

Sexual Conflict in Primates

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Sexual conflict is increasingly recognized as a major force for evolutionary change and holds great potential for delineating variation in primate behavior and morphology. The goals of this review are to highlight the rapidly rising field of sexual conflict and the ongoing shift in our understanding of interactions between the sexes. We discuss the evidence for sexual conflict within the Order Primates, and assess how studies of primates have illuminated and can continue to increase our understanding of sexual conflict and sexual selection. Finally, we introduce a framework for understanding the behavioral, anatomical, and genetic expression of sexual conflict across primate mating systems and suggest directions for future research.

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Sexual conflict is defined as “a conflict between the evolutionary interests of individuals of the two sexes.”¹ This conflict may increase fitness in one sex while reducing or constraining fitness in the opposite sex.² It can be manifested in myriad behavioral, anatomical, and physiological traits related to reproduction, including penile spines, vaginal plugs, mating frequency, timing of fertilization, cryptic choice, infanticide, and relative parental effort.³ Because these characteristics favor the reproductive interests of one sex while decreasing fitness in the other, counterstrategies can evolve, triggering an evolutionary “arms race” between the sexes. At an extreme, sexual conflict can lead to speciation through reproductive isolation.^{2,4}

Interest in sexual conflict is growing across multiple fields, including evolutionary anthropology and primatology.^{5–14} While no single review can thoroughly examine all aspects of this rapidly expanding field, our first aim here is to examine behavioral, anatomical, and genetic examples of sexual conflict in primates. We highlight how integrating sexual conflict theory into primate studies can advance theoretical developments in our understanding of sexual selection and lead to new insights

into primate behavior and evolution. We propose that primate social complexity and the high diversity of mating systems makes the Order Primates particularly fertile ground for sexual conflict research.

HISTORICAL BACKGROUND AND SHIFTING PERSPECTIVES

Darwin^{15:256} defined sexual selection as being dependent on “the advantage which certain individuals have over *others of the same sex* and species, in exclusive relation to reproduction.” He also recognized two fundamental processes that influence sexual selection, mate competition and mate choice. Darwin's definition emphasized *intrasexual* levels of competition, or competition and conflict occurring between members of the same sex. Though intersexual conflict may or may not have been nascent in Darwin's original formulation of sexual selection theory, more than a century passed before the conflicting reproductive interests between males and females were explicitly recognized as a fundamental evolutionary force.^{1,16} In 1979, Parker emphasized that as a consequence of the divergent evolutionary interests of the two sexes, all reproductive interactions between the sexes, including mate choice, mating rates, and parental investment, imply a conflict.¹ In historical context, the slow recognition of sexual conflict as an important evolutionary force is perhaps not surprising. For one, reproduction was viewed as a cooperative effort between the sexes,⁸ particularly in our own species, whereby fitness depends on both maternal and paternal cooperation and is negatively affected by lack of one or the

other.^{17,18} In addition, female sexual reserve and passivity were expected.

Theoretical and empirical research by key evolutionary anthropologists and primatologists, notably Robert Trivers, Sarah Blaffer Hrdy, and Barbara Smuts, contributed greatly to both the understanding of sexual selection and development of the study of sexual conflict. Trivers, building on Bateman's¹⁹ experiments with fruit flies, emphasized the divergent reproductive interests of males and females, including sex differences in parental investment.²⁰ This work set the stage for future focus on differing sexual roles and strategies between the sexes. Hrdy's empirical studies of wild langurs led to her then-controversial hypothesis that infanticide by males was a sexually selected evolutionary tactic as opposed to simply aberrant behavior.²¹ Notably, Hrdy also challenged the notion of the "coy" female by highlighting the prevalence of female promiscuity among primates and proffering it as a female counterstrategy to infanticide.²² More recently, Smuts and Smuts¹⁶ expanded on Darwin's traditional components of sexual selection, mate choice and male competition, by identifying coercion as a third component. This work brought new theoretical attention to conflict between the sexes.

Despite considerable potential for sexual conflict to explain intersexual dynamics and evolutionary pressures, further theoretical development and experimental research on sexual conflict and its consequences has been slow to emerge. The dynamic of intersexual conflict still has a relatively limited role in traditional sexual selection theory.^{4,23,24} Moreover, the explanatory power of sexual conflict has only recently been emphasized, partly due to improved methodologies that facilitated the understanding of reproductive mechanisms.⁸ Indirectly, this emerging shift in our field can be seen in publication records. Few primate papers referenced sexual conflict or intersexual selection until this decade, but a marked increase has occurred just in the last few years (Fig. 1a). Concepts such as sperm competition and the evolution of sexual dimorphism are

still overwhelmingly ascribed to intrasexual mechanisms (for example, male-male competition), with little attention is given to the potential influence of intersexual mechanisms (Fig. 1b, c). Specifically, female strategies such as multi-male mating counter male reproductive control and provide selective pressure for male co-evolution. The slow emergence of sexual conflict in traditional sexual selection theory may be due

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HOW PRIMATES CAN INFORM EXISTING SEXUAL CONFLICT MODELS

Currently, the predominant challenge within the field of sexual conflict is to develop a unified theoretical framework⁸ that will enable predictions of the ways in

which sexual conflict is expressed within and across species. To date, the majority of the theoretical models, hypotheses, predictions, and empirical research on sexual conflict are based on insects, especially *Drosophila* and, to a lesser extent, on birds and fish.^{31,33–40} These studies have been fundamental for providing strong evidence of conflict between the sexes leading to selection and counter-selection (sexually antagonistic selection).

While such studies of sexual conflict have proliferated, the models, assumptions, and conclusions derived from insect-focused studies may be largely inapplicable to primates for several reasons. First, primates are highly social animals; their mating strategies are flexible, complex, polyadic, and can change over time. Second, traditional sexual conflict models assume differences in optimal mating rates between the sexes. Specifically, assumptions include low mating costs for males and high mating costs for females so that females evolve resistance to males who may "manipulate" them into mating more than is necessary to ensure fertilization.^{41,42} However, many female primates are promiscuous and sexual behavior often serves female reproductive interests in more ways than simply fertilization.^{9,43–45} Because infanticide is a considerable risk in many primate species,⁴⁶ additional benefits gained from confusing paternity through promiscuity may counter or outweigh costs incurred from mating. Therefore, the costs and benefits of mating among primates do not fit a traditional "sex as reproduction" framework. Moreover, male primates incur considerable mating costs as well (including energetic costs, injuries, sperm depletion, and sexually transmitted diseases (STDs)^{47,48} which are not considered in traditional models. Third, whereas immediate behaviors are the focus of insect studies of sexual conflict, longitudinal behaviors such as coercion (for example, conditioning aggression⁴⁹) may be more important among primates because of their stable social networks, individual recognition, long-term memory, and higher cognitive function, thus leading to different predictions and

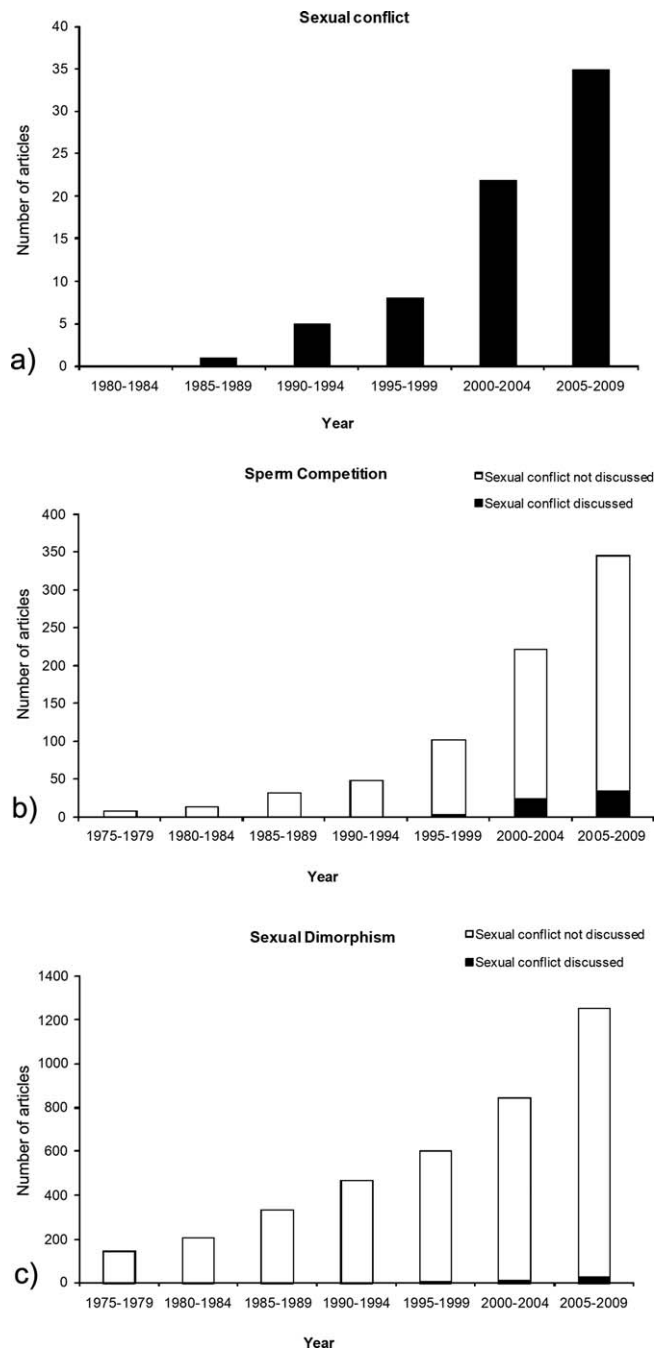


Figure 1. a) Simple count of articles referring to sexual conflict in primates. A search was conducted in PubMed, PrimateLit, and Google Scholar using the key words "sexual conflict," "intersexual conflict" or "intersexual selection" and "primates." Articles were screened to ensure that they discussed intersexual conflict and that there were no repeats between different search terms. Figures 1b and 1c depict the number of articles found using PubMed that discuss sexual conflict and either b) sperm competition or c) sexual dimorphism in primates. A PubMed search was conducted using the term "sperm competition" or "sexual dimorphism" paired with the terms "conflict," "antagonistic," or "antagonism." The number of articles found discussing sexual conflict was subtracted from the total number of articles found when using only the term "sperm competition" or "sexual dimorphism" to calculate the number of articles on these subjects that do not discuss sexual conflict. Articles were separated into those that discuss sexual conflict (black portion) and those that did not (white portion).

assumptions related to sexual conflict. Finally because raising offspring is so costly, sexual conflict over parental investment is an important consideration in primates, in contrast to other orders that are characterized by little to no parental investment.

The diversity of primate mating systems provides an ideal system for refining our understanding of sexual conflict and challenges the assumptions of traditional models. Specifically, different primate mating systems, such as polyandry and monogamy, are expected to produce different manifestations and intensities of sexual conflict, including sexual role reversals. Thus, incorporating primate studies of sexual conflict into traditional models has the potential to contribute to a more unified framework of sexual conflict.

Sexual Conflict in Primate Behavior

Insight into the evolutionary dynamics of the sexual arms race between primate males and females provided important early advances in understanding sexual conflict. Hrdy and Smuts were among the first to use a sexual conflict framework for understanding sexual selection and sexual dialectics, due in large part to their focus on females. Moreover, where primates have figured prominently in sexual conflict theory, the emphasis has largely been on behavior.^{7,16,49,50} Because behavioral sexual conflict has received more detailed treatment elsewhere,^{7,16,49,50} here we briefly describe some of the main examples that highlight how sexual conflict theory has enriched our understanding of male and female coevolution and sexual selection.

Perhaps the most compelling evidence of sexual conflict in primates is infanticide. Originally viewed as simply an aberrant behavior, Hrdy²¹ proposed that infanticide by males is a sexually selected strategy. By eliminating rival males' offspring and shortening lactational amenorrhea in the victim's mother, an infanticidal male increases his mating opportunities and reproductive potential rela-

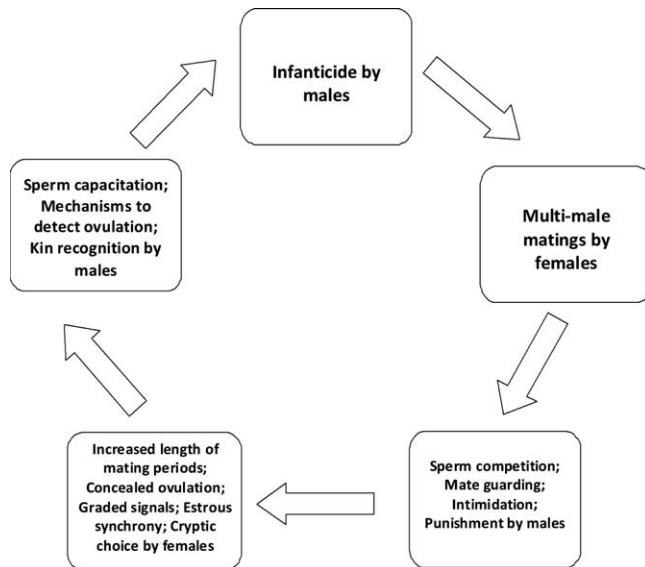


Figure 2. This diagram illustrates a hypothetical example of the behavioral strategies and counter-strategies in sexually antagonistic coevolution. For example, in polygynandrous mating systems, males may evolve infanticidal behavior because of the benefits gained by reducing the time until a female can conceive again. Because loss of an infant is so costly, females counter by mating with multiple males, thereby confusing paternity. Males respond to multiple matings by increasing sperm competition and attempting to prevent multiple matings through behavioral strategies such as mate guarding. Females then evolve further strategies, such as concealed ovulation, which lengthens the mating period and makes behaviors like mate guarding more difficult for the male. It also decreases some of the effectiveness of sperm competition, as a male is likely to mate with a female when she is nonconceptive. Again, males attempt to overcome this by evolving further strategies, such as kin recognition. The ability to differentiate his own offspring from a rival male's offspring decreases the costs associated with infanticide for a male, leading to selection for behavior strategies and counter strategies in the continuous "arms race" that is sexual conflict.

tive to that of other males. For primate females with heavy offspring investment and limited reproductive potential, the loss of an infant is extremely costly.

Infanticide has been documented extensively among catarrhines in both one-male groups when a new male takes over the group (for example, guenons and gorillas) and multi-male groups (for example, red colobus, chacma baboons, and chimpanzees).⁵¹ Although infanticide has been less commonly observed among strepsirrhine and platyrrhine taxa, it has nonetheless been reported in several of them.^{52–62} Because this behavior is rare and not easily observed, it may be more prevalent in these taxonomic groups than currently is recognized.

Through long-term, detailed observations of wild baboons, Smuts and Smuts identified coercion (which

could take the form of forced copulation, harassment, intimidation, punishment and, in its extreme form, infanticide),¹⁶ as an important selective force. Males are thought to benefit from sexual aggression through increased mating opportunities, but females suffer costs, including loss of mate choice, decreased foraging, injury, increased stress, and spontaneous abortion.^{63–68}

Females have co-evolved several counterstrategies in response to male coercion and infanticide (Fig. 2).^{9,22} Multi-male mating benefits female primates especially at risk of infanticide by confusing paternity and thus inhibiting males from killing the infants of former mates.^{21,45} Evidence from diverse primate taxa indicates that females actively solicit matings from multiple males,^{69,70} particularly when conception is unlikely,⁹ and that this behavior

extends to pregnancy, especially when new males appear after the female has conceived. For example, female long-tailed macaques (*Macaca fascicularis*) maintain swelling size, frequency of proceptive behaviors, and copulations throughout the first two-thirds of pregnancy.⁷¹ Similarly, orangutan females are particularly proceptive during early pregnancy.⁷² It is argued that these multi-male matings are a female counterstrategy to infanticide and coercion, manipulating "paternity assessment"⁷³ and decreasing selection for persistent or aggressive males.⁷⁴

Female mate selectivity, which includes any behavior or trait that biases male mating success toward certain male phenotypes,^{8,73,75,76} is another sexually selected trait that creates selective pressure on male reproductive interests and constitutes a form of conflict.^{77–80} Strategies of multi-male mating and female mate selectivity are not mutually exclusive. Indeed, evidence suggests that they can be applied in tandem through a mixed strategy of paternity confusion and mate selectivity.^{9,80,81}

Females can also employ social strategies in response to sexual conflict. Among orangutans, associating with a dominant male is argued to be a female behavioral counterstrategy to forced mating.^{80,82} Among chacma baboons (*Papio hamadryas ursinus*), both "friendships", a term referring to close associations between lactating females and specific adult males, as well as female defensive coalitions against males, are suggested to be anti-infanticide strategies, providing protection to females and their offspring.^{16,51} Male friends respond to infanticidal attacks in different ways than do other males; these responses include physically fighting the attacker, initiating chases, and issuing direct threats and vocalizations.⁸³ Secondary transfer, which is associated with weak within-group social relationships and increased coercion by extra-group males at the end of the breeding male's tenure,⁸⁴ may also be a female defensive strategy. Teichroeb and colleagues,⁸⁵ observing six groups of *Colobus vellerosus* over seven years, recorded that 90% of voluntary female

emigrations occurred when new adult males immigrated and the social environment destabilized due to frequent male-male aggression and evictions. Similar findings have been reported among Thomas's langurs (*Presbytis thomasi*) and gorillas (*Gorilla* sp.), with emigrations generally occurring when a female's present offspring reach independence or die.⁸⁴ These examples illustrate that primate behavior is a dynamic process involving strategies and counterstrategies between males and females, enlivening theoretical development and testable hypotheses to explain patterns of primate behavior and evolution.

Sexual Conflict in Primate Anatomy and Physiology

In addition to behavior, evaluating primate anatomy and physiology in light of sexual conflict theory also contributes to a greater understanding of primate evolution. In particular, sexual conflict is likely to have a significant effect on the reproductive organs,⁸⁶ since there is strong selection to enhance insemination and fertilization, even if those adaptations impose a cost to a sexual partner. Traits that enhance one sex's opportunities for mating and fertilization, but impinge on the other sex's opportunities, lead to adaptation and counter-adaptation between the sexes.

One driving force of sexual conflict is the competition between the sexes for control over paternity. In males, this conflict manifests in physiological adaptations related to rates of sperm production, as well as sperm length and speed, testes size, and volumes of the sperm midpiece (where mitochondria associated with sperm motility reside).^{87,88} These features all correlate positively with levels of female promiscuity across primates^{87,89-91} and increase a male's control over paternity. While these features are traditionally viewed in the context of male-male competition, it is important to emphasize that they evolve in response to female behavior and physiology and, in many cases, enhance male reproductive success while imposing a cost on females.

For example, primate seminal fluid is rich in biochemical compounds that aid in sperm motility and fertilization. However, hormones and prostaglandins found in seminal fluid also affect females through immunosuppression, induction of ovulation, incitation of uterine muscle contractions to aid sperm transport, and decreased female sexual receptivity,⁹²⁻⁹⁵ all of which limit female control over paternity and reproductive health. In another example, penile spines are argued to enhance conception likelihood^{13,34,96} yet may damage the female reproductive tract,³⁴ decrease a female's willingness to mate with other partners, and increase female susceptibility to STDs, arguably⁹⁷ advantageous to males in species where additional mating opportunities with the same female are unlikely.

Selective pressure resulting from these male adaptations to influence paternity are high for females. Costs include fertilization by non-preferred males, fertilization by more than one sperm (polyspermy) causing zygote mortality, and reduction of female fertility.^{8,98} One counter-strategy of female primates to increase control over paternity is to manipulate male mating behavior, including infanticide and male coercion, by modifying ovulatory timing and signals. For example, by synchronizing ovulatory cycles, females limit control of multiple fertile females by a single male.⁹⁹ Alternatively, females are argued to conceal ovulation to decrease male reproductive control and increase paternity uncertainty.^{87,100} Specifically, concealed ovulation in the form of long ovarian cycles, follicular phases, and extended periods of sexual swellings in several Old World primates counteract the cost of male coercion and infanticide.⁷⁰ Nunn⁸¹ proposed the graded-signal hypothesis to explain the evolution of exaggerated sexual swellings in primates. This hypothesis states that gradual increases in swelling size are general indicators to males of the likelihood of conception, so that the signal and extended duration of receptivity attracts males and encourages mating. Because males may not recog-

nize the precise time of ovulation, paternity confusion ensues. Sexual swellings and mating during pregnancy^{71,101,102} enhance the effect. By confusing and concentrating paternity, sexual swellings manipulate male behavior.^{81,103} Other taxa, such as prosimians and platyrrhines, may conceal ovulation and manipulate males through olfactory cues from pheromones or scent gland secretions.⁷⁰

Cryptic choice is another counter-adaptation to increase control over paternity. Eberhard^{86:7} defines cryptic choice as "a female-controlled process or structure that selectively favors paternity by conspecific males with a particular trait over that of others that lack the trait when the female has copulated with both types." Thus, within the female reproductive tract, diverse anatomical or physiological processes may favor gametes of particular males and/or counteract damaging effects of male seminal substances.^{86,93} Oviduct length in mammals, including primates, correlates positively with testes size, ejaculate size, and sperm midpiece volume,^{104,105} suggesting that females have evolved in response to sperm competition. Inside the vagina, sperm are exposed to a hostile acidic environment and phagocytotic attacks.^{93,106} Although seminal fluid buffers the pH of the vagina and helps with sperm transport, it is effective only for a few hours.¹⁰⁷ Therefore, only sperm capable of surviving the vaginal tract can fertilize an egg.⁹³ The vaginal environment may demonstrate post copulatory sexual selection by differential selection among male sperm. Biochemical properties of the cervical mucus and vaginal secretions released during orgasm affect sperm survival.¹⁰⁷ Moreover, uterine contractions occurring during orgasm may facilitate transport of the sperm of particular males.¹⁰⁸ The Bruce Effect¹⁰⁹ (that is, reabsorption of an embryo after exposure to a new male) is argued to be a female strategy to avoid investment in an infant that would most likely be killed.^{21,73} Although it is best known in rodents, cases of abortions related to the arrival of a new male have been

reported in baboons, langurs, and gibbons.⁷³ These various anatomical and biochemical mechanisms in males and females affect individual fitness and are argued to have evolved not only in response to intra-sexual competition, but also in response to sexual conflict.

Sexual Conflict in Primate Genes

While most evidence of primate sexual conflict has come from behavior studies and, to a lesser extent, morphological studies, evolution is ultimately a genetic process. It is therefore important to examine how a sexual-conflict perspective can inform our understanding of genetic outcomes. Because genetic technology has only recently become accessible to a large range of researchers, the field of primate genetics in general, let alone primate genetics in relation to sexual conflict, remains largely unexplored. To date, most studies looking at primate genetics have come from fields outside of anthropology and have taken a very broad approach, looking at mammals in general. Therefore, evidence of genetic sexual conflict in primates is rare. Most of the studies cited here reference several mammalian species. Nevertheless, because the rapidly growing field of genetics is likely to have a large impact on primatological studies and theories, we feel it is important to highlight how sexual conflict can enrich interpretation of genetic variation.

Intralocus Conflict. A beneficial trait in one sex, such as the bright coloration of peacocks or the large canines of several primate males, may not be beneficial, or may even be detrimental, in the other sex. However, because males and females largely share the same genes, selection on a trait in one sex leads to a correlated response in the other sex,¹¹⁰ so that both sexes express the trait even if only one sex benefits from its presence. The result is intralocus conflict; that is, selection on these loci is sexually antagonistic.

This conflict can be resolved through the evolution of sex-limited gene expression, or sexual dimorphism.¹¹¹ An extension of this process likely played a role in the formation of sex chromosomes.¹¹² Indeed, the presence of sexual dimorphism across a large number of primate taxa provides support in itself for sexual conflict, as dimor-

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phism is not likely to evolve if, for example, the presence of large canines is beneficial for both sexes.¹¹³ However, several factors can allow for the persistence of intralocus conflict. Due to the constraints imposed, dimorphism can evolve very slowly.¹¹⁰ There may also be a limit to the degree of dimorphism that can evolve, so that one or both sexes cannot obtain the ideal phenotype. As well, it may be that not all genes are exclusively expressed in one sex.¹¹¹ Although most extensively studied in *Drosophila*,^{114,115} a handful of studies have demonstrated intralocus conflict in wild animals, including mammals.^{116,117} In haplorrhine primates, Lindenfors and Tullberg¹¹⁸ demonstrated that where there is strong male intrasexual selection, there is a general trend to increase the body size of males and, to a lesser degree, females (but see Brockman, Coblen, and Whitten⁶⁰). However, further analysis showed that the

increase in body size negatively affects female reproductive rates,¹¹⁹ demonstrating a conflict over ideal body size in primates that may not be entirely resolved through sexual dimorphism.

Genomic imprinting, perhaps the most persuasive genetic evidence for intralocus sexual conflict, exemplifies the insight to be gained from understanding this phenomenon from the perspective of sexual conflict. Imprinting is traditionally viewed as a form of parent-offspring conflict,^{120,121} with offspring maximizing maternal investment at a cost to the mother's future reproduction. However, this wording minimizes the conflict between maternal and paternal DNA.^{122,123} Genomic imprinting occurs when two alleles have different expression levels depending on which parent provided the allele. The most common explanation for genomic imprinting is that it is the result of conflict over maternal investment.^{124,125} In a given primate genome, an estimated 100–200 genes are likely to be imprinted.^{126,127} In mammals, most imprinted genes are associated with embryonic growth and development, with the majority involved with development of the placenta as well as post natal development, such as suckling.^{128,129} Conflict occurs because paternal alleles maximize maternal investment and growth, whereas maternal alleles inhibit growth, presumably to balance investment between current and future offspring.^{121,124,125,130,131} In support of a link to sexual conflict, genomic imprinting has been found across placental mammals, but not in oviparous birds and monotremes, with their considerably reduced maternal fetal investment.¹³² Even the mechanisms behind imprinting have been argued to demonstrate sexual conflict.^{133,134}

Interlocus Conflict. Interlocus conflict, predicted to be a driving force of speciation,^{2,41} is another realm in which the sexual-conflict perspective can aid our understanding of primate evolution. Interlocus conflict, which refers to competition between traits encoded by different genes in different individuals,^{31,36}

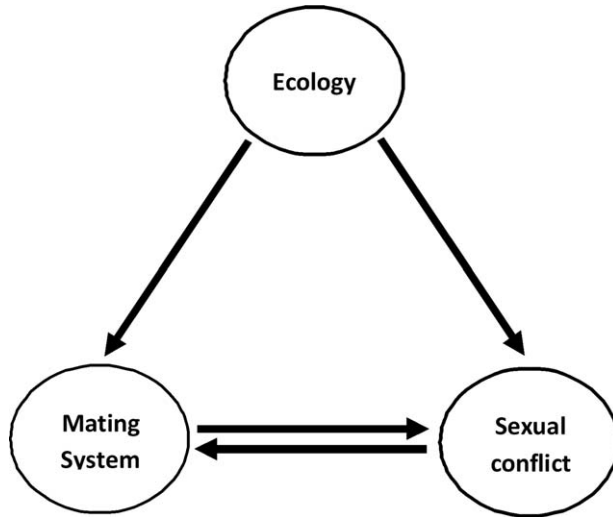


Figure 3. A diagram showing the interactions among sexual conflict, mating systems, and ecology. The evolution of sexual conflict will take place within the conditions set by both ecology and the species' mating system (which is also affected by ecology). However, there is a two-way interaction between sexual conflict and mating systems so that the coevolution of males and females may result in shifting behavioral strategies that change the dynamics of a mating system (modified from Arnqvist and Rowe, 2005).

allows for continual evolution of traits in both sexes that manipulate the outcome of male-female sexual interactions. Because any feature involved in some sort of “arms race” will tend to evolve at a high rates, evidence of these processes can be found by looking at base pair substitution rates within and between species. Conflict between the sexes should result in a high ratio of nonsynonymous to synonymous substitutions (d_N/d_S) in loci involved with reproduction.³⁶ Furthermore, sexual conflict should also lead to the rapid evolution of gene expression differences related to reproduction. If sexual conflict leads to speciation, we should see a high level of divergence between species in reproductive gene sequences and expression levels.¹³⁵

In fact, across a variety of taxa including chimpanzees and humans, male and female reproductive traits such as proteins involved in sperm competition and gamete recognition are found to evolve more rapidly through positive selection than do nonsexual traits,^{136–139} a pattern that is consistent with intersexual conflict.^{27,136,140–148} Although these studies clearly demonstrate positive selection in relation to reproduction, this pattern can also be explained in terms of more traditional sexual selec-

tion theory, such as sperm competition, without invoking sexual conflict.

To identify sexual conflict, it is necessary to include consideration of male-female interactions to demonstrate that males, rather than evolving in response to other males, evolve in response to particular aspects of the female reproductive system and vice-versa. The evolution of the mammalian egg provides a persuasive example. In primates and other mammals, the proteins of the *zona pellucida*, the coating of the egg, evolve very rapidly,¹⁴⁰ particularly in areas that directly interact with sperm and are associated with sperm reception and species recognition.^{141,142,149} Sexual conflict over sperm penetration rate through the *zona pellucida* provides a compelling explanation for this rapid evolution.¹⁵⁰ Male sperm are selected to penetrate the *zona pellucida* as quickly as possible, particularly in promiscuous mating systems. However, females have evolved polymorphic responses to enhance discrimination and minimize the possibility of polyspermy, or multiple sperm entering the egg at once. This tug of war between males and females leads to a runaway process resulting in the rapid evolution of both sexes' gametes as they evolve in response to each other.^{141,142}

A NEW FRAMEWORK FOR UNDERSTANDING THE EXPRESSION OF SEXUAL CONFLICT ACROSS PRIMATES

Much variability in morphology and behavior across primates cannot be explained by either phylogeny or socioecology. Individual reproductive success depends on multiple factors, including ecology, spatial and temporal distribution of mates, and operational sex ratio (OSR); that is, the ratio of sexually active males to sexually receptive females at any one time. Just as these factors drive the evolution of mating and social systems,¹⁵¹ these factors should also influence the expression of sexual conflict, such as patterns of ornamentation, coercion, and female choice. Moreover, while ecology and mating systems are expected to drive the expression of sexual conflict, mating systems are also predicted to have evolved in response to sexual conflict (Fig. 3).¹⁵²

Variation in primate morphology and behavior permits hypothesis testing and predictions for the way in which sexual conflict is expressed in this Order. Recently, attempts have been made to explain the presence of particular examples of sexual selection and conflict such as infanticide⁷³ and penile spines.⁸⁷ Here we introduce an overall framework for understanding the expression of sexual conflict and selection more broadly across primate mating systems. For one, the manifestation and intensity of sexual conflict is predicted to differ markedly across primate mating systems in response to differing selective pressures (Fig. 4). This is predicated on two assumptions. First, individuals of each sex are expected to maximize their fitness, leading to intersexual interactions that are competitive and beset by conflict. Second, the selection pressures on male and females ultimately determine the intensity and manifestation of sexual conflict. Specifically, as a consequence of differences in mating system parameters, such as the number of mates acquired, the manner of mate acquisition, the presence and characteristics of pair bonds, and the patterns of parental care provided by each sex,¹⁵¹ optimal strategies are expected to vary, resulting in the

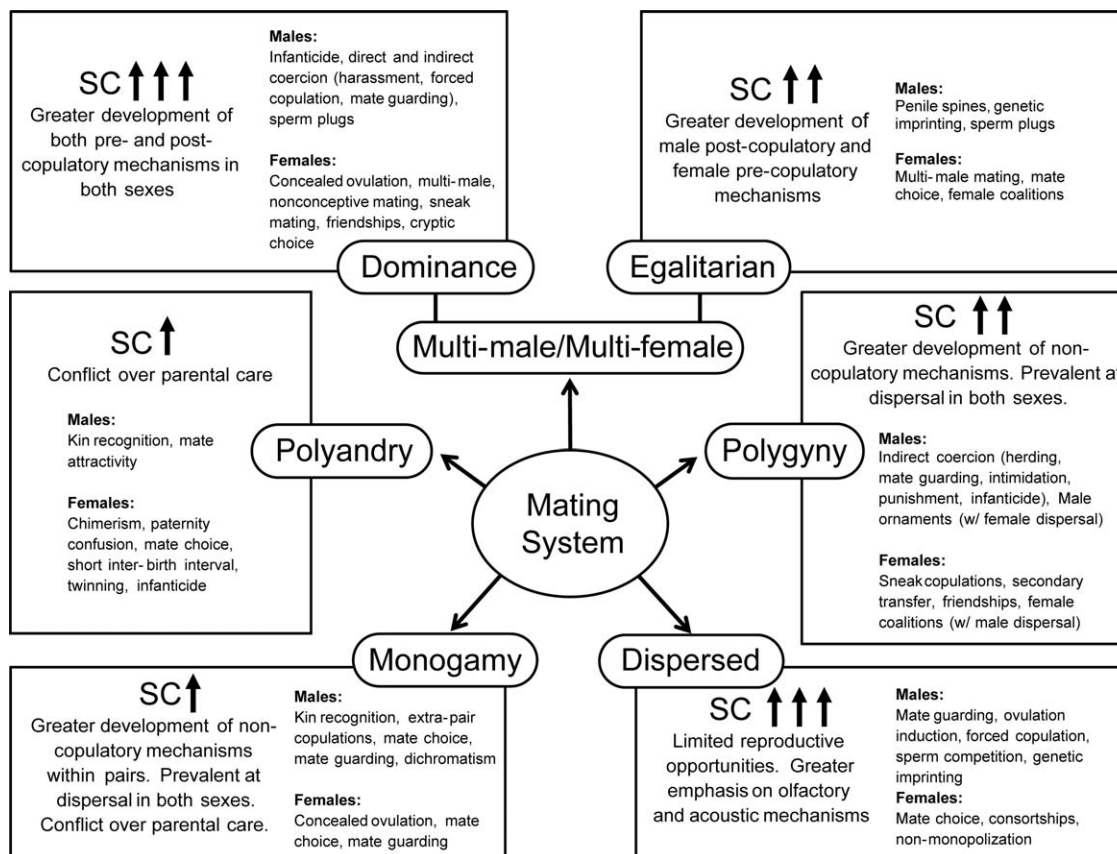


Figure 4. A model for sexual conflict and selection across different primate mating systems. Primate mating systems include monogamy (for example, *Indri indri*, *Aotus* spp., *Hylobates* spp., *Symphalangus* sp.), polyandry (for example, *Callithrix* spp., *Saguinus* spp.); polygyny (for example, *Papio hamadryas*, *Theropithecus gelada*, *Gorilla gorilla gorilla*); dispersed (for example, *Pongo pygmaeus*, *Microcebus murinus*); multimale-multifemale egalitarian (for example, *Alouatta caraya*, *A. pigra*, *Brachyteles arachnoides*, *Pan paniscus*); and multi-male-multifemale dominance-based (for example, *Macaca fascicularis*, *Papio cynocephalus ursinus*, *Pan troglodytes*). Across mating systems, the intensity and manifestation of sexual conflict are expected to vary. For each mating system, we show the expected level of sexual conflict (SC) (one arrow ↑ = low; two arrows ↑↑ = intermediate; three arrows ↑↑↑ = high), highlight areas where sexual conflict will most likely manifest, and list examples of male and female strategies and traits known or expected to occur in these mating systems. These mating systems differ in the number of mates acquired, the manner of mate acquisition, the presence and characteristics of pair bonds, and patterns of parental care provided by each sex. As a consequence of differences in these mating system parameters, optimal strategies shift, resulting in the molding of adaptive mechanisms of sexual conflict to mating system constraints.

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Thus, while sexual conflict is predicted to be ubiquitous across primates, mating systems with highly divergent male and female reproductive interests (for example, polygynandry) are expected to exhibit more extensive and elaborate mechanisms of sexual conflict. Specifically, sexual conflict should be more intense in primate species characterized by high OSRs, high mating competition, strong hierarchies, and extensive sexual dimorphism. For example, sexual conflict is predicted to be greater in many catarrhine species than it is among platyrrhines or strepsirrhines

with reduced or reversed sexual dimorphism and OSRs.

Figure 4 presents a framework outlining predictions for the differing expression of sexual conflict across five primate mating systems: multi-male, multi-female (polygynandry), polygyny, polyandry, monogamy, and dispersed. For example, among multi-male multi-female mating systems characterized by male dominance to females, both direct coercion (for example, behaviors to increase a male's mating opportunities, such as forced copulation, harassment, and intimidation) and indirect coercion (for example, behaviors that attempt to prevent females from reproducing with other males, such

as mate guarding, punishment, copulation interference, herding, sequestering, and infanticide)¹⁴ are predicted to be more prevalent. Because the overt expression of female choice is challenging in male-dominant polygynandrous mating systems, females are predicted to manifest attempts to influence paternity through more subtle means, such as variation in sexual receptivity, and graded signals which both confuse and concentrate paternity. In addition, due to high male contest competition and the challenges of expressing overt female choice, post-copulatory mechanisms such as sperm competition and cryptic choice are expected to be more prevalent here than in other mating

systems. Because females have less influence over precopulatory mate choice than in they do other mating systems, postcopulatory mechanisms, such as sperm competition and cryptic female choice, are expected to be more prevalent in these species.

In multi-male, multi-female mating systems characterized by egalitarian male-female relationships, such as several lemuroids, bonobos and many New World monkeys, we predict limited direct or indirect coercion from males. Because males do not benefit from much sexual dimorphism in size, thus making coercion less tenable, male postcopulatory mechanisms including sperm competition, are predicted to be more extensive than precopulatory ones such as coercion. In these less sexually dimorphic or female-dominant species, females are predicted to exhibit more precopulatory mechanisms, (including mate choice, resistance, proceptivity, and female coalitions) and fewer postcopulatory mechanisms (for example, cryptic choice) than in male-dominant polygyny.

Finally, multi-male, multi-female mating systems (dominant or egalitarian) are predicted to demonstrate a greater prevalence of genomic imprinting than other mating systems, perhaps with the exception of dispersed. Genomic imprinting is thought to maximize maternal investment on the current sire's offspring at a cost to the female and her investment in future offspring, and females in these mating systems are less likely to reproduce again with the same male. In addition, the rapid evolution of genes related to reproduction should be most prevalent in polygynandrous species, where the reproductive interests of males and females are most at odds.

Among polyandrous species, we predict that most sexual conflict will be expressed as conflict over paternal care. We expect multiple mechanisms to induce paternal care because, by persuading males to increase parental care, females can produce multiple offspring and rapidly invest energetic resources in future offspring shortly after birth. Females may induce paternal care by basing future mate choice decisions on male parental care; males may

attract females and influence female choice by exploiting this mechanism.¹⁵³ Another mechanism found in this mating system, genetic chimerism, may induce paternal investment. Chimerism occurs when high rates of placental fusion and delayed embryonic development during placental fusion increase the possibility for stem cell exchange between siblings before advanced differentiation of embryonic tissues.^{154,155} Thus, fraternal twins share alleles in multiple cells, possibly including germ lines, leading to a greater than average coefficient of relatedness as compared to full siblings.¹⁵⁶ Ross, French, and Orti¹⁵⁶ argue that marmoset chimerism may result in female-imposed costs to males in the form of high investment in paternal care through kin recognition mechanisms such as phenotypic matching. This effect may be even more important in groups of unrelated males. We predict that similar mechanisms to induce alloparenting will be found in other polyandrous species.

Another mechanism characteristic of polyandrous primates is female reproductive suppression, which is traditionally considered an example of female-female competition. However, when considered through the lens of sexual conflict, reproductive suppression of the ovulatory function of other females permits dominant females to limit male mating opportunities, thereby raising male costs. Males sometimes succeed at obtaining additional mates, yet dominant females often kill the offspring of these matings. Infanticide by dominant polyandrous females may be considered yet another mechanism for sexual conflict because females constrain male fitness by substantially increasing the costs of expending male mating effort in exchange for parental care relative to the benefits.

In polygynous mating systems, direct coercion is expected to be rare because mechanisms for female mate choice and male persuasion should be most active before group formation and not during sexual activity. Thus, sexual interactions are predicted to be relatively free of conflict. Specifically, females are predicted to initiate a large proportion of

matings, while female resistance to mating is predicted to be minimal. However, because the largest reproductive threat to males in polygynous mating systems is female abandonment in favor of another male, indirect coercion is predicted to be intense, often expressed in a nonsexual context, and is the most prominent form of coercion.

Polygynous mating systems can be divided into two main types: one characterized by female dispersal into a new unit or group and the second by male takeovers of existing groups. In polygynous species characterized by female or bisexual dispersal, such as gorillas and mandrills, intersexual selection in the form of female choice of mates is predicted to be predominantly expressed at dispersal (that is, during female immigration into a group). Thus, we predict that these polygynous species will exhibit a high prevalence of male persuasive signaling tactics in the form of elaborate male ornaments to attract females. Such ornaments include the bright coloration of drills and mandrills, as well as the silver-back of gorillas, which do not directly increase fighting ability.¹⁵⁷ Previously, ornamentation has been explained by the coercion defense model, in which species characterized by females that are able to avoid coercion exhibit the development of male ornaments instead of weapons.¹⁵⁷ Alternatively, we propose that coercion (particularly indirect) is still an important selective pressure on females. Rather, selection for male ornamentation is primarily an outcome of female choice at dispersal. We therefore expect that ornaments evolve in species where female choice of mate is manifest before prolonged association with a male, thereby leading to exaggerated male signals to attract females.

In contrast, in polygynous species characterized by male takeovers, such as langurs, male ornamentation is not expected to be under strong selection because females do not actively choose males. Rather, males take over a group and eject resident males. Intersexual conflict in these polygynous species should select for enhanced female fighting ability to prevent the resultant decrease in fit-

ness through infanticide, and manifest as female resistance to incoming males, such as physical resistance, reduced sexual dimorphism, female-female alliances, and support for resident males.

In monogamous species such as titi monkeys and gibbons, sexual conflict in parental care is predicted to be moderate since fitness for both sexes depends on biparental care and is often maximized by shared parental effort. Sexual and social relationships generally endure; thus, the expression of male coercion is also predicted to differ from that in other mating systems. Indirect coercion, such as mate guarding, to secure and protect long-term access to females is predicted to be more common, whereas direct coercion should be relatively rare. Similar manifestations to maintain the pairbond are also expected for females. Thus, mutual mate guarding, territorial defense, reduced canine and body dimorphism, and concealed ovulation or frequent mating are expected.

In a dispersed mating system, individuals occupy separate but overlapping ranges. Mating opportunities are relatively rare, of short duration, and fleeting. Thus, sexual selection on males is expected to drive mechanisms to ensure conception and limit remating by other males, such as forced copulation, genital locks, penile spines, and ovulation induction,^{13,87,158,159} as well as mechanisms to increase maternal investment such as genomic imprinting. Because females are isolated and vulnerable to coercion, selection for female influence on paternity is predicted to be manifest through association patterns (such as temporary consortships) and postcopulatory mechanisms. Male mechanisms to attract females and female mechanisms to signal receptivity are predicted to emphasize acoustic or olfactory tactics in dispersed compared to more aggregated mating systems.^{160–162}

Of course, plasticity in mating systems and sexual conflict is expected. Sexual conflict strategies may vary within mating systems and within species based on such factors as age or rank. For example, male coercion is

predicted to be high in multi-male multi-female mating systems, and to vary by male identity. Higher ranking males are predicted to use indirect coercion to attempt to prevent females from mating with other males and decrease the relative reproductive success of other males, whereas lower ranking or nonpreferred males are pre-

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dicted to use direct coercion more frequently to increase their immediate mating opportunities.¹⁴ Similarly, in monogamous species, paired males are more likely to exhibit indirect coercion, in contrast to more direct coercion by nonpaired males.

While we have attempted to explain and predict patterns of behaviors and morphologies through a framework of sexual conflict across mating systems, we recognize that these are incomplete. We view this framework as a stimulus for further research and expect that these predictions will be applicable on a broader scale to other mammalian orders. In a forthcoming paper, we elaborate on and test this framework, in which different mating systems and ecological conditions correspond to differences in the manifestations of sex conflict across primates.

MOVING RESEARCH ON PRIMATE SEXUAL CONFLICT FORWARD

The developing field of sexual conflict is inducing a paradigm shift in sexual selection theory by emphasizing the conflicting dynamics in reproductive interactions, as well as adaptation and counter-adaptation between the sexes. As sexual interactions are increasingly viewed less as a cooperative undertaking and more as grounds for conflict, this shift in focus is dramatically altering our understanding of the evolution of anatomical, physiological, genomic, and behavioral traits across species. Darwin's original conceptualization of sexual selection as being largely precopulatory has expanded to include copulatory and postcopulatory mechanisms, as well as intergenomic interactions.^{1,22,121} This shifting perception is also arguably a consequence of a greater research focus on females, resulting in new discoveries and changing perceptions of female agency in sexual interactions.^{69,86,163,164} While data on primate sexual conflict largely come from catarrhines, making this, in itself, an area for hypothesis testing, the increasing reports of sexual conflict in other suborders^{165–170} suggest that sexual conflict is more prevalent across noncatarrhine primates than currently recognized.

Progress toward understanding the evolutionary impact of sexual conflict and selection among primates requires clearer definitions, concepts, and operational measures.^{3,25,171} Currently, multiple definitions exist for sexual conflict,³¹ along with at least nine for sexual selection.²⁹ Similarly, the word "mate" is applied to both the copulatory and the reproductive partner,¹⁷² yet the distinction is great. Importantly, most descriptions of sexual selection invoke the false dichotomy between intersexual and intrasexual selection. Both of these modes of selection clearly impact both sexes. For example, while features of male primate anatomy and physiology are traditionally viewed in the context of male-male competition (for example, sperm competition), they also evolved in response to intersexual conflict and

female-mediated selection.^{157,173} Similarly, coercion and female choice are often categorized as examples of intersexual selection because the conflicting interests of males and females drive evolution in both sexes. However, these behaviors also evolve in response to intrasexual conflict. Thus, an individual's reproductive success is affected by competing strategies of both the opposite and the same sex, while also driving selection on both the same and opposite sex. Ultimately, however, how well an individual competes reproductively *relative to others of the same sex* is what determines the strength of selection.¹⁷⁴

Genetic studies of primates, with such a diversity of mating systems, provide tremendous potential for understanding intersexual conflict. Evidence of rapid evolution in genes related to reproduction highlights potential sexual conflict. Further studies that identify the functional consequences of these molecular changes will help to clarify how intersexual and intrasexual selection drive molecular evolution.^{135,175} Quantitative genetics is another compelling tool for examining sexual conflict in primates. Recently, Foerster and coworkers¹¹⁷ applied quantitative genetics to examine intralocus conflict in a wild red deer population. Specifically, they showed that the daughters of successful males had relatively low fitness, presumably because traits that made a male successful were detrimental when passed onto their female offspring. It should be feasible to replicate studies such as this in primates, particularly in breeding centers where detailed data exist on pedigrees and reproduction.

Clear methods for identifying selection on behavioral tactics between the sexes are also needed. For example, male coercion and female mate choice are difficult to tease apart, given the challenge of assessing whether mating was the result of female preference for a particular male or pressure from male intimidation. Moreover, continual counterbalancing adaptations between the sexes may obscure the antagonistic interaction and evolutionary

change resulting from sexual conflict.^{8,176} More refined methods for distinguishing between these include examining the behavioral, ontogenetic, and temporal plasticity of male and female strategies (for example, across the menstrual cycle) and their effectiveness.^{9,14,67,74,177,178} More broadly, the coupling of behavioral and genetic (for example, paternity) data is paramount to assessing the effectiveness of different sexual strategies and the costs and benefits of sexually antagonistic selection on individual fitness. Parental care is another fruitful area for examining sexual conflict, as this characteristic is of particular relevance to primates, carries a heavy cost, and is under substantial selective pressure. Examining the interaction between male and female neurological, hormonal, and behavioral mechanisms influencing paternal care¹⁷⁹ within a sexual conflict framework holds enormous potential to shed light on the evolution of this important, yet rare and poorly understood behavior.

Studies of primate morphology and physiology are also critical to evaluate sexual conflict. In particular, female traits affecting postcopulatory sexual selection may be under strong selection, but these mechanisms remain poorly understood¹⁸⁰ and understudied. A recent phylogenetically controlled analysis of 16 waterfowl species indicated that vaginal elaboration correlated positively with phallus morphology, suggesting the co-evolution of female-male morphological complexity and female counterstrategies to forced mating.^{181,182} These studies can be translated to primates, particularly focusing on clades with more elaborate penile structures, such as the strepsirrhines, and in mating systems characterized by direct coercion. Cross-disciplinary advances such as laser optical trapping could be applied to examine primate sperm motility across different mating systems⁹¹ and provide additional means and possibilities for examining sexual conflict across primates.

The growing recognition of sexual conflict as a significant evolutionary force offers a rich theoretical framework for understanding intersexual

dynamics in primatology and evolutionary anthropology. What is most interesting are the myriad ways that sexual conflict is expressed across different primate mating systems. Further research across primates will enable testing of the framework and predictions introduced in this paper. Integrating clearer operational definitions, new methodologies, long-term observations, and new models for exploring male and female interactions will offer a richer understanding of sexual conflict in this order, and opens up new comparative directions where primate research can certainly play an important role. There is much work to be done.

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