

SHORT COMMUNICATION

Sex investment ratios in eusocial Hymenoptera support inclusive fitness theory

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relatedness;
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Inclusive fitness theory predicts that sex investment ratios in eusocial Hymenoptera are a function of the relatedness asymmetry (relative relatedness to females and males) of the individuals controlling sex allocation. In monogynous ants (with one queen per colony), assuming worker control, the theory therefore predicts female-biased sex investment ratios, as found in natural populations. Recently, E.O. Wilson and M.A. Nowak criticized this explanation and presented an alternative hypothesis. The Wilson–Nowak sex ratio hypothesis proposes that, in monogynous ants, there is selection for a 1 : 1 numerical sex ratio to avoid males remaining unmated, which, given queens exceed males in size, results in a female-biased sex investment ratio. The hypothesis also asserts that, contrary to inclusive fitness theory, queens not workers control sex allocation and queen–worker conflict over sex allocation is absent. Here, I argue that the Wilson–Nowak sex ratio hypothesis is flawed because it contradicts Fisher's sex ratio theory, which shows that selection on sex ratio does not maximize the number of mated offspring and that the sex ratio proposed by the hypothesis is not an equilibrium for the queen. In addition, the hypothesis is not supported by empirical evidence, as it fails to explain 'split' (bimodal) sex ratios or data showing queen and worker control and ongoing queen–worker conflict. By contrast, these phenomena match predictions of inclusive fitness theory. Hence, the Wilson–Nowak sex ratio hypothesis fails both as an alternative hypothesis for sex investment ratios in eusocial Hymenoptera and as a critique of inclusive fitness theory.

Introduction

Inclusive fitness theory aims to provide a framework for understanding the evolution of sociality and social behaviour across all scales of biological organization (Queller, 2000; Boomsma, 2009; Bourke, 2011a). First proposed by Hamilton (1964), the theory, also known as kin selection theory, has attracted particular controversy over the past decade. Over this time, criticisms have been directed at its theoretical foundations, its usefulness and its empirical evidence base (Wilson &

Hölldobler, 2005; Nowak *et al.*, 2010; Wilson, 2012; Allen *et al.*, 2013; Wilson & Nowak, 2014; Nowak & Allen, 2015). In turn, each of these criticisms has been contested (Foster *et al.*, 2006; Abbot *et al.*, 2011; Bourke, 2011a,b, 2014; Gardner *et al.*, 2011; Rousset & Lion, 2011; Liao *et al.*, 2015; Marshall, 2015). For example, Liao *et al.* (2015) showed that the conclusion that relatedness does not affect the likelihood of the origin of eusociality is not supported by the alternative model of eusocial evolution of Nowak *et al.* (2010).

Sex investment ratios in eusocial Hymenoptera (ants, bees and wasps with a sterile or partially sterile worker caste) have provided some of the strongest evidence for inclusive fitness theory. Recently, as part of their wider criticism of inclusive fitness theory, Wilson (2012) and

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Wilson & Nowak (2014) disputed the theory's explanation of sex investment ratios in eusocial Hymenoptera and proposed an alternative hypothesis with particular application to the ants. Here, I argue that this hypothesis (henceforth, the 'Wilson–Nowak sex ratio hypothesis') is both theoretically flawed and unsupported by the data. Hence, the criticisms of inclusive fitness theory in Wilson (2012) and Wilson & Nowak (2014) centred on sex investment ratios do not succeed.

Inclusive fitness theory's explanation of sex investment ratios in the eusocial Hymenoptera

Sex ratio refers to the relative allocation of resources to rearing females and males, with the numerical sex ratio referring to the relative numbers of females and males reared and the sex investment ratio to sex allocation in terms of biomass. (In the following, sex investment ratio is expressed as the ratio, biomass of females/biomass of males; in the eusocial Hymenoptera, 'females' refers to new queens.) The theory underpinning current understanding of sex investment ratio in all sexual organisms is Fisher's (1930) sex ratio theory. This states that the stable sex investment ratio for the party controlling sex investment arises when the fitness returns to that party from raising a female or a male, per unit cost, are equal (e.g. Benford, 1978). Linking inclusive fitness theory (Hamilton, 1964) and Fisher's (1930) sex ratio theory, Trivers & Hare (1976) showed that, within populations of eusocial Hymenoptera, the stable sex investment ratio for any party within the colony equals that party's relatedness asymmetry, that is its relative relatedness to females and males. Under conditions of monogyny (one queen per colony), monandry (single queen mating), worker sterility and random mating, the queen's relatedness asymmetry is 1 : 1 (relatedness to daughters, 0.5/relatedness to sons, 0.5) and the workers' relatedness asymmetry is 3 : 1 (relatedness to sisters, 0.75/relatedness to brothers, 0.25). Hence the predicted population-level sex investment ratios are 1 : 1 for the queen and 3 : 1 for workers (Trivers & Hare, 1976). This finding shows that there is potential queen–worker conflict over sex investment ratio in eusocial Hymenoptera and predicts that, if workers control sex allocation, the sex investment ratio should be female biased (Trivers & Hare, 1976).

Boomsma & Grafen (1990, 1991) extended Trivers & Hare's (1976) reasoning to explain within-population sex investment ratio variation. In some populations, workers' relatedness asymmetry varies across colonies (e.g. because of multiple mating (polyandry) in queens). Boomsma & Grafen (1990, 1991) showed that, if workers control sex allocation, workers in colonies with high relatedness asymmetry should

produce relatively more females and workers in colonies with low relatedness asymmetry should produce relatively more males. In short, there should be so-called split (bimodal) sex ratios, with colony-level sex investment ratios covarying with workers' relatedness asymmetry.

Empirical studies have largely confirmed inclusive fitness theory's predictions for sex investment ratio at the level of both the population (Bourke & Franks, 1995; Crozier & Pamilo, 1996; Bourke, 2005; West, 2009) and the colony (Queller & Strassmann, 1998; Bourke, 2005; Meunier *et al.*, 2008; West, 2009). In particular, in monogynous ants, population sex investment ratios are significantly female biased (Crozier & Pamilo, 1996; Bourke, 2005). Empirical studies therefore support the concept of worker control of sex allocation, which is a reasonable one as workers, not queens, rear sexual brood to adulthood (Trivers & Hare, 1976). However, inclusive fitness theory does not preclude queen control, provided queens have the power to exert it. One relevant mechanism could involve queens controlling the ploidy and hence the sex of eggs by controlling release of sperm from the spermatheca (sperm storage organ); another could involve queens laying worker-biased female eggs (Bourke & Franks, 1995; Helms, 1999; Passera *et al.*, 2001; De Menten *et al.*, 2005). Indeed, sex investment ratios in ants often appear to be evolutionary compromises arising from ongoing queen–worker conflict over sex allocation (Helms, 1999; Ratnieks *et al.*, 2006; Rosset & Chapuisat, 2006; Helanterä & Ratnieks, 2009; Aron, 2012). It has also been recognized that many other factors aside from relatedness asymmetry and queen–worker conflict influence variation in sex investment ratio at both population and colony levels (Bourke, 2005; Meunier *et al.*, 2008; West, 2009; Kümmerli & Keller, 2011). For example, in polygynous ants (with multiple queens per colony), unbiased sex investment ratios are thought to arise from either reduced workers' relatedness asymmetry, or local resource competition between related queens to head new colonies, or a combination of these factors (Bourke & Franks, 1995; Crozier & Pamilo, 1996; Bourke, 2005).

The Wilson–Nowak sex ratio hypothesis for sex investment ratio in ants

Wilson (2012, p. 178) presented the Wilson–Nowak sex ratio hypothesis as follows:

The goal of the whole colony is to put as many future parents into the next generation as possible. In ant species generally, males are smaller and lighter than virgin queens, often strikingly so, because of the heavy fat reserves the queens must carry in order to start new colonies. Males cost less to make, and if the ratio of energy investment were 1 : 1, more males

than queens would be available for mating. Most commonly the young reproductives have only one chance to mate, so that, on average, producing an excess of males would be a waste for the colony. ...

As a result, it is in the best interest of both the mother queen and her worker daughters to bias energy investment in favor of virgin queens.

Wilson & Nowak (2014) likewise highlighted the fact that, in monogynous ants, queens show claustral, independent colony foundation, rearing their first worker offspring without foraging externally using energy derived from stored bodily reserves. They pointed out that claustrality explains the sexual size dimorphism seen in monogynous ants, whereby queens typically greatly exceed males in size. They then argued that claustrality is 'the decisive factor in the sex allocation of resources', essentially following the reasoning presented in Wilson (2012). In addition, Wilson & Nowak (2014) disputed the concept, from inclusive fitness theory, of worker control over sex allocation, calling it an 'error' and stating that 'the mother queen, not the workers, is in principal charge of which sex is preferred' because of her control of sperm release from the spermatheca. Polygynous ants lack claustral colony foundation, or at least do not show it to the same extent. It is for this reason, Wilson & Nowak (2014) argued, that polygynous ants show relatively unbiased population sex investment ratios.

To summarize, the Wilson–Nowak sex ratio hypothesis argues that, if the sex investment ratio in monogynous ants were 1 : 1, the numerical sex ratio would be male biased (given sexual size dimorphism with queens larger than males), and so some males would never mate (given both sexes generally mate once) and would represent 'waste'. Natural selection therefore selects for a 1 : 1 numerical sex ratio and hence a female-biased sex investment ratio. The hypothesis therefore assumes that selection on the sex ratio acts to maximize the number of females and males that are mated. Moreover, it asserts that queen and workers share a common interest in producing the same sex ratio, queens have principal control of sex allocation, and queen–worker conflict over sex allocation is absent.

Critique of the Wilson–Nowak sex ratio hypothesis

The facts that queens in monogynous and polygynous ant species show, respectively, claustral and nonclaustral colony foundation, and that this difference explains the relatively larger queens found in monogynous ants, are well established and not disputed (e.g. Cronin *et al.*, 2013). The facts that in most ant species both queens and males mate once or at most a few times, with multiple mating in both sexes occurring but being relatively rare, are likewise not disputed (Bourke & Franks,

1995; Strassmann, 2001; Boomsma *et al.*, 2005). What is disputed is the conclusion drawn from these facts by the Wilson–Nowak sex ratio hypothesis. The hypothesis has several flaws:

Contradicts Fisher's (1930) sex ratio theory

Fisher's (1930) sex ratio theory, which is supported by a huge body of later theory and empirical evidence (Charnov, 1982; Hardy, 2002; West, 2009), shows that selection on the population sex ratio is frequency dependent and does not act to maximize the number of females and males that are mated. In general, selection on the sex ratio is frequency dependent because the rarer sex will gain higher mating success, creating selection for overproduction of the rarer sex and so redressing imbalance in the sex ratio. There is no selection to maximize the number of females and males that are mated because selection acts on the average fitness return from rearing a member of either sex, while permitting variation about this average. To be more specific, consider the standard case in which a nonsocial female parent rears daughters and sons that mate randomly. Let c equal the cost ratio (per capita cost of a female/per capita cost of a male) and let the stable numerical sex ratio = $X : 1$ females : males. Then, if the mating success (average per capita number of mates) of females is set at 1 unit, that of males equals X units (there are X females for every male). By Fisher's (1930) sex ratio theory, the stable sex investment ratio occurs when per capita fitness returns on each sex per unit cost are equal (henceforth, the 'Fisherian condition'). Given the mother is equally related to sons and daughters, this occurs when

$$\text{female mating success}/c = \text{male mating success}.$$

In the present case, this condition is therefore $1/c = X$, from which, if costs are equal (i.e. if $c = 1$), $X = 1$. In short, as is well known, the stable sex ratio in this case is 1 : 1 and both sexes have equal mating success (of 1 unit). There are no terms for the mating frequencies of the sexes in the Fisherian condition. A numerical example shows why. Say that in the above case each female mated once and each male could mate 10 times. Take any set of 10 females and assume each is mated. As all 10 matings could have been gained by one male, nine of every 10 males could be unmated. Nonetheless, because 1 in 10 males would mate 10 times, male mating success would equal $((1 \times 10) + (9 \times 0))/10 = 1$ and hence would be unchanged. Thus, the Fisherian sex ratio is stable even if many males (in this case 90%) never mate and represent 'waste'. In this example, according to the Wilson–Nowak sex ratio hypothesis, natural selection would produce a numerical sex ratio of 10 : 1 females : males to avoid such

'waste'. However, this sex ratio would not be stable. If female mating success equalled 1 unit, male mating success would equal 10 units, and so mothers would be selected to overproduce males, driving the population sex ratio back to the 1 : 1 equilibrium.

Correspondingly, if in the starting example the numerical sex ratio were 1 : 1, this would be stable only for the case of $c = 1$, regardless of mating frequency. If the cost ratio were not 1, then the Fisherian condition would not be satisfied, as the fitness return from females would be $1/c$ and that from males would be 1. For example, with $c = 2$, mothers would be selected to overproduce males until the stable numerical sex ratio of 1 : 2 females : males was reached. Note that, at this equilibrium, 50% of the males would be unmated. Therefore, the Wilson–Nowak hypothesis contradicts Fisher's (1930) sex ratio theory even for the case of nonsocial organisms. Overall, from Fisher's theory, the ratio of mating successes is set by the relative numbers of females and males in the population-wide mating pool and not by the mating frequency of either sex (Trivers, 1985; Bourke & Franks, 1995). It follows that there is no selection to maximize the proportion of individuals mated. Consistent with this insight, there are many examples in nature, including in the eusocial Hymenoptera, where more males are produced than can ever achieve a mating. For instance, in the honeybee (*Apis mellifera*), the numerical sex ratio is very highly male biased and most males die never having mated (Winston, 1987).

Fisher's logic can now be applied to the case of monogynous ants. Because the stable sex ratio for the queen is the same as for a nonsocial mother, the sex ratio predicted in monogynous ants by the Wilson–Nowak sex ratio hypothesis (1 : 1 numerical sex ratio with $c > 1$) would not be an equilibrium for the queen. The Fisherian condition for the queen would be $1/c = 1$, which can only be satisfied when $c = 1$, contradicting the assumption of $c > 1$. A 1 : 1 numerical sex ratio could be an equilibrium for the workers, if $c = 3$. Then, the Fisherian condition for workers would be $0.75 \times 1/3 = 0.25 \times 1$, with 0.75 and 0.25 being workers' relatednesses to females (sisters) and males (brothers), respectively, and so would be satisfied. But, as Trivers & Hare (1976) showed, the stable sex ratios for the queen and workers would differ, negating the assumption of the Wilson–Nowak sex ratio hypothesis that both parties favour the same equilibrium. In sum, the Wilson–Nowak sex ratio hypothesis is a direct contradiction of the long-standing game-theoretical logic of Fisher's (1930) sex ratio theory in both nonsocial and social taxa.

Fails to explain split sex ratios

Both inclusive fitness theory and the Wilson–Nowak sex ratio hypothesis predict female-biased population

sex investment ratios in monogynous ants and unbiased population sex investment ratios in polygynous ants, each of which is observed (Bourke & Franks, 1995; Crozier & Pamilo, 1996; Bourke, 2005). However, in many eusocial Hymenoptera, including many monogynous ants, populations exhibit split sex ratios, with some colonies concentrating on female production and others on male production (Boomsma & Grafen, 1990). The Wilson–Nowak sex ratio hypothesis offers no explanation for split sex ratios. By contrast, inclusive fitness theory explains split sex ratios as a function of either variation in workers' relatedness asymmetry (via Boomsma & Grafen's (1990, 1991) split sex ratio theory) or ongoing queen–worker conflict over sex allocation (Helms, 1999; Bourke, 2005; Rosset & Chapuisat, 2006; Helanterä & Ratnieks, 2009; Kümmerli & Keller, 2009).

Evidence that colony-level sex investment ratios covary with either workers' relatedness asymmetry or the distribution of power to influence sex allocation between queens and workers is considerable (Queller & Strassmann, 1998; Bourke, 2005; Ratnieks *et al.*, 2006; Meunier *et al.*, 2008; Helanterä & Ratnieks, 2009; Kümmerli & Keller, 2009; West, 2009). These factors do not explain all cases of split sex ratios (e.g. Wiernasz & Cole, 2009; Debout *et al.*, 2010), and inclusive fitness theory recognizes that sex ratios at both population and colony levels are affected by many factors (Bourke, 2005; Meunier *et al.*, 2008; West, 2009; Kümmerli & Keller, 2011). However, in cases that are discriminating, available data support inclusive fitness theory but not the Wilson–Nowak sex ratio hypothesis. For example, the hypothesis cannot explain cases in monogynous ants in which colony-level sex ratios covary with workers' relatedness asymmetry and variation in workers' relatedness asymmetry arises through partial multiple mating by queens (e.g. Sundström, 1994; Sundström *et al.*, 1996), as mode of colony founding in these conditions is constant. Similarly, it cannot explain cases in facultatively polygynous ants in which colony-level sex ratios covary with workers' relatedness asymmetry independently of queen number (Evans, 1995; Heinze *et al.*, 2001). Finally, it cannot explain the results of studies finding that experimentally altering workers' relatedness asymmetry changes sex investment ratios in the direction predicted by inclusive fitness theory (Mueller, 1991; Evans, 1995).

Contradicts empirical evidence for queen–worker conflict over sex allocation

Contrary to the Wilson–Nowak sex ratio hypothesis, the empirical literature supports the occurrence of both queen and worker control and of ongoing queen–worker conflict over sex allocation. First, split sex ratios that covary with workers' relatedness asymmetry argue for worker control, because in these cases

queens' relatedness asymmetry is invariant and hence queens do not favour split sex ratios (Boomsma & Grafen, 1990, 1991). Second, in such populations, evidence suggests that workers achieve a female bias in colonies with high workers' relatedness asymmetry by either selectively destroying queen-derived male brood or selectively rearing an excess of new queens from developing queen-derived females (Sundström *et al.*, 1996; Hammond *et al.*, 2002). Similarly, in an ant in which queens controlled the primary sex ratio by varying the proportion of male, haploid eggs laid, workers increased allocation to females by selectively destroying queen-derived male brood (Rosset & Chapuisat, 2006). Such manipulations are unexplained by the assumption that queens and workers are in evolutionary agreement.

Wilson & Nowak (2014) dismissed these phenomena by arguing that workers' selective destruction of male brood is costly; that there is no reason to assume it does not serve the queen's and the colony's interests; and that many factors affect the caste of developing females. However, models show that workers' self-interested destruction of male brood can evolve despite its cost to colony productivity (Chapuisat *et al.*, 1997; Reuter *et al.*, 2004; Helms *et al.*, 2005). Inclusive fitness theory provides the reason why such selective destruction favours workers and not the queen, whose stable sex ratio is less female biased (Boomsma & Grafen, 1990, 1991), and the very fact that such a mechanism reduces colony productivity shows that colony interests are not met. The existence of other factors affecting caste does not explain findings suggesting that workers, via biasing caste determination, rear an excess of queens in colonies with a high workers' relatedness asymmetry (Hammond *et al.*, 2002). More generally, in some cases in which split sex ratios occur in the absence of between-colony variation in workers' relatedness asymmetry, evidence suggests that this arises from ongoing queen-worker conflict over sex allocation as predicted by inclusive fitness theory (Helms, 1999; Bourke, 2005; Rosset & Chapuisat, 2006; Helanterä & Ratnieks, 2009; Kümmerli & Keller, 2009).

Conclusion

Inclusive fitness theory for sex investment ratios in eusocial Hymenoptera is built on Fisher's (1930) sex ratio theory and offers a comprehensive framework for understanding sex allocation in all taxa within the group, including ants. The framework is strongly predictive, having successfully predicted several major phenomena *a priori*, including female-biased sex allocation in monogynous ants (Trivers & Hare, 1976) and split sex ratios covarying with workers' relatedness asymmetry (Boomsma & Grafen, 1990, 1991). By contrast, the Wilson–Nowak sex ratio hypothesis

contradicts Fisher's (1930) sex ratio theory for both nonsocial and social organisms and is a *post hoc* explanation for patterns of sex allocation observed in ants. In addition, unlike inclusive fitness theory, it is not supported by the empirical evidence regarding split sex ratios and queen–worker conflict over sex allocation. For these reasons, the Wilson–Nowak sex ratio hypothesis fails both as an alternative hypothesis for sex allocation in eusocial Hymenoptera and as a critique of inclusive fitness theory.

Inclusive fitness theory has been used to predict sex investment ratios across a very broad array of colony life cycles and mating systems in eusocial Hymenoptera, incorporating factors such as polyandry, polygyny, social parasitism, local mate competition and local resource competition (Trivers & Hare, 1976; Bourke & Franks, 1995; Crozier & Pamilo, 1996; West, 2009). As with any wide-ranging theory applied to complex phenomena, its predictions are not universally successful (e.g. Kümmerli & Keller, 2011). But, overall, the fit to data is strong (Bourke, 2005; Meunier *et al.*, 2008; West, 2009). Inclusive fitness theory therefore remains strongly supported by the evidence of sex investment ratios in eusocial Hymenoptera.

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