Review

The sociobiology of sex: inclusive fitness consequences of inter-sexual interactions

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The diversity of social interactions between sexual partners has long captivated biologists, and its evolution has been interpreted largely in terms of 'direct fitness' pay-offs to partners and their descendants. Inter-sexual interactions also have 'indirect effects' by affecting the fitness of relatives, with important consequences for inclusive fitness. However, inclusive fitness arguments have received limited consideration in this context, and definitions of 'direct' and 'indirect' fitness effects in this field are often inconsistent with those of inclusive fitness theory. Here, we use a sociobiology approach based on inclusive fitness theory to distinguish between direct and indirect fitness effects. We first consider direct effects: we review how competition leads to sexual conflict, and discuss the conditions under which repression of competition fosters sexual mutualism. We then clarify indirect effects, and show that greenbeard effects, kin recognition and population viscosity can all lead to episodes of indirect selection on sexual interactions creating potential for sexual altruism and spite. We argue that the integration of direct and indirect fitness effects within a sociobiology approach enables us to consider a more diverse spectrum of evolutionary outcomes of sexual interactions, and may help resolving current debates over sexual selection and sexual conflict.

Keywords: sexual selection; kin selection; sexual conflict; greenbeard; Fisherian runaway

1. INTRODUCTION

In sexually reproducing organisms—from yeast to primates—interactions between reproductive partners over mating and/or fertilization are exceptionally diverse and often extravagant. In some species, partners feed and groom each other to form a long-term cooperative bond, while in other species they regularly kill or cannibalize each other. The evolutionary significance of this diversity has been largely interpreted in the light of a balance between direct fitness payoffs to partners and resulting progeny, with focus on the role of sexual selection. While at a proximate level (i.e. regardless of fitness payoffs), successful sexual reproduction ultimately requires a degree of cooperation between partners, as with most transactions between cooperators, sexual reproduction is also fraught with evolutionary tension.

The possibility for members of one sex both to help and to harm members of the opposite sex was already implicit in Darwin's idea of sexual selection [1]. Darwin [1] recognized that sex can introduce two sources of variation in individual fitness: competition among members of one sex over access to reproductive opportunities, and choosiness by members of one sex of reproductive partners of the opposite sex. Together, these mechanisms create opportunity for sexual

selection. Owing to the disparity in size of male versus female gametes (anisogamy), it is males that often compete more intensely over access to ova and females that—as a result—display more conspicuous choosiness of potential partners and/or their sperm [2,3]. However, females may also compete, sometimes more fiercely than males [4], and males may discriminate among different females [5].

This approach has therefore helped elucidate conditions under which—at a functional level—the direct fitness interests of partners are aligned or diverge, and thus where sexual and viability selection interact to foster mutualistic or antagonistic interactions between males and females. Indeed, much of the recent research can be framed within a framework that seeks to establish the extent to which sexual interactions are driven by cooperation or conflict between the sexes. However, this framework fails to consider that inter-sexual interactions do not only affect the fitness of the interactants but often also that of their relatives. This has critical repercussions for inclusive fitness and for the evolutionary significance of social interactions between sexual partners.

One of the major advances in modern evolutionary theory stems from the Hamiltonian insight of inclusive fitness, 'which allows for interactions between relatives on one another's fitness' [6], by decomposing selection into direct and indirect components, where the latter is mediated by the relatedness-weighted effects on the fitness of social partners. Natural selection leads organisms to appear designed as if to maximize their

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Table 1. Behaviours that improve the fitness of the actor are 'mutually beneficial' if they also improve the fitness of the recipient ($c < 0$, $b < 0$) and are 'selfish' if they reduce the recipient's fitness ($c < 0$, $b < 0$). Behaviours that reduce the fitness of the actor are 'altruistic' if they improve the recipient's fitness ($c > 0$, $b > 0$), and 'spiteful' if they reduce the fitness of the recipient ($c > 0$, $b < 0$). Behaviours that improve the fitness of the recipient ($b > 0$) are termed 'helping' and those that reduce the recipient's fitness ($b < 0$) are 'harming', irrespective of the fitness consequences for the actor. If behaviours impact upon the fitness of multiple recipients, helping some and harming others, then classification can be done according to the effects felt by the actor's 'primary' recipients. Finally, helping behaviours that have evolved, at least in part, owing to the benefits that they grant the recipient are termed 'cooperation'. This includes all altruistic and some mutually beneficial behaviours.

		effect on recipient			
		+	–		
effect on actor:	+	mutual benefit	selfishness	direct effects	favoured owing to:
	–	altruism	spite	indirect effects	
		helping	*harming*		

inclusive fitness, which is the sum of their direct and indirect fitness [6–8]. There are two routes by which the organism may increase inclusive fitness, either by increasing the organism's own reproductive success (direct fitness effect) or else by increasing the reproductive success of the organism's genetic relatives (indirect fitness effect) [6]. The overall condition for natural selection to favour a social behaviour that incurs a cost c for the actor and provides a benefit b to the recipient is Hamilton's rule $rb > c$, where r is the genetic relatedness of these two individuals [6,7,9]. If multiple individuals are affected, then Hamilton's rule may be written as $\sum_i r_i b_i > c$, where b_i and r_i are the benefit and relatedness corresponding to the ith recipient [8]. Hamilton's rule is a fully general separation of natural selection into its direct and indirect components [10].

Hamilton [6,9] showed that natural selection could drive the evolution of altruistic behaviours, so long as the recipients of altruism are sufficiently related to the actor. More generally, Hamilton's rule predicts when any trait—i.e. altruism, selfishness, mutual benefit, spite and also non-social characters—are favoured by natural selection. The intentional language employed in the study of social evolution is sometimes felt to be undesirable, and efforts have been made in the past to purge the field of such loaded, anthropomorphic terminology. However, this concern is misguided. The intentional language is formally justified by the mathematical correspondence between the dynamics of natural selection and the analogy of the individual organism as 'maximizing agent' [8,11,12]. Moreover, such language defines whole programmes of scientific research in behavioural ecology, for example, on sexual 'conflict'. If agents and their intentions are part

of the question, then they must also form a part of the solution [13].

There is growing appreciation that the study of sexual interactions, including studies of sexual selection and sexual conflict, would stand to gain by embracing an inclusive fitness approach, and recent efforts have been made in this direction [14–19]. However, at present, these efforts remain isolated and focused on specific questions. Here, we integrate these studies within a broader sociobiology approach based on inclusive fitness theory, to explain the diversity of social interactions observed among sexual partners across a range of sexual organisms by simultaneously considering direct and indirect selection episodes.

2. AN INCLUSIVE FITNESS APPROACH

In most organisms, sex is a social trait, an interaction between an actor and recipient(s) of two discrete categories (males and females), which has the potential to change the fitness of each party. The consequences of sexual interactions for the selective process can therefore be categorized using a standard inclusive fitness approach, which decomposes genetic change into 'direct selection'—i.e. owing to the impact of the trait upon the individual's own reproductive success—and 'indirect selection'—i.e. owing to the impact of the trait upon the reproductive success of the individual's genetic relatives. The separation of direct and indirect selection (table 1) provides the basis for classifying social behaviours [6,20], and represents the most fundamental branching in the hierarchy of explanations for Darwinian adaptations, such as cooperation [21].

The idea that natural selection comprises direct and indirect effects is well known in the sexual selection

literature. However, there is a diversity of meanings attached to these terms, which requires some clarification. In sexual selection literature, the mechanisms driving sexual preferences are often divided into those conveying net fitness benefits to the individual selecting mates (i.e. preference for specific mates increases its lifetime reproductive success of an individual), and those conveying net benefits to the offspring produced by mating with preferred mates, through genetic covariance between ornament and viability ('good genes') and/or linkage disequilibrium between preference and ornament genes ('Fisherian runaway'). Traditionally, the former benefits are defined as 'direct' and the latter as 'indirect' [22,23]. However, the distinction between 'direct' and 'indirect' effects can cause confusion, as offspring survival may be viewed as part of the parent's reproductive success and, as such, a direct (rather than indirect) contribution to the parent's fitness. Considerable debate has focused on whether 'direct' fitness costs imposed by an actor on its partner(s) might be rescued by 'indirect' benefits associated with reproducing with harmful partners [24–26], and on whether 'good genes' and 'Fisherian runaway' represent two distinct indirect mechanisms [26–28]. Key to resolving these debates is the correct assignment of direct and indirect effects. Here, we employ the formal definitions of direct and indirect fitness that are provided by inclusive fitness theory, as they are unambiguous and fundamentally connected to the design objective of all Darwinian adaptation.

3. DIRECT FITNESS EFFECTS
(a) *Selfishness and sexual conflict*
Conflict arises whenever two prospective partners maximize fitness through different, mutually exclusive reproductive decisions at any stage of the reproductive process, from mating to parental investment [15]. This tension can occur whenever multiple reproductive opportunities are available to members of at least one sex, for the combination of two inter-related factors. First, by its very nature, reproductive investment incurs a fitness cost. This means that the reproductive resources available to an individual are limited and investment in reproduction with a particular partner will automatically reduce the availability of resources for reproduction with other current or future partners.

Therefore, evolutionary conflict between interacting males and females is implicit in any mechanism of mate choice, postmating gamete selection or postzygotic differential reproductive investment. Second, owing to limited availability of reproductive opportunities, there is competition among members of one sex to access sexual partners. Intrasexual competition can promote traits that enable the carrier to outcompete rivals even when they harm reproductive partners. The 'tragedy of the commons' provides a useful metaphor [29–31]. This refers to a situation in which individuals compete selfishly over access to a resource, which as a result becomes depleted to the detriment of the whole group. One could argue that males themselves can often be regarded as a tragedy of the

commons, because although relatively few would be required to guarantee the growth of a population, it often pays individuals to produce more than required. In the context of sexual selection, competition between sexual rivals can damage the reproductive ability of members of the opposite sex, and thus reduce the whole mating group's fitness. For example, male harassment of females in their pursuit of mating opportunities can be so damaging to females as to lead local populations to extinction (figure 1a). Harm can also be mediated by insemination costs (figure 1b,c). For example, in several invertebrates, insemination is 'traumatic'. In contrast to orthodox genitalic intromission, traumatic insemination occurs through the puncture of the female body wall by highly derived male organs [40]. Similarly, when females mate with multiple males, males are often selected to inseminate larger ejaculates in order to outcompete the sperm of their rivals [41]. However, in many organisms, if too many sperm penetrate the oocyte, the resulting excess of centrosomes may jeopardize zygote development (pathological polyspermy [42]), resulting in a post-mating tragedy of the commons.

(b) *Mutual benefits*
Mutual benefits occur when a male and a female stand to gain simultaneously from the same reproductive decision. The only way to enforce complete sexual mutualism is through the absence of sexual selection. Imagine a species with lifetime monogamy, even sex ratio and zero variance in intrinsic individual fecundity or reproductive quality. Here, we have essentially removed intrasexual competition and individual variation in reproductive success due to differential access to mating and fertilization, the ingredients of sexual selection. Under such conditions, the interests of an individual will coincide with those of its reproductive partner, such that the only way for an individual to increase its own fitness is to increase that of its partner. Such 'repression of competition' is one of the mechanisms driving major transitions in evolution, whereby social groups that effectively abolish their internal conflicts can be viewed as single adaptive individuals in their own right [43–46]. For example, an ancestral condition of strict lifetime monogamy has probably been a catalyst for the evolution of eusociality [47,48].

The complete absence of sexual selection is clearly rare. However, specific ecological conditions can lead to mating systems in which sexual selection is strongly limited. For example, when reproductive resources are limited and spatially dispersed, strict lifetime monogamy is often the best reproductive strategy, for a range of organisms (figure 1d,e). Some potential for mutualism for specific reproductive decisions persists even under sexual selection. For example, inbreeding or hybridization may result in such low reproductive success that both partners might 'agree' to avoid mating [14,15,17]. Similarly, in species where males can stimulate female fecundity (for example, through nuptial gifts or spermatophylaxes, figure 1f) to a degree where female reproductive success more than doubles if the female mates with two males, then all
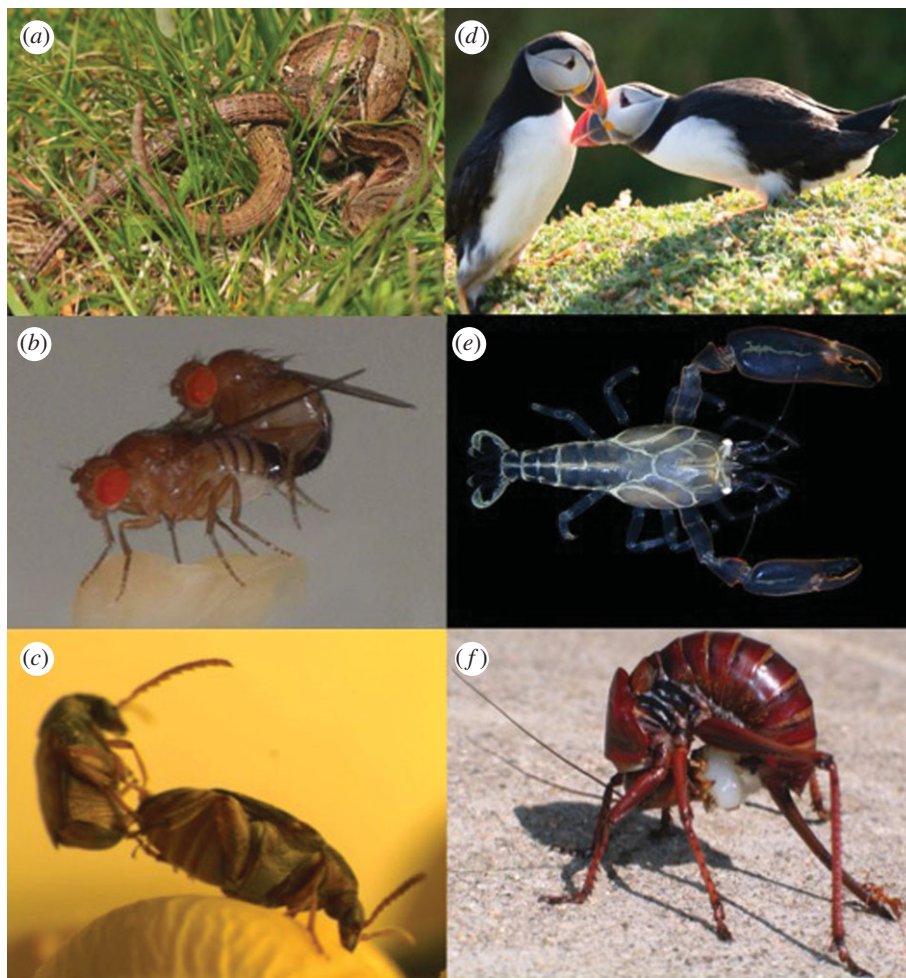
Figure 1. Sexual conflict and mutual benefits. Conflict: (*a*) in experimental populations of viviparous lizards, *Lacerta vivipara*, male sexual harassment can be so costly to females as to drive populations to local extinctions [32]. Photo credit: P. S. Fitze. (*b*) The accessory gland products (Acp) released in the seminal fluid of the male fruit fly, *Drosophila melanogaster*, favour the fertilizing success of an ejaculate in sperm competition by facilitating female sperm storage, by inhibiting female receptivity to new mating, and by stimulating egg production [33], and males evolve more manipulative Acps under more intense sperm competition [34]. However, Acps also have a toxic side effect on females, which pay a net fitness cost when exposed to high insemination rates [35]. Credit: R. Dean. (*c*) In the bean beetle, *Callosobruchus maculatus*, male genitalic spines damage the female reproductive tract [36], and longer spines convey higher reproductive success to males but impose higher costs to females [37]. Credit: F. Champion de Crespigny. Mutual benefits: (*d*) many seabirds, such as these Atlantic puffins, *Fratercula arctica*, partners form long-term, highly cooperative and monogamous pair bonds. Credit: C. M. Perrins. (*e*) In the symbiontic shrimps, *Pontonia margarita*, a single heterosexual pair typically inhabits the same host (pearl oyster). The size of the hosts, their limited availability and high predation risk between hosts can all contribute to maintain monogamy in this system [38]. Credit: A. Anker (Universidade Federal do Ceará, Brazil). (*f*) In some organisms, males can boost female fecundity, e.g. through the provision of a highly nutritious nuptial gift or, as in some orthopterans, a spermatophylax (credit: N. W. Bailey). When male stimulation more than doubles female fecundity, both male and female gain if the female remates with another male [39].

three individuals may do better if the female mates with both males [39]. Clearly, the mutualism of this 'ménage à trois' is limited to the decision of whether or not a female should mate with both males. Her promiscuity will generate competition between the sperm of the two males over fertilization (sperm competition) and thus sexual conflict over differential sperm utilization and fertilization [39]. Similarly, when male sperm reserves are limited, females might mate suboptimally, paying a fertility cost. However, high mating rates driven by strong male competition might reduce this particular conflict by automatically leading to assortative mating, e.g. more fertile males mating with more fecund females [49]. In fact, we

can find some potential of mutualism even in behaviours such as sexual cannibalism. The females of a diverse range of invertebrate species typically eat the often smaller partners [50]. One would expect this to lead irrevocably to conflict, but this is not necessarily the case. Conflict clearly occurs when the male is eaten before he mates with a female [50]. However, when cannibalism occurs during or after mating, things are different. In some species such as the redback spider, *Latrodectus hasselti*, a male has a low chance of mating successfully with more than one female, while females are likely to mate with more than one male [51,52], which means that the ejaculate of a male is likely to face sperm competition. During

mating, the male red-backed spider somersaults to offer his abdomen to the female mouthparts, and cannibalism ensues. By feeding himself to the female, a male increases the fecundity of the female and doubles his share of paternity by prolonging mating [53]. Even if a male survived a female, mating damages the male twin intromittent organs (pedipalps) so as to render a male effectively sterile after two copulations [54]. Clearly, a male red-backed spider might have more to gain by defending his paternity with a female than by leaving her to the attention of other males in search of new females. This arrangement would also benefit females unless there are strong benefits associated with polyandry. Therefore, under some conditions, male self-sacrifice might represent a mutually beneficial strategy. Clearly, this is a precarious balance: males should avoid such sexual sacrifice as soon as ecological conditions shift to make remating beneficial for either sex. And this is what may happen in other species, where males feign their own death [55] or preferentially target well-fed females to reduce the risk of cannibalism [56].

In short, while the potential for sexual conflict appears to increase proportionally with the opportunity of sexual selection, sexual selection and sexual conflict are two distinct evolutionary mechanisms [20], and the former does not necessarily lead to the latter.

(c) Enforcing sexual cooperation

Cooperation can be enforced even when evolutionary conflict would otherwise occur between partners. There is a diversity of mechanisms through which cooperation can be secured in spite of conflict. These fall into two non-mutually exclusive categories: cooperation can be traded for concessions and fitness rewards to cooperating partners, or it can be coerced with the threat of sanctions and punishments of non-cooperating partners. For example, female dunnocks, *Prunella modularis*, often mate and form pair bonds with two males simultaneously. Because these female sexual concessions give both males a realistic chance of paternity, both provide paternal care (albeit proportionally to perceived confidence of paternity), enabling females to invest less into maternal care [57]. Similarly, field observations suggest that in Adélie penguins, *Pygoscelis adeliae*, females might obtain nest material by engaging in extra-pair copulations with unpaired males [58]. A particular case of reciprocal concessions occurs in non-selfing simultaneous hermaphrodites [59]. Here, anisogamy means that each individual produces more sperm than eggs, and at mating will benefit more by giving sperm to fertilize its partner's eggs rather than receiving its partner's sperm to fertilize its own eggs. Therefore, there is a conflict of interest over male (giving sperm) and female (accepting sperm) roles. This stalemate can be resolved by partners taking turns, through reciprocal spawning or inseminations. However, the equilibrium of this tit-for-tat can be vulnerable to the invasion of cheating strategies in which an individual can impose its own reproductive interests (i.e. give sperm). A number of extravagant traits appear to have this function, from the 'love darts' of some snails, coated with allohormones which inhibit sperm digestion by the recipient [60] to the 'penis-fencing'

[61], traumatic inseminations and 'sperm-sucking' of some flatworms [62] and the apophallation of the banana slug, *Ariolimax columbianus* [63].

An additional mechanism to enforce cooperation is by punishing partners when they do not cooperate, i.e. when they behave in a way that reduces the fitness of the focal individual [64,65]. In principle, sexual punishment occurs when an actor is able to prevent a recipient from acting selfishly by imposing (or threatening to impose) fitness costs to refrain the recipient from being selfish [64]. In practice, however, sexual punishment is difficult to demonstrate experimentally, although a number of behaviours might have this function. In several mammalian societies, males have been observed to attack females that refuse to mate with them or stray away from their territory [65]. In socially monogamous birds with bi-parental care, males have been speculated to punish their partner when she mates with other males (extra-pair copulations) [66]. For example, in lesser grey shrikes, *Lanius minor*, where partners often leave the nest to engage in extra-pair copulations, males attacked their social mates when these were experimentally removed from and returned to the nest while fertile (shortly before the onset of egg-laying) but not when the same manipulation was performed when females were no longer fertile (all the eggs were already laid) [67]. A similar pattern may occur in monogamous termites, where inter-sexual aggression (especially male aggression of females) may function to pre-empt rejection [68]. Finally, the high mating costs imposed by males in some species might function as a form of sanction to discourage females from remating [69], or encourage them to invest more in the current reproductive event [70].

4. INDIRECT FITNESS EFFECTS

(a) Sexual altruism and sexual spite

Altruism occurs when the actor pays a direct fitness cost to convey a fitness benefit to a recipient. Hamilton [6] showed that genes for altruism can be favoured provided that the recipients of altruism are sufficiently genetically related to the actor. Spite is the more sinister flipside of altruism, whereby the actor incurs a cost in order to harm the recipient, and can be favoured if the relatedness between recipient and actor is less than the average relatedness between individuals in their economic neighbourhood (negative relatedness [7,71–73]). In other words, harming the recipient at your own cost might increase your inclusive fitness if the recipient is in competition with your relatives. Often altruism and spite are interchangeable: the same action may benefit some recipients while harming others, so classification depends upon which individuals are deemed the 'primary' recipients and which are merely 'secondary' recipients [74,75].

While altruism has been extensively explored in several social contexts, its role in sexual interactions has received much less attention. Here, indirect benefits can arise for two reasons: (i) the recipient is related to the actor; or (ii) the actor is related to a third party, who will at some point also interact with the recipient. The former case represents inbreeding, as
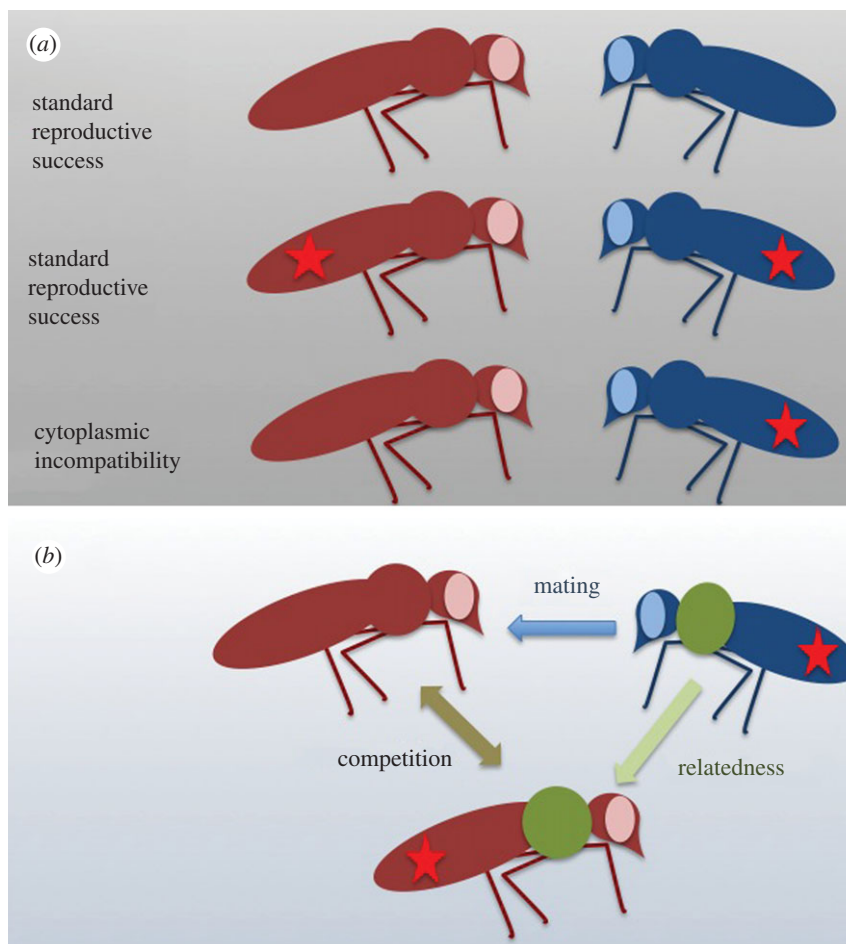
Figure 2. Spiteful *Wolbachia*. *Wolbachia* is a genus of bacteria, which live symbiotically in many species of invertebrates. (*a*) Mating between infected males (star) and non-infected females leads to cytoplasmic incompatibility, which depresses reproductive success, while assortative matings result in healthy reproductive success. (*b*) In structured populations, infected males might pay a reproductive cost to mate with uninfected females. The resulting cytoplasmic incompatibility will depress the fitness of the competitors of the male's female relatives [79,80].

it concerns the reproductive decisions of related partners (see below). The latter refers to, for example, situations in which intrasexual competition occurs mainly among relatives. In this case, behaviours that harm a partner might also reduce the fitness of the actor's related competitors. Recent theoretical work demonstrates the potential for indirect selection to buffer sexual selection for male harm of females [18,19]. Few studies have explicitly tested these predictions. However, a recent study of killifish, *Heterandria formosa*, demonstrated that females mated to three males genetically unrelated to each other suffer from higher mortality rates than females mated to three full-sib males (unrelated to the female) [76]. Proximally, these results may be mediated by a number of factors, e.g. higher immunological costs associated with responding to three genetically different ejaculates; however, functionally, these results are also consistent with the prediction that males are more benign to their partners when male relatedness increases.

A plethora of intra- and inter-sexual behaviours have also been interpreted as spiteful in the past. On closer scrutiny, many of these examples represent the outcome of costly selfish competition. Conditions for spite are stringent [75]. However, under some

situations, an actor could be indirectly selected to pay a cost for harming partners of negatively related competitors. For example, male punishment of asexual females has recently been proposed as an explanation for the maintenance of sexual reproduction [77,78]. Cytoplasmic incompatibility induced by maternally inherited symbionts, such as *Wolbachia*, may also create potential for sexual spite [79,80] (figure 2).

Both altruism and spite require that non-zero genetic relatedness arises between social partners. Inclusive fitness theory has shown that there are three basic mechanisms for generating this: the greenbeard effect, kin discrimination and population viscosity.

(b) *Fisherian greenbeards*

Greenbeards are single genes (or multiple genes, in linkage disequilibrium with each other) that enable their carriers to recognize each other and also behave so as to increase each other's fitness [6,81]. Such genes may be selectively favoured owing to genetic relatedness at the greenbeard locus, even when social partners are not genealogical kin. The Fisherian runaway process, defined as the coevolution of preference and ornament under linkage disequilibrium [28,82], can be usefully thought
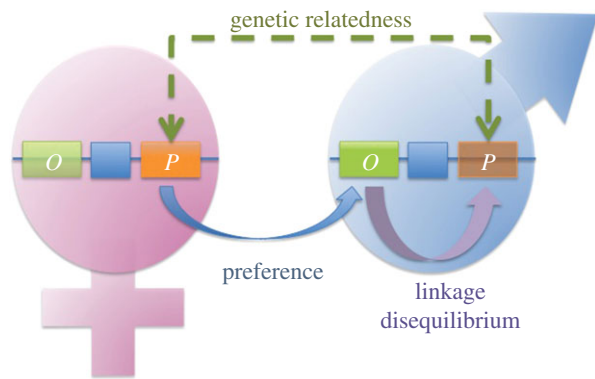
Figure 3. Fisherian greenbeards. The greenbeard effect is mediated by linkage disequilibrium between a locus coding for a phenotypic marker and a locus coding for a behavioural response to the marker [81]. In a sexual context, allele *O* codes for a greenbeard ornament and allele *P* codes for a sexual preference for partners expressing *O*. Linkage disequilibrium between *O* and *P* evolves through assortative mating. Owing to the preference and linkage disequilibrium associations, there is an overall relatedness association (dashed green line). It is likely that allele expression is specific to two discrete categories: individuals expressing *O* but not *P* (e.g. males), and individuals expressing *P* but not *O* (females), as indicated by reciprocal transparency of *P* and *O* loci.

of as a greenbeard effect (*sensu* [81]). Here, a gene encoding a male sexual ornament is in linkage disequilibrium with a gene encoding a female preference for the ornament, because offspring of preferring females tend to have ornamented fathers. The female preference in this case is indirectly favoured because females who express the preference gene will increase the relative reproductive success of ornamented males who will tend to carry copies of the female preference gene, i.e. the preference gene is helping out copies of itself (figure 3).

The extent to which the Fisherian runaway and good genes are distinct mechanisms has been the subject of recent debate [26–28]. While these mechanisms are not mutually exclusive and in fact are likely to occur simultaneously, the distinction between direct and indirect effects helps us to identify their inherent difference. The Fisherian runaway works in a greenbeard-like fashion because of indirect selection caused by linkage disequilibrium, while good genes work largely because of the direct effect of viability benefits conveyed to the offspring through the genetic covariance between the ornament and viability, independently of linkage disequilibrium between preference and ornament. Specifically, the Fisherian runaway requires that preference is exerted within a generation in which there is linkage disequilibrium between the female preference gene and the male ornament, whereas the good genes mechanism does not. That is, if the female preference gene were 'switched on' in only one generation, it would not be favoured under the Fisherian runaway (it would generate an association with the ornament in the subsequent generation, but the ornament would no longer benefit its bearers), but it would be favoured under good genes (it would generate an association with the ornament, and hence with the good genes, and the latter would remain beneficial to their bearers even in the absence of female preference behaviour).

Although greenbeards are known to occur in the natural world—particularly in microbes—they are generally expected to be rare owing to the possibility that 'falsebeard' [81] genotypes arise that express the phenotypic marker but not the social behaviour, and thus free-ride on the social benefits provided by greenbeards. However, in the context of Fisher's runaway model, cheating is less likely because any breakdown of the association between male ornament genes and female preference genes will be countered by the build-up of this association owing to preferential mating of discriminating females with ornamented males. Thus, Fisher's runaway model represents an example of a greenbeard effect that is intrinsically protected against usurpation by falsebeards. An additional peculiarity of sexual greenbeard effects is that they could lead to higher rates of inbreeding [83,84], especially in structured populations, where the preference and ornament genes are rare, so inbreeding depression may pose a barrier to its evolution that is not experienced by other kinds of greenbeard gene.

(c) *Kin discrimination*

Parker [85] had already recognized that inbreeding decisions create potential for both direct and indirect effects, which can result in sex-specific selection on kin discrimination. Imagine a male that has the opportunity to increase his reproductive success by mating with a related female. Because inbreeding may result in inbreeding depression, the male would simultaneously increase his reproductive success but also reduce the reproductive success of his relative (who might otherwise have mated with an unrelated partner, thus avoiding the costs of inbreeding depression). When the female is sufficiently closely related to the male and inbreeding depression is sufficiently strong, the male will increase his inclusive fitness by altruistically foregoing his chances of mating with his relative [14,15,17]. Similarly, a female might maximize her inclusive fitness by altruistically increasing the reproductive success of a relative rather than mating with an unrelated male [14,15,17]. However, because parental investment is often higher in females than in males, the male may tolerate a greater cost of inbreeding than would the female, leading to sexual conflict over the threshold for inbreeding. As expected, when experimentally exposed to only one female at a time, male red junglefowl, *Gallus gallus*, will readily mate with their sisters. However, females will typically neutralize the sperm of their brothers following copulation [86]. Interestingly, when they are simultaneously exposed to multiple related and unrelated females, males become more discriminant and prefer unrelated partners (Løvlie & Pizzari 2012, unpublished).

(d) *Reduced sexual 'virulence' in a viscous world*

Having clarified that genetic relatedness can strongly mediate the intensity of sexual conflict, we emphasize the importance of population demography. In viscous populations, where dispersal is limited, the genetic relatedness of neighbours will differ from the population average creating potential for indirect selection on social behaviours. The realization that population

structure might have a strong influence on sexual dynamics is surprisingly recent [87,88]. However, the role of population viscosity has been extensively explored in the context of the evolution of pathogen-induced harm to its host (virulence). Here, the level of virulence is expected to change with the viscosity of the pathogen population and the mechanism underpinning harm [89]. Similar arguments can be developed to study the way population viscosity impacts on the extent to which members of opposite sex are selected to harm each other ('sexual virulence').

Recent theoretical efforts in this direction have revealed that patterns of sex-specific dispersal and the scale of competition can have a fundamental influence. In general, when sexual interactions occur on a local scale, individuals have higher potential to simultaneously help and compete with kin. Imagine, for example, a rather typical situation in which males are sexually selected to harm females (see above). When male competition is largely restricted among male relatives (e.g. male dispersal before mating is limited), sexual selection leading to female harm will be counteracted by inclusive fitness costs due to reductions in the reproductive success of male relatives caused by female harm [18,19]. Interestingly, when females mate locally they can be evolutionarily indifferent to male harm because inclusive fitness benefits and costs cancel each other out [19]. Imagine now a situation where males disperse before mating but females disperse after mating. Here, the scale of competition for males and females can change drastically. In general, we would expect females to always prefer the smallest amount of male-induced harm, and males to prefer a level of sexually selected harm inversely proportional to local relatedness [19]. The biological reality is likely to be often more complex. For example, in species where a female mates with only one out of several males in a patch and then moves on to a new patch to mate with yet another male, male competition for mating opportunities will be local but sperm competition will occur more globally. It is also likely that—just as in the case for pathogen virulence—the mechanisms through which males reduce female fitness (e.g. by shortening their life or by stimulating oviposition rates) interact with relatedness to influence selection on sexual harm.

5. CONCLUSIONS AND FUTURE DIRECTIONS

Resolving the evolutionary significance of sexual interactions is the first step towards understanding inter-sexual coevolution. Current debate over the evolutionary significance of sexual interactions is strongly polarized between those proposing that sexual selection necessarily leads to sexual conflict and those advocating that the theory of sexual selection should be rejected and replaced by a theoretical framework entrenched in cooperation. So what do we need to move the field forward? First, we do not need to replace Darwin's theory of sexual selection, as has been proposed recently [90]. This body of theory has clearly withstood the test of time as a very successful heuristic tool, providing parsimonious, adaptive explanations for a bewildering diversity of traits and

patterns, and revealing the almost universal potential for sexual conflict. However, we have argued here that direct selection alone (mediated by viability and intrasexual competition) is not always sufficient to explain the entire diversity of inter-sexual interactions, and that it is fundamental to integrate direct with indirect effects within an inclusive fitness approach to reach a fuller understanding of the evolutionary significance of such diversity. We show that this requires a clear definition of direct and indirect fitness and that, out of the two sexual selection models traditionally considered to involve indirect selection—good genes and Fisherian runaway—only the latter conforms to indirect selection as defined by inclusive fitness theory (through a greenbeard-like effect), while the former represents direct selection. This distinction transcends semantics: we argue that when both direct and indirect effects are considered and correctly measured, this enables one to detect a wider range of evolutionary outcomes of sexual interactions (conflict, cooperation, altruism and even spite), and make more sophisticated predictions about how such outcomes are modulated by specific socio-ecological factors, such as population structure, sex-biased dispersal, kin recognition and inbreeding depression.

We identify two main integrated goals for future research. First, we need to bring sexual selection and sexual conflict theory more firmly within the wider framework of social evolution. Several authors have recently lamented the gap between sexual selection and social evolution studies, despite the fact that sex is by its very nature a social trait [16,18,91]. Second, we need more emphasis on the ecological details of sexual interactions. Recent work clearly indicates that, for example, the physiological mechanisms through which males manipulate females, and the social structure of the population, can have drastic consequences on the evolutionary significance of sexual interactions, shifting from conflict to altruism or mutual benefit.

REFERENCES

1 Darwin, C. 1871 *The descent of man and selection in relation to sex*. London, UK: John Murray.
2 Trivers, R. L. 1972 Parental investment and sexual selection. In *Sexual selection and the descent of man 1871–1971* (ed. B. Campbell), pp. 136–179. Chicago, IL: Aldine.
3 Pizzari, T. & Bonduriansky, R. 2010 Sexual behaviour: conflict, cooperation and co-evolution. In *Social behaviour: genes, ecology and evolution* (eds T. Szekely, A. J. Moore & J. Komdeur), pp. 230–266. Cambridge, UK: Cambridge University Press.
4 Clutton-Brock, T. R. 2007 Sexual selection in males and females. *Science* **318**, 1882–1885. (doi:10.1126/science.1133311)
5 Bonduriansky, R. 2001 The evolution of male mate choice in insects: a synthesis of ideas and evidence. *Biol. Rev.* **76**, 305–339. (doi:10.1017/S1464793101005693)

6 Hamilton, W. D. 1964 Genetical evolution of social behaviour. I. *J. Theor. Biol.* **7**, 1–16. (doi:10.1016/0022-5193(64)90038-4J)

7 Hamilton, W. D. 1970 Selfish and spiteful behaviour in an evolutionary model. *Nature* **228**, 1218–1220. (doi:10.1038/2281218a0)

8 Grafen, A. 2006 Optimization of inclusive fitness. *J. Theor. Biol.* **238**, 541–563. (doi:10.1016/j.jtbi.2005.06.009)

9 Hamilton, W. D. 1963 The evolution of altruistic behavior. *Am. Nat.* **97**, 354–356. (doi:10.1086/497114)

10 Gardner, A., West, S. A. & Wild, G. 2011 The genetical theory of kin selection. *J. Evol. Biol.* **24**, 1020–1043. (doi:10.1111/j.1420-9101.2011.02236.x)

11 Grafen, A. 2002 A first formal link between the Price equation and an optimization program. *J. Theor. Biol.* **217**, 75–91. (doi:10.1006/jtbi.2002.3015)

12 Grafen, A. 2009 Formalizing Darwinism and inclusive fitness theory. *Phil. Trans. R. Soc. B* **364**, 3135–3141. (doi:10.1098/rstb.2009.0056)

13 Gardner, A. 2009 Adaptation as organism design. *Biol. Lett.* **5**, 861–864. (doi:10.1098/rsbl.2009.0674)

14 Kokko, H. & Ots, I. 2006 When not to avoid inbreeding. *Evolution* **60**, 467–475. (doi:10.1111/j.0014-3820.2006.tb01128.x)

15 Parker, G. A. 2006 Sexual conflict over mating and fertilization: an overview. *Phil. Trans. R. Soc. B* **361**, 235–259. (doi:10.1098/rstb.2005.1785)

16 Boomsma, J. J. 2007 Kin selection versus sexual selection: why the ends do not meet. *Curr. Biol.* **7**, R673–R683. (doi:10.1016/j.cub.2007.06.033)

17 Puurtinen, M. 2011 Mate choice for optimal (k)inbreeding. *Evolution* **65**, 1501–1505. (doi:10.1111/j.1558-5646.2010.01217.x)

18 Rankin, D. J. 2011 Kin selection and the evolution of sexual conflict. *J. Evol. Biol.* **24**, 71–81. (doi:10.1111/j.1420-9101.2010.02143.x)

19 Wild, G., Pizzari, T. & West, S. A. 2011 Sexual conflict in viscous populations: the effect of the timing of dispersal. *Theor. Popul. Biol.* **80**, 298–316. (doi:10.1016/j.tpb.2011.09.002)

20 West, S. A., Griffin, A. S. & Gardner, A. 2007 Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *J. Evol. Biol.* **20**, 415–432. (doi:10.1111/j.1420-9101.2006.01258.x)

21 West, S. A., Griffin, A. S. & Gardner, A. 2007 Evolutionary explanations for cooperation. *Curr. Biol.* **17**, R661–R672. (doi:10.1016/j.cub.2007.06.004)

22 Arnqvist, G. & Rowe, L. 2005 *Sexual conflict.* Princeton, NJ: Princeton University Press.

23 Andersson, M. & Simmons, L. W. 2006 Sexual selection and mate choice. *Trends Ecol. Evol.* **21**, 296–302. (doi:10.1016/j.tree.2006.03.015)

24 Eberhard, W. G. & Cordero, C. 2003 Female choice of sexually antagonistic male adaptations: a critical review of some current research. *J. Evol. Biol.* **16**, 1–6. (doi:10.1046/j.1420-9101.2003.00506.x)

25 Pizzari, T. & Snook, R. R. 2003 Perspective: sexual conflict and sexual selection: chasing away paradigm shifts. *Evolution* **57**, 1223–1236. (doi:10.1554/02-517)

26 Cameron, E., Day, T. & Rowe, L. 2003 Sexual conflict and indirect benefits. *J. Evol. Biol.* **16**, 1055–1060. (doi:10.1046/j.1420-9101.2003.00584.x)

27 Kokko, H. 2001 Fisherian and 'good genes' benefits of mate choice: how (not) to distinguish between them. *Ecol. Lett.* **4**, 322–326. (doi:10.1046/j.1461-0248.2001.00224.x)

28 Prum, R. O. 2010 The Lande–Kirkpatrick mechanism is the null model of evolution by intersexual selection: implications for meaning, honesty, and design in intersexual signals. *Evolution* **64**, 3085–3100. (doi:10.1111/j.1558-5646.2010.01054.x)

29 Hardin, G. 1968 Tragedy of the commons. *Science* **162**, 1243–1248. (doi:10.1126/science.162.3859.1243)

30 Frank, S. A. 1998 *Foundations of social evolution.* Princeton, NJ: Princeton University Press.

31 Rankin, D. J., Dieckmann, U. & Kokko, H. 2011 Sexual conflict and the tragedy of the commons. *Am. Nat.* **177**, 780–791. (doi:10.1007/s10886-007-9393-z)

32 Le Galliard, J. F., Fitze, P. S., Ferriere, R. & Clobert, J. 2005 Sex ratio bias, male aggression, and population collapse in lizards. *Proc. Natl Acad. Sci. USA* **102**, 18 231–18 236. (doi:10.1073/pnas.0505172102)

33 Wigby, S., Sirot, L. K., Linklater, J. R., Buehner, N., Calboli, F. C. F., Bretman, A., Wolfner, M. F. & Chapman, T. 2009 Seminal fluid protein allocation and male reproductive success. *Curr. Biol.* **19**, 751–757. (doi:10.1016/j.cub.2009.03.036)

34 Wigby, S. & Chapman, T. 2004 Female resistance to male harm evolves in response to manipulation of sexual conflict. *Evolution* **58**, 1028–1037. (doi:10.1554/03-568)

35 Wigby, S. & Chapman, T. 2005 Sex peptide causes mating costs in female *Drosophila melanogaster. Curr. Biol.* **15**, 316–321. (doi:10.1016/j.cub.2005.01.051)

36 Crudgington, H. S. & Siva-Jothy, M. T. 2000 Genital damage, kicking and early death—the battle of the sexes takes a sinister turn in the bean weevil. *Nature* **407**, 855–856. (doi:10.1038/35038154)

37 Hotzy, C. & Arnqvist, G. 2009 Sperm competition favors harmful males in seed beetles. *Curr. Biol.* **19**, 404–407. (doi:10.1016/j.cub.2009.01.045)

38 Baeza, J. A. 2008 Social monogamy in the shrimp *Pontonia margarita*, a symbiont of *Pinctada mazatlanica*, off the Pacific coast of Panama. *Mar. Biol.* **153**, 387–395. (doi:10.1007/s00227-007-0815-9)

39 Alonzo, S. H. & Pizzari, T. 2010 Male fecundity stimulation: conflict and cooperation within and between the sexes: model analyses and coevolutionary dynamics. *Am. Nat.* **175**, 174–185. (doi:10.1086/649596)

40 Stutt, A. D. & Siva-Jothy, M. T. 2001 Traumatic insemination and sexual conflict in the bed bug *Cimex lectularius. Proc. Natl Acad. Sci. USA* **98**, 5683–5687. (doi:10.1073/pnas.101440698)

41 Parker, G. A. & Pizzari, T. 2010 Sperm competition and ejaculate economics. *Biol. Rev.* **85**, 897–934. (doi:10.1111/j.1469-185X.2010.00140.x)

42 Snook, R. R., Hosken, D. J. & Karr, T. L. 2011 The biology and evolution of polyspermy: insights from cellular and functional studies of sperm and centrosomal behaviour in the fertilized egg. *Reproduction* **142**, 779–792. (doi:10.1530/REP-11-0255)

43 Maynard Smith, J. & Szathmary, E. 1995 *The major transitions in evolution.* Oxford, UK: Oxford University Press.

44 Queller, D. C. 2000 Relatedness and the fraternal major transitions. *Phil. Trans. R. Soc. Lond. B* **355**, 1647–1655. (doi:10.1098/rstb.2000.0727)

45 Gardner, A. & Grafen, A. 2009 Capturing the superorganism: a formal theory of group adaptation. *J. Evol. Biol.* **22**, 659–671. (doi:10.1111/j.1420-9101.2008.01681.x)

46 Bourke, A. F. G. 2011 *Principles of social evolution.* Oxford, UK: Oxford University Press.

47 Hughes, W. O. H., Oldroyd, B. J., Beekman, M. & Ratnieks, F. L. W. 2008 Ancestral monogamy shows kin selection is key to the evolution of eusociality. *Science* **320**, 1213–1216. (doi:10.1126/science.1156108)

48 Boomsma, J. J. 2009 Lifetime monogamy and the evolution of eusociality. *Phil. Trans. R. Soc. B* **364**, 3191–3207. (doi:10.1098/rstb.2009.0101)

49 Hardling, R., Gosden, T. & Robin, A. 2008 Male mating constraints affect mutual mate choice: prudent male courting and sperm-limited females. *Am. Nat.* **172**, 259–271. (doi:10.1086/589452)

50 Elgar, M. A. & Schneider, J. M. 2004 Evolutionary significance of sexual cannibalism. *Adv. Study Behav.* **34**, 135–163. (doi:10.1016/S0065-3454(04)34004-0)

51 Andrade, M. C. B. 2003 Risky mate search and male self-sacrifice in redback spiders. *Behav. Ecol.* **14**, 531–538. (doi:10.1093/beheco/arg015)

52 Fromhage, L., Elgar, M. A. & Schneider, J. M. 2005 Faithful without care: the evolution of monogyny. *Evolution* **59**, 1400–1405. (doi:10.1554/04-680)

53 Andrade, M. C. B. 1996 Sexual selection for male sacrifice in the Australian redback spider. *Science* **271**, 70–72. (doi:10.1126/science.271.5245.70)

54 Andrade, M. C. B. & Banta, E. M. 2002 Value of male remating and functional sterility in redback spiders. *Anim. Behav.* **63**, 857–870. (doi:10.1006/anbe.2002.2003)

55 Hansen, L. S., Gonzalez, S. F., Toft, S. & Bilde, T. 2008 Thanatosis as an adaptive male mating strategy in the nuptial gift-giving spider *Pisaura mirabilis. Behav. Ecol.* **19**, 546–551. (doi:10.1093/beheco/arm165)

56 Johnson, J. C., Trubl, P., Blackmore, V. & Miles, L. 2011 Male black widows court well-fed females more than starved females: silken cues indicate sexual cannibalism risk. *Anim. Behav.* **82**, 383–390. (doi:10.1016/j.anbehav.2011.05.018)

57 Davies, N. B. 1992 *Dunnock behaviour and social evolution.* Oxford, UK: Oxford University Press.

58 Hunter, F. M. & Davis, L. S. 1998 Female Adelie penguins acquire nest material from extrapair males after engaging in extrapair copulations. *Auk* **115**, 526–528.

59 Axelrod, R. & Hamilton, W. D. 1981 The evolution of cooperation. *Science* **211**, 1390–1396. (doi:10.1126/science.7466396)

60 Koene, I. M. 2006 Tales of two snails: sexual selection and sexual conflict in *Lymnaea stagnalis* and *Helix aspersa. Int. Comp. Biol.* **46**, 419–429. (doi:10.1093/icb/icj040)

61 Michiels, N. K. 1998 Mating conflicts and sperm competition in simultaneous hermaphrodites. In *Sperm competition and sexual selection* (eds T. R. Birkhead & A. P. Møller), pp. 219–254. London, UK: Academic Press.

62 Scharer, L., Littlewood, D. T. J., Waeschenbach, A., Yoshida, W. & Vizoso, D. B. 2011 Mating behavior and the evolution of sperm design. *Proc. Natl Acad. Sci. USA* **108**, 1490–1495. (doi:10.1073/pnas.1013892108)

63 Leonard, J. L. & Pearse, J. S. 2001 Sex in banana slugs: different clades do different things. *Am. Zool.* **41**, 1504.

64 Clutton-Brock, T. H. & Parker, G. A. 1995 Sexual coercion in animal societies. *Anim. Behav.* **49**, 1345–1365. (doi:10.1006/anbe.1995.0166)

65 Clutton-Brock, T. H. & Parker, G. A. 1995 Punishment in animal societies. *Nature* **373**, 209–216. (doi:10.1038/373209a0)

66 Barash, D. P. 1976 Male response to apparent female adultery in mountain bluebird (*Sialia currucoides*). Evolutionary interpretation. *Am. Nat.* **110**, 1097–1101. (doi:10.1086/283129)

67 Valera, F., Hoi, H. & Kristin, A. 2003 Male shrikes punish unfaithful females. *Behav. Ecol.* **14**, 403–408. (doi:10.1093/beheco/14.3.403)

68 Shellman-Reeve, J. S. 1999 Courting strategies and conflicts in a monogamous, biparental termite. *Proc. R. Soc. Lond. B* **266**, 137–144. (doi:10.1098/rspb.1999.0613)

69 Johnstone, R. A. & Keller, L. 2000 How males can gain by harming their mates: sexual conflict, seminal toxins, and the cost of mating. *Am. Nat.* **156**, 368–377. (doi:10.1086/303392)

70 Lessells, C. M. 2005 Why are males bad for females? Models for the evolution of damaging male mating behaviour. *Am. Nat.* **165**, S46–S63. (doi:10.1086/429356)

71 Grafen, A. 1985 A geometric view of relatedness. *Oxf. Surv. Evol. Biol.* **2**, 28–90.

72 Queller, D. C. 1994 Genetic relatedness in viscous populations. *Evol. Ecol.* **8**, 70–73. (doi:10.1007/BF01237667)

73 Gardner, A. & West, S. A. 2004 Spite and the scale of competition. *J. Evol. Biol.* **17**, 1195–1203. (doi:10.1111/j.1420-9101.2004.00775.x)

74 Gardner, A., Hardy, I. C. W., Taylor, P. D. & West, S. A. 2007 Spiteful soldiers and sex ratio conflict in polyembryonic parasitoid wasps. *Am. Nat.* **169**, 519–533. (doi:10.1086/512107)

75 West, S. A. & Gardner, A. 2010 Altruism, spite and greenbeards. *Science* **327**, 1341–1344. (doi:10.1126/science.1178332)

76 Ala-Honkola, O., Friman, E. & Lindström, K. 2011 Costs and benefits of polyandry in a placental poeciliid fish *Heterandria formosa* are in accordance with the parent–offspring conflict theory of placentation. *J. Evol. Biol.* **24**, 2600–2610. (doi:10.1111/j.1420-9101.2011.02383.x)

77 Dagg, J. L. 2006 Could sex be maintained through harmful males? *Oikos* **112**, 232–235. (doi:10.1111/j.0030-1299.2006.14196.x)

78 Rankin, D. J. 2008 Can punishment maintain sex? *Oikos* **117**, 173–176. (doi:10.1111/j.2007.0030-1299.16271.x)

79 Frank, S. A. 1997 Cytoplasmic incompatibility and population structure. *J. Theor. Biol.* **184**, 327–330. (doi:10.1006/jtbi.1996.0276)

80 Haygood, R. & Turelli, M. 2009 Evolution of incompatibility-inducing microbes in subdivided host populations. *Evolution* **63**, 432–447. (doi:10.1111/j.1558-5646.2008.00550.x)

81 Gardner, A. & West, S. A. 2010 Greenbeards. *Evolution* **64**, 25–38. (doi:10.1111/j.1558-5646.2009.00842.x)

82 Kirkpatrick, M. & Barton, N. H. 1997 The strength of indirect selection on female mating preferences. *Proc. Natl Acad. Sci. USA* **94**, 1282–1286. (doi:10.1073/pnas.94.4.1282)

83 Fromhage, L., Reid, J. M. & Kokko, H. 2009 Evolution of mate choice for genome-wide heterozygosity. *Evolution* **63**, 684–694. (doi:10.1111/j.1558-5646.2008.00575.x)

84 Aparicio, J. M. 2011 The paradox of the resolution of the lek paradox based on mate choice for heterozygosity. *Anim. Behav.* **81**, 1271–1279. (doi:10.1016/j.anbehav.2011.03.017)

85 Parker, G. A. 1979 Sexual selection and sexual conflict. In *Sexual selection and reproductive competition in insects* (eds M. S. Blum & N. A. Blum), pp. 123–166. New York, NY: Academic Press.

86 Pizzari, T., Løvlie, H. & Cornwallis, C. K. 2004 Sex-specific, counteracting responses to inbreeding in a bird. *Proc. R. Soc. Lond. B* **271**, 2115–2121. (doi:10.1098/rspb.2004.2843)

87 Eldakar, O. T., Dlugos, M. J., Pepper, J. W. & Wilson, D. S. 2009 Population structure mediates sexual conflict in water striders. *Science* **326**, 816. (doi:10.1126/science.1180183)

88 Oh, K. P. & Badyaev, A. V. 2010 Structure of social networks in a passerine bird: consequences for sexual selection and the evolution of mating strategies. *Am. Nat.* **176**, E80–E89. (doi:10.1086/655216)

89 Buckling, A. & Brockhurst, M. A. 2008 Kin selection and the evolution of virulence. *Heredity* **100**, 484–488. (doi:10.1038/sj.hdy.6801093)

90 Roughgarden, J., Oishi, M. & Akçay, E. 2006 Reproductive social behavior: cooperative games to replace sexual selection. *Science* **311**, 965–969. (doi:10.1126/science.1110105)

91 Pizzari, T. & Foster, K. R. 2008 Sperm sociality: cooperation, altruism, and spite. *PLoS Biol.* **6**, e130. (doi:10.1371/journal.pbio.0060130)