



Queens versus workers: sex-ratio conflict in eusocial Hymenoptera

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Studies of sex-ratio conflict in the eusocial Hymenoptera (ants, bees and wasps) have provided the most rigorous tests of kin selection theory. The hymenopter haplodiploid system of sex determination generally renders workers more closely related to their sisters than to their brothers, whereas queens are equally related to their sons and daughters. Kin selection theory therefore predicts that resource allocation into male or female reproductives is a source of queen–worker (i.e. parent–offspring) conflict. Under the traditional assumption of worker control, sex ratios should evolve towards female bias, shifting away from the optimum of the queen, an even sex ratio. Three decades of research on sex-ratio conflict largely supported worker control, but recent studies have revealed queen-controlled sex ratios even in societies previously thought to operate under worker control. Recent studies have further documented that queen–worker sex-ratio conflict is modulated by other within-colony conflicts, such as those over colony growth or worker reproduction. Shared-control, multiconflict models are now needed to encompass the dynamic balance between queen and worker power over the colony sex ratio.

Kin selection (inclusive fitness) theory is the key hypothesis for explaining a wide variety of evolutionary phenomena, including the maintenance of eusociality [1]. True eusociality occurs in vertebrate and invertebrate social systems, yet the extreme forms are found in hymenopteran insects (ants, bees and wasps). Social insect colony workers usually forgo reproduction and help the mother queen(s) to produce collateral kin (siblings), thus augmenting the inclusive fitness of the worker. As a consequence of the hymenopteran haplodiploid system of sex determination, workers are generally more closely related to sisters than to brothers (in the extreme case, three times more related to sisters than to brothers), whereas the queen is equally related to her sons and daughters [1]. This asymmetry in relatedness generates conflict over sex allocation (investment in male versus female reproductives produced by a colony), and thus, creates evolutionary potential for both kinship-mediated cooperation and within-colony conflict.

In 1976, Trivers and Hare [2] outlined a theoretical framework specifying the differing sex-ratio optima for a

queen and her workers. This seminal work integrated and extended both sex-ratio theory, as developed by Fisher [3], and kin selection theory, as developed by Hamilton [1,4]. Trivers and Hare [2] argued that relatedness asymmetries generate selection that favors workers that behave more nepotistically toward sisters than they do toward brothers. In particular, workers should bias the colony investment sex ratio [3] toward their more closely related sisters and away from their more distantly related brothers, up to a point where the reproductive value of the more closely related females is exactly offset by the increased mean reproductive value (mating success) of males in a female-biased population. By contrast, reproductive queens are related equally to their male and female offspring, and selection should favor queens that counter any female bias induced by the workers. According to Trivers and Hare [2], sex allocation in eusocial Hymenoptera is therefore characterized by parent–offspring (queen–worker) conflict over the colony sex ratio.

To test the hypothesis of queen–worker conflict, Trivers and Hare [2] expanded on Fisher's sex-ratio theory [3] and derived the sex ratios expected if either the queen or workers had complete control over the allocation of resources in the two sexes. Because empirical data of population-wide sex ratios of ants closely matched the female-biased sex ratios expected under worker control, Trivers and Hare [2] argued that the queen–worker conflict in colonies of ants is resolved in favor of workers (Box 1). Using an augmented data set of ant sex ratios, Nonacs [5] later confirmed the population-wide female bias among ants. Since then, numerous studies of various hymenopterans have supported this view that workers often control sex-investment ratios [6,7]. However, recent work has provided surprising examples of queen control over sex ratios, urging the development of shared-control models that encompass the dynamic power balance between queen and worker influences over colony sex ratios.

Primary versus secondary sex ratios

Sex-investment ratios can be measured at different life stages. Primary sex ratios refer to proportions of haploid (male) and diploid (female) reproductive-destined eggs laid by a queen. Secondary sex ratios, however, refer to proportions of male and female reproductives at later developmental stages (e.g. pupal or adult colony sex ratio). Queens presumably control primary sex ratios during oviposition (given that this ratio refers to the proportion of

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Box 1. Potential factors affecting sex ratios

Most theories of queen–worker sex-ratio conflict focus on how relatedness asymmetry modulates the optimal worker sex ratio and thus the intensity of queen–worker conflict. For example, relatedness asymmetry is reduced by an increase in queen mating frequency, thus more closely aligning the sex-ratio interests between queen and workers [a,b]. However, population-wide investment sex ratios are the joint product of many selective forces operating in concert with relatedness asymmetry. The presence of a female-biased sex ratio therefore does not constitute evidence for worker control unless other factors can be discounted. Some of these alternate factors involve conditions under which females have higher reproductive value than do males.

For example, under the following conditions, even the optimal sex ratio of the queen is female-biased: (1) competition for mates or resources is stronger between sons than between daughters, reducing the relative value of sons (local mate or resource competition [b–e]); (2) daughters cooperate synergistically to enhance their joint reproduction, increasing the relative value of daughters (local resource enhancement [e]); or (3) only female offspring can facultatively assume either worker or reproductive roles depending on environmental conditions [f]. In addition, females are more valuable to the queen if there is an excess of males in the population (e.g. because of the presence of male-specialist colonies arising from queen sperm depletion or worker reproduction following queen loss (sex-ratio compensation; [b,e]). In the absence of queen–worker conflict, female-biased sex ratios can be induced by maternally inherited parasites or selfish genetic elements, such as *Wolbachia* [g,h] or cytoplasmic and mitochondrial genes. Finally, biased sampling procedures can generate artifacts of female bias [i,j].

Even in the absence of all the complicating factors listed above, potential queen–worker conflict over the sex ratio might not occur if selection causes male brood to ‘mimic’ female brood, thus depriving workers of recognition cues for favoring sisters [k]. However, male brood might not be able to maintain this mimicry indefinitely during development, because such mimicry will eventually result in a sub-optimal developmental trajectory, especially in a sexually dimorphic species. This might force older male brood eventually to reveal their sex, which could explain why worker sex-ratio manipulations sometimes do not occur until the later brood stages [k]. This mimicry hypothesis

predicts that the greater the sexual dimorphism of a species: (1) the earlier the onset of male elimination by workers; and (2) the greater the overall bias (because elimination of small males is less costly). Interestingly, sex ratios tend to be more female biased in more sexually dimorphic species of ants, bees and wasps [i,l].

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reproductive-destined eggs laid by the queen), whereas workers traditionally have been assumed to control secondary sex ratios because they rear and feed the brood. Thus, queen–worker control over sex allocation is likely to vary according to the developmental stage. The precise quantification of sex-investment ratios has proved challenging [8,9] and only recently have empirical studies begun to examine and compare primary and secondary ratios [10–13]. These experiments provide support for worker control over the secondary sex ratio, by alteration of the queen-controlled primary sex ratio (e.g. by selectively eliminating male brood) [10–13]. Thus, these studies strongly support the idea that the queen and workers pursue different sex ratio optima and that both parties have at least some leverage in the sex-ratio conflict (see Box 2 for an additional intriguing test for queen control involving slave-making ants).

Sex-ratio biasing mechanisms

The mechanisms that enable queens and workers to control sex allocation have only recently received attention [6,7,14]. Each party can bias sex ratios through either direct or indirect tactics.

Direct mechanisms

Because workers rear and feed the brood, they can adjust sex-investment ratios by selectively eliminating males (i.e.

fratricide) [10–13,15,16], preferentially feeding or rearing females [17], facultatively manipulating female caste fate (i.e. switching worker-destined brood to become reproductive females) [18], or even by imprisoning males and thus preventing their access to food [19]. Such manipulations assume that workers are capable of distinguishing between the sexes (which might be difficult at early developmental stages); otherwise, these tactics are costly, because offrequent misdirected harm to females (Box 1) [20].

Mechanisms by which queens control sex allocation are less well known [7,21–23], but are implicated by recent studies of hymenopterans with split sex ratios (i.e. population-wide bimodal sex-ratio distributions with co-occurring colonies that specialize in the production of either male or female reproductives). For example, in monogynous (single-queen) colonies of the fire ant *Solenopsis invicta*, queens seem to control sex ratios by limiting the number of female eggs laid, thus forcing workers to rear males in male-specialist colonies [24]. In the ant *Pheidole desertorum*, it is hypothesized that queens from male-specialist colonies manipulate sex ratios by producing worker-destined instead of reproductive-destined female eggs (i.e. affect female caste determination) [21]. In spite of this influence, both *P. desertorum* and *S. invicta* workers are capable of biasing sex ratios toward females [13,17]. For example, experimental manipulations showed that *P. desertorum* workers from male-specialist colonies

Box 2. Is there queen–worker conflict in slave-making ants?

Slave-making ants represent an exception to the simple formulation of queen–worker sex-ratio conflict [a]. Slave makers seize brood of other species and eventually enslave these workers to be solely responsible for heterospecific brood care (the slave-making workers are assumed to contribute very little or nothing to brood care). Because the slaves are genetically unrelated to the brood, slave workers are not under selection to bias the slave-maker sex ratio toward females. Therefore, under the assumption that brood is reared free of slave-maker worker influences, queens from slave-making colonies should exclusively control sex allocation [a].

This prediction was supported by early work [a–c]; however, a recent study implicates the potential for queen–worker conflict over sex ratios in slave makers [d]. Even though the mean population investment sex ratio across 11 slave-maker data sets (compiled for three obligate slave-making ant species) is close to the queen optimum of 0.50, an analysis of each data set on its own showed that six of these significantly deviated

from an even sex ratio. Thus, whereas the overall pattern across all 11 species seems to confirm queen control, sex-allocation evolution does not appear uniform across all slave-making species [d], raising the possibility of sex-ratio influences of slave-making workers or even of the slave workers themselves.

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preferentially rear reproductive female brood over male brood [17]. Thus, both queens and workers have some leverage over the colony sex ratio and work in opposition, implying queen–worker conflict.

Similar to *S. invicta* and *P. desertorum*, the bumblebee *Bombus terrestris* is characterized by split sex ratios, yet queens also seem to achieve partial control over sex allocation [25]. This could be explained by mechanisms reinforcing queen control over male parentage (i.e. workers can produce males in *B. terrestris*) [25]. Queens from male-specialist colonies appear to force workers to rear queen-produced males by laying haploid eggs preferentially during the early phase of colony development, thus contrasting with the late laying of haploid eggs by queens from female-specialist colonies. Assuming that workers postpone egg laying until they can assess whether it serves their genetic interests, and also assuming that workers can discriminate the sex of brood no earlier than the larval stage, queens from male-specialist colonies lay haploid eggs as early as possible, because workers are unable to detect these males until it is too costly for them to replace them with their own sons. Moreover, the queen's sons cannot be replaced with female reproductives, because the queen controls the primary sex ratio [25]. Interestingly, the population investment sex ratio is at the queen optimum of 1:1 for *P. desertorum* [21] and is either male biased or close to 1:1 in *B. terrestris* [26,27]. Because male- and female-specialist colonies do not differ in relatedness asymmetry or productivity, queen control has therefore been hypothesized to explain the evolution of split sex ratios in these two species [21,25]. That is, queens completely control the sex ratio in some colonies [i.e. by laying only male and worker-destined eggs (as in *P. desertorum*) or by laying haploid eggs early (as in *B. terrestris*)], and such colonies therefore become male-specialists. Other colonies in the same population are selected to become female-specialists through a process called sex-ratio compensation, because the value of males relative to that of females decreases with increasing frequency of male-specialist colonies in the population [22].

Indirect mechanisms

Indirect sex-ratio biasing mechanisms regulate sex ratios through worker manipulation of colony conditions (e.g.

nutrient supplements) that induce queens to change the sex-ratio output at oviposition. Workers influence queen behaviour by providing her with incentives for the production of females, effectively making it the optimal strategy for her to overproduce females. One indirect tactic involves workers providing the queen with incentives to lay fertilized eggs. For example, female fitness might increase faster with investment than does male fitness [28,29]; hence, in mass-provisioning bees, presenting the queen with a large investment in a cell (provisioning mass on which an offspring is reared) would induce her to lay a fertilized egg [30,31]. Thus, indirect mechanisms are an alternative to direct influences, but the indirect nature of these mechanisms makes them harder to study empirically.

Integrating sex-ratio conflict with other queen–worker conflicts

Even though sex-ratio conflict according to Trivers and Hare [2] strictly pertains to investment in queen-produced sexuals, recent research has demonstrated that sex-ratio conflicts are entangled with other intracolony conflicts. Ultimately, a theory of the simultaneous resolution of all conflicts is necessary for a full understanding of the properties of eusocial hymenopteran societies.

Conflict over male production

The optimal allocation ratio of a queen and the workers changes with the proportion of males in the population that are sons of workers. Worker reproduction (generally limited to sons, because workers in many species are unfertilized) thus influences the sex-allocation conflict [29]. Chemical cues and various ritualized behaviors provide queens with potential mechanisms to limit worker reproduction. For example, recent work with the ponerine ant *Pachycondyla apicalis* [32] implicates that queens emit a pheromone that inhibits workers from producing males. However, such inhibition does not necessarily entail conflict, because workers might use the pheromone as an indicator of the presence of a healthy mother queen and thus as a predictor for higher expected payoffs when forgoing reproduction and rearing full sisters instead of their own sons and nephews [33]. In addition to chemical cues, ritualized interactions between queens and workers might also enable the queen to control reproduction. In two

Australian species of stingless bees, the queens appear to suppress worker reproduction by performing a series of ritualized behaviors during oviposition [34]. Such displays are consistent with conflict between the queen and the workers, because such conventional displays are expected when interactants are signalling relative fighting or competitive ability [35].

Another social mechanism for controlling worker reproduction is worker policing. According to kin selection theory, workers are expected to police each other's reproduction in colonies with multiply mated queens because workers are on average more closely related to males produced by the queen (brothers) than to males produced by other workers (nephews) [29]. Using the vespine wasp *Dolichvespula saxonica*, Foster and Ratnieks [36] found support for this prediction by showing in a few colonies that worker policing occurs in societies with a multiply mated queen but not in those with a singly mated queen. Thus, queen mating frequency seems to affect both worker policing and queen–worker sex-ratio conflict, and a queen might be able to promote both her optimum sex ratio and improve her control of male production by increasing her mating frequency. Thus, it is a puzzle as to why multiple mating is not more common in the Hymenoptera. Although there are many factors that can select against multiple mating (e.g. sexually transmitted diseases or predation risks), single mating might be prevalent in the social Hymenoptera because males can avoid mating with already mated queens. Such queens are less valuable to males as mates because they would tend to specialize in producing sons when there are split sex ratios, and males gain genetic representation only in their daughters [37].

Worker policing of male production also occurs in polyandrous honeybees [38], but is absent in monandrous stingless bees [39], in accordance with theory. However, worker policing occurs in a variety of other hymenopterans, including the common wasp [40], hornets [36,41,42], and queenless ants [43–45], even though theory does not predict worker policing for these species (where workers are more closely related to nephews than to brothers). Worker policing in such cases can result when workers have limited ability to recognize sex [46]. For example, if workers are unable to distinguish sister- versus brother-destined brood in colonies with a singly mated queen, their average relatedness to all reproductive brood is $(1/2)(3/4) + (1/2)(1/4) = 1/2$, which exceeds the mean relatedness of $3/8$ to nieces and nephews. Therefore workers will police against worker egg laying (assuming that workers can differentiate between queen-laid and worker-laid eggs, as is hypothesized to occur in honey bees [47]).

Conflict over reproductive partitioning among queens

Conflicts among queens over the partitioning of reproduction (reproductive skew) can be connected to queen–worker sex-ratio conflict. For example, Bourke [48] showed recently that, when workers cause a female-biased population sex ratio, a dominant queen has added incentive to share reproduction with a subordinate related queen, thereby increasing the relative power of queens vis-à-vis the workers. In other words, the queen yields some reproduction to other queens (reducing reproductive

skew) to diminish the worker-induced sex-ratio bias. Shared reproduction between multiple related queens decreases the relatedness asymmetry of the workers to the average brood, leading to greater investment in males by workers, and shifting the colony sex ratio towards the queen-preferred sex-ratio optimum.

Conflict over life-history decisions (colony growth)

One major recent theoretical development is the extension of queen–worker conflict over sex allocation to life-history allocation, that is, the relative investment of resources in colony growth (production of workers) versus colony reproduction (production of sexuals) [29]. The applicability and scope of this type of conflict in various kin-structured hymenopteran societies has recently stimulated controversy. Bourke and Chan [49] argued against the generality of queen–worker conflict over life-history decisions [50]. They suggested that conflict should be absent in colonies with the simplest social organization (i.e. characterized by a monogynous, monandrous queen and sterile workers) because only queens can produce reproductives in these societies, essentially aligning the interests of the workers and queens in maximizing colony fitness. Herbers *et al.* [51] and Reuter and Keller [52] contributed to the theoretical resolution of this controversy by developing models that link conflict over life-history allocation (colony growth) to conflict over sex ratios. Herbers *et al.* [51] concluded that there is potential for queen–worker conflict over life-history allocation only when: (1) sex-ratio conflict occurs; and (2) there is variation in population-wide sex ratios (i.e. split sex ratios). Reuter and Keller [52] also showed that queen–worker conflict over colony growth occurred only if neither party had complete control over sex allocation.

Conclusions and future directions

Two major advances arising from recent empirical and theoretical work on sex-ratio conflict include: (1) the synthesis of sex-ratio conflict with other queen–worker conflicts; and (2) the elucidation of cases of queen control over the sex ratio. The integration of multiple queen–worker conflicts not only enables a more realistic approach to the study of conflict evolution, but also should lead to new predictions about the resolution of conflicts in eusocial Hymenoptera. The original paradigm of worker-controlled sex ratios clearly has been an oversimplification. This is especially evident in societies where the queen controls the primary sex ratio whilst workers control relative investment in worker broods versus reproductive females [52]. Future empirical work needs to address whether there are other potential mechanisms of queen control (e.g. indirect mechanisms might be a promising area), whether queen–worker conflict is evident in other types of social insect societies besides those characterized by split sex ratios, and whether queen control is dependent on genetic, social or ecological contexts. A further understanding of the genetic, chemical and physiological means by which queens might bias sex ratios is also worth investigating. For example, if queens can determine female caste fate, how is this achieved, and what leverage might the brood have in these caste decisions? Once these chemicals or hormones are identified (given that ants communicate

primarily through the use of chemical signals), then manipulative experiments, similar to those reviewed here, could be performed to elucidate further the resolution of queen–worker conflict over sex allocation.

What is now needed is a synthetic theory of how sex-ratio conflicts will be resolved; that is, a theory of the actual sex ratio that results in different genetic, ecological and social contexts. Such a theory would parallel reproductive skew theory, which combines kin selection and game theory models to make predictions about actual reproductive partitioning when group members have different genetic interests about who should breed [53]. Similar game-theoretic models of sex-ratio conflict resolution among relatives will greatly extend Trivers and Hare's theory and pave the way for the next generation of empirical analyses of sex-ratio conflicts in social organisms. Clearly, the study of the resolution of queen–worker sex-ratio conflicts has barely begun.

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