

## CURRENT ISSUES – PERSPECTIVES AND REVIEWS

### **Toward a New Sexual Selection Paradigm: Polyandry, Conflict and Incompatibility (Invited Article)**

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#### **Abstract**

Darwin's recognition that male–male competition and female choice could favor the evolution of exaggerated male traits detrimental to survival set the stage for more than a century of theoretical and empirical work on sexual selection. While this Darwinian paradigm represents one of the most profound insights in biology, its preoccupation with sexual selection as a directional evolutionary force acting on males has diverted attention away from the selective processes acting on females. Our understanding of female reproduction has been further confounded by discreet female mating tactics that have perpetuated the illusion of the monogamous female and masked the potential for conflict between the sexes. With advances in molecular techniques leading to the discovery that polyandry is a pervasive mating strategy, recognition of these shortcomings has brought the study of sexual selection to its current state of flux. In this paper, we suggest that progress in two key areas is critical to formulation of a more inclusive, sexual selection paradigm that adequately incorporates selection from the female perspective. First, we need to develop a better understanding of male  $\times$  female and maternal  $\times$  paternal genome interactions and the role that polyandry plays in providing females with non-additive genetic benefits such as incompatibility avoidance. Consideration of these interaction effects influencing natural selection on females is important because they can complicate and even undermine directional sexual selection on males. Secondly, because antagonistic coevolution maintains a balance between opposing sides that obscures the conflict itself, many more experimental evolution studies and interventionist investigations (e.g. gene knockouts) are needed to tease apart male manipulative adaptations and female counter-adaptations. It seems evident that the divisiveness and controversy that has plagued sexual selection theory since Darwin first proposed the idea has often stalled progress in this important field of evolutionary biology. What is now needed is a more pluralistic and integrative approach that considers natural as

well as sexual selection acting on females, incorporates multiple sexual selection mechanisms, and exploits advances in physiology and molecular biology to understand the mechanisms through which males and females achieve reproductive success.

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*'For what a man would like to be true, that he more readily believes.'* (Bacon 1620)

### Introduction

According to Kuhn (1962), scientific endeavor proceeds through cycles. Long periods of what he describes as 'normal science' are devoted to the mopping-up operations of realizing the promise and refining the articulation of the prevailing paradigm. Such periods of relative stability come to an end when, in the process of carrying out that normal science, researchers uncover an anomaly in nature that cannot be forced '... into the preformed and relatively inflexible box that the paradigm supplies' (Kuhn 1962). The discipline enters a crisis, transition phase characterized by a proliferation of divergent articulations, involving ad hoc adjustments of the paradigm that attempt to resolve the problem of the anomaly. 'Though there is still a paradigm, few practitioners prove to be entirely agreed about what it is' (Kuhn 1962). Long-standing paradigms, however, are not readily rejected. What is required is a new framework that convincingly assimilates the disturbing anomaly by reconstructing the field from new fundamentals. Only after this new paradigm has been enunciated and has gained consensus support is the old paradigm discarded. The revolution is now complete and normal science can proceed anew. Drawing on such notable examples from the physical sciences as the Copernican and Newtonian revolutions, Kuhn (1962) points out that paradigm shifts may be triggered when '... a piece of equipment designed and constructed for the purpose of normal research fails to perform in the anticipated manner, revealing an anomaly that cannot, despite repeated effort, be aligned with professional expectation.'

In the biological sciences, the agent of change has not been a particular piece of equipment but rather a set of molecular tools that has enabled researchers to see through the individual organism to the molecular and genetic processes that underlie its development and reproduction. In just 50 years since Watson & Crick (1953) described the double-helical structure of DNA, the central dogma of molecular biology has been established (DNA makes RNA makes protein), recombinant DNA techniques have made possible genetic engineering, and the entire genomes of several species, including *Homo sapiens*, have been sequenced. Along with these advances have come unexpected discoveries. For example, horizontal gene transfer is now known to be a common feature of prokaryotic evolution (Wolf et al. 2002). Potentially disruptive transposable elements have been found to be a predominant component of many eukaryotic genomes (Bestor 2003). Cellular endosymbionts such as *Wolbachia* have been shown to manipulate

sex and reproductive behavior in a staggering diversity of arthropod hosts (Charlat et al. 2003), while genomically imprinted genes in mammalian embryos violate Mendelian principles by varying their expression, depending on whether they are inherited through sperm or eggs (Wilkins & Haig 2003). Such selfish genetic elements operating within the individual are not easily reconciled with the Modern Synthesis concept of a co-adapted genome that is a harmonious ‘... parliament of genes, which so regulated itself as to prevent cabals of a few conspiring for their own selfish profit at the expense of the commonwealth’ (Leigh 1977). The preponderance of selfish genetic elements that has been revealed by comparative genomics is, however, consistent with a view of evolution that ranks the gene as the fundamental unit of selection and the individual as an ephemeral, phenotypic manifestation of an uneasy alliance between genes whose conflicting interests may often result in an irreconcilable arms race over transmission to the next generation (Dawkins 1976, 1982; Cosmides & Tooby 1981).

For ethologists and behavioral ecologists engaged in the study of sexual selection, the landmark advance in molecular technology came with Alec Jeffreys’s discovery of hypervariable DNA and its utility for DNA fingerprinting (Jeffreys et al. 1985). Previously limited to extrapolating reproductive success from observations of mating success, researchers now had a tool for unambiguously assigning paternity in the wild. Quite unexpectedly, the new technique would rapidly reveal one of nature’s best-kept secrets, namely, that females across a wide array of species frequently mate with more than one male. The question of why females so commonly engage in polyandry, despite the potentially high risks and costs associated with copulation (Rowe et al. 1994; Chapman et al. 1995; Watson et al. 1998; Holland & Rice 1999), has shifted the focus of attention in sexual selection research from what was previously a preoccupation with male mating strategies (for exceptions, see Kirkpatrick 1987; Kirkpatrick & Ryan 1991) to a consideration of reproduction from the female perspective. More importantly, the discovery that polyandry is a pervasive feature of natural populations has uncovered an anomaly that cannot easily be aligned with the Darwinian paradigm of the promiscuous male and the choosy, essentially monogamous female (Darwin 1871; Williams 1966; Trivers 1972). As a consequence, the last decade has seen a proliferation of empirical and theoretical investigations of female mating behavior that have variously: (i) interpreted the data in a manner consistent with the existing sexual selection paradigm (e.g. Petrie & Kempenaers 1998), (ii) modified the paradigm to accommodate the anomalous data (e.g. Keller & Reeve 1995), or (iii) looked beyond the bounds of the paradigm for an explanation of the selective forces favoring the evolution of polyandry (e.g. Zeh & Zeh 1996, 1997). With little agreement on the relative importance of pre- and post-copulatory female choice, male/female antagonistic coevolution and ‘good genes’ vs. incompatibility avoidance, sexual selection research currently exhibits characteristics symptomatic of a scientific discipline in the throes of Kuhnian crisis.

In this Perspectives and Reviews article, we focus on the need for a new, pluralistic paradigm of sexual selection, one that retains fundamental Darwinian

concepts but expands the framework to incorporate recent insights into sensory physiology, genomic conflicts, and sexually antagonistic coevolution. To this end, we first provide a brief historical overview of the field, with particular emphasis on the controversies that have plagued the study of sexual selection since its inception. We then consider the anomalies that have led to the current crisis, and the hypotheses that have been proposed to account for them. Finally, we suggest a number of issues that need to be addressed in reaching a new, consensus view of the selective forces shaping male and female reproductive behavior.

### **The Darwinian Sexual Selection Paradigm**

... *'so it appears that female birds in a state of nature, have by a long selection of the more attractive males, added to their beauty or other attractive qualities.'* (Darwin 1871)

From its modest debut as a three-paragraph aside in Darwin's 490-page 'abstract' of his theory of evolution by natural selection (Darwin 1859) to its current status as a major field of evolutionary biology, the concept of sexual selection has been fraught with controversy. Realizing that characteristics conferring a competitive advantage in mating could be favored, even if opposed by natural selection, Darwin proposed sexual selection to explain the paradoxical evolution of exaggerated male traits detrimental to survival. Such selection could occur either through direct male competition for mating opportunities or as a consequence of females choosing to mate with attractive males (Darwin 1871). Male-male competition as a potent evolutionary force was neither a highly controversial proposal nor a particularly novel one, having been considered by Darwin's grandfather, Erasmus, over 60 yr earlier (Darwin 1794). By contrast, the suggestion that sexual selection might occur through female choice, particularly choice based on esthetics, was received with extreme skepticism and even ridicule (Wallace 1889). Andersson (1994) notes that, ironically, it was one of Darwin's most vehement critics who laid the groundwork for the development of a genetically explicit theory of mate choice. Commenting on the feasibility of female choice as a mechanism of sexual selection, the geneticist, Morgan (1903), remarked: 'Shall we assume that still another process of selection is going on, ... that those females whose taste has soared a little higher than that of the average ... select males to correspond, and thus the two continue heaping up the ornaments on one side and the appreciation of these ornaments on the other? No doubt an interesting fiction could be built up along these lines, but would anyone believe it, and, if he did, could he prove it?' Morgan's gibe precisely anticipated Fisher's (1930) 'runaway' model of the joint evolution of female preference and preferred male trait. Indeed, as Andersson (1994) points out, Fisher (1915) was undoubtedly aware of Morgan's comment when he first sketched out both the runaway and the viability-indicator mechanisms for the evolution of female choice.

**Sexy Sons Run Away Courtesy of their Choosy Mothers**

*'In the first place competition between males for mates, accompanied by any form of female choice, is not the common phenomenon postulated by Darwin.'* (Huxley 1938).

The scientific community of the early 20th century did not consider female choice to be a significant agent of evolutionary change, and Fisher's model of runaway sexual selection was largely ignored. Indeed, sexual selection was relegated to a position of obscurity in the classic works of the Modern Synthesis (Huxley 1942; Mayr 1942; Dobzhansky 1951). Only Mayr (1942) even made reference to the topic, arguing that female choice functioned not in sexual selection but rather in species recognition. It was not until the 1960s that the theoretical and empirical study of sexual selection finally experienced a renaissance, set against the backdrop of the women's liberation movement in North America. In pioneering, computer-simulation studies of sexual selection by female choice, O'Donald (1962, 1967) used a diploid, two-locus model to quantify the effect of preferential mating on linkage disequilibrium between alleles at the female-preference locus and the male-trait locus, and was able to establish the general plausibility of the Darwin/Fisher self-reinforcing mechanism. Nonetheless, O'Donald (1983) cautioned that the dynamics of the process were extremely complex, and depended on whether the alleles were dominant or recessive, their initial frequencies, and the behavioral model of preference expression (absolute or relative preference). He also rejected Fisher's (1930) assertion that the preference allele must always increase exponentially: in some simulations the female preference allele had barely increased in frequency and in no case did it ever reach fixation. Ultimately, it was the ground-breaking theory of Lande (1981), who used a quantitative genetics approach to obtain analytical solutions to models of the runaway process, that led to widespread acceptance of the Fisherian mechanism in the 1980s.

**Truth in Advertising: Good Genes Gain Ground**

The 1960s also witnessed a resurgence of interest in Fisher's (1915) hypothesis that sexually selected traits in males can serve as indicators of viability for female choice. Frequently portrayed as a strict alternative to Fisherian runaway selection, the viability-indicator mechanism was re-introduced by Williams (1966) and gave rise to a class of hypotheses variously termed 'handicap,' 'good genes,' or 'indicator' models. Most contentious of these was the handicap model proposed by the ethologist, Zahavi (1975), who argued that the ability to express a trait that handicaps survival provides a test of a male's genetic quality. Such costly traits enforce honest signaling by males and thus serve as reliable, mate-choice cues for females (Zahavi 1975; Kodric-Brown & Brown 1984). Thanks in part to his criticism of the runaway hypothesis, theoreticians pounced on Zahavi's verbal model, dismissing it as a theory whose premises and logic were fundamentally flawed (Davis & O'Donald 1976). As subsequently

became evident, however, it was the simplifying assumptions of the early mathematical models of the handicap mechanism, rather the process itself, that may have been unrealistic (Andersson 1994). In a recent, quantitative-genetics model (Houle & Kondrashov 2002), the incorporation of such complexities as condition-dependent expression, polygenic input of deleterious mutation, and assessment errors in female choice has shown that the good-genes, handicap process does not require runaway selection to be a potent force driving the evolution of exaggerated male traits. With the development of more sophisticated, good-genes models in the 1980s and 1990s, particularly those that provided for the maintenance of additive genetic variation in male quality (e.g. Iwasa et al. 1991), the study of female choice for genetic benefits has become, according to Kokko et al. (2002), a ‘tale of two hypotheses’ in which the runaway and good genes mechanisms have been ‘pitted against one another as alternatives.’ In response to this Fisherian/good-genes dichotomy, Kokko et al. (2002) present a unifying model of female choice in which selection favors preference for males siring offspring of high reproductive value (survivorship  $\times$  mating success). According to this model, the relative contributions of survivorship and mating success to offspring reproductive value depend on the cost to female choice. At the low-cost endpoint, offspring reproductive value derives primarily from Fisherian, ‘sexy-son’ benefits, while, at the high-cost end of the continuum, good-genes effects predominate. However, Cameron et al. (2003) argue that, although the mechanisms exhibit similar dynamics, they differ fundamentally in that one (good genes) can affect values for the male trait and female preference at equilibrium, while the other (sexy-son) cannot.

### **The Emergence of Anomalies**

#### **Truth in DNA Profiling: the Anomaly of Multiple Paternity**

*‘The causes which prevent the action of Sexual Selection... The chief cause, first, so-called communal marriages or promiscuous intercourse.’ (Darwin 1871)*

By the late 1980s, the scene appeared set for normal science to proceed with ‘mopping up’ the details of the female-choice component of Darwin’s theory of sexual selection. Theoretical modeling and manipulative field experiments had validated female choice as a potentially important evolutionary mechanism in natural populations (reviewed in Andersson 1994). By identifying large, costly eggs as a limiting resource for abundant, cheap sperm, Trivers (1972) had provided a conceptual framework for understanding the evolution of promiscuous males and choosy, essentially monogamous females. New and powerful molecular tools (multi-locus and then single-locus, minisatellite DNA profiling, followed soon thereafter by PCR-amplified, microsatellite typing) now made it practicable to directly measure male reproductive success in the wild. The first, DNA-based, field studies of paternity were carried out on pair-bonding birds (Burke & Bruford 1987; Wetton et al. 1987), and the results were quite

unexpected. The discovery of multiple paternity in 10–15% (Wetton & Parkin 1991) of the broods of females previously thought to be paragons of monogamy clearly did not conform to professional expectations. As DNA paternity-assignment techniques were applied to a growing number of bird species, the evidence of polyandry became increasingly anomalous (Dunn & Lifjeld 1994; Birkhead & Møller 1995). For example, in the aquatic warbler, 44% of broods were found to be sired by three or four males (Schulze-Hagen et al. 1993), while the level of extrapair paternity in superb fairy wrens was an astonishing 76% (Mulder et al. 1994). Such findings necessitated the invention of the term, 'social monogamy,' to define the mating system of many bird species.

The now widespread use of DNA profiling in studies of animal behavior has led to growing recognition that female mating strategies in many species cannot be determined reliably through field observation alone. To conceal their polyandrous behavior from conspecific males, females frequently mate with multiple males in a manner that is clandestine and therefore difficult to assess at the behavioral level (Hughes 1998). As a classic example, Davies's (1992) account of a female dunnoek disappearing behind a bush to mate with a waiting male before rejoining her oblivious partner, is not only entertaining but also revealing. As a consequence of this strategy of subterfuge on the part of females, paternity cannot be inferred either from observed copulations and social relationships or from male dominance hierarchies. In Soay sheep, for example, comparison of rutting behavior census data with genetic paternity assignment has demonstrated that only 27% of lambs were sired by rams seen in consort with the estrous female (Coltman et al. 1999). In the highly polyandrous superb fairy wrens (Mulder et al. 1994), radiotelemetry has recently shown that extrapair young result from pre-dawn, extra-territorial forays and infidelity by fertile females (Double & Cockburn 2000). Despite extensive genetic sampling and long-term, behavioral observations of gray seal breeding colonies, between 50 and 70% of pups were sired by unknown males, apparently as the result of aquatic copulations (Wilmer et al. 1999, 2000). Microsatellite data have revealed that, contrary to the traditional assumption of extreme variance in male mating success in such harem mating systems, 'behavioural dominance leading to enhanced fitness is a feature of only a handful of males located near the center of the breeding colony. The vast majority of pups are fathered by any of a large number of males who all share approximately equal success ...' (Wilmer et al. 2000).

#### **Conflict not Cooperation: the Anomaly of Sexual Antagonism**

The adequacy of the Darwinian sexual selection paradigm is being called into question not only by the discovery of widespread polyandry but also by growing evidence that the reproductive interests of males and females frequently differ and therefore generate sexual conflict rather than cooperation (Chapman et al. 2003). In both Fisherian and good-genes models, choosy females benefit indirectly from mate choice by producing high-viability offspring and/or sexy sons. Until recently, this view of cooperative male/female interactions dominated the theoretical

literature on sexual selection (reviewed in Holland & Rice 1998). In nature, however, when males compete and females choose, the simultaneous action of these two mechanisms may inevitably result in conflict. Sexual conflict can be overt and extreme, as with competing male *Scatophaga* flies that harass and sometimes drown females attempting to oviposit on cowpats. Observations of such behavior led Parker (1979; pers. comm.) to define analytically the boundaries of sexual conflict for a novel male trait that not only imposed harm on females but also enhanced the fitness of their male offspring through a sexy-son advantage. In computer simulations of conflict in which the arms level of each sex could increase in order for males to achieve or females to avoid mating, he showed that such sexually antagonistic effects could lead to rapid and unpredictable evolutionary change (evolutionary chases). Unfortunately, Parker's insights were largely unappreciated until the study of sexual conflict was revitalized in the 1990s (Rice 1992, 1996; Rowe et al. 1994).

The importance of conflict in sexual selection has gained increasing recognition with the realization that polyandrous mating systems may be the norm rather than the exception. Indeed, theory predicts that mating system is a critical determinant of the intensity of sexual conflict (Rice 2000), a fact that has long been recognized in the parental investment literature (Mock & Parker 1997). At the extreme of strict monogamy, male and female reproductive interests coincide, resulting in selection that favors cooperative males who maximize their mates' lifetime reproductive success. By contrast, when both sexes copulate with multiple partners, the interests of males and females diverge, and conflicts can occur over, for example, mating frequency, timing and pattern of fertilization, relative parental effort, female re-mating behavior, female reproductive rate and clutch size (Chapman et al. 2003). Recent evidence is revealing that such sexual conflict is manifested at the post-copulatory stage in the female reproductive tract as a 'tug-of-war' between male offensive and defensive strategies for monopolizing access to the female's eggs and female resistance to male manipulation of her physiology and male control of her reproductive options (e.g. Rice 1992, 1996; Chapman et al. 1995, 2003; Eberhard 1996; Holland & Rice 1999; Wolfner 2002).

In contrast to the blatantly harmful, pre-copulatory conflict experienced by female dung flies, sexual conflict occurring at post-copulatory stage may involve chemical coercion that is both covert and insidious. In *Drosophila melanogaster*, for example, seminal fluid contains accessory gland proteins that stimulate ovulation and egg production, inhibit re-mating by females, mediate sperm storage and reduce female longevity (Simmons 2001a; Wolfner 2002; Chapman et al. 2003). It has been estimated from expressed sequence tag screening of male accessory gland RNA that more than 80 genes are involved in coding for the peptides and proteins that make up seminal fluid (Swanson et al. 2001). A number of these protein-coding loci exhibit evidence of positive, Darwinian selection (higher rates of non-synonymous than synonymous substitution), a pattern consistent with both female choice and conflict-based mechanisms of sexual selection (Pizzari & Snook 2003). However, a compelling case for the hypothesis



that sexual conflict drives the evolution of seminal fluid products comes from experimental evolution studies of *D. melanogaster* that have revealed the existence of both male manipulative adaptations and female counter-adaptations (Rice 1996; Holland & Rice 1999).

### **Responses to the Anomalies**

#### **The Anomaly of Multiple Paternity**

Among the hypotheses to explain polyandry in a manner consistent with Darwinian sexual selection theory, forced copulation provides perhaps the most obvious avenue through which choosy females could produce offspring sired by more than one male. Although striking examples of forced copulation have been well documented (e.g. Parker 1979; Thornhill 1980; McKinney et al. 1983), females of many species have control over copulations (Reynolds 1996; Zeh et al. 1998), and rape therefore fails to provide a general explanation for the prevalence of multiple paternity in nature. A recent meta-analysis of 122 experimental studies of insects does suggest, however, that coercion by males may play a role in polyandry by elevating mating rate above the level that is optimal for female reproductive success (Arnqvist & Nilsson 2000). An alternative approach to addressing the problem of multiple paternity focuses on the constraints that females may experience in exercising choice. According to the Darwinian paradigm, females should mate with the best available male. In practice, however, females may be limited in their initial choice of mate, and may only subsequently have the opportunity to copulate with a superior male (Kempnaers et al. 1992; Hasselquist et al. 1996). This 'trading-up' hypothesis, involving extra-pair copulations to compensate for a mate of relatively poor quality, has been proposed as a general explanation for mixed paternity in socially monogamous birds (Petrie & Kempnaers 1998; Jennions & Petrie 2000). Within the framework of this hypothesis, polyandry can be viewed not as an anomaly but rather as a cryptic strategy that females utilize for choosing attractive or high-quality fathers for their offspring when breeding territory and parental care requirements limit their options for choice of social mate.

As DNA evidence of multiple paternity has accumulated for organisms as ecologically and phylogenetically divergent as fruit flies (Imhof et al. 1998) and humpback whales (Clapham & Palsboll 1997), sexual selection research over the last decade has increasingly focused on investigating the material and/or genetic benefits that females derive from engaging in polyandry. The hypothesis that females can gain material benefits by mating with more than one male predates the DNA profiling era, and has its origins in behavioral observations of polyandrous female insects receiving various forms of nuptial gifts and/or nutrients contained in spermatophores or seminal fluid (Thornhill & Alcock 1983; Gwynne 1984; Zeh & Smith 1985). Direct material benefits that may enhance female fecundity and/or survivorship (Eberhard 1996; Reynolds 1996) have now been extended to include: (i) ensuring an adequate sperm supply

(Ridley 1988); (ii) additional paternal care or access to male territories (Davies 1992), and (iii) sexually transmitted, anti-predator defense chemicals (González et al. 1999). The multifarious material benefits that females may gain by mating with more than one male are often conspicuous. Perhaps largely because of this, material benefits have been widely accepted as explanations for polyandry (see Parker 1992; Yasui 1998), while the argument that polyandry provides genetic benefits remains controversial (Simmons 2001b). Certainly, there are numerous examples of mating systems, particularly in Orthoptera and Lepidoptera, in which males make material contributions that enhance the reproductive success and/or survivorship of their mates. However, the general extent to which females derive a nutritional benefit from male donations during copulation has been called into question by several recent studies (Zeh 1997; Sadowski et al. 1999; Sakaluk 2000; Vahed 2003). For example, in the decorated cricket, the number of spermatophylaxes consumed by food-deprived females was found to have no effect on egg mass or number of nymphs produced (Will & Sakaluk 1994). Moreover, most studies that have investigated material benefits have not adequately controlled for potential genetic benefits (Newcomer 1998).

A variety of genetic-benefit hypotheses have been proposed for polyandry, and an important distinction can be made between those that are fundamentally consistent with Darwinian theory and those whose implications call for a significant shift of the sexual selection paradigm. In the former category, hypotheses share with classic male competition/mate choice theory an emphasis on the intrinsic, i.e. additive effects of paternal genes on female fitness (Zeh & Zeh 1996, 1997, 2001; Tregenza & Wedell 2000). Specifically, the 'intrinsic male quality' hypothesis proposes that sperm competition or female choice of sperm increases the probability of fertilization by high-quality sperm or sperm from high-quality males (Watson 1991; Madsen et al. 1992; Birkhead et al. 1993), while the 'sexually-selected sperm' hypothesis argues that females benefit from polyandry because their sons produce competitively superior sperm or ejaculates (Keller & Reeve 1995; Pizzari & Birkhead 2002). To accommodate polyandry within the traditional framework, both these hypotheses require only that the opportunity for sexual selection be extended beyond mating in order to increase the probability of fertilization by high-quality or competitively superior sperm. With this type of selective advantage to polyandry, multiple paternity is the incidental consequence of constraints, such as mating order effects, that limit the effectiveness of post-copulatory sexual selection. By contrast, other additive-effect hypotheses propose that multiple paternity per se represents a bet-hedging strategy that provides a genetic benefit to polyandry by increasing the geometric mean fitness of females in the face of mate choice and/or environmental uncertainties (Watson 1991, 1998; Fox & Rauter 2003). Similarly, it is the genetic diversity associated with multiple paternity that itself provides the benefit proposed by the 'sibling competition avoidance' hypothesis (Ridley 1993). Because the bet-hedging and sibling competition avoidance hypotheses posit an adaptive advantage to multiple paternity, polyandry for such genetic benefits

cannot be accommodated without significant modification of the traditional sexual selection paradigm.

Whereas the preceding hypotheses all propose genetic benefits accruing from intrinsic (additive) effects of paternal genes in offspring, the second major category of genetic benefit hypotheses emphasizes non-additive effects associated with maternal  $\times$  paternal genome interactions (Zeh & Zeh 1996, 1997, 2001; Tregenza & Wedell 2000) and/or male  $\times$  female interactions (Clark 2002). As a consequence of dominance, overdominance, intra- and inter-genomic conflict, fetomaternal interactions and immune system function, sexual reproduction involves the merging in embryos of parental genomes likely to vary in the extent to which they are genetically compatible (Zeh & Zeh 1996, 1997, 2000; Jennions 1997; Brown 1998; Jennions & Petrie 2000; Tregenza & Wedell 2000). Genetic incompatibility occurs not only in the context of interspecific matings but can also pose a significant threat to reproductive success within species and populations. In particular, female fitness can be undermined by many agents of genomic conflict (cellular endosymbionts, transposable elements, segregation distorter alleles, maternal effect lethals, and genomically imprinted genes) that render certain combinations of maternal and paternal haplotypes incompatible within the developing embryo (Zeh & Zeh 1996, 1997). If offspring fitness depends on an interaction between maternal and paternal haplotypes, gene effects will not be strictly additive. More importantly from the perspective of female choice, genetic incompatibility, unlike intrinsic male quality, will generally not be apparent at the phenotypic level (Zeh & Zeh 1996). The 'genetic incompatibility avoidance' hypothesis therefore proposes that polyandry enables females to exploit post-copulatory mechanisms in order to reduce the risk and/or cost of fertilization by genetically incompatible sperm (Zeh & Zeh 1996, 1997). Polyandry, in combination with an immunologically hostile female reproductive tract, provides a physiological screening process capable of weeding out incompatible genotypes in sperm and/or embryos (Zeh & Zeh 1997). It should be noted that the 'inbreeding avoidance' hypothesis that polyandry diminishes the cost of inbreeding when females cannot avoid mating with close relatives (Brooker et al. 1990; Stockley et al. 1993) is a special case of polyandry for genetic incompatibility avoidance.

The genetic incompatibility avoidance hypothesis was originally proposed to address the potential for polyandry as a defense against deleterious maternal/paternal genetic interactions in offspring, i.e. at the post-fertilization stage. However, it is becoming increasingly clear that strong interaction effects also characterize the post-copulatory, pre-fertilization stage of reproduction (Wilson et al. 1997; Archer & Elgar 1999; Clark et al. 1999, 2000). In *Drosophila*, for example, it has been demonstrated that sperm competitive ability is not an intrinsic characteristic of each male but rather depends on a complex interplay between competing male genotypes as well as the genotype of the female involved (Clark 2002). Theoretical studies indicate that non-transitive sperm precedence and strong male  $\times$  female interactions can act to maintain high levels of polymorphism in genes determining sperm competitive ability (Clark 2002). Indeed, empirical research has shown that male seminal products in *Drosophila*

are highly polymorphic and that male success at manipulating female reproduction exhibits extensive variability that depends on both male and female genotype (Clark et al. 1999). As a consequence, a monandrous female may risk pairing with a male whose genotype produces manipulative seminal fluid products ineffective at overcoming her level of resistance (for circumstantial evidence of such an effect, see Archer & Elgar 1999). As with other forms of incompatibility, females could reduce this risk by mating with more than one male, thereby obtaining a benefit through the acquisition of polymorphic, seminal-fluid products. Clearly, the problem inherent in 'good genes' models of sexual selection of explaining the persistence of additive genetic variance in fitness (reviewed in Andersson 1994) is eliminated, if non-additive genetic effects and male  $\times$  female interactions exert a significant influence on female reproductive success. Polyandry for incompatibility avoidance may frequently undermine the intensity of directional sexual selection acting on males (Zeh & Zeh 2000), and the traditional Darwinian concept of female choice provides an incomplete and potentially misleading picture of the selective forces shaping the evolution of female mating tactics.

#### **The Anomaly of Sexually Antagonistic Coevolution**

*'It is highly implausible that for every possible mutation there exists an immediate and reciprocal reversible selection possibility which would exactly cancel the exploitive phenotypic effect.'* (Cosmides & Tooby 1981)

The 'chase-away' sexual selection hypothesis (Holland & Rice 1998; Rice & Holland 1999) represents the most fully articulated response to the anomaly of sexually antagonistic coevolution. As Holland & Rice (1998) point out, 'the major distinction between this chase-away model and previous models is that coevolution between the male trait and female attraction is antithetic rather than reinforcing.' In proposing their hypothesis as an alternative to extant sexual selection models, Holland & Rice (1998) cite three lines of evidence that, taken together, cannot be easily aligned with either Fisherian, good-genes or strict sensory-exploitation mechanisms. First, the authors present evidence that sexual conflict is pervasive and often intense. Secondly, they discuss several cases in which female preferences exist for traits that have not evolved in conspecific males but are present in closely related species. Finally, they point to examples in which females have evolved resistance to exaggerated male display traits, as evidenced by the stronger preference exhibited by females of closely related species lacking the exaggerated trait. To account for these patterns, the chase-away sexual selection model proposes that exaggerated male traits evolve as a consequence of an evolutionary arms race between males and females for control of various aspects of reproduction (e.g. mating rate, female propensity to remate, female proximate fecundity). Initially, a rudimentary male display trait evolves to exploit a pre-existing sensory bias in females (West-Eberhard 1984; Ryan 1990; Basolo 1998), and, as a consequence, females may be coerced into mating in a sub-optimal manner. This generates counter-selection on females to evolve resistance to the trait, followed by selection favoring a more

extreme male trait to overcome female resistance. The resultant cyclic antagonistic coevolution may ultimately lead to viability selection checking further elaboration of the male trait in question, at which point, sexual selection will favor the evolution of a new display trait in males. A similar model was analyzed formally by Parker (1979, 1983). He concluded that evolutionary chases between males and females can produce a Nash equilibrium, at least temporarily, until new evolutionary possibilities become available.

Although publication of the theory generated immediate controversy (Getty 1999; Rice & Holland 1999; Rosenthal & Servedio 1999), interest in the chase-away model of sexual selection is currently gaining considerable momentum, as investigators increasingly emphasize conflict rather than cooperation as the basis for male/female interactions (Chapman et al. 2003). Nonetheless, the general importance of sexually antagonistic coevolution continues to be the subject of heated debate, with recent criticisms focusing on: (i) the failure by some researchers to consider alternative hypotheses in interpreting empirical patterns (Pizzari & Snook 2003), and (ii) the failure of many theoretical models to offset the direct fitness costs that females may suffer as a consequence of mating with manipulative males by incorporating the indirect benefits they may gain through the production of manipulative sons (Cordero & Eberhard 2003; Eberhard & Cordero 2003, but see Gavrillets et al. 2001; Cameron et al. 2003). An indirect, sexy-son benefit of sufficient magnitude could theoretically outweigh direct costs, resulting in an overall benefit for females. Such a hypothetical outcome has led to the suggestion that apparent male/female conflicts of interest may actually form part of a reproductive interaction between the sexes whose net coevolutionary effect is cooperative rather than antagonistic, and therefore in accordance with traditional sexual selection theory (Cordero & Eberhard 2003; Pizzari & Snook 2003).

The major difficulty in demonstrating any form of conflict-driven evolution, intersexual or otherwise, is that, almost by definition, the coevolutionary process of adaptation and counter-adaptation maintains a balance between opposing sides that obscures the conflict itself. Consequently, in order to uncover a history of antagonistic interactions, it may be necessary either to perform comparative, phylogenetically based analyses (e.g. Arnqvist & Rowe 2002), or, alternatively, to engineer a natural disruption or perturbation of the interaction through experimental evolution studies (e.g. Rice 1996; Holland & Rice 1999; Pitnick et al. 2001a,b; Martin & Hosken 2003), or some other interventionist approach (e.g. gene knockout techniques). A particularly illustrative example of the type of research needed to investigate antagonistic coevolution involves male/female conflicts of interests played out at genomically imprinted loci during fetal development in mammals (Haig & Graham 1991; Haig 1993, 1997). Genomic imprinting is a form of non-Mendelian, autosomal inheritance in which methylation and expression of an allele depend on whether it is inherited through sperm or egg (Sapienza 1995; Bartolomei & Tilghman 1997). During embryonic development, maternally and paternally inherited alleles at imprinted loci exhibit radically different patterns of expression.

The antagonistic nature of the interaction between maternal and paternal genes in embryos was revealed quite unexpectedly by nuclear transplantation experiments in which the genomes of mouse oocytes were engineered to consist of either two maternal or two paternal copies. These experiments demonstrated that it is largely paternal genome expression that is responsible for the growth of the trophoblast and the placenta, the embryonic organs that act to sequester nutrients from the mother (McGrath & Solter 1984; Surani et al. 1984). By contrast, morphological differentiation of the embryo proper, at least during early developmental stages, is controlled by maternal genome expression (Villar & Pedersen 1997). Subsequent studies, involving gene-knockout experiments, have elucidated the function of specific imprinted loci. For example, insulin-like growth factor II (IGF-II), which stimulates nutrient transfer from mother to fetus, is transcribed only from the paternal copy of the *Igf2* gene. This pattern is reversed at the *Igf2r* locus where the paternal allele is inactive and transcription of the maternal allele results in degradation of IGF-II (Barlow et al. 1991). Knockout experiments have demonstrated that normal fetal development depends on a balance between the antagonistic effects of these two reciprocally imprinted genes: loss-of-function mutations in paternal *Igf2* alleles result in a 40% reduction in growth, while fetuses containing maternal *Igf2r* knockouts are oversized and ultimately inviable. Interestingly, the double mutant is completely viable and of normal size (reviewed in Tilghman 1999). Development thus involves a balance between the opposing effects of maternal and paternal genes, and imprinting disruption has been implicated in a growing list of embryonic abnormalities, growth disorders, cancers and unstable DNA diseases in humans (reviews in Hall 1999; Tycko 1999; Ariel et al. 2000).

Of the hypotheses put forward to explain the evolution of genomic imprinting, only the 'conflict' hypothesis proposed by Haig & Westoby (1989), Moore & Haig (1991), and Haig (1997) is capable of explaining the diversity of imprinting patterns (Wilkins & Haig 2003). The essential feature of the conflict hypothesis is that multiple paternity is the key factor generating antagonism between fetal maternal and paternal genomes. Because embryonic paternal genes are unrelated to genes of the mother and genes in half-siblings, the optimal rate of nutrient transfer from mother to embryo is likely to be greater for paternally inherited alleles than it is for maternally inherited alleles (Haig & Westoby 1989). The resultant tug-of-war conflict between embryonic maternal and paternal alleles over maternal resource transfer is hypothesized to be the driving force behind the evolution of genomic imprinting. If this conflict hypothesis is correct, the components of this interplay should be constantly evolving in viviparous species, due to a coevolutionary arms race over maternal resource allocation.

### Toward a New Consensus

*'I intend to redress a balance, not to be balanced myself.'* (Grafen 1987)

Darwin's recognition that male–male competition and female choice could favor the evolution of exaggerated male traits detrimental to survival set the stage for more than a century of theoretical and empirical work on sexual selection. While the Darwinian paradigm of sexual selection stemmed from what was undoubtedly one of the most profound insights in biology, its preoccupation with sexual selection as a directional evolutionary force acting on males has had the unfortunate effect of diverting attention away from the selective processes acting on females. Our understanding of female reproduction has been further confounded by discreet female mating tactics that have perpetuated the illusion of the monogamous female and masked the extent of the potential for conflict between the sexes. It is recognition of these shortcomings that has brought the study of sexual selection to its current state of flux.

We suggest that progress in two key areas is of critical importance to the formulation of a more inclusive sexual selection paradigm that adequately incorporates selection from the female perspective. First, we need to develop a better understanding of the causes and consequences of male  $\times$  female and maternal  $\times$  paternal genome interaction and the role that polyandry can play in providing females with non-additive genetic benefits. As we have argued elsewhere (Zeh & Zeh 1996, 1997, 2001), cellular endosymbionts, transposable elements, segregation distorters, maternal-effect lethals and genomically imprinted genes are all agents of genomic conflict that can modify maternal and paternal haplotypes in ways that render them incompatible within the developing embryo. Reciprocal evolutionary change between such selfish genetic elements and their suppressors, combined with the capacity of these elements for horizontal transfer between species, is likely to ensure the persistence of genetic incompatibility as a threat to female reproductive success. Similarly, maternal/paternal gene interaction resulting from balancing selection at MHC loci (Hedrick 1999) is likely to act as a strong, unrelenting, selective force promoting polyandry as adaptive mating strategy for non-additive genetic benefits (Hedrick & Thomson 1988; Tregenza & Wedell 2000; Zeh & Zeh 2001). Consideration of these interaction effects influencing natural selection on females is especially important because they can greatly complicate or even completely undermine the effects of directional sexual selection acting on males (Hedrick 1992; Birkhead 1998; Tregenza & Wedell 2000; Zeh & Zeh 2001). Moreover, it should be pointed out that, as the majority of evidence for genetic benefits to polyandry involves incompatibility avoidance (e.g. Bishop et al. 1996; Olsson et al. 1996; Zeh 1997; Newcomer et al. 1999; Stockley 1999, 2003; Tregenza & Wedell 2002; Foerster et al. 2003; Garner & Schmidt 2003; Hohoff et al. 2003), non-additive effects seem especially likely to exert an important influence on female mating decisions.

Secondly, even if, as has been argued (Cordero & Eberhard 2003; Pizzari & Snook 2003), a certain amount of intersexual conflict is implicit in traditional models, the explicit incorporation of antagonistic male/female coevolution in formal models represents a major advance in theoretical approaches to the study of sexual selection. Until recently, nearly all mathematical models of sexual selection dealt exclusively with female choice as the driving mechanism (Maynard-Smith

1987), undoubtedly because male competition is obvious and therefore uncontroversial. The incorporation of both male competition and female choice within a single theoretical framework of sexual selection, however, greatly complicates male and female evolutionary dynamics and is likely to generate sexually antagonistic coevolution (Parker 1979). As discussed above, demonstrating sexually antagonistic coevolution is often difficult in practice because counterbalancing adaptations obscure the antagonistic interaction. Pizzari & Snook (2003) suggest that antagonistic coevolution can be differentiated from traditional sexual selection on the basis of the average effect on male and female fitness. However, the truly novel and important aspect of sexual conflict theory is not the average effect on the population but rather that females evolve counter-adaptations to male attempts to manipulate their reproduction. We therefore suggest that future research should take the form of comparative, phylogenetic analyses or experimental evolution and other interventionist approaches that have the capacity to tease apart male manipulative adaptations and female resistance.

In conclusion, it seems evident that the divisiveness and controversy that has plagued sexual selection theory since Darwin first proposed the idea in 1859 has, in many cases, stalled progress in this important, intriguing and complex field of evolutionary biology. Nearly every important idea in sexual selection, i.e. female choice, runaway selection, good genes, genetic incompatibility avoidance and sexually antagonistic coevolution, has initially met with extreme skepticism or has even been ignored. What is clearly needed now to advance the field is a more pluralistic and integrative approach that considers natural as well as sexual selection acting on females, incorporates multiple sexual selection mechanisms (e.g. Colegrave et al. 2002; Reinhold 2002), and exploits advances in physiology and molecular biology to understand the mechanisms through which males and females achieve reproductive success.

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