Patterns of split sex ratio in ants have multiple evolutionary causes based on different within-colony conflicts

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Split sex ratio—a pattern where colonies within a population specialize in either male or queen production—is a widespread phenomenon in ants and other social Hymenoptera. It has often been attributed to variation in colony kin structure, which affects the degree of queen–worker conflict over optimal sex allocation. However, recent findings suggest that split sex ratio is a more diverse phenomenon, which can evolve for multiple reasons. Here, we provide an overview of the main conditions favouring split sex ratio. We show that each split sex-ratio type arises due to a different combination of factors determining colony kin structure, queen or worker control over sex ratio and the type of conflict between colony members.

Keywords: sex allocation; colony kin structure; control over sex ratio; reproductive conflict; social insects

1. INTRODUCTION

In colonies of social Hymenoptera, there is a potential conflict between queens, males and workers over optimal sex allocation (Trivers & Hare 1976; Queller & Strassmann 1998; Chapuisat & Keller 1999; Bourke 2005; Meunier *et al.* 2008; West 2009). This potential conflict arises because of the haplodiploid sex determination mechanism (females and males develop from fertilized and unfertilized eggs, respectively). This results in males transmitting their genes to the next generation only through daughter queens, and workers transmitting more of their genes through sisters (relatedness coefficient $r = 0.75$) than through brothers ($r = 0.25$). Hence, males and workers prefer a female-biased sex allocation, which contrasts with the queen's interest of an even sex allocation as she is equally related to her daughters and sons ($r = 0.5$). While queens and workers have both considerable power over sex allocation (Reuter & Keller 2001; Beekman & Ratnieks 2003; Mehdiabadi *et al.* 2003), this is not the case for males, who die shortly after mating.

The degree of this potential conflict depends on the relatedness asymmetry ($RA = r_{w \rightarrow f} / r_{w \rightarrow m}$) within a colony, where $r_{w \rightarrow f}$ and $r_{w \rightarrow m}$ are the relatedness of

workers towards female and male offspring, respectively. RA is highest (3 : 1) in colonies with one singly mated queen and becomes weaker ($1 : 1 \leq RA < 3 : 1$) when queens mate multiple times, when the colony is headed by multiple related queens (polygyny) (Bourke & Franks 1995), or when queens are replaced by daughters (Boomsma 1991). Under worker control, theory predicts that, if RA varies among colonies in a population, colony sex ratio should be split (Boomsma & Grafen 1991), with colonies having an RA above the population average specializing in gyne (virgin queen) production, while colonies with a below-average RA specializing in male production. Indeed, split sex ratio linked to between-colony variation in RA is a widespread phenomenon in social Hymenoptera (Bourke 2005). However, theoretical work showed that split sex ratio can also emerge under other conditions, such as queen control (Pamilo 1982; Roisin & Aron 2003) or competition among co-breeding queens (Frank 1987; Fournier *et al.* 2003). Compatible with this idea, recent studies have uncovered split sex-ratio patterns in ants that are unlinked to between-colony variation in RA (Vargo 1996; Helms 1999; Brown & Keller 2000; Fournier *et al.* 2003; Rosset & Chapuisat 2006), indicating that split sex ratio seems to have multiple evolutionary causes. In this paper, we provide a general framework of the main conditions favouring split sex ratio.

2. KIN STRUCTURE AND SEX-RATIO CONTROL MECHANISMS

Assuming no inbreeding, RA within a colony is mainly determined by the effective number of queens ($n_{e,q}$), the relatedness among queens (r_q) and the number of effective matings per queen (m_e) (figure 1), whereby the relatedness of workers towards females ($r_{w \rightarrow f}$) and males ($r_{w \rightarrow m}$) can be expressed as

$$r_{w \rightarrow f} = \frac{m_e + 2}{4m_e n_{e,q}} + \frac{r_q}{4} \left(\frac{n_{e,q} - 1}{n_{e,q}} \right), \quad (2.1)$$

and

$$r_{w \rightarrow m} = \frac{1}{4n_{e,q}} + \frac{r_q}{4} \left(\frac{n_{e,q} - 1}{n_{e,q}} \right), \quad (2.2)$$

(Queller 1993). Multiple mating decreases RA because it lowers $r_{w \rightarrow f}$ but not $r_{w \rightarrow m}$. The presence of multiple related queens results in $r_{w \rightarrow f}$ decreasing more rapidly than $r_{w \rightarrow m}$ because the second term in the equations contributes relatively more to the overall relatedness in equation (2.2) than in equation (2.1). In contrast, if co-breeding queens (and their mates) are unrelated, $r_{w \rightarrow f}$ and $r_{w \rightarrow m}$ decrease proportionally such that RA remains 3 : 1.

The predicted association between colony sex allocation and kin structure also depends on the party controlling sex allocation (figure 1). At the proximate level, queens can exert control by biasing the primary sex ratio (haploid to diploid eggs). For example, queens can force workers to rear males by limiting the number of diploid eggs (Passera *et al.* 2001). Alternatively, queens can influence the caste fate (workers or gynes) of their diploid eggs by modifying juvenile hormone and ecdysteroid titres (Suzzoni *et al.* 1980; de Menten *et al.* 2005; Schwander *et al.* 2008). Finally, queens can deceive workers over larval sex and therefore prevent worker bias (Nonacs & Carlin 1990).

One contribution of 16 to a Special Feature on 'Sexual conflict and sex allocation: evolutionary principles and mechanisms'.

¹Colonies in a population have either one queen, multiple related (solid lines) or unrelated (dashed lines) queens.

²Queens in a population are either singly or multiply mated.

^aDue to high RA in all colonies, workers prefer a 0.75 female-biased population sex allocation. Once this equilibrium is achieved, there is no selection on colony sex ratio, which may lead to random single-sex brood in some colonies.

^bQueens prefer an 0.5 population sex allocation regardless of the RA within their colony. Split sex ratio can occur to prevent worker manipulation, whereby half of the colonies within a population specialize in either female or male production.

^cColonies with a high RA specialize in female production, whereas colonies with a low RA specialize in male production. Population sex allocation varies between the relatedness asymmetries of the high and low RA colony classes depending on the proportion of high- and low-RA colonies in the population.

^dThere is little scope for workers to bias sex ratio as the workers' and queens' optimum merge (i.e. 0.5 population sex allocation) with high mating frequency and queen number.

^eCompetition over female production among unrelated co-breeding queens can lead to split sex ratio: multiple-queen colonies specialize in gyne production, while single-queen colonies specialize in male production. Population sex allocation is ≥ 0.5 depending on the proportion of monogynous and polygynous colonies.

^fLocal resource competition (LRC) among related co-breeding queens can lead to split sex ratio. Colonies with many queens are subject to high LRC and should specialize in male production, while colonies with few queens have reduced levels of LRC and should produce females to recruit new queens. Population sex allocation is extremely male biased.

Figure 1. Colony kin structure, its effect on between-colony variation in relatedness asymmetry (RA, i.e. the asymmetry in the relatedness of workers towards female and male offspring) and the resulting potential for split sex ratio under worker or queen control.

While queens control the primary sex ratio, workers have power over the secondary sex ratio (the number of eggs of each sex reared to adulthood). Workers have been reported to exert control by killing males (Sundström *et al.* 1996), or by increasing the proportion of diploid eggs that turn into gynes instead of workers (Hammond *et al.* 2002).

3. PATTERNS OF SPLIT SEX RATIO IN ANTS

(a) *Queen control in high conflict situation*

Split sex ratio may occur here because queens produce a haploid- or diploid-biased egg clutch to force workers to rear mainly males or gynes (Pamilo 1982; Roisin & Aron 2003). This mechanism has been suggested to lead to split sex ratio in *Pheidole desertorum* (Helms 1999; Helms *et al.* 2000; figure 2a) and *Solenopsis invicta* (Vargo 1996; Passera *et al.* 2001) in populations with singly mated one-queen colonies (high RA); and in a population of *Formica selysi* where RA varied among colonies (Rosset & Chapuisat 2006; figure 2b).

(b) *Worker control when RA varies among colonies*

Split sex ratio can occur here because the workers' optimal sex allocation is all-female biased in colonies

with one singly mated queen (high RA), and all-male biased in colonies with a multiply mated queen or multiple related queens (low RA) (Boomsma & Grafen 1991). Split sex ratio associated with between-colony variation in mating frequency occurs in *Formica exsecta* (Sundström *et al.* 1996; figure 2c) and *Formica truncorum* (Sundström 1994), while between-colony variation in queen number was associated with split-sex ratio in *Myrmica tahoensis* (Evans 1995; figure 2d), *Myrmica ruginodis* (Walsh & Seppä 2001) and *Leptothorax acervorum* (Chan & Bourke 1994).

(c) *Conflict among unrelated queens*

In such populations, the number of queens, but not RA, varies among colonies, which may affect the relative control of queens and workers over the sex ratio. While queens may limit the production of diploid eggs to force workers to raise males in single-queen colonies, competition among unrelated co-breeding queens should result in queens maximizing egg production, which would favour queens who produce diploid eggs, as these eggs are preferentially reared by workers due to the high RA within colonies (Fournier *et al.* 2003). Thus, polygynous colonies are predicted to specialize in gyne production, while monogynous

Figure 2. Selected examples of split sex-ratio patterns in ants in populations where colonies are characterized by: (a) having one singly mated queen and queen control (*Pheidole desertorum*, $n = 95$); (b) variation in relatedness asymmetry (RA) and queen control (*Formica selysi*, $n = 65$); (c) predominantly worker control and variation in RA due to variance in mating frequency (*Formica exsecta* (monogyne), $n = 38$) or (d) queen number (*Myrmica tahoensis*, $n = 39$); (e) conflict among unrelated queens (*Pheidole pallidula*, $n = 21$) and (f) conflict among related queens (*Formica exsecta* (polygyne), $n = 248$). Sex allocation is given as the percentage dry weight investment in gynes, except for (a) and (e), which are based on numerical sex ratios (i.e. proportion of gynes). n , number of colonies. For (b), (c) and (f) data and n represent averages across multiple study years.

colonies should specialize in male production—a split sex-ratio pattern observed in the ant *Pheidole pallidula* (Fournier *et al.* 2003; de Menten *et al.* 2005; figure 2e).

(d) Conflict among related queens

Split sex ratio can emerge under these conditions because in highly polygynous species new queens frequently remain in the parental colony after mating (Bourke & Franks 1995), leading to local resource competition (LRC). Because the benefit of recruiting new queens is highest for colonies containing few queens (because of egg limitation or colony extinction risk), gyne production should only occur in colonies where the queen number is below a given threshold. This concept, which has been termed ‘queen-replenishment hypothesis’, predicts split sex ratios correlated with queen number and the degree of LRC (Brown & Keller 2000)—a pattern observed in highly polygynous populations of *F. exsecta* (Brown & Keller 2002; Kümmerli *et al.* 2005; Kümmerli & Keller 2008; figure 2f).

4. DISCUSSION

Our overview reveals that split sex ratio in ants can emerge for a number of reasons—each representing a different combination of factors determining colony kin structure, queen or worker control over sex ratio and the type of conflict (queen–worker or queen–queen conflict). Consequently, detailed knowledge on these factors is needed to predict patterns of split sex ratio and their evolutionary causes in nature.

That such knowledge is crucial is best demonstrated in the ant *F. exsecta*, where reasons for split sex ratio vary between populations. While in monogynous populations split sex ratio is based on workers biasing sex ratio according to between-colony variation in RA (Sundström *et al.* 1996), split sex ratio in polygynous populations occurs because of between-colony variation in queen number and levels of LRC (Brown & Keller 2002; Kümmerli & Keller 2008).

Finally, theoretical work has revealed additional reasons for split sex ratio to evolve than those outlined in this paper. For example, split sex ratio could occur owing to between-colony variation in the relative cost of male and gyne production (Nonacs 1986; Rosenheim *et al.* 1996), caused by local mate competition (Frank 1987), inbreeding (Reece *et al.* 2004) or variation in the cost of worker sex-ratio manipulation among colonies (Reuter *et al.* 2004).

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