



REVIEW

Sexual conflict and life histories

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There is burgeoning interest in the costs of mating and in how this leads to sex differences in the optimal mating rate. Here, we attempt to look beyond an exclusive focus on matings to examine the fundamental conflicts that arise out of the fact that sexual reproduction involves investment in offspring by typically unrelated individuals. Conflicts between mates stem from the ever present potential for individuals to reduce their investment relative to that of their sexual partner in order to seek alternative reproductive opportunities elsewhere. All aspects of life histories, the partitioning of time and energy into growth, survival and reproduction, are inextricably caught up in, and moulded by these conflicts of interest, the most profound expression of which is the differentiation between male and female types. This differentiation creates a new set of conflicts because alleles with positive effects on fitness when expressed in one sex may have negative fitness effects in the other. This type of conflict may influence the evolution of separate juvenile and adult life stages as in metamorphosis, although a major outstanding question is why sex limitation does not evolve more rapidly. We review the impact of conflicts of interest between males and females on all aspects of life history, revealing at least as much evidence for sexual conflict over life history traits such as investment in gametes and parental care as there is for conflicts over matings.

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The traditional approach to understanding life histories is to consider animals as maximizing their lifetime reproductive success in the face of competition and environmental selection pressures. A frequently neglected consideration is that reproductive success is influenced not only by these environmental factors but also by conflicts caused by differences in optimal trait values between males and females. These conflicts stem from the fact that sexual reproduction typically requires two unrelated individuals to invest resources in a shared enterprise, a situation that favours individuals that manipulate their mates to maximize their own fitness even if this has negative consequences for their partners. This conflict over parental investment does not require any differences between the sexes, but theory suggests that it

will lead to the evolution of sexual differentiation, such that in most organisms one sex invests heavily in offspring, while the other effectively parasitizes this sex. Sex differentiation creates a whole new set of conflicts between mates, caused by differences in the optimal reproductive strategies of males and females. In addition, sex differentiation creates an entirely new type of potential conflict caused by alleles that have opposite effects on fitness according to the sex of the individual in which they are expressed.

The implications of sexual conflict for traits associated with mating and sexual selection have been considered in a number of recent papers (Partridge & Hurst 1998; Rice 1998a; Lessells 1999; Chapman et al. 2003). In this review we consider how sexual conflict can affect life history strategies, how widespread and important the effects of such conflicts are likely to be, and the particular aspects of life histories that are likely to be most influenced by sexual conflict, and vice versa.

All aspects of investment in offspring are likely to be subject to conflict: the size of the gametes themselves, subsequent investment in the zygote, gestation, parental care and the timing of these investments. The only escape

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from conflict comes in species where monogamy is obligate and lifelong, with no prospect of remating even if one partner dies. If there is any chance that one partner will mate with another individual, sexual conflict begins. The stringency of the monogamy requirement for complete avoidance of conflict is such that we cannot think of any species that might be expected to lack sexual conflict entirely (can you?).

The evolutionary impact of sexual conflict will depend not just on the extent of the potential for conflict over a trait, but also on whether there is genetic variation available for selection and on the costs associated with conflict adaptations. This distinction between potential and actual conflict has been discussed in relation to conflicts of interest in social insects. Ratnieks & Reeve (1992) suggested that the extent of actual conflict will depend on the benefit minus the cost of manipulation and countermanipulation, and the effectiveness of countermanipulation. Quantifying these constraints on the evolutionary power of sexual conflict remains a major challenge for the field.

INTRALOCUS CONFLICT

Intralocus conflict is driven by the differences between the sexes. It can be defined as a situation in which the same allele has opposite effects on the fitness of the two sexes (Fisher 1930; Lande 1980). Because of the different selection pressures facing males and females, the genes that build a better male may not build a better female (Rice 1996). For instance, in humans, a narrow pelvis may be beneficial for males as it is more efficient for locomotion, whereas a broader one may be beneficial for child-bearing females (see Rice & Chippindale 2001a). A new mutation that decreases pelvis width may be selected for when it is carried by males, but selected against when in females. This mutation is under 'sexually antagonistic selection': the direction of selection on an allele differs between the sexes. In general, antagonistic selection acts as a constraint on trait evolution. Even if the trait is favoured in males it will be selected against when expressed in females, so each sex holds back adaptation of the other (Rice 1984). If the benefits of a trait in one sex outweigh the costs in the other and the allele is expressed equally frequently in the two sexes (typically because it is on an autosome) then sexually antagonistic alleles can be favoured by selection and will increase in prevalence (Rice 1987). This creates strong selection pressure for the evolution of sex-limited expression (Rice 1984), either through the action of modifiers or through translocation of sexually antagonistic alleles to the sex chromosomes. How rapidly such sex limitation can evolve will determine whether intralocus conflict is a relatively unimportant, transient phenomenon or a powerful influence on adaptation. The issue of how difficult it is to evolve sex limitation is a major question facing evolutionary biology. At present, the importance of intralocus conflict in driving evolution remains largely unknown, although studies of *Drosophila melanogaster* (Rice 1992, 1998a, b; Gibson et al. 2002) suggest that such conflicts are in progress.

Sexual Size Dimorphism

Perhaps the most obvious area of intralocus conflict between the sexes is in the type of body to build. Females need a morphology suited to the production of large gametes, and frequently for investing in offspring, whereas males are more commonly involved in competition for mates. Therefore, alleles that produce a fitter male may produce a less fit female. It has been suggested that, in some mammals and birds, benefits of large male size arising from competition among males may generate a corresponding increase in female size (Fairbairn & Preziosi 1994; Lindenfors 2002), implying a genetic correlation in male and female body size (Andersson 1994), which is often very high (Roff 1997). There is evidence in haplorhine primates (tarsiers, monkeys, apes and humans) that male–male competition has promoted the evolution of large male body size and, to a lesser degree, also large female size (Lindenfors & Tullberg 1998). The increase in female size does not appear to be explained by selection on females to bear larger offspring.

Life Cycles

Juveniles of both sexes are likely to maximize their future reproduction by simply pursuing rapid growth while maximizing survival. However, as sexual maturity is approached, the best strategies for maximizing fitness diverge according to the sex of the individual, with males typically having a greater emphasis on achieving fertilizations (Chippindale et al. 2001; Rice & Chippindale 2001a, b). This divergence results in greater expression of intralocus conflicts. Hence, it is possible that sexually antagonistic alleles are partly the cause of the delay in expression of sex differences seen in most organisms. Imagine an allele under antagonistic selection in males and females that has a negative effect on one sex regardless of the life stage at which it is expressed and has a positive effect on the fitness of the other sex that increases at sexual maturity. In such a situation, selection will favour a variant of the allele in which expression is delayed until a point at which the benefits it bestows when it is found in one sex outweigh the costs it imposes in the other. Such a scenario appears biologically plausible. For instance, mature males may benefit from larger body size, and it might be easier for them to attain large bodies by growing faster throughout their lives. However, costs to females of more rapid growth might mean that the most successful growth allele is one that has delayed expression in both sexes leading to exaggerated differences between juveniles and mature individuals. It is possible that sexual conflict may have influenced the evolution of metamorphosis, which sharply delimits juvenile and adult phases. If so, we would predict that species with metamorphosis may be characterized by larger degrees of sexual dimorphism than those without (although whether sufficient numbers of phylogenetically independent contrasts are available is questionable).

INTERLOCUS CONFLICTS

In contrast with intralocus conflicts, which can be resolved through the evolution of sex-limited expression, sexual reproduction creates a constant selection pressure in favour of genotypes that increase an individual's ability to exploit its mates. Sexual reproduction involves two individuals that have no genetic interest in each other, but produce offspring sharing their genes. It therefore pays an individual 'A' to get its mate 'B' to invest as much as possible in A's offspring, regardless of the cost to B in terms of B's other offspring (Lessells 1999). Furthermore, mates may not have the same optima in respect of other aspects of offspring production, such as the sex ratio of the brood, resulting in selection on each sex to modify these traits in its own favour. This situation has been termed interlocus conflict. Interlocus conflict does not require there to be any differences between the sexes, but tends to lead evolutionarily to one sex investing less in each gamete while the other sex invests more (Parker et al. 1972; Parker 1978). The sexes are broadly defined by this difference: eggs are large and sperm small. Female reproductive success is therefore generally limited by resources invested in reproduction, whereas male reproductive success is strongly influenced by number of mating partners (Bateman 1948). This creates an asymmetry between the sexes with wide-ranging implications for the evolution of life histories.

Conflicts over Mating Events

The best-documented examples of sexual conflict are over whether or not to mate. These conflicts are of two types: over whether an individual will benefit from an additional mating (males typically have a higher optimal mating frequency than females) and, second, over whether an individual will benefit from mating with a particular member of the opposite sex (males typically are less choosy than females about mates). Although it has been recognized that females often gain benefits from mating with multiple males (reviewed in Arnqvist & Nilsson 2000; Knight 2002; Hosken & Stockley 2003), males typically have more to gain from inseminating additional females (Bateman 1948). The observation that males tend to have a higher optimal mating rate than females has been confirmed by various experimental studies (Arnqvist & Nilsson 2000). Nevertheless, because males typically do not have the opportunity to mate with very large numbers of females, and ultimately are constrained to have the same average mating rate as females, they are adapted to a lower mating rate than their theoretical maximum. This means that the results of experiments in which mating rates are manipulated and the reproductive success of males and females is measured need to be treated with caution. Studies that allow mating rate to evolve may prove more revealing if we are interested in the size of the potential conflict over mating rate. Males cannot increase their reproductive success indefinitely, as matings involve considerable costs, particularly in terms of ejaculate production (reviewed in Wedell et al. 2002). Hence,

studies on conflicts over whether a particular mating is beneficial can find either the male or the female likely to benefit or suffer from a particular mating.

Females are expected to resist mating attempts by males frequently, because of the costs imposed by the copulation itself and because females may wish to use precopulatory mate choice to determine the paternity of their offspring. Costs associated with copulations include time, energy, risk of disease transmission, injuries, exposure to predation and negative effects of males' attempts to reduce females' subsequent mating rate (e.g. Magnhagen 1991; Chapman et al. 1995; Rice 1996; Watson et al. 1998; McLain & Pratt 1999; Jormalainen et al. 2001). To secure matings, males can use one of five strategies: (1) provide genetic benefits to offspring that outweigh the costs of the mating; (2) provide females or offspring with direct benefits that outweigh the costs of the mating; (3) exploit sensory biases in females such that females mate with a male even though the costs of doing so outweigh the benefits; (4) impose large costs on resisting females so that it is less costly for them to mate than to resist; (5) physically force females to mate.

Strategy 1 differs from the others because it is based on genetic benefits to offspring rather than direct benefits to the female; conferring such benefits does not impose any cost on the male. Strategies 1 and 2 include some situations where a mating is mutually beneficial, although there will continually be selection to minimize the size of the costs to males of providing direct benefits to females. There are numerous examples of males providing females with food gifts at mating. For example, males of many insects provide nutrients in the ejaculate, resulting in increased female reproductive output (Vahed 1998). Male contributions may take the form of paternal care, and exclusive male care may have evolved both in arthropods (Tallamy 2000) and in territorial fish (Ah-King 2003) because females prefer males that care and thus caring males gain increased mating success. In some instances, male investment in reproduction exceeds that of females (e.g. Simmons 1992), resulting in sex role reversal and even male mate choice (e.g. Berglund & Rosenqvist 2003; LeBas et al. 2003).

Conflict over mating can lead to males coercing females into mating. This coercion can be divided into three types (3–5 above). In strategy 3, males seduce females into matings that reduce fitness. This creates an evolutionarily unstable situation because females can improve their fitness if they avoid seduction, and such avoidance is not inherently costly. The persistence of male seduction is likely to indicate constraints on female sensory systems rather than a balance between male and female costs and benefits. Persuasive evidence comes from observations such as those of the Glandulocaudine tetra fish in which females are attracted by an extension of the gill cover that has been modified to resemble a prey item and which the male twitches to enhance this appearance (discussed by Arnqvist & Rowe 2005).

In strategy 4, males make it less costly for females to mate than to resist. Hence, females are making an optimal decision by mating and, unlike strategy 3, this situation is not inherently unstable. Females are under selection to

evolve adaptations that allow them to avoid the costs associated with refusing to mate, so we expect a coevolutionary process between males and females. Strategy 5, physically forcing females to mate, differs from strategy 4 because strategy 4 allows females to make state-dependent strategic decisions whether to mate or not. To illustrate: if you are accosted by a robber who demands your purse, you can make a strategic decision whether to hand it over or risk an assault according to your assessment of the value of the purse and how dangerous any assault might be, but if you are knocked unconscious and your purse is stolen no strategic decisions are possible. Hence, strategy 4 will tend to lead to more dynamic coevolutionary situations particularly where there is a cost to males of imposing costs on females.

To determine whether females are making strategic decisions about matings or are being unavoidably physically coerced requires studies that can reveal females avoiding matings when they are more costly or less beneficial. Female water striders suffer costs of mating (reviewed in Rowe et al. 1994; Arnqvist 1997), but dislodging a male is also costly (Watson et al. 1998), and it does not pay to resist when males are abundant. Accordingly, females are less reluctant to mate at male-biased operational sex ratios, thereby avoiding being harassed by other males (Arnqvist 1992). Sex ratio variation generates large intraspecific variation in mating behaviours across species of water strider (Rowe & Arnqvist 2002). Furthermore, males have grasping structures and females of some species possess antigrasping structures, which are used during premating struggles (Arnqvist & Rowe 1995). Conflict over mating has promoted coevolution of grasping and antigrasping structures, and across species the levels of male and female armaments are closely correlated (Arnqvist & Rowe 2002a, b). In species where males guard females before mating, conflict may arise over guarding duration. In the marine isopod, *Idotea baltica*, females are sexually receptive for only a brief period after moulting and males guard unreceptive females before copulation. There is conflict over the guarding duration because males try to initiate pairings at an earlier stage than is optimal for females. Experiments show that the conflict is mainly resolved in the female's interest, but females pay a cost for resisting in terms of smaller eggs, which results in smaller and less fit offspring (Jormalainen & Merilaita 1995; Jormalainen et al. 2001). Thus, early guarding by males can evidently be selected for despite reduced female reproductive success, a fitness cost that males share with their females (Jormalainen et al. 2001).

In other cases, males use more drastic means to improve their mating success. Males may kill and sometimes cannibalize the offspring of females to increase the likelihood that females will become receptive and mate (Elgar & Crespi 1992; Schneider & Lubin 1996, 1997). This has been documented in several taxa, including arachnids, rodents, lions and primates (Hiraiwa-Hasegawa 1988; Elwood 1992; Pusey & Packer 1994; Schneider & Lubin 1996). In the spider, *Stegodyphus lineatus*, as a countermeasure to male infanticide, females reduce the risk of losing eggs by extending the time between mating and

oviposition (Schneider 1999), with the length of the delay before oviposition varying according to the risk of infanticide.

Conflicts over Remating

Closely related to the conflict over whether or not to mate is the issue of how soon after a mating either partner remates with a different individual. Generally, the focus of this conflict is over how soon the female remates, since this will generally reduce paternity of the previously mating male. However, there are also situations where the female may benefit from preventing the male from mating with other females since this may lead to him dividing his future investment between a larger number of offspring. This type of conflict has been demonstrated in several species of birds and in fish, with examples of females preventing their partner from attracting a new female by aggressive behaviours towards new females (e.g. Veiga 1990; Sandell & Smith 1996; Sandell 1998; Kokita & Nakazono 2001), and even destroying the young of rival females (Veiga 1993; Hansson et al. 1997).

More commonly, the male has more to gain by reducing female remating rate, and males have evolved numerous adaptations to reduce female receptivity and increase their fertilization success, often at a cost to females (Stockley 1997; Chapman 2001; Chapman et al. 2003). There are a few polyandrous species where the first male to mate gains a greater share of paternity than subsequent males (Birkhead & Møller 1998; Simmons 2001). However, examples of such first-male sperm precedence are rare (presumably because they tend to evolve rapidly towards monandry, and hence can no longer be detected).

In the majority of species where females store sperm, the last male to mate gains the greatest share of fertilizations (Birkhead & Møller 1998; Simmons 2001). There is no qualitative difference between first- and last-male sperm precedence, but greater last-male precedence creates greater selection on males to mate frequently and to attempt to prevent females from remating even if it adversely affects the overall reproductive success of the female (Rice 1996; Johnstone & Keller 2000; Jormalainen et al. 2001). There is ample evidence of male adaptations to sperm competition (Stockley 1997; Birkhead & Møller 1998), notably the very large number of sperm commonly found in a single ejaculate. In many insects, males transfer factors in the ejaculate that manipulate female reproductive physiology to increase their reproductive success (Gillott 2003). For example, *D. melanogaster* males transfer a cocktail of over 80 different seminal peptides that manipulate female reproductive physiology resulting in higher reproductive success (Chapman 2001; Wolfner 2002; Kubli 2003). Concurrently, these manipulations are costly to females, reducing their longevity (Chapman et al. 1995; Rice 1996).

In the most extreme scenario, rather than females being harmed as a side-effect of male manipulation (which may be disadvantageous to the male as well), males might deliberately injure females in such a way that future copulations become more costly (Constantz 1984). This

adaptive harm hypothesis (Morrow et al. 2003) suggests that it is the reduction in survival of the female that the damage causes that is the primary effect, and that this invokes consequences that increase male fitness (Michiels 1998; Lessells 1999; Johnstone & Keller 2000). In particular, females may make a terminal investment in oviposition in response to increased risk of mortality. Although such a scenario is theoretically possible (Johnstone & Keller 2000; Lessells 2005), theory suggests that costs need to escalate over subsequent matings for such a situation to evolve.

Examples of the spectrum of male strategies to delay or prevent a female remating or to accelerate her rate of investment in those offspring that are more likely to be sired by the male are numerous. Males of several insects pass nutrients, so called 'nuptial gifts', to females at mating (Thornhill 1976; Boggs & Gilbert 1979; Gwynne 1983; Vahed 1998). A large gift not only enhances female fecundity, longevity and offspring fitness, but also gives more time for ejaculate transfer and/or a longer interval before the female remates, which improves the chances that the male becomes the father of the offspring (Simmons & Gwynne 1991; Wedell 1991, 1994; Wiklund et al. 1993; Simmons 1995).

Other male adaptations that reduce female remating propensity include physical interventions by males. In some species, males directly punish unfaithful females. For example, in shrikes, *Larus minor*, males appear to reduce the incidence of female extrapair behaviour by physically retaliating against unfaithful females (Valera et al. 2003). In other species, males guard their mates or physically prevent them from remating through the use of mating plugs (e.g. Baer & Schmid-Hempel 1999; Baer et al. 2001; Moore et al. 2001; Montrose et al. 2004). Male bruchid beetles, *Callosobruchus maculatus*, have sclerotized spines on the tip of their intromittent organ (Crudgington & Siva-Jothy 2000). Unlike spines in odonates (Waage 1979), these spines do not remove any sperm, but damage the female's reproductive tract, possibly to postpone female remating and hence increase the male's paternity. Females have evolved a counteradaptation, kicking the copulating male, which reduces the damage by shortening the duration of copulation (Crudgington & Siva-Jothy 2000). Similarly, male bed bugs, *Cimex lectularius*, damage females by piercing their body wall with their intromittent organ during insemination (Morrow & Arnqvist 2003). Again, females have evolved a counteradaptation to this antagonistic male trait (Morrow & Arnqvist 2003; Reinhardt et al. 2003).

As well as attempting to manipulate female mating rate, males are under selection to increase the proportion of the female's offspring that result from fertilizations by their sperm. This can be advantageous to females if males successful in sperm competition are of higher genetic quality, as seems to be the case in yellow dung flies, *Scatophaga stercoraria* (Hosken et al. 2003a). However, manipulation by males can create a conflict of interests since male adaptations to increase the competitive success of sperm may be directly detrimental to females (e.g. Stockley 1997), and will tend to reduce the control that females have over paternity. All adaptations of males to increase

their share of paternity are potentially in conflict with female interests because choice over paternity is taken away from the female. Females have evolved counteradaptations to male attempts to manipulate paternity. Female postcopulatory choice occurs when multiply mated females are able to influence which male's sperm is used for fertilization (Eberhard 1996). For example, in the yellow dung fly, females have multiple sperm storage organs, making it possible for a female to store sperm from different males separately (Hellriegel & Bernasconi 2000). The optimal father for a female's offspring depends on whether she oviposits on a dung pat in a sunny location or not, and females use sperm from their previous mates according to the position of the dung pat (Ward et al. 2002).

The question of whether to remate or not is related to the key life history decision of whether to devote all reproductive effort to a single period (semelparity) or to spread it over multiple events (iteroparity). Males are expected to be continuously exerting pressure on females to put more effort into current reproduction, making sexual conflict a potentially important force in the evolution of female semelparity (Lessells 2005).

GAMETE SIZE

The fundamental level of sexual conflict is over gamete size. Indeed, it seems likely that the evolution of the fundamental difference between the genders has evolved as a result of a conflict over gamete investment. Parker and colleagues' (Parker et al. 1972; Parker 1978; Bulmer & Parker 2002) models reveal that conflict between undifferentiated parents over gamete size can lead to evolution of gamete dimorphism and subsequently to disassortative mating between large and small gametes. Given a fixed quantity of resource for gamete production, production of more gametes can happen only at the expense of gamete size: parents producing large gametes have the advantage of zygotes with high fitness, and parents producing small gametes have the advantage of numerous gametes, which are effectively parasites on the larger gametes. When the fitness of the zygote depends strongly on its size, disruptive selection for gamete size can result. This may especially be the case in organisms with extensive growth between the zygote and adult stage, and the resultant prediction that selection for anisogamy is stronger in such organisms is supported in green algae, with species that are larger as adults having bigger eggs and a greater degree of gamete dimorphism (Randerson & Hurst 2001).

Once gametes are size dimorphic (anisogamy), there is a conflict between the gametes over fusion partners since both small and large gametes do better when fusing with large gametes. Small gametes have won this evolutionary conflict. Possible reasons for this include: (1) stronger selection on small gametes to mate disassortatively since they have much to gain; (2) lack of suitable fusion partners for mutant ova that could fuse only with other ova (since individuals producing such ova will face competition with the vastly more numerous sperm); and (3) the costs for larger gametes of maintaining the

mobility necessary for fusion with other large gametes exceeding the benefits of such large-large gamete fusions.

There are alternative theories for the evolution of the sexes involving intragenomic rather than parental conflict as the main selection pressure for the evolution of two mating types (e.g. Cosmides & Tooby 1981; Hurst 1990, 1992; Law & Hutson 1992; Randerson & Hurst 1999). However, these theories do not rule out parental conflict as the major selection pressure responsible for the evolution and maintenance of anisogamy.

REPRODUCTIVE RATES

Although both sexes potentially gain fitness through reproduction, sexual conflict may occur over reproductive rates. Females are, of course, the mother of any offspring that they produce over their entire life span, whereas a male's paternity is reduced when the female remates, except when there is complete first-male sperm precedence. As a result, males are usually selected to manipulate females into investing more in the period when they can father the female's offspring, even if the female could achieve greater overall reproductive output by investing at a lower rate over a longer period.

The best example to date of male manipulation reducing female lifetime reproductive success is the use of accessory gland proteins in *D. melanogaster* (Chapman 2001; Wolfner 2002). In this species, male ejaculates increase male fertilization success by manipulating female reproductive physiology and, presumably as a side-effect, reduce female life span (Chapman et al. 1995).

An alternative explanation for this reduction in female life span is that, by imposing a high cost of mating on females in species that breed repeatedly, males can lower the females' residual reproductive value, thereby promoting an increased investment in current reproduction (Constantz 1984; Lessells 1999, 2005; Crudgington & Siva-Jothy 2000). In simultaneous hermaphrodites, for example, costly sperm injection may have evolved to manipulate the partner into increasing its investment in the current reproductive event (Michiels 1998). The same explanation could apply in other species that increase oviposition rate after harmful matings, including guppies, Poeciliidae (Constantz 1984), bruchid beetles (Crudgington & Siva-Jothy 2000), bed bugs (Stutt & Siva-Jothy 2001) and dung flies, *Sepsis cynipsea* (Hosken et al. 2003b).

The above arguments were formulated chiefly for species where the female makes the major investment in offspring, including whatever parental care is provided. However, sexual conflict over reproductive rates may also occur in species with biparental care. Mathematical models for the evolutionarily stable amount of parental investment by male and female parents suggest that in some situations the resultant fitness of male and female parents may be maximized at different family sizes (Houston & Davies 1985), creating sexual conflict over family size. Females presumably have immediate control over the family size produced, but males could then reduce family size to their optimum by destroying eggs or offspring. Such infanticide is not widely reported in

species with biparental care, but may occur in some fish or frogs with paternal care.

GESTATION AND GENOMIC IMPRINTING

In species where the female continues to invest in the zygote after fertilization, conflicts of interest between males and females can be mediated by the manipulation of gene expression in the offspring by either parent. Genes that are otherwise identical can vary in their expression according to the parent from which they are inherited. This process, known as genomic imprinting, has been shown in a wide range of taxa including plants, fungi, insects and mammals (Lloyd 2000), and appears to be caused by changes in DNA methylation affecting allelic dominance (Monk et al. 1987; Sanford et al. 1987). Autosomal imprinted genes increase embryo growth and size in mice, *Mus musculus*, when inherited from the father, but decrease growth and size when inherited from the mother (Mochizuki et al. 1996). Imprinting can be explained in terms of sexual conflict because an embryo's paternally derived genes will typically not be related to the mother and so will be under selection to secure a greater proportion of the female's resources than it is optimal for her to provide (Haig & Westoby 1989; Moore & Haig 1991; Lessells & Parker 1999). This effect is driven by the fact that each offspring is in competition for maternal resources with its siblings and half siblings, present and future. Estimates of the number of imprinted genes in mammals vary widely, with more than 70 identified in mammals (Murphy & Jirtle 2003). In mice and humans a disproportionate number of these involve placental and juvenile growth (Barlow 1995), and thus act in the period when females are continuing to invest in offspring. Theoretical models of the evolution of imprinting suggest that a placental hormone that increases resources available to offspring will evolve to full expression when paternally inherited and to zero expression when maternally inherited (Haig 1996). In addition, mathematical models show that imprinting does not evolve in strictly monogamous situations, but can occur with even low levels of multiple paternity (e.g. Mochizuki et al. 1996; Spencer et al. 1998; Hurst 1999; Spencer 2000).

Differences in costs and benefits of parental investment to males, females and their offspring result in conflict. This conflict can be influenced by genes expressed in mothers as well as maternal and paternal genes expressed in offspring (genomic imprinting). In mice, there is evidence of antagonistic coadaptation between the sexes over offspring investment (Hager & Johnstone 2003). The extent of investment provided by mothers, including litter size, is influenced by paternal genotype (strain). The mechanism by which paternal genes influence litter size is not clear but may be caused by paternally derived imprinted genes in embryos affecting the likelihood of embryo resorption. Bigger litters also enjoy greater maternal investment after birth (despite birth weight of individual pups being negatively related to litter size). However, female genotype also influences postnatal provisioning: females from the strain whose males provoke females

into producing larger litters provide fewer resources. Thus females appear to adjust their postnatal provisioning to balance the negative effects of increased litter size on their fitness (Hager & Johnstone 2003). It has been argued that paternal imprinting will be more common than maternal imprinting because mothers can influence their investment directly, whereas fathers cannot, and because actual levels of maternal investment will tend to be further from the paternal optimum creating stronger selection on males (Burt & Trivers 1998).

Female lactation is an extension of female investment beyond gestation and tends to be energetically even more costly (Cameron 1998; Dufour & Sautner 2002). Indiscriminate nursing of related and unrelated offspring in communally nesting mammals may reflect a sexual conflict that has been won by the males (Roulin & Hager 2003). Roulin & Hager argued that polygynous males benefit if all the females in their communal nest nurse indiscriminately (although they do not say why, this may be a more efficient system), whereas females would benefit from preferentially nursing their own young, resulting in selection for paternally derived genes that suppress kin recognition during lactation.

PARENTAL CARE

Conflicts over investment in offspring are particularly apparent when both parents continue to care for young after birth. Investment in parental care, such as protection and feeding of young, reduces future reproductive success (Trivers 1972; Clutton-Brock 1991). While these costs of parental care are generally paid separately by each parent, the benefits of care are accrued by both parents, regardless of who provides the care. As a result, each parent's fitness is maximized by the other parent doing most of the work, putting pressure on parents to restrict the amount or duration of investment in the current family. This restriction will often reduce the inclusive fitness of the partner either because it will have less-fit offspring or because it has to invest more of its own resources in the offspring.

Conflict over parental care rarely appears to be resolved through manipulation or coercion. Instead, each parent controls its own level of care. Mathematical models suggest that this will lead to evolutionarily stable biparental care when selection favours incomplete compensation of any change in care by the other parent (Houston & Davies 1985). Such undercompensation has been shown in experiments on wild birds where one parent was temporarily handicapped or removed (Wright & Cut-hill 1989; Markman et al. 1995, 1996). The unmanipulated parent increased its work rate, but did not fully compensate for the decrease in, or absence of, the other parent's care, and the chicks gained less weight. In these experiments brood size was not altered, but a recent experiment on zebra finches, *Taeniopygia guttata*, investigated the level of care provided by females caring for half the brood alone compared with the whole brood together with the male (Royle et al. 2002). Models like that of Houston & Davies (1985) predict an unchanged level of care per offspring (Lessells 2002), but intriguingly single mothers

provided more care per offspring (resulting in more attractive sons) and incurred a greater cost to themselves. This may come about because parents 'negotiate' on a behavioural timescale over the level of parental care. Such negotiation lays each parent open to exploitation by the other, and the predicted consequence of negotiation rules that reduced exploitability is a lower level of care, and greater sexual conflict, than predicted by Houston & Davies (McNamara et al. 1999, 2003).

Life history theory predicts that reproductive effort will increase with increasing age, because there is less future reproduction for which to save resources (Roff 1992). In particular, towards the end of life, individuals often make a terminal investment, that is, increase their effort in current reproduction. This has been found, for example, among old female collared flycatchers, *Ficedula albicollis*, which feed their young at higher rates and lose more weight than do middle-aged females (Pärt et al. 1992). However, the influence on the young is low, which may be the result of sexual conflict over parental care. Old females may have no option but to invest heavily in their current brood, since they cannot expect a further breeding season. Younger males can then exploit their older mates by reducing their own investment (Pärt et al. 1992).

Conflict over offspring care can sometimes lead to one of the parents abandoning parental care altogether. The parent left 'holding the baby' has to decide whether to abandon or continue to invest in the offspring. This situation parallels the one leading to the evolution of anisogamy: as one sex invests less and less, it can pay the other to invest more and more. Because either sex has the option to abandon its mate and brood, males sometimes take over the sole parental responsibilities. Parents may attempt to deceive one another, as in penduline tits, *Remiz pendulinus*, where females attempt to conceal their eggs until the entire brood has been laid so that they can abandon them to the care of the male (Valera et al. 1997).

Other female strategies to extract more paternal care include obscuring the paternity of their offspring, for example through concealed ovulation in mammals and polyandry in birds and mammals. This has several benefits. In species where males commonly commit infanticide as a means of bringing the female into oestrus (e.g. primates and carnivores) this may be one way of reducing such risks (Hausfater & Hrdy 1984; Packer & Pusey 1984). By mating with several males, female birds may also extract more parental care by recruiting more males to care for their young (Davies 1992). Conversely, females may gain by concealing extrapair paternity of offspring because males may provide care in relation to their paternity (Westneat & Sherman 1993; Sheldon 2002). The reverse scenario also exists, with females rewarding a male that provides a lot of care to her first brood with a higher paternity share in the second (Freeman-Gallant 1996).

Because males can father several sets of offspring at the same time, conflicts arise because fathers may divide their parental effort between several females to the detriment of them all. In polyterritorial birds, males often pair up with a secondary female while the first female is incubating the male's first clutch (e.g. Alatalo & Lundberg 1984; Slagsvold et al. 1992; Smith & Sandell 1998; Stenius 2001). Males

may try to hide their mating status by moving away from the first territory before attracting a second mate (Alatalo & Lundberg 1984). This is not in the interest of either of the females, because they have to carry most of the load of rearing the young, as the male is dividing his time between two nests. The cost to females of polyterritoriality can also be in terms of increased predation risk. In the wood warbler, *Phylloscopus sibilatrix*, the male sings to indicate to the incubating female that there are no egg predators in the vicinity. This informs the female when it is safe to leave the nest to feed, a benefit that is reduced when the male has to divide his time between two nests (Stenius 2001).

Females are not passive victims of male promiscuity. For example, in house sparrows, *Passer domesticus*, secondary females will kill the first female's young, thereby removing competition and achieving greater male care (Veiga 1990). Similarly, European starling, *Sturnus vulgaris*, females can be so aggressive towards the secondary female that they effectively prevent her from breeding, ensuring a monogamous pairing with the male (Sandell & Smith 1996; Sandell 1998). Among insects, female burying beetles, *Nicrophorus defodiens*, provide an example of how females can reduce male promiscuity. A female that has secured a carcass larger than is needed for her own young adopts various behaviours to reduce the male's pheromone production, reducing his chances of attracting a second female to the carcass (Eggert & Sakaluk 1995).

Extreme conflicts over parental care can occur when one partner not only fails to provide care for offspring, but also harms them to increase its own future reproductive success. In many species of paternally caring fish, the guarding male may eat some or all of the eggs in his nest (FitzGerald 1992; Manica 2002). If the male manages to care for the rest of the brood successfully, by eating some of the eggs, it can be argued that this is also beneficial to the female (although of course it may not be; Sargent 1992). In contrast, if the male eats all the eggs it can only be seen as an investment in his own future reproduction, at the expense of his and the female's current reproductive success. Females have developed means to avoid having their eggs eaten. In fish with paternal care and filial cannibalism, females commonly prefer to spawn with males that already have eggs in their nest (e.g. Marconato & Bisazza 1986; Kraak & Groothuis 1994; Forsgren et al. 1996). As a consequence, these females reduce the risk of having all their eggs eaten, since males typically eat all the eggs only in small clutches (Sargent 1992). They also reduce the risks associated with partial clutch cannibalism through dilution effects (Forsgren et al. 1996). A simulation study of the evolution of cannibalism and female mate choice strategies suggests that the coexistence of male filial cannibalism and female preference for mates with eggs is likely to be evolutionarily stable (Lindström 2000).

Another paternally caring fish provides an interesting scenario of sexual conflict over care. In the sex-reversed pipefish, *Syngnathus typhle*, males typically mate with multiple females (Berglund et al. 1988; Jones et al. 1999) and provide care by carrying developing eggs in a brood pouch, providing the embryos with oxygen,

osmoregulation and possibly nutrients until birth. However, failure to support some embryos in the brood pouch throughout the care period is a frequent occurrence (Ahnesjö 1992). Eggs of small females survive less well when sharing the pouch with eggs of a large as opposed to a small female (Ahnesjö 1996). This may be because males favour eggs of large females by allocating more resources to them, possibly by resorbing nutrients from a small female's eggs and reallocating them to the eggs of large females. Alternatively, the eggs of large females may take resources from the eggs of small females, either directly or through exploitation competition. Both processes may result in offspring from advantaged eggs surviving substantially better later in life, thereby compensating for reduced brood size. If this is the case, both large females and males benefit from brood reduction, so that small females are in conflict with both large females and males. However, if improved offspring quality from egg competition does not compensate for the reduction in offspring numbers, then males and small females are in conflict with large females.

SEX RATIO AND SEX ALLOCATION

Relative investment in offspring of each sex is another crucial life history decision. Because the sexes make an equal contribution to the genes in the next generation, over a population we expect equal total investment by parents in sons and daughters (Fisher 1930). In some species, rearing male offspring is more costly than rearing female offspring. This is particularly true in sexually dimorphic species. In grey seals, *Halichoerus grypus*, rearing a male pup is more costly than rearing a female pup (Anderson & Fedak 1987) and in fallow deer, *Dama dama*, males and females suckle for similar lengths of time, but males drink faster so are more expensive energetically to the mother (Birgersson et al. 1998). There is similar evidence that sons are more costly to rear in many other polygynous mammals including red deer, *Cervus elaphus*, goats, *Capra hircus*, bison, *Bison bison*, African elephants, *Loxodonta africana* (Gomendio et al. 1990), primates (Bercovitch 2002) and some human populations (Bereczkei & Dunbar 1997). When the relative cost of rearing sons and daughters differs between the parental sexes, the sex ratio that generates equal investment in sons and daughters differs between the sexes, so that the two parental sexes are selected to produce different sex ratios. In mammals, this conflict typically occurs because males do not provide parental care, so sons and daughters are equally costly to males to produce and hence males prefer a 1:1 sex ratio among their offspring. However, females will prefer a female-biased sex ratio if sons are more costly to rear (Trivers & Willard 1973).

SEXUAL CONFLICT AND UNDERSTANDING LIFE HISTORIES

We have shown that sexual conflict will have a large impact on the life histories of organisms. Costs of mating directly affect key life history traits such as survival and

fecundity, which, in combination with their sensitivity to density, are the major determinants of population dynamics (Roff 1992; Mueller & Joshi 2000). Sexual conflict exacerbates costs of reproduction because of costs to both mating partners of attempting to impose their sex's optimal strategy on their mate, and avoid their mate's attempts to do the same. Additional costs arise from pleiotropic and adaptive harm. The costs of conflict have implications for key life history traits, including how reproductive effort is distributed over the adult life span. Life history traits that we have previously tried to understand by using optimality models incorporating selection on only one sex may be the outcome of sexual conflict. For example, mathematical models suggest that male mating harm that has evolved to provoke the female into modifying her life history in the male's favour may, at least in theory, lead to the evolution of semelparity in females (Lessells 2005). Explaining such a life history trait would be impossible without taking sexual conflict into account. The flip side of this is that conflicts themselves need to be understood in terms of life history; for instance, male harm of females may be explained as a method of exploiting plasticity in life history in relation to life expectancy. Selection is likely to promote ways to enable females to ameliorate mating costs (e.g. Rice 1996).

To date, there are only a handful of studies where negative consequences of mating have been conclusively demonstrated (e.g. fruit flies, *Drosophila melanogaster*: Chapman et al. 1995; bed bugs: Stutt & Siva-Jothy 2001; dung flies: Martin & Hosken 2003). We need experimental studies conclusively demonstrating fitness costs of mating, with careful measurement of potential direct and genetic benefits that might balance these costs, before we can evaluate the generality of this phenomenon. The influence of sexual conflict on life histories is important in understanding patterns of development. Intralocus conflicts may be reduced by delaying the expression of alleles with antagonistic fitness effects. This suggests a role for sexual conflict in explaining why many organisms have pronounced differences in their immature and mature life stages. In *D. melanogaster*, there appears to be no intralocus conflict in the juvenile stage, but in adults a large number of alleles are beneficial in one sex and detrimental in the other (Chippindale et al. 2001; Rice & Chippindale 2001a). Studies of the timing of expression of conflict alleles will throw light on the importance of sexual conflict in explaining observed developmental physiologies.

Life history differences between populations are generally explained in terms of the different environments they experience. However, differences in life histories may be adaptations to sexual conflict rather than to the environment, and the arbitrary nature of coevolutionary arms races means that correlations between life history and the environment may be weak. That sexual conflict can speed up the evolution of reproductive isolation has recently been shown in an experimental study on the dung fly *S. cynipsea* (Martin & Hosken 2003). Although sexual conflict can lead to life history differences between populations without there being habitat or density differences, environmental factors will interact with aspects of sexual conflict. For instance, population density will influence

the encounter rate between potential mates such that conflicts over matings may be more severe in high-density populations.

Finally, although some degree of conflict is an intrinsic and unavoidable consequence of all interactions between unrelated individuals, it is worth bearing in mind that sexual reproduction is noteworthy more for the prevalence of cooperation than for the existence of conflict. What is clear is that for all organisms, the optimal partitioning of time and energy into growth, survival and reproduction depends on interactions between individuals and their sexual partners and on how the inevitably occurring conflicts are resolved.

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