

## Bateman Revisited: The Reproductive Tactics of Female Primates<sup>1</sup>

CHRISTINE M. DREA<sup>2</sup>

*Department of Biological Anthropology and Anatomy, Duke University, Box 90383, Durham, North Carolina 27708-0383*

**SYNOPSIS.** The breeding system of an animal population is thought to depend on the ability of one sex (usually the male) to acquire mates, either directly through association with females or indirectly through defense of the resources desired by females. The sex that contributes most to infant care (usually the female) is constrained by parental involvement and thereby limits reproduction of the opposite sex. Accordingly, males, but not females, enhance their reproductive success by acquiring additional mates. This classical view has emphasized the role of male–male competition in sexual selection, at the expense of fully exploring the potential for female choice. A more recent shift in focus has revealed substantial variation in female reproductive success and increasingly accentuates the importance of female intrasexual competition and male mate choice. A comparative review of primate reproduction, therefore, challenges expectations of male control and female compliance, and calls for a comprehensive treatment of costs and benefits that extends beyond conventional mention of heavy female investment *versus* male negligence or absenteeism. For individuals that manipulate their social environment or reproductive output, consideration of more subtle, even cryptic, aspects of female behavior and physiology (*e.g.*, social strategizing, sexual solicitation or rejection, sexual advertisement or concealed ovulation, multiple mating, and reproductive failure) raises the question of whether females can be effectively ‘monopolized.’ Widespread patterns that counter Bateman’s paradigm call for a reexamination of the predictions generated by dichotomizing gametes into ‘expensive eggs’ and ‘cheap sperm,’ and encourage continued mechanistic research focused on conception quality rather than quantity.

### THE DARWIN–BATEMAN PARADIGM

Darwin’s first mechanism of sexual selection—male–male competition over access to females—was readily accepted by his contemporaries, but his second mechanism of female choice was less well received and has engendered enduring controversy. Darwin (1871) contended that choosy females were responsible for the flamboyant physical and behavioral traits of males. Ironically, one of his most notable examples of presumptive female choice—the extraordinary coloration and extravagant ornamentation of male mandrills (*Mandrillus sphinx*)—involves traits that were more likely to have been driven by intrasexual selection (Abernethy *et al.*, 2002), aptly illustrating the difficulty inherent in separating these two mechanisms (Wiley and Poston, 1996). Despite limited corroboration that female choice of males drives sexual dimorphism, the Primate Order boasts ample evidence of showy males and drab females. Historically, male extravagance became equated with male control over female reproduction and fueled an early perception of males as initiators of sexual behavior (Zuckerman, 1932). Likewise, the comparatively low profile of the female became equated with behavioral accommodation and she was traditionally seen as sexually submissive (Daly and Wilson, 1978; Keverne, 1976).

This view of demure females acquiescing to the sexual advances of assertive males was elaborated by Bateman in 1948. Bateman’s experiments on fruit flies

(*Drosophila melanogaster*) are credited for showing that males experience a reproductive advantage by mating with multiple females, whereas females are unlikely to increase their progeny as a function of additional mates (Fig. 1b in Bateman, 1948). Oddly, his concurrent, but contradictory, finding that female reproductive success (RS) actually does increase with additional mates (Fig. 1a in Bateman, 1948) went largely unnoticed. Nonetheless, based on his popular empirical findings that male flies have greater variance in RS and profit more from multiple mating than do females, Bateman argued that males are subject to more intense sexual selection than are females. Trivers (1972) subsequently expanded this theoretical framework by implicating the relative parental investment of the sexes as the driving force in sexual selection. Thus, Trivers argued, because fertilization and gestation occur in the female, her maximum reproductive output is limited compared to that of the male.

Together, these insights perpetuated notions about the universality of sex differences in behavior. In particular, differential investment in reproduction predicts (1) male sexual ardor *vs.* female sexual passivity, (2) male promiscuity (indiscriminate mate selection) *vs.* female monandry (mate discrimination), and (3) paternal disinvestment *vs.* maternal care. The expectation of female monandry, for instance, became so entrenched that models of parental investment failed to incorporate correction factors for female remating (see Wade and Shuster, 2002).

Theoretical discussions and empirical evidence have long contested these sexual stereotypes (Eberhard, 1996; Gowaty, 1997; Hrdy, 1981; Small, 1989), arguing that early emphasis on the outcome of intermale

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<sup>2</sup> E-Mail: cdrea@duke.edu

competition both obscured important processes occurring in the female and assumed shared reproductive interests between the sexes. The historical focus on male behavioral and morphological traits that are showy, at the expense of female traits that may be subtle or even cryptic, produced enduring contradictions or paradoxes, evident between “female passivity” and “female choice” or in the female’s purported relinquishment of reproductive control despite her greater reproductive investment. Since then, a shift in emphasis, paired with technological advances, has provided better appreciation of the female’s active role in sexual selection, and has revealed significant sexual conflict and interaction that calls for a reassessment of established hypotheses (Hughes, 1998). In light of these more recent findings, the present discourse re-evaluates the general applicability of the Darwin–Bateman predictions with respect to the Primate Order.

#### PRIMATES AS AN EXTREME TEST CASE

Discussions of the Darwin–Bateman paradigm often center on species in which sexual activity is tightly linked to female fertility and in which females produce fast-developing broods or clutches (note 1 in Trivers, 1972). Such species also typically form anonymous societies characterized by transient male–female relationships and limited behavioral flexibility. This section outlines how primates differ from those species in a manner that provides an extreme test case of the paradigm’s predictions.

#### *Life history variables and reproductive considerations*

Females within the Primate Order possess certain distinguishing characteristics. First, because they evolved from the ‘primitive’ mammalian condition of strictly circumscribed sexual receptivity to a more “advanced” state of situation-dependent receptivity (Hrdy and Whitten, 1987), most female primates show a decoupling of sex and fertility. Whereas prosimians display estrus, anthropoids lack estrus, such that their sexual receptivity is emancipated from hormonal control and they can engage in copulation at any stage of their cycle (Wallen, 1990). Second, because of the energetic demands of producing highly encephalized infants, primate mothers are heavily invested in their young, more so than are other mammalian mothers of similar size. Costs assumed by primate mothers include lengthy gestation and prolonged periods of lactation and infant dependency (Harvey *et al.*, 1987). Slow development further extends the juvenile period (Pereira and Fairbanks, 1993) and delays sexual maturity. Finally, most primates produce only one infant per pregnancy.

Aside from the conventionally recognized constraints on female fertility (*e.g.*, concealed release and short-term survival of only one egg per fertile period), many primates are more cryptically constrained by reproductive inefficiency or gamete wastage, such that even fertile females can be notoriously ‘infertile’

(Short, 1976; Wasser and Barash, 1983). In women, for instance, approximately 50% of cycles are anovulatory or too short to allow implantation (Einon, 1998). If cycles are fertile, sexually active women may still fail to conceive or implant. Additionally, pregnant women may suffer low embryo viability, miscarriage, premature delivery, or perinatal death (Short, 1976). Likewise, in wild vervet monkeys (*Cercopithecus aethiops*), 50% of conceptions may result in miscarriage (Turner *et al.*, 1987).

The maternal burden in primates therefore combines energetically costly infants with low reproductive output. In wild yellow baboons (*Papio cynocephalus*), for instance, the mean number of offspring surviving to four years varies between only 0.48–2.07 (Wasser *et al.*, 2004). Moreover, by coupling the enhanced behavioral potential for nonfertile mating with the physiological constraints on reproduction, it becomes apparent that observed mating success can be an extremely poor predictor of RS (Drea and Wallen, 2003).

Contrary to expectation, consideration of these hallmark features raises logistical difficulties for those who might interpret Bateman’s (1948) landmark study as a demonstration of the seemingly limitless potential for fatherhood. This harem myth—the distorted notion that successful male primates can father hundreds of offspring by merely increasing sexual activity—ignores, not only the exceptional status of harems in the primate world, but the low probability of conception associated with each copulatory act (Einon, 1998; Short, 1976). In humans, for instance, males are hard pressed to improve over women’s odds of reproduction, so the range in male and female lifetime RS tends to be equal.

The premise that reproduction is “expensive” for females, but “cheap” for males might adequately characterize some species, but in many cases, the currency of a sperm–egg comparison oversimplifies the male’s contribution and disregards his substantial stake in the reproductive process. Unlike the female’s post-fertilization investment, the male’s pre-fertilization investment (including his emphasis on growth at the expense of delaying puberty and postponing RS) is often minimized in the comparative assessment of reproductive costs. Specifically, the expense of producing (Dewsbury, 1982) and maintaining (Thomsen *et al.*, 2003) viable ejaculate should be factored into the male’s uncertain paternity (*e.g.*, through sperm competition) and the need for repeat performance (*e.g.*, to ensure fertilization). Primates pose somewhat of an enigma, therefore, as the more profound and pervasive the difficulties associated with conception, the greater the investment necessitated by both sexes. Female fertility constraints, while raising the cost of eggs, also impose further reproductive investment on the male, undoubtedly increasing the cost of sperm.

#### *Social complexity and behavioral flexibility*

Another unusual feature of most primates is that their complex societies combine enduring social and

kin relationships with year-round male residency (Cheaney *et al.*, 1986). In hierarchical organizations, dominant status is commonly seen to confer mating rights to select males; yet, 'individualized' primate societies are also marked by opportunities for the exploitation or cultivation of relationships (Byrne and Whiten, 1988; de Waal and Tyack, 2003), providing increased potential for social factors to influence behavior, mating tactics, and reproductive outcome (Altmann and Alberts, 2003; Bercovitch, 1991; Silk *et al.*, 2003). From the female's perspective, social strategizing and coalition formation allow some females to dominate males that are individually stronger, even in patriarchal societies (Parish, 1996), while other females might consort with an adult male to reduce potential sexual harassment from additional suitors (Fox, 2002). Likewise, while friendships with males provide protection for females and their offspring (Palombit *et al.*, 1997; Smuts, 1985), social integration amongst females can ultimately enhance infant survival (Silk *et al.*, 2003).

The complexity of social interaction among primate group members can blur the distinction between male intrasexual contest and female choice: Consider, for example, that a male's dominance status is usually attributed to his fighting ability, when the achievement or maintenance of his rank may require female support (Bernstein and Sharpe, 1966). When paired with reproductive constraints, such behavioral flexibility casts doubt on the adequacy of one "best" male for all females.

#### MALE SEXUAL ARDOR VS. FEMALE SEXUAL PASSIVITY

Sexual drive in the male primate is well established (although not incompatible with male choice), but the idea of female passivity has long been refuted (Gowaty, 1997; Hrdy, 1981). Female primates may set the stage for male competition, but they are also actively discriminating and competitive over mates. Renewed interest in mechanisms of mate choice and intrasexual competition has broadened the scope for sexual selection to influence the coevolution of male and female traits (Wiley and Poston, 1996; Paul, 2002). For instance, "direct" mate choice (*i.e.*, discriminating between the attributes of individuals) and "indirect" mate choice (*i.e.*, limiting the set of potential mates through morphological or behavioral traits) both produce assortative mating. The present section highlights critical aspects of female reproductive control through discussion of female sexual initiation, advertisement of sexual status, and elimination of rival females. It notes that, as females differ in quality and fecundity, knowledge of the variability in female attributes (and reliable detection of female fertility) would facilitate male mating strategies, placing males under similar evolutionary pressure to be choosy.

#### *Female mate choice (precopulatory mechanisms)*

While some female primates appear to merely accept copulation with eager males (Smuts, 1985), others either effectively reject (Huffman, 1987) or actively

solicit (Janson, 1984) sex, often showing clear partner preferences (Small, 1989). Uncooperative females can prevent intromission by failing to adopt certain postures or can terminate copulation prior to ejaculation (see reviews in Drea and Wallen, 2003; Reeder, 2003). Consideration of individual variation in female proceptivity and receptivity (Beach, 1976) has revealed far greater scope of mating patterns and has provided a better understanding of the female's regulation of sexual activity (Wallen, 1990).

The mating pattern of male rhesus monkeys (*Macaca mulatta*), for example, involves multiple female partners and fluctuates wildly over the breeding season, revealing little about the animals' sexual motivation; however, peaks in female estradiol concentration (*i.e.*, fertility) are mirrored in her sexual solicitations, both of which significantly predict male ejaculation frequencies (Wallen and Tannenbaum, 1997). The mating behavior of orangutans (*Pongo pygmaeus*) reveals a similarly powerful influence of female sexual motivation. In captivity, male-controlled social interaction increased sexual activity (including forced copulation) without being procreative, whereas female-controlled social interaction decreased rates of copulation, yet resulted in pregnancy (Nadler, 1982). Likewise, in the wild, female consortship with a male—a likely indicator of female choice—better predicted paternity than did the males' physical attributes or dominance status (Utami *et al.*, 2002). Together, these studies illustrate how females might bias paternity by influencing the timing of copulation, which highlights the critical importance of male attendance to female invitational cues, even for species in which sexual initiation and control historically have been attributed to the male.

#### *Female sexual advertisement*

Scent marking is well established as a prominent form of communication among prosimian and New World primates (Schilling, 1979; Epple *et al.*, 1993), whereas the importance of olfactory cues in "microsmatic" Catarrhine primates only recently has been gaining appreciation. Absence of a clear territorial function in female scent marks points to its role in intersexual communication, including sexual advertisement and proceptivity (Heymann, 2003). Given that odors contain information about an individual's sex, reproductive state, dominance status, identity (Epple *et al.*, 1993), and even degree of genetic relatedness (*e.g.*, via the major histocompatibility complex or "MHC": Penn and Potts [1998]), scent signals may communicate mate quality (Wedekind *et al.*, 1995), and thereby influence mate choice. Odor cues could be additionally useful to males discriminating between females that are dispersed, but relatively synchronized in their reproductive cycles (Drea *et al.*, 2004).

Female primates also advertise their reproductive status through visual means. Aside from behavioral and postural displays, visible cues include facial reddening and sexual swellings, particularly in the peri-

neal region (Hrdy and Whitten, 1987; Dixson, 1998). Swellings may indicate fecundity, in that maximal tumescence correlates with the peak probability of ovulation (Nunn, 1999), but they are both excessive (Pagel, 1994) and imprecise cues (Heistermann *et al.*, 1996). Sexual swellings occur in species representing all major primate radiations and are more specifically associated with multimale–multifemale (MM–MF) breeding systems (Dixson, 1998). Exaggerated swellings, which occur only in the Old World anthropoids, appear to be relatively costly: Swollen females experience substantial weight gain, greater energy expenditure during travel, water retention, increased parasite load, susceptibility to bruising, and even discomfort (Nunn, 1999).

Assuming these costs are offset by reproductive benefits, the various hypotheses advanced to explain the evolution of sexual swellings dispute whether these signals serve to concentrate paternity amongst choice males (Clutton-Brock and Harvey, 1976), to confuse paternity (Hrdy, 1981), or even to increase male confidence in paternity (Hamilton, 1984). Attractive cues to the male, swellings are associated with increased male attention and sexual arousal (Bielert, 1982). Moreover, males will endure the costs of receiving aggression from other males and providing grooming services to females in order to preferentially mate with females that have larger perineal swellings (Domb and Pagel, 2001). Accordingly, sexual swellings appear to represent highly derived, sexually selected ornamentation in females.

#### *Female–female competition and reproductive success*

Compared to male–male competition, its female counterpart has received far less attention (Hrdy, 1981; Silk, 1993). Among species in which both sexes display dominance hierarchies and expend significant effort on rank maintenance, social status is likely to confer reproductive benefits, not only to males (as we shall see later), but also to females. Indeed, there is strong evidence of rank-related reproductive skew in females, which often can be attributed to differential access to resources (Pusey *et al.*, 1997; van Noordwijk and van Schaik, 1999); however, growing evidence also suggests that female competitive social relationships can have profound fitness consequences independent of dominance or resource allocation.

Among the well-studied, cooperatively breeding calitrichid primates, reproduction is strongly biased through intrasexual influences in both sexes (French, 1997; Saltzman, 2003). The mated or dominant female suppresses ovulation in subordinate females through behavioral and olfactory cues modulated by cryptic neuroendocrine mechanisms, thereby blocking her male partner's opportunities for extra-pair breeding. Among cercopithecines, more overt mechanisms of female competition are in place, as the period of peak estradiol concentration is associated with increased rates of female–female aggression (Wallen and Tannenbaum, 1997). Female primates interfere with the

copulatory behavior, fertility, and reproductive output of other female group members through attack coalitions, harassment, infanticide, and physical eviction from the group (Silk, 1993; Wasser and Barash, 1983; Wasser and Starling, 1988; Vervaecke *et al.*, 2003).

The myriad forms of female–female competition contribute to rank-related variance in female RS: Compared to subordinates, dominant females mature earlier, live longer, have a longer reproductive life span, have a lower incidence of miscarriage, produce more offspring that are more likely to survive to reproductive age, and have shorter inter-birth intervals with shorter periods of lactation (Wasser *et al.*, 2004). In such cases where female fecundity varies, it stands to reason that males should be choosy.

#### MALE PROMISCUITY VS. FEMALE MONANDRY

Because sexual selection theory holds that males should seek to maximize their reproductive output through indiscriminate mating, whereas females should be highly selective and mate only with the choice male, monogamous mating systems, in which the male mates with only *one female*, and systems in which females mate with *numerous males*, challenge the conventionally expected sex differences in RS. In the former case, the reproductive output of males and females would necessarily converge; in the latter case, female RS would likely improve with multiple matings. Whereas less than 3% of nonprimate mammals form exclusive pair bonds (Kleiman, 1977), between 14–18% of primates are monogamous (Hrdy, 1981; Rutberg, 1983), so male promiscuity is far from universal. Nevertheless, as Bateman (1948) and Trivers (1972) recognized the exceptional status of monogamous (and polyandrous) systems, this section first reviews male RS in polygynous, MM–MF, and dispersed societies, and then addresses the issue of female promiscuity.

#### *Constraints on male reproductive success*

Reproductive skew should be most apparent in one-male breeding units or multi-male systems in which only select males achieve RS by 'monopolizing' fertile females (Emlen and Oring, 1977). Because dominance status provides priority of access to resources, including sexual partners, male rank might function as a queue for mating opportunities (Altmann, 1962). Early studies that reported male reproductive skew used social rank as a proxy of male quality, seasonality as a proxy of the male's ability to monopolize females, and male mating success (defined as the number of consorts, copulations, ejaculations, or partners) as a proxy of male RS—all of which can be problematic. Nevertheless, with the advent of molecular genetic techniques, various paternity studies indeed revealed a positive correlation between male dominance status and RS (see reviews in Cowlshaw and Dunbar, 1991; Di Fiore, 2003) and showed that increased mating by dominant males can accurately predict RS (Altmann *et al.*, 1996); however, short-term measures of RS (as

typically assessed by paternity studies) do not account for differential infant survival, social instability, or variance in the males' ability to monopolize females, and may not translate into accurate estimates of lifetime RS (Alberts *et al.*, 2003; Altmann *et al.*, 1996; Clutton-Brock, 1988).

More broadly, but especially among primates, the relationship between status, mating success, and RS has been equivocal: The outcome of male–male competition does not invariably influence mating success nor does mating success necessarily predict RS (reviewed in Ellis, 1995). Lack of concordance between these variables may derive in part from uniform adherence to the premise of male defensibility of females, which (1) presupposes female compliance when males are not universally poised to govern females (Drea and Wallen, 2003), (2) minimizes the effectiveness of alternative male strategies, such as sneak copulation (Berard *et al.*, 1994) and coalition formation (Noé and Sluijter, 1990), and (3) assumes that males either can effectively guard a female throughout her fertile period (despite associated costs: Alberts *et al.*, 1996) or have perfect knowledge of female fertility (which may be especially unrealistic if females conceal ovulation: Drea and Wallen, 2003). Consideration of these factors is necessary to appreciate that subordinate males can father a significant proportion of offspring despite intense monopoly of females by dominant males (Heistermann *et al.*, 2001). Even among pair-living species, evidence of extra-pair copulation (Palombit, 1994; Reichard, 1995) and fertilization (Fietz *et al.*, 2000) calls into question female fidelity and the exclusivity of male mating rights.

More to the point, departure from the predicted pattern minimizes the effectiveness of female choice, independent of male dominance (Huffman, 1987; Manson, 1992), which may be required to explain that male RS can be better predicted by a male's genotype (specifically heterozygosity of the MHC) than by his dominance status (Widdig *et al.*, 2004).

By underscoring the efficacy of alternative male tactics and the significance of female choice in shaping male RS (Di Fore, 2003), recent DNA fingerprinting studies reveal uncertainty in the extent to which the priority-of-access model is applicable across species. Factors reported to influence the fit of the model include male age and length of residency, sex ratio and dispersal patterns, number of competitors, costs of mateguarding, and environmental conditions (Cowlshaw and Dunbar, 1991; Alberts *et al.*, 2003). Nevertheless, incorporation of female resistance into models of female choice is suggested by the growing recognition that sexual conflict plays a prominent role in sexual coevolution (Chapman *et al.*, 2003). Such consideration would cast doubt on the ability of one sex to routinely "monopolize" the other. Accordingly, compatibility between parental genotypes (Zeh and Zeh, 2003) may also feature as an important source of variation in male RS. In either case, departure from the model suggests the need for a more unified and

integrated framework for understanding reproductive skew in all types of social systems.

#### *Female multiple, indiscriminate, and nonprocreative mating*

Serial sexual associations with multiple males have long challenged the idea of the monandrous female (Hrdy, 1981): Ample empirical evidence (derived from all major primate radiations) indicates that females copulate with more than one partner per fertile period and at times that could not be procreative (Dixson, 1998; Soltis, 2002; Reeder, 2003). Moreover, because females can appear to be indiscriminate, copulating with almost every male in the group rather than with the one "best" male, promiscuity has been seen as incompatible with female selectivity (Small, 1989). Indiscriminate mating, however, does not necessarily imply that fertile mating is randomly distributed: Even opportunistic females might display mate preferences that could bias paternity (Matsumoto-Oda, 1999).

The potentially negative consequences of a female's multiple liaisons suggest that promiscuity may entail compensatory benefits. The costs associated with sexual intercourse, including energy expenditure, loss of foraging time, susceptibility to predation (owing to compromised vigilance), and risk of disease exposure or parasite transmission (Daly, 1978), are likely to increase proportionately with the number of copulatory events or partners (Nunn *et al.*, 2000). Far from being monandrous, therefore, females are apparently under strong selection pressure to be promiscuous.

Hypotheses advanced to explain why female primates should assume the cost of mating with multiple partners fall into two broad categories of potential compensatory benefits: nonprocreative and procreative. Nonprocreative benefits of multiple mating include depleting the sperm available to rival females, recruiting males to the social group, trading sex for resources, and confusing paternity, either to reduce the risk of infanticide or to secure infant care from additional males (reviewed in Soltis, 2002). While most of the theoretical and empirical support favors paternity confusion, it is also likely that different benefits obtain for different species.

#### *Cryptic female choice (postcopulatory mechanisms)*

The procreative benefits of multiple mating may simply include ensuring insemination (to counteract potential infertility); however, because a male's likelihood of paternity is a function of the number of rival mates, multiple mating by females sets the stage for postcopulatory mechanisms of sexual selection, including sperm competition and cryptic female choice (Birkhead, 2000; Eberhard, 1996; Parker, 1970). Consequently, additional procreative benefits may include "trading up" for a superior mate's sperm through a "good genes" model, minimizing genetic incompatibilities that could result in reproductive failure, and increasing genetic diversity or viability (*e.g.*, inbreed-

ing avoidance) among progeny (see reviews in Jennions and Petri, 2000; Zeh and Zeh, 2003).

Despite the difficulties associated with demonstrating sperm competition and cryptic female choice, several lines of evidence suggest that these mechanisms are functioning in primates. Although this area of investigation is in its infancy, as with previous biases, sperm competition has received relatively more attention than has cryptic female choice. Primate research has traditionally relied on relative testis size as a proxy for male sperm competition because it is indicative of the volume of seminiferous tubules and sperm production, and is greater in species in which females mate multiply (Harcourt *et al.*, 1981). Likewise, the coagulation of semen and formation of copulatory plugs (that may prevent sperm loss), and the presence of complex penile morphologies (that may facilitate prolonged or deeper intromission, as well as sperm transfer) tend to coincide with female promiscuity (Dixon, 1998).

Females, on the other hand, can impose constraints on males following sperm deposition, by ejecting sperm or manually removing copulatory plugs (Reeder, 2003). Various anatomical and physiological barriers present in the female reproductive tract may also serve to impede sperm deposition, transport, and viability (Dixon, 1998). Following fertilization, females have additional control mechanisms to manipulate pregnancy (Drea and Wallen, 2003). Thus, female primates can potentially select against less viable sperm or less viable embryos. In female macaques and humans, increased similarity between parental genotypes is associated with increased reproductive failure (Knapp *et al.*, 1996; Ober *et al.*, 1998). The possibility that genetic compatibility may drive mate or gamete choice is gaining theoretical and empirical support, with further study promising to shed new light on mechanisms of sexual selection (Tregenza and Wedell, 2000; Stockley, 2003; Zeh and Zeh, 2003).

#### PATERNAL DISINVESTMENT VS. MATERNAL CARE

A female mammal's obligatory investment in lengthy gestation and lactation ensures her commitment to the young; however, her male partner is exempt from the same physical responsibilities. Thus, the majority of female mammals (>90%) care for their young alone (Kleiman and Malcolm, 1981). Primates are somewhat exceptional in this regard, as many males routinely protect, rescue, patrol, baby-sit, adopt, carry, shelter, feed, play with and groom infants (Whitten, 1987; Wright, 1990).

Because parental care limits reproductive opportunities, male investment is expected when confidence in paternity is high (Trivers, 1972) or when additional care is essential to infant survival (Kurland and Gaulin, 1984). Both of these conditions are met in several monogamous and polyandrous New World monkeys, where adult males perform most of the carrying (see Taub, 1984) and extensive male investment is critical to successful breeding (Goldizen, 1987). Nevertheless,

not all monogamous males partake in infant care (Van Schaik and Dunbar, 1990) and extensive male care is not necessarily associated with monogamy or paternal confidence (Whitten, 1987; Wright, 1990). With notable exceptions (Leighton, 1987), surprisingly few of the monogamous lesser apes provide infant care—surprising because absence of male care under conditions of paternal confidence counters the expectations of kin selection theory. Moreover, male presence in dissuading potential attackers occurs in various MM–MF groups where paternity is uncertain (Hector *et al.*, 1989; Packer, 1980; Pollock, 1979). Thus, some males may endure the costs of care (evident in expended energy, reduced foraging time, and aggression received from other males) without necessarily having genetic ties to their infant charge.

Although early descriptive accounts of male care could not quantify the degree of genetic relatedness between caregiver and infant, more recent paternity studies are producing similarly mixed results: Whereas some genetic studies in MM–MF societies validate male care by nonkin (Paul *et al.*, 1996), others show evidence of genetic relatedness between infants and their male providers. For instance, male savannah baboons (*P. cynocephalus*) show true paternal care, selectively supporting their genetic offspring in agonistic disputes (Buchan *et al.*, 2003). Likewise, among langurs (*Presbytis entellus*), only the fathers or males that had been residents at the time of conception were observed to protect infants from potentially infanticidal attacks (Borries *et al.*, 1999).

Although monogamy increases confidence in paternity, the variance in, and especially absence of, male care among monogamous species suggests that, contrary to the predictions generated by sexual selection theory (Trivers, 1972), paternal certainty is not prerequisite to the evolution of male care (Wright, 1990). The existence of male care in promiscuous species with minimal paternal certainty bolsters this argument; although, in some cases, it highlights the need for a better understanding of the mechanisms of paternal kin recognition. Other hypotheses that could account for these findings, such as mating effort or agonistic buffering (Paul *et al.*, 1996) also merit further scrutiny.

#### CONCLUDING REMARKS

This review has highlighted numerous disparities between the behavioral sex differences predicted by the Darwin–Bateman paradigm and the actual sex roles displayed within the Primate Order. Although primates may present an extreme test case of these predictions, the exceptions noted herein are more broadly representative of other taxonomic groups. In mammals alone, a male's RS can be compromised by sperm depletion (*e.g.*, Preston *et al.*, 2001), by the effectiveness of alternate male strategies (*e.g.*, Wilmer *et al.*, 1999), and by female choice, as countless females profit from mating with more than one male (*e.g.*, Hoogland, 1998) and/or from selecting dissimilar mates (*e.g.*, Amos *et al.*, 2001). Likewise, significant

variance in female lifetime RS (e.g., von Holst *et al.*, 2002), implicates a more pervasive role for female intrasexual competition and male choice of mates (e.g., Szykman *et al.*, 2001). That mating success may not predict RS increasingly suggests that females bias paternity through behavioral and physiological means (Hughes, 1999). Thus, detailed studies have provided evidence of sexual conflict and emphasized female mechanisms of reproductive control to a greater extent than previously recognized.

While the *potential* for sex differences in RS is uncontested, the number of sexual partners and the size of their gametes may reveal little about actual lifetime variance in RS—far less than would the manner in which the sexes and their gametes interact. Contrary to Bateman's paradigm, therefore, measures of sexual selection should be based on paternity or number of fertilizations rather than on mating success or number of partners. Much of the controversy resides not in the theory so much as in our emphasis on and interpretation of its component parts; nevertheless, some authors have proposed a reformulation of sexual selection theory that places greater emphasis on female selection via genome interaction (Tregenza and Wedell, 2000; Zeh and Zeh, 2003).

Much of the attention in sexual selection theory has been concerned with the “why” questions. The time is ripe to focus on the “how” questions, with continued study of the proximal neuroendocrine mechanisms regulating sexual desire, the behavioral details of mate choice, the physiological constraints on conception, and the molecular genetics of parental compatibility. Future research faces important challenges, such as determining appropriate measures of individual mate quality (in males and females) and expanding the number of long-term studies that can compare lifetime RS within and between sexes. The strategies by which males and females maximize their RS cannot be fully appreciated without a better understanding of the multiple mechanisms operating, in both sexes, to influence fertilization.

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