The origin of sexual reproduction involved the evolution of zygotes from separate genomes and, like other social processes, should therefore be amenable to analysis using kin selection theory. I consider how kin structure affects sexual interactions in three contexts—the evolution of sexual reproduction, sex allocation and sexual conflict. Kin structure helps explain the even-handed replication of paternal and maternal genes under outbreeding. Under inbreeding, it predicts altruistic failure to replicate by one half of the diploid genome. Kin structure predicts optimal sex ratios and potential conflicts over sex ratio within social groups and individuals. Sexual conflict predictably occurs as a function of (i) the probability that current sexual partners will reproduce together in future and (ii) between-partner relatedness. I conclude that systematically analysing the kin structure of sexual interactions helps illuminate their evolution.

Keywords: evolution of sex; kin selection; relatedness; sex allocation; sex ratio; sexual conflict

1. INTRODUCTION

The evolution of sexual reproduction in eukaryotes was a momentous step in the history of life, qualifying as one of Maynard Smith & Szathmáry’s (1995) major transitions in evolution. Among other things, it involved the evolution of a new kind of individual (Buss 1987), namely the zygote (and its multicellular offshoot, the body into which a zygote develops). A zygote is a chimera formed from the union of two separate genomes (one from each gamete). Several of the major transitions defined by Maynard Smith & Szathmáry (1995) involved the grouping together of previously separate entities to form a new kind of individual, whether a single cell, a multicellular organism or a eusocial colony. Because such unions have an obvious social dimension, they are amenable to analysis with Hamilton’s (1964) theory of kin selection (inclusive fitness theory). In this article I consider the evolution of sexual reproduction and other sexual phenomena (sex allocation and sexual conflict) from the standpoint of kin selection theory. Note that I take kin selection to include interactions in which the partners are not genetically related since relatedness is a continuous variable ranging from negative values, through zero, to positive values.

Previous authors have also investigated the social aspects of sexual reproduction (e.g. Queller 1997; Keller & Reeve 1999; Wenseleers & Ratnieks 2001; McNamara et al. 2006) and kin selection theory is well established as the major tool for understanding sex allocation (e.g. Croziers & Pamilo 1996). I do not consider the social aspects of sexual reproduction in this article, I seek to integrate and extend the message of these authors. My hope is that applying kin selection thinking systematically to sexual interactions and the evolutionary conflicts they engender will help illuminate their selective basis.

2. EVOLUTION OF SEXUAL REPRODUCTION

Queller (1997) divided the major evolutionary transitions into ‘egalitarian’ ones, which occur between unrelated entities, and ‘fraternal’ ones, which occur between related entities. The evolution of sex is an egalitarian transition in that it involves the union of unrelated gametes at least under outbreeding. Another such transition was the origin of the eukaryotic cell by the symbiosis of two prokaryotic genomes (Maynard Smith & Szathmáry 1995). Sex differs from this transition, however, in that the union creating the new individual, the zygote, occurs anew each generation. The basic prediction from kin selection theory for social interactions between non-relatives is that they will be cooperative, i.e. each party must gain a direct fitness benefit for the partnership to remain stable (West et al. 2007). In the eukaryotic cell, this is borne out by the continued replication of both the nuclear and organelle genomes. In sexual reproduction, it is borne out by the continued replication of both maternally and paternally derived genes. Meiosis usually involves each allele at a locus (i.e. each maternally and paternally derived gene) receiving the same chance (0.5) of entering a gamete. As pointed out by Keller & Reeve (1999), this is as expected from kin selection theory, which predicts low reproductive skew (i.e. an egalitarian sharing of reproduction) when social partners are unrelated. However, potential conflict is present because, as in other mutualisms, each party (here, each allele) potentially benefits from increasing its reproduction at the expense of the other (West et al. 2007). Such conflict is expressed during meiotic drive, in which a gene gains over-representation in gametes relative to its allele (Burt & Trivers 2006). Meiotic drive is therefore unstable from the perspective of the allele of the drive gene, which hence should be selected to resist drive. In practice, however, drive genes are suppressed by modifier genes at other loci (given drive generally causes pleiotropic fitness costs to these loci too), perhaps because their greater number makes appropriate mutations at other loci more likely (Leigh 1977).

Such considerations lead naturally to thinking about what should happen if gametes are related, i.e. if...
there is inbreeding. This was done by Wenseleers & Ratnieks (2001), who found that selection for meiotic drive would be reduced by inbreeding. Wenseleers & Ratnieks (2001) also noted, in keeping with a core prediction of kin selection theory, that relatedness between alleles at a locus creates conditions for altruism (one party sacrifices its reproduction to aid the other). What would altruism between related alleles at a locus look like? One possibility is that one half of the diploid genome might sacrifice its own reproduction in order to enhance that of the half from the opposite sex. To be more specific, an allele A from one gamete paired in a zygote with the same allele A from the other gamete might forgo entering a gamete (or surviving in the zygote) if this allowed more than one copy of A (two copies of A × 0.5 chance of entering a new gamete under a fair meiosis) to be passed to the next generation. This would satisfy Hamilton’s (1964) rule for altruism \( r_b c > 0 \), since in this case \( r = 1 \), making the condition for altruism only that the benefit \( b \) should exceed the cost \( c \). This level of benefit could easily be achieved if females gave up meiosis and so removed the twofold cost of sex. Because inbreeding (on average) increases homozygosity across all loci simultaneously, a result of inbreeding might therefore be any of the various ‘asymmetric’ genetic systems, such as paternal genome elimination, pseudogamy, arrhenotoky and thelytoky, in which one half of the genome (usually the male half) fails to replicate equally (Normark 2006). Such a process would also be facilitated under extreme inbreeding because sex would no longer confer the benefits of additional genetic variation (Hamilton 1967).

This perspective predicts that inbreeding should precede the evolution of asymmetric genetic systems rather than, as Normark (2006) suggested, being a consequence of them. Although detailed phylogenetic evidence appears lacking, there is a close association between inbreeding and such systems in terrestrial arthropods (Hamilton 1967) if not in plants (Charlesworth 1980). In sum, although other conclusions are possible under different initial assumptions (e.g. Charlesworth 1980; Bull 1981), kin selection suggests that inbreeding creates conditions for asymmetric genetic systems, including asexuality, by allowing genomes of one sex to sacrifice their reproduction altruistically on behalf of genomes of the other.

### 3. SEX ALLOCATION

Restated in terms of kin selection, Fisher’s sex ratio theory predicts that the stable sex ratio is set by the relatedness asymmetry of the party controlling sex allocation, i.e. the ratio of relatednesses with females and males (Hamilton 1967; Trivers & Hare 1976). Using this formulation, kin selection generates many familiar predictions in sex ratio theory (e.g. Crozier & Pamilo 1996). It also shows how potential conflict over sex ratio occurs when different parties have unequal relatedness asymmetries (Trivers & Hare 1976).

Less familiarly, sex ratios for non-nuclear genes are also predicted by their relatedness asymmetries. For example, the stable sex ratio for cytoplasmic elements (e.g. mitochondria or endosymbiotic bacteria) is all-females, given by the ratio of their relatedness to female gametes \( r = 1 \), because cytoplasmic elements reproduce asexually and male gametes \( r = 0 \), because cytoplasmic elements are not transmitted paternally. This accounts for phenomena such as cytoplasmic male sterility in plants, in which mitochondrial genes hinder pollen production and increase ovule production, and male killing in invertebrates, in which endosymbiotic bacteria destroy male embryos and so induce female-biased sex ratios (Burt & Trivers 2006). However, because (autosomal) nuclear genes have a relatedness asymmetry of 1 : 1, nuclear genes restoring a 1 : 1 sex ratio are selected for in affected hosts (Burt & Trivers 2006). Alternatively, some cytoplasmic endosymbionts may induce haplodiploidy or thelytoky in their hosts (Engelstädter & Hurst 2006; Adachi-Hagimori et al. 2008), demonstrating that the relatedness asymmetries of non-nuclear genes may also catalyse the evolution of asymmetric genetic systems.

### 4. SEXUAL CONFLICT

One way of seeing how kin structure influences sexual conflict is by considering the case of conflict over mating frequency. This is one of the best-studied forms of sexual conflict and is believed to underlie the transfer by male *Drosophila* of toxic peptides to females during mating (Chapman 2006). The presence or absence of potential sexual conflict here can be predicted by a two-way classification of mating in terms of (i) the probability that the focal partner will produce additional offspring with its partner beyond the current mating and (ii) between-partner relatedness (figure 1). This predicts sexual conflict in *Drosophila* because the mating system (polygamy) is such that males are very unlikely to re-mate with their current partner and are unrelated to females, i.e. there is outbreeding (region A in figure 1). Males therefore have no evolutionary interest in the survivorship or reproduction of females after females have produced the young from the current mating, whereas females retain an evolutionary interest in their future reproduction, so creating high potential conflict. (The kinship theory of genomic imprinting posits an analogous male–female conflict based on the fitness interests of male genomes from the previous generation (Haig 2004).) Specifically, males are not selected to refrain from selfish manipulations that increase their fitness from the current mating but reduce females’ long-term survivorship (Chapman 2006).

By contrast, when there is monogamy, irrespective of relatedness (regions B and C in figure 1), there is low potential sexual conflict, since a focal partner harming its mate would damage its own long-term fitness (Lessells 1999). (Note, however, that monogamy may itself be the outcome of previous conflict (Hosken et al. 2009). Note also that, to concentrate on any effects of relatedness *per se*, I ignore costs of inbreeding in these comparisons.) Such a reduction in sexual conflict is likely in the social Hymenoptera, in which, because of sperm storage and lack of female re-mating, a male commits each ejaculate to a single female throughout the female’s lifetime. Evidence for the resulting sexual cooperation comes from the ant *Cardiocondyla obscurior*,...
in which mating increased the longevity of queens (Schrempf et al. 2005). The contrast between regions A and B in figure 1 also represents a specific instance of a well-known result from the study of reciprocity in cooperating non-relatives (Trivers 1971). This is that single encounters encourage the inflicting of costs (defection), whereas repeated encounters (here, repeated batches of offspring under monogamy) do not. Finally, when there is polygamy with inbreeding, there should again be reduced potential sexual conflict because a focal partner’s relatedness with mates would constrain the degree of selfish damage inflicted on them (region D in figure 1).

5. CONCLUSION

Sexual reproduction involves a complex set of phenomena and I do not propose that kin selection theory holds the key to them all. Indeed, two integral features of sex, recombination and segregation, although not outside the scope of inclusive fitness analysis (e.g. Haig & Grafen 1991), represent longstanding evolutionary puzzles that endure to the present (Barton & Charlesworth 1998; Agrawal 2006). Nonetheless, by systematically investigating the underlying kin structure of sexual interactions, we stand to gain a deeper, more integrated understanding of their evolutionary causes and the conflicts they create.

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