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Review

Family feuds: social competition and sexual conflict in complex societies

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Darwin was initially puzzled by the processes that led to ornamentation in males—what he termed sexual selection—and those that led to extreme cooperation and altruism in complex animal societies—what was later termed kin selection. Here, I explore the relationships between sexual and kin selection theory by examining how social competition for reproductive opportunities—particularly in females—and sexual conflict over mating partners are inherent and critical parts of complex altruistic societies. I argue that (i) patterns of reproductive sharing within complex societies can drive levels of social competition and reproductive conflict not only in males but also in females living in social groups, and ultimately the evolution of female traits such as ornaments and armaments; (ii) mating conflict over female choice of sexual partners can influence kin structure within groups and drive the evolution of complex societies; and (iii) patterns of reproductive sharing and conflict among females may also drive the evolution of complex societies by influencing kin structure within groups. Ultimately, complex societies exhibiting altruistic behaviour appear to have only arisen in taxa where social competition over reproductive opportunities and sexual conflict over mating partners were low. Once such societies evolved, there were important selective feedbacks on traits used to regulate and mediate intra-sexual competition over reproductive opportunities, particularly in females.

Keywords: kin selection; sexual selection; social selection; sexual conflict; reproductive conflict; mating conflict

1. INTRODUCTION

The presence of elaborate ornaments (i.e. traits used for mate attraction) and armaments (i.e. traits used in competitive interactions) in males of many species has long intrigued biologists. Darwin provided the first explanation for these complex male traits when he coined the term 'sexual selection' [1,2]. According to Darwin's view, sexual selection was primarily a contest within the sexually selected sex, usually males in most species [3]. Sexual selection, or intra-sexual competition for mates, can take two forms: (i) male–male combat and threat; and (ii) male courtship of females that can result in female choice of mates. Although most early biologists, including Darwin, viewed this intra-sexual selection (i.e. social competition) as a clear example of social conflict over reproduction, the traditional view of reproduction between the sexes (i.e. female choice) was historically one of harmony and cooperation [2]. Later, however, it became apparent that the interests of males and females are often not aligned, as inter-sexual selection (i.e. sexual conflict) can also include cases of sexual and social conflict between males and females over reproduction [4–7]. It is now generally accepted that male and female genetic interests are rarely aligned, and that the resulting conflict over mating opportunities can, in many species, lead to an evolutionary arms race between the sexes [6]. Thus, competition and conflict within and between the sexes play an important role in sexual selection and reproduction in general. Understanding the causes and consequences of this social competition and sexual conflict is important for determining not only how morphological traits such as ornaments and armaments develop, but also how other types of behavioural traits evolve, including complex social behaviour.

Although social competition is typically emphasized in males [3], female–female competition is common in many species [3,8–10]. Moreover, female–female competition occurs commonly not only around reproduction, but also in a variety of other social contexts [11–13]. In other words, females do not always fight with other females for direct access to mates. Instead they often compete over traits such as social rank, territories, breeding sites or other resources, which may or may not be indirectly related to reproduction [12–15]. Social competition among females for mates, social rank or other resources—termed social selection [14–16]—is clearly important in many species of insects, birds, non-primate mammals and other mammals [9,13,15,17], including humans [11]. Although not as well studied as social competition in males [18], competition in females in both reproductive and non-reproductive contexts may be

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One contribution of 11 to a Theme Issue 'Sexual selection, social conflict and the female perspective'.

important for the evolution of female ornaments and armaments [19], particularly for species living in groups [14,15,19].

Breeding is sufficiently costly in some species that successful reproduction requires parental cooperation in rearing offspring [20]. For example, in many socially monogamous birds, males and females form a pair-bond and remain together throughout the breeding season because both sexes are required to successfully care for and raise young [21]. In other species where raising offspring is even more costly, more than two individuals are sometimes needed to cooperatively care for young. Eusociality in insects represents the most extreme form of reproductive cooperation, with up to millions of workers forgoing reproduction to help raise offspring of a queen or a groups of queens [22,23]. Although eusocial insect colonies are unlikely to form solely because of the costs of rearing offspring, cooperative care of young—along with reproductive division of labour and overlapping generations—is a defining characteristic of these complex altruistic societies [22]. Workers are typically related to the queens and are essential to colony growth and survival. Similarly, cooperatively breeding societies represent the most extreme example of reproductive cooperation in vertebrates. Cooperatively breeding groups are defined as those in which some individuals forgo independent breeding to help raise others' offspring [24,25]. In most, but not all, cooperatively breeding species, the non-breeding helpers are related to at least one of the breeding individuals in a group. Helpers aid in feeding young and protecting them from predators, and in many species the presence of helpers increases the fitness of the breeders [26].

Although cooperation is the critical feature that defines all complex altruistic societies, reproductive conflict, which can be defined as conflict between same-sex individuals over breeding opportunities and the resources essential for reproduction, is also inherent in any group of genetically different entities [27–30]. Inclusive fitness theory has shown that potential conflict over reproduction is a key influence on the dynamics of most social animals [31]. Much of the empirical work on reproductive conflict in social species has been conducted in Hymenoptera (ants, bees and wasps) [28,32–35] and in vertebrates [36–39]. In vertebrates, where all individuals in a group are totipotent and able to reproduce throughout their lives, there is often intense competition over direct reproductive opportunities. Even in cases where mates are limiting and some individuals are therefore effectively sterile, reproductive conflict over limited breeding positions may still be quite intense. In some social polygynous Hymenoptera, female queens compete for reproductive opportunities as intensively as breeders in many social vertebrate species [30]. Moreover, although workers are unmated in most species of Hymenoptera and thus lack the ability to reproduce sexually (i.e. produce diploid females), they can still produce infertile eggs that become haploid males. Reproductive conflict in Hymenoptera therefore can also arise from competition among workers (or among queens and workers) to produce male eggs or in some cases to develop mature ovaries, and results in workers often 'policing' other workers' reproductive behaviours [28,30,33,34]. Thus, reproductive conflict over who gets to breed in a group occurs in most social species and can take a variety of forms [28,30].

In addition to social competition and reproductive conflict over breeding opportunities, sexual conflict over mating decisions also occurs frequently in social societies. In particular, mating conflict, which can be defined as conflict over who a female mates with, can occur in both insect and vertebrate societies [40,41]. Mating conflict differs from reproductive conflict in that the former describes how reproductive success is limited by access to specific mates, whereas the latter describes the ability of an individual to reproduce at all. In vertebrates, mating conflict is almost exclusively between males and females, but in many social insects, such as all Hymenoptera, because males and females do not often form pair-bonds, mating conflict over polyandrous matings typically occurs between female workers and queens [28]. It is worth reiterating that this form of intra-sexual mating conflict over choice of queen mating partners is quite different from the intra-sexual competitive reproductive conflict over worker reproductive options described above [28]. Reproductive conflict describes disagreement over the opportunity to breed at all, whereas mating conflict describes disagreement over who to mate with. Although recent evidence suggests that mating conflict may be lower in social than non-social species [42], the opportunity for females to mate multiply may greatly influence the evolution of sociality (i.e. formation of complex altruistic societies) because it dictates patterns of genetic relatedness within groups [40,43–45].

Both the processes that lead to ornamentation in males—sexual selection—and those that contribute to the formation of complex altruistic societies—what was later termed kin selection by Maynard Smith [46]—puzzled even Darwin [1,2]. For decades, these two domains of behavioural ecology have largely been separated (but see earlier studies [14,15,40,43]), and yet many of the underlying concepts such as reproductive sharing, cooperation and conflict are central to both. Here, I explore the relationships between sexual, social and kin selection theory by examining how social competition for reproductive opportunities and sexual conflict over mating partners are inherent and significant parts of complex altruistic societies. This conflict has important consequences for species living in social groups, and it may even have played a central role in the formation of those societies in the first place (figure 1). First, I discuss how intense social competition and reproductive conflict in both sexes, a hallmark of social species, may lead to atypical patterns of trait evolution, particularly in females. Second, I examine how reduced mating conflict in social species may be a critical driver of social evolution by influencing kin structure within groups. Third, I explore the idea that social competition, reproductive conflict and pattern of reproductive sharing among same-sex individuals could also play a central role in the evolution of complex societies. Ultimately, this review will provide a link between sexual, social and kin selection theory

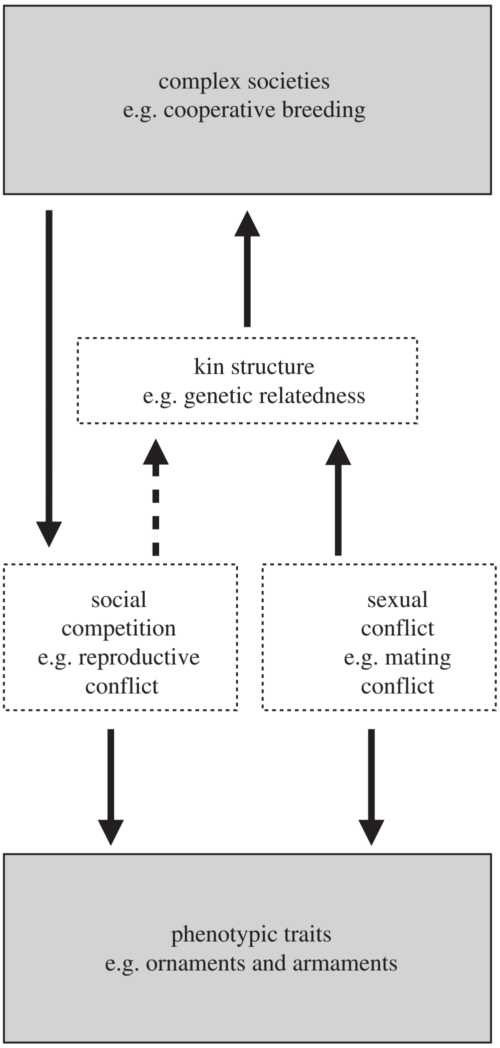

Figure 1. A diagram of the relationships between complex altruistic societies, social competition, sexual conflict, and phenotypic trait elaboration. Comparative work in African starlings suggests that living in cooperative breeding groups leads to unusually high levels of intra-sexual competition among females (i.e. reproductive conflict), which can result in the elaboration of female phenotypic traits [19]. Additionally, comparative work in birds [42] and insects [45] suggests that sexual conflict over female mating patterns (i.e. mating conflict) may have influenced the evolution of cooperative breeding behaviour and eusociality by driving kin structure within groups. Finally, although there have been few studies of how reproductive conflict over breeding opportunities might influence the formation of complex societies, theory suggests it may be an important and understudied avenue of social evolution.

and shed new light on the roles (i) that social-living plays in trait evolution and (ii) that social competition and sexual conflict play in the evolution and maintenance of sociality.

2. SOCIAL COMPETITION AND THE EVOLUTION OF ORNAMENTS AND ARMAMENTS IN COMPLEX SOCIETIES

Sociality is widespread in the animal kingdom and observed in numerous birds [24], mammals [47], insects [22,23] and other invertebrates [48,49]. Because the concept of family is central to social evolution, sociality is often defined as family-living, or group-living with kin structure [50]. Kin selection, or reproductive strategies that favour an organism's relatives, has come to form the basis of our understanding of cooperation and the formation of complex altruistic societies characterized by relatives [50–55] (but see earlier studies [56,57]). Although genetic relatedness alone is unlikely to lead to the evolution of complex altruistic societies, as demonstrated theoretically by Hamilton [51] and shown empirically in numerous species [58], it is clearly a central concept in the evolution of altruism and social complexity.

Genetic relatedness among group members, however, not only may influence whether cooperation arises among individuals and stable social groups form, but also it can drive levels of social competition and sexual conflict within groups [59,60]. Numerous theoretical [61–64] and empirical [65,66] studies have examined how relatedness among group members influences conflict and reproduction in addition to group formation. In general, competition among relatives can reduce the kin-selected benefits of cooperation [59], and low within-group conflict may therefore be necessary for complex societies to form [64].

Although insect societies are often described as being more complex than those of vertebrates [22,67], they range in complexity from simple (i.e. primitive) to complex (i.e. advanced) [27,68]. Similarly, cooperatively breeding systems in vertebrates are equally variable, also ranging in structure from simple (i.e. single breeding pair per group) to complex (i.e. multiple breeding pairs per group) [24,69] (figure 2). The simplest type of cooperatively breeding society is called singular breeding. Singular breeding groups consist of a single breeding pair and a variable number of non-breeding auxiliaries, or helpers [24,69]. Because helpers are often related to one or both members of the breeding pair, reproductive conflict in singular breeders may be relatively low because most breeding options for helpers would therefore result in inbreeding. Plural breeding societies, on the other hand, are typically more complex than singular breeding societies. These extended family groups are characterized by more than one breeder of at least one sex, which typically means multiple breeding pairs in most vertebrates, and a variable number of helpers [50]. Because reproductive opportunities for subordinate individuals are greater in plural breeding groups than they are in those of singular breeders, since options to mate with unrelated individuals from within the group exist, reproductive conflict is generally higher in plural breeders. In both singular and plural breeding societies, however, one or a few individuals of each sex monopolize reproduction and many individuals in the group do not breed. This low reproductive sharing, or high reproductive skew, is the defining characteristic of most complex altruistic societies [70].

Reproductive skew, or the unequal division of reproduction, that defines complex altruistic societies across disparate taxa [70], is also central to the concept of sexual selection. High reproductive skew, be it in a social group or the broader population, results in a high variance in reproductive success because a few individuals of one sex monopolize most of the

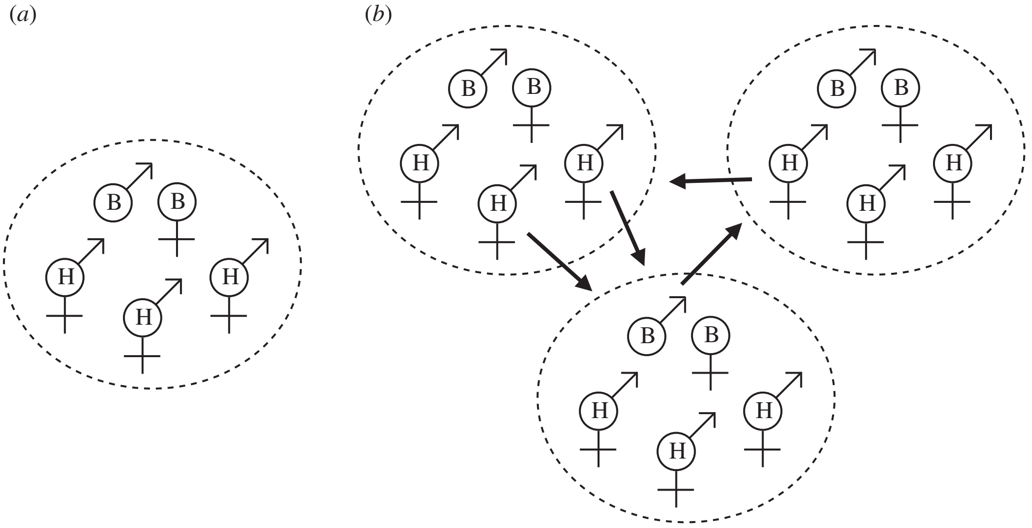

Figure 2. A diagram of typical (*a*) simple (i.e. singular breeding) and (*b*) complex (i.e. plural breeding) vertebrate social systems. Singular breeding systems are characterized by a single breeding pair (i.e. simple family unit), whereas plural breeding systems are typically characterized by multiple breeding pairs (i.e. extended family unit) [24,50]. Helpers are most often offspring of the breeding pair, and in birds they are typically male, whereas in mammals they are usually female (indicated by the male and female helper symbols). Because helpers are often related to one or both members of the breeding pair in singular breeding groups, reproductive conflict may be relatively low in these groups. In contrast, because reproductive opportunities for subordinate individuals within the group are greater in plural breeding species than they are in those of singular breeders, reproductive conflict is generally higher in plural breeders. Breeding pairs in plural breeding groups may breed jointly in the same structure, or separately in different breeding structures. Helpers in these groups may help multiple pairs simultaneously, and in some species breeders may also aid other breeding pairs. Help includes not only feeding young, but also providing defence from predators, conspecifics or heterospecifics.

reproduction, whereas most other individuals of that sex gain no reproductive success. Classic sexual selection theory predicts that selection on traits that enhance reproductive opportunities or access to mates and other resources should be stronger in the sex with the higher variance in reproductive success [3]. In other words, because only a few individuals of each sex will gain any reproductive success, selection should operate strongly on traits that help individuals improve their chances of gaining a reproductive share. In most species, males have a higher variance in reproductive success than females because they have more to gain from mating multiply than do females [71], thus resulting in stronger selection on male ornaments and armaments used for competition or mate attraction [72,73]. Because, in most species, females are likely to gain higher fitness from investing more resources in young rather than competing for additional mates [71], sexual selection is unlikely to act as strongly on female armaments or ornaments as those of males (though social selection could still act more strongly on females in some cases [13]). Thus, the elaborate, sexually selected traits observed in males of many species, as well as the resulting extreme sexual dimorphism between male and female traits, are ultimately the result of greater reproductive competition in males than in females.

The typical patterns of higher male than female variance in reproductive success and extreme sexual dimorphism in trait elaboration seen in most non-social vertebrates are reversed in many social species, as females often have a higher variance in reproductive success than males [74], and males and females often have equally elaborated traits [19]. In cooperatively breeding systems where not all individuals are able to breed, competition for reproductive opportunities, and thus ultimately reproductive skew, is high in both sexes [29]. Because non-socially paired males have the option to reproduce via extra-pair matings but females in most species generally do not, females tend to have higher variance in reproductive success than males in cooperatively breeding species [74]. Although the relationships among reproductive skew, reproductive variance and trait elaboration are similar in social and non-social species, there are some important differences in how skew and variance in reproductive success is measured in time and space in the two groups of species. First, reproductive variance in classic sexual selection theory—which is typically applied to non-social species—is based on lifetime fitness measures (though it is rarely quantified this way) [72], whereas in social species, variance in reproductive success is typically measured across individuals of different social ranks in a given breeding period [74]. However, because there is also likely to be high skew in lifetime reproductive success in cooperative breeders [75], this difference in the period over which variance in reproduction is measured may not ultimately matter (unless the variance is due simply to age, i.e. young individuals always help, whereas old individuals always breed). Second, reproductive skew in non-social species is measured across a population, whereas in social species it is measured within a social group. Again, however, this is unlikely to matter as scaling up across social groups within a population should still result in a pattern of high skew at the population level. Thus, the concepts of reproductive skew and reproductive variance are important for understanding selection on ornaments and armaments

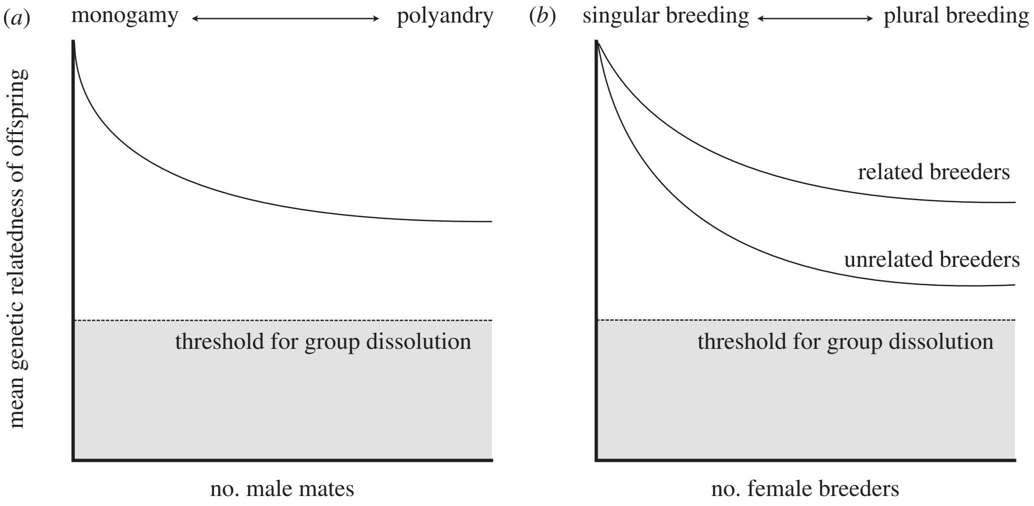

Figure 3. Relationship between the mean genetic relatedness of offspring and (*a*) the number of mates a single female breeds with as well as (*b*) the number of female breeders in a group. As the number of mates increases (a continuum from genetic monogamy to polyandry/promiscuity) and the number of breeders in a group increases (a continuum from singular to plural breeding), the relatedness of offspring will decrease. Relatedness of offspring will be higher when co-breeders are related than when they are unrelated. Below a certain threshold of genetic relatedness, groups should dissolve (given some value of direct or material benefits). This threshold will vary among species and will probably be related to ecological factors and other external constraints on group formation.

in both social and non-social species even if they are quantified differently in time and space in the two groups. One key emerging concept that differs between social and non-social species, however, is that competition for reproductive opportunities is likely to be high in both sexes in social species [19], and therefore females in these species will often have a higher variance in reproductive success than males [74].

High intra-sexual competition in both sexes has important implications for the evolution of phenotypic traits in social species [76] because selection should therefore act strongly on both sexes, and not just on males [19]. A comparative analysis of African starlings showed that there was reduced sexual dimorphism in plumage colouration and body size in cooperatively breeding compared to non-cooperatively breeding species [19]. Furthermore, this reduced dimorphism in social species was due to increased selection on female traits that were likely used in intra-sexual competition for breeding opportunities or social rank. In particular, the high reproductive skew that defines social groups leads to intra-sexual competition in both males and females, higher variance in reproductive success in females, and ultimately selection on ornaments and armaments in both sexes. Intense female–female competition is not unique to cooperatively breeding birds. Females in many social mammals also compete with same-sex individuals for access to reproductive opportunities [9,13] or resources [17]. This competition can influence morphology, physiology and behaviour [76], sometimes in radical ways. For example, in the spotted hyena, extreme female–female competition for dominance rank and resources is likely to have led to their unique masculinized morphological and physiological adaptations [77]. Female–female competition is also a hallmark of many social insect societies, particularly in Hymenoptera [28,30,34], and can result in morphological differences between individuals of different castes [68]. It is important to point out, however, that males and females could be using the same trait to signal similar information (e.g. territorial defence signals in males and females [78]) or different information (e.g. mate choice intra-sexual signal in males versus competitive signals in females [79]), as has been in shown in a variety of non-social species. Alternatively, males and females in social species could be using different traits in the same signalling context (e.g. to establish or maintain social rank). Future research in social species should examine the function of both monomorphic and dimorphic traits used by males and females in sexual and non-sexual signalling contexts.

3. MATING CONFLICT AS A DRIVER OF SOCIAL EVOLUTION

Complex altruistic societies are thought to form in many species because the inclusive fitness benefits of cooperating with relatives outweigh the costs of trying to breed independently [46,52]. That is, when genetic relatedness among potential group members is high, the potential inclusive fitness benefits may select for group formation. Moreover, a key means of reinforcing kin structure and maintaining high relatedness among group members—and reducing mating conflict—is through genetic monogamy and long-term pair-bonds [40,44]. This is because as the number of males a female mates with increases, the genetic relatedness among her offspring declines (figure 3*a*). Yet, at the individual level, it is often advantageous for both sexes to mate with multiple partners [80]. This sets up a tension between the cohesive influence of relatedness and the dissolutive influence of polyandry/promiscuity on group dynamics [68]. Thus, conflict over mating and preferences for females to mate multiply may be at odds with group formation, and for sociality to evolve, mating conflict within groups may need to be low to ensure high relatedness among group members [40,44].

The relationship between mating conflict and sociality has been studied in both social insects and vertebrates. Although monogamy is extremely common in the most socially diverse group of insects, the Hymenoptera, multiple mating by females (i.e. polyandry) occurs [80–82]. A variety of benefits relating to the increased genetic diversity from females mating with multiple males have been proposed for social insects [83–85]. The resulting mating conflict over these polyandrous matings typically occurs between female workers and queens in most Hymenoptera species [28]. However, in most social vertebrates—particularly birds—where females commonly have opportunities to mate multiply via polyandry or extra-pair matings, conflict over mating opportunities occurs between breeding partners (i.e. sexual conflict) [41]. Females in cooperatively breeding systems have a range of mating options inside and outside of a pair-bond (e.g. pure social and genetic monogamy in Florida scrub-jays [86], polygyny in acorn woodpeckers [87] or extreme infidelity in superb fairy wrens [88]). As in insects, there are a number of potential direct and indirect benefits to mating multiply in vertebrates [89]. Thus, conflict over the number of mates that a female has occurs commonly in both social vertebrates and invertebrates and may be relevant to understanding social evolution.

Monogamy, which results in low mating conflict, has been argued to be critical to the evolution of eusociality in insects because it generates the high kin structure necessary for cooperation among relatives to form [40,44]. Monogamy's role in social evolution was studied comparatively in 267 species of eusocial ants, bees and wasps [45]. Not only was monogamy found to be ancestral for all eusocial lineages, but polyandry (i.e. multiple mating by females) was observed only in lineages whose workers had lost the ability to reproduce [45]. Together, these results suggest that monogamy and low re-mating frequencies were critical in the evolution of eusociality, presumably by maintaining high genetic relatedness among group members.

The role of female mating behaviour in social evolution in vertebrates has not been studied to the same degree that it has in insects. Furthermore, the general relationships between eusociality in insects and cooperative breeding in vertebrates has long been debated. While some have suggested that social vertebrates and insects share many similar traits [90–93], others have argued that eusocial insects are fundamentally different from social vertebrates because most group members are physiologically incapable of producing (diploid) offspring [94–99]. Kin selection and relatedness are clearly important to social evolution in both taxa [50–55], but the role that males play in the social structure of many vertebrates is quite different from that in insects, largely because of the role of direct benefits in vertebrates, particularly in birds. In many social insects, males provide sperm and little else, but in nearly all cooperatively breeding birds, males and females form a pair-bond during breeding. This breeding structure in birds sets up the potential for high mating conflict over female breeding opportunities outside of the pair-bond [41].

Birds also provide an interesting system within which to examine the relationships among monogamy, mating conflict and social evolution because some of the highest rates of extra-pair paternity were recorded in cooperative breeders [88,100]. Additionally, direct benefits—including those derived from extra-pair matings—are thought to be more important in birds than in insects [25,26]. Moreover, the presence of helpers in the group could actually release female breeders from the constraints of parental care and allow them to pursue extra-pair fertilizations because a potential retaliatory reduction in paternal care as a result of females being unfaithful to their mates could be compensated for by the additional helper care [88,101]. The relationship between extra-pair paternity (promiscuity) and sociality was studied in a sample of 267 species of birds [42]. Promiscuity rates were found to be lower in cooperatively breeding species than in non-cooperatively breeding ones, and cooperation—as measured by the presence of helpers at nests—was lower in nests with higher rates of promiscuity [42]. Together, these results suggest that monogamy (i.e. low promiscuity) and low mating conflict are important in the evolution of sociality in birds, and not just in insects.

Despite key differences in the reproductive physiology and morphology of social vertebrates and insects, reduced conflict over female mating behaviour appears to be an important unifying feature in animal social evolution. Conflict over female preference for multiple mates occurs primarily between queens and female workers in social insects, whereas in vertebrates, it occurs between female and male pair-bonded breeders. In both instances, however, female mating choices for partner frequency greatly affect kin structure within groups and ultimately seem to have played a key role in the evolution of sociality. In insects, the evolution of eusociality and the associated loss of the ability of workers to reproduce appears to have released females to mate multiply again [40,44,45]. Given that some species of cooperatively breeding birds have exceptionally high levels of extra-pair paternity [88,100], it remains to be studied why these species differ from most other cooperative breeders in this regard.

4. CAN REPRODUCTIVE CONFLICT INFLUENCE SOCIAL EVOLUTION?

Maintaining kin structure and high genetic relatedness among group members is clearly important to the evolution of sociality in both vertebrates and invertebrates. Multiple mating by females, however, is not the only mechanism that can lead to reduced kin structure in complex altruistic societies. Having multiple breeding females in a group—termed polygyny in insects and plural breeding in vertebrates—will also lead to reduced genetic relatedness of the offspring [43,102]. There is a negative relationship between polyandry and polygyny in eusocial Hymenoptera [82,102], suggesting a potential trade-off in these two underlying drivers of kin structure within groups [103]. In general, as the number of breeders in a group increases, the genetic relatedness among offspring would be expected to decrease (figure 3*b*). Clearly, when female breeders are related to each other, their offspring will tend to be more related than when breeders are unrelated. Because complex altruistic societies might be predicted to dissolve below some threshold of average group relatedness (given some value of direct or material benefits), selection should act to preserve some optimal number of breeding females in the group that maintains high relatedness among offspring, while also minimizing reproductive conflict.

Although mating conflict may very well be lower in social than non-social species [42], potential reproductive conflict nevertheless always remains present in species where non-breeders maintain the ability to reproduce sexually. This is especially true in species where unrelated mates are available in the group, as in most plural breeding vertebrates, or in species where multiple females found groups together, as in many social wasps. Theory predicts that reproductive conflict increases with group size in species where all group members are physiologically capable of reproducing [36]. In certain types of social dominance hierarchies, reproductive conflict within a group can be reduced by increasing the number of breeders (i.e. sharing reproduction more equitably) [36]. Importantly, such reproductive conflict is driven not by the absolute number of group members, but by the ratio of breeders to non-breeders in the group [36]. Although increasing the number of breeders in a group should theoretically lead to a reduction in reproductive conflict over breeding opportunities, it will also lead to reduced genetic relatedness among offspring, thereby counteracting the unifying influence of genetic relatedness in social evolution [68]. Thus, understanding how both reproductive and mating conflict influence kin structure simultaneously will be important to understanding social evolution.

Reproductive skew can be quantified in a variety of ways [104,105]. However, the simplest way to assess skew in terms of breeding roles is simply to estimate the number of breeding females and the ratio of breeding to non-breeding females in a group. This effectively gives a measure of reproductive structure, which is analogous to reproductive skew as described previously. Evidence that relatedness increases with reproductive skew across species (i.e. a decrease in the number of breeding females) would be consistent with the hypothesis that high genetic relatedness is an important prerequisite for the evolution of complex altruistic societies. Simultaneous examination of levels of polyandry or promiscuity, or studies in taxa where levels of polyandry or promiscuity are extremely low, will also be needed to determine the role that patterns of reproductive skew and reproductive conflict play in social evolution. Few studies have examined the roles of reproductive skew and breeding structure in driving social evolution across species via changes in kin structure, despite the theoretical importance and the trade-offs seen in social Hymenoptera between polyandry (i.e. multiple mates per queen) and polygyny (i.e. multiple queens per colony) [82,102,103].

5. SUMMARY AND CONCLUSIONS

Conflict over reproductive and mating opportunities is important not only to sexual selection theory [6], but also to kin selection theory and social evolution in general [59,64]. Central to both theories are the concepts of reproductive skew and reproductive variance in the context of intra-sexual competition. Both males and females compete with other individuals of their sex for reproductive opportunities, which often leads to high reproductive skew and high variance in reproductive success. Classic sexual selection theory emphasizes male–male competition [3], but female–female competition is also common, particularly in social species where females compete for breeding opportunities, social rank, breeding sites or other resources [3,76]. Intense competition among females in social species acts as an important and perhaps under-appreciated selective force that has led to morphological, physiological and behavioural trait elaboration in a variety of birds [19], mammals [3,76] and insects [68]. The increased variance in female reproductive success resulting from high reproductive skew in social species is probably the underlying cause of this trait elaboration [19]. These elaborate ornaments and armaments are critical for females to gain access to breeding resources and opportunities that are typically easier for them to access when not living socially. Thus, reproductive conflict resulting from high reproductive skew in social species plays an important role in the evolution of female morphological, physiological and behavioural traits.

In addition to competition over reproductive opportunities, conflict over mating partners, particularly those of the female, is also common in most sexually reproducing species, including social ones. When a female mates with multiple partners, the genetic relatedness of her offspring decreases [40]. For species that live in social groups, this could lead to a breakdown of kin structure and ultimately the dissolution of the group. It has been hypothesized [40,44] and shown [45] in insects that eusociality did not arise until after lineages went through a period of monogamy, which ensured high relatedness among offspring. Similarly, in birds, cooperative breeding behaviour is associated with low levels of promiscuity [42]. Thus, in both vertebrates and invertebrates social evolution is associated with high kin structure and low mating conflict.

High polyandry or female promiscuity is not the only mechanism by which kin structure can be eroded within groups. When multiple females breed in a group, the genetic relatedness of the offspring produced will also decline. However, increasing the number of breeders in a group may also lead to reduced reproductive conflict in certain types of social dominance hierarchies because there are more socially dominant individuals to compete with the larger pool of socially subordinate individuals [36]. Thus, within groups of totipotent individuals, there may be tension between maximizing genetic relatedness and minimizing reproductive conflict [68]. Understanding how these mechanisms influence social evolution will be important, particularly when also simultaneously considering mating conflict and female mating patterns.

In summary, there are clearly strong links between the processes that lead to the evolution of elaborate traits and those that lead to the formation of complex altruistic societies (figure 1). It is interesting to consider that two phenomena that initially puzzled Darwin, social evolution and the evolution of elaborate ornaments and armaments, are actually more related than we tend to think. I have argued that (i) patterns of reproductive sharing within complex societies can drive levels of social competition and reproductive conflict not only in males but also in females living in social groups, and ultimately can drive the evolution of female traits such as ornaments and armaments; (ii) mating conflict over female choice of sexual partners can influence kin structure within groups and drive the evolution of complex societies; and (iii) patterns of reproductive sharing and conflict among females may also drive the evolution of complex societies by influencing kin structure within groups. Complex altruistic societies appear to have only arisen in taxa where social competition over reproductive opportunities and sexual conflict over mating partners were low. Moreover, once complex societies evolved, there were important selective feedbacks on traits used to regulate and mediate intra-sexual competition over reproductive opportunities, particularly in females. Empirical tests of many of these ideas have only just begun, but are still generally lacking in a diverse array of social taxa. Future comparative studies should consider social mammals (see recent study [106]) and other invertebrates, and empirical studies need to be conducted in many more species. Linking sexual, social and kin selection theory will enhance our understanding of the evolution of complex morphological, physiological and behavioural traits, and even the evolution of sociality itself in taxa as diverse as insects, birds and mammals, including humans.

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