

Split sex ratios in the social Hymenoptera: a meta-analysis

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The study of sex allocation in social Hymenoptera (ants, bees, and wasps) provides an excellent opportunity for testing kin-selection theory and studying conflict resolution. A queen–worker conflict over sex allocation is expected because workers are more related to sisters than to brothers, whereas queens are equally related to daughters and sons. If workers fully control sex allocation, split sex ratio theory predicts that colonies with relatively high or low relatedness asymmetry (the relatedness of workers to females divided by the relatedness of workers to males) should specialize in females or males, respectively. We performed a meta-analysis to assess the magnitude of adaptive sex allocation biasing by workers and degree of support for split sex ratio theory in the social Hymenoptera. Overall, variation in relatedness asymmetry (due to mate number or queen replacement) and variation in queen number (which also affects relatedness asymmetry in some conditions) explained 20.9% and 5% of the variance in sex allocation among colonies, respectively. These results show that workers often bias colony sex allocation in their favor as predicted by split sex ratio theory, even if their control is incomplete and a large part of the variation among colonies has other causes. The explanatory power of split sex ratio theory was close to that of local mate competition and local resource competition in the few species of social Hymenoptera where these factors apply. Hence, three of the most successful theories explaining quantitative variation in sex allocation are based on kin selection. *Key words:* meta-analysis, queen–worker conflict, relatedness asymmetry, sex allocation, social insects, split sex ratio. [*Behav Ecol* 19:382–390 (2008)]

Kin selection extends natural selection to include the indirect transmission of copies of genes through relatives (Hamilton 1964). This theory is fundamental to understanding a wide variety of evolutionary phenomena such as the evolution of altruism and spite, the emergence of eusociality, and the presence of kin conflicts (Hamilton 1964, 1970, 1972; Bourke and Franks 1995; Gardner and West 2004; Ratnieks et al. 2006; West et al. 2007). Some of the clearest opportunities for testing kin-selection theory are provided by conflicts over sex allocation in the social Hymenoptera (Trivers and Hare 1976; Bourke and Franks 1995; Crozier and Pamilo 1996; Chapuisat and Keller 1999). Social Hymenoptera are haplodiploid with diploid females produced from fertilized eggs and haploid males from unfertilized ones. This sex-determination system results in relatedness asymmetries between workers (females who raise the brood) and sexual individuals (queens and males). When colonies are headed by 1 single-mated queen, workers are 3 times more related to sisters than to brothers, whereas queens are equally related to daughters and sons (Trivers and Hare 1976). Hence, kin selection predicts a potential conflict between queens and workers, with queens favoring a balanced sex allocation and full-sibling workers a 3 times larger investment in females than in males.

The quantitative predictions vary with changes in social structure, which affect relatedness asymmetry. Specifically, relatedness asymmetry is expected to decrease when (i) the queens mates with more than one male, (ii) the queen is replaced by one of her daughters, (iii) multiple related queens

reproduce in the same colony, and (iv) workers produce males (Hamilton 1972; Trivers and Hare 1976; Boomsma and Grafen 1990, 1991; Boomsma 1991, 1993; Foster and Ratnieks 2001). Under worker control, these changes in relatedness asymmetry should result in less female-biased sex allocation relative to the case with 1 single-mated queen, and on average, the degree of queen–worker conflict should decrease.

Variation in relatedness asymmetry can occur among species, among populations, and among colonies within populations. The comparison of sex allocation and relatedness asymmetry across ant species and populations provides evidence for partial worker control, with female-biased sex allocation in species that have a single queen per colony (monogyne colonies) and slightly male-biased sex allocation in species with multiple queens per colony (polygyne colonies; Trivers and Hare 1976; Pamilo and Rosengren 1983; Nonacs 1986a; Pamilo 1990; Bourke 2005). However, this pattern is open to multiple explanations due to correlated factors. In particular, queens from polygyne colonies often stay in their natal nest while males disperse, and this local resource competition (LRC) among queens also promotes male-biased sex allocation independently of the decrease in relatedness asymmetry (Crozier and Pamilo 1996; Chapuisat and Keller 1999).

The most powerful method for testing the queen–worker conflict over sex allocation is to examine if sex ratio is split according to relatedness asymmetry variation among colonies within populations. The theory predicts that under worker control, colonies with relatively high or low relatedness asymmetry should specialize in producing females or males, respectively (Boomsma and Grafen 1990, 1991; Boomsma 1991). In as many as 19 out of 25 species or populations studied so far, colony sex allocation is indeed split according to measured or putative variation in relatedness asymmetry (Queller and Strassmann 1998; Chapuisat and Keller 1999; Mehdiabadi et al. 2003; Bourke 2005). This general pattern is consistent

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with widespread worker control and provides strong qualitative support to kin-selection theory (Queller and Strassmann 1998; Chapuisat and Keller 1999; Bourke 2005). However, the magnitude of adaptive sex allocation biasing by workers has not been quantified so far.

In this study, we performed a meta-analysis on empirical tests of split sex ratio theory. Our first aim was to use all published studies to quantify the impact of worker control over colony sex allocation in the social Hymenoptera. Our second aim was to examine if the degree of sex allocation adjustment depends on the source and/or magnitude of relatedness asymmetry variation. Relatedness asymmetry can vary among colonies because of queen replacement, variation in queen mating frequency, and variation in queen number under certain conditions. All types of studies have been used to qualitatively test split sex ratio theory, but they are likely to differ with respect to information constraints and strength of selection on worker behavior, which depends on the magnitude of variation in relatedness asymmetry (Boomsma et al. 2003; Bourke 2005). For example, the replacement of a queen by one of her daughters is probably easy to detect by workers, and it results in the highest decrease in relatedness asymmetry (3:1 to 1:1). In contrast, workers might have more difficulty to assess the number of males that have mated with the queen because queens mate before the birth of the workers and store the sperm for the rest of their life. Workers therefore have to infer mate number from the level of colony genetic diversity, which might be a difficult task particularly if the cost of nepotistic behavior selects against genetically based odor cues (Boomsma et al. 2003). Higher number of queens also decreases relatedness asymmetry when queens are related (Boomsma 1993; Bourke and Franks 1995). However, changes in relatedness asymmetry might be small, continuous, and somewhat erratic because of the dynamics of queen replacement, and therefore they are likely to be difficult to assess for workers in polygynous colonies. Our third aim was to compare the explanatory power of split sex ratio theory to the other most successful areas of sex allocation—local mate competition (LMC, which predicts a bias toward females when related males compete over access to females; Hamilton 1967) and LRC (which predicts a bias toward males when related females compete over resources; Clark 1978).

METHODS

Collection of data

We performed a large-scale search for studies that contained relevant data and read abstracts to select studies on social Hymenoptera. We combined several methods: (1) searching for references in reviews of the subject (Herbers 1979; Nonacs 1986a, 1986b; Bourke and Franks 1995; Crozier and Pamilo 1996; Queller and Strassmann 1998; Chapuisat and Keller 1999; Mehdiabadi et al. 2003; Bourke 2005; Ratnieks et al. 2006); (2) searching the Institute for Scientific Information Web of science on 7 May 2007 for all articles containing at least one of the following expressions: “sex ratio variation,” “relatedness asymmetry,” “sex investment ratio,” “queen mating,” “monoandrous,” “monandrous,” “polyandrous,” or “split sex ratio”; and (3) searching citations in all papers found by the above method. We obtained more than 700 studies out of which 27 were relevant for our aims.

We did not include studies for which appropriate effect sizes could not be calculated, such as studies without data on both colony sex allocation and variation of colony relatedness asymmetry or breeding system (Brian 1979; Pamilo and Rosengren 1983; Ward 1983; Strassmann 1984; Elmes 1987; Herbers 1990; Stark 1992; Fuchs and Schade 1994; Vargo

1996; Helms 1999). Because the meta-analysis requests an estimate of the correlation between sex allocation and relatedness asymmetry, we had to exclude studies in which there was no variation in relatedness asymmetry among colonies within populations (Passera et al. 2001; Duchateau et al. 2004). We also excluded studies based on experimentally selected colonies (Kikuchi et al. 2002) or on worker relatedness without information on queen number, queen relatedness, or queen mating frequency in a slave-making ant species (Pamilo and Seppä 1994). In few cases, we contacted the authors to obtain additional information on published data sets (Yanega 1989; Queller et al. 1993; Pearcy and Aron 2006).

We separately collected studies that investigated the impact of competitive interactions among relatives on sex allocation in social Hymenoptera. We used the data set of West et al. (2005), complemented by searching the Institute for Scientific Information Web of science on 7 May 2007 for all articles containing at least one of the expressions “local resource competition” or “local mate competition” in social Hymenoptera. As a result, we added 3 new studies published since 2005 to the 9 studies on social Hymenoptera reviewed in West et al. (2005).

Data analysis

We analyzed our data using meta-analysis methods, where the calculated effect size of each study is used as a response variable in a global analysis (Rosenthal 1991; Rosenberg et al. 2000). Each effect size (r) is a correlation coefficient providing an estimate of how colonies adjust their sex allocation in response to relatedness asymmetry variation, queen number variation, or competitive interactions (LRC plus LMC). We defined a positive effect size when colonies with higher relatedness asymmetry (or smaller queen number, lower LRC, and higher LMC) had a more female-biased sex allocation and negative when colonies with lower relatedness asymmetry (or larger queen number, higher LRC, and lower LMC) had a more female-biased sex allocation. Hence, a positive, large effect size indicates that sex allocation followed the predicted pattern.

We calculated effect sizes using standard methodology (Rosenthal 1991; Rosenberg et al. 2000). The values sometimes come from the Spearman rank correlation coefficient (r_s) provided in the publication. In other cases, the effect size could be calculated from the statistics (e.g., t , χ^2 , F , Z , or P values) and sample size using standard formulas (Rosenthal 1991; Rosenberg et al. 2000). If the test statistics were derived from the analysis of variance (ANOVA) with more than 2 treatments, we applied an ordered heterogeneity (OH) test (see Rice and Gaines 1994). Finally, when values were not available, we used raw data given in figures or tables. The proportion of variance in colony sex allocation that is explained by the factor is given by r^2 .

All analyses were performed using the software package Metawin 2.0 (Rosenberg et al. 2000) with random-effect model (Møller and Jennions 2002; West et al. 2005) and the statistical software R.2.5.0 (Ihaka and Gentleman 1996). Statistical analyses were conducted on Z -transformed r values (Zr) to correct for asymptotic behavior of large values of r (Sheldon and West 2004), and the bias-corrected 95% confidence interval (CI) were obtained by bootstrapping (Rosenberg et al. 2000). We tested for statistical differences between the mean effect sizes with randomized ANOVA in which effect sizes were randomly permuted 10 000 times between factors (Manly 1997). Results were back transformed to r values for presentation.

We conducted each analysis with 1 mean effect size per species in each factor category (relatedness asymmetry variation, queen number variation, and competitive interactions

Table 1
Mean effect sizes of studies investigating sex allocation adjustment in response to relatedness asymmetry variation, queen number variation, and competitive interaction among relatives

Class of study Factor	Mean effect size (r)	95% CI	Number of species
Relatedness asymmetry variation	0.457**	0.211–0.674	7
Queen replacement	0.552**	0.300–0.786	3
Mate number	0.368*	0.003–0.648	4
Queen number variation	0.223**	0.107–0.323	15
Monogyne versus polygyne colonies	0.090	–0.216–0.320	9
Count of queens in polygyne colonies	0.240**	0.071–0.426	4
From relatedness variation	0.354**	0.292–0.484	6
Competitive interactions among relatives	0.501**	0.375–0.619	10
LRC	0.496**	0.285–0.660	7
LMC	0.473**	0.222–0.601	4

Asterisks indicate effect sizes that are significantly greater than 0 (* $P < 0.05$, ** $P < 0.01$).

among relatives; Table 1 and Appendix). When the same species was studied in several populations or over several years, we calculated an average Zr , weighted by sample size. We summed up sample sizes when different colonies were sampled and calculated an average when the same colonies were sampled repeatedly.

We used several methods to detect a potential publication bias—a tendency to be more likely to publish studies with significant results. First, we plotted the effect sizes against sample sizes. In the absence of publication bias, the plot should have a funnel shape with the values of effect sizes equilibrating to the average when sample size increases (Møller and Jennions 2001). In contrast, a significant negative correlation between effect size and sample size suggests that studies with significant results have been preferentially published, which causes a deficit of studies with nonsignificant results and small sample sizes. Second, we applied the “trim and fill” method to evaluate the bias in the funnel plot and the significance of the result (Johnson et al. 2000). This method estimates the number (L_0) and effect size of studies that are missing from a meta-analysis due to publication bias and then adds them to the data set, recalculates the mean effect size, and derives its statistical significance (Møller and Jennions 2002). Finally, we calculated the “fail-safe number” (X), which is the number of unpublished studies with an effect size of 0 that would be needed to change the result from significant to not significant (Rosenthal 1991). Interpretation of the meaning of X depends in part on the subjective assessment of whether so many unpublished studies are likely to exist. A quantitative criterion is that a result is robust if $X > 5n + 10$, where n is the number of studies on which the meta-analysis was based, although this criterion is hard to meet with small sample sizes (Rosenberg et al. 2000).

We investigated whether the degree of worker control was linked to the magnitude of relatedness asymmetry variation between colonies in the population. This magnitude of relatedness asymmetry variation was estimated as the proportion $\frac{RA_{high}}{RA_{high} + RA_{low}}$ in which RA_{high} and RA_{low} were mean relatedness asymmetries in the highest and lowest relatedness asymmetry classes, respectively (see Appendix for details). In some cases, these relatedness asymmetries were directly measured with microsatellite or allozyme markers. In other cases, they were inferred from social structure variation (mate number, mother or sister queen, queen number). The relatedness asymmetry within polygyne colonies was estimated as

$1 + \frac{2}{1 + r_q(n-1)}$, where n is the number of queens and r_q the relatedness among queens that we assumed to be equal to the relatedness among workers because queens are usually recruited back into their natal colony in species with polygyne colonies (Boomsma 1993; Crozier and Pamilo 1996). When not available, the number of queens was estimated as $\frac{3-r_w}{(r_w - \frac{r_q}{4}) \times 4}$, where r_w is the relatedness among workers (Hughes et al. 1993; Boomsma 1993).

RESULTS

Relatedness asymmetry variation

We found 7 studies with quantitative data on sex allocation adjustment in response to relatedness asymmetry variation among colonies due to queen replacement or mate number variation (Appendix). Data on queen replacement by daughter were available for 3 species of sweat bees, and data on mate number variation were available for 3 ant and 1 bumblebee species.

Overall, sex allocation was significantly correlated with relatedness asymmetry, in the direction predicted by worker control, with a mean effect size of $r = 0.457$ (Table 1). Hence, worker control according to relatedness asymmetry explains 20.9% of the variance in sex allocation. The extent of sex allocation adjustment did not depend on the cause of relatedness asymmetry variation. Specifically, there was no significant difference between the mean effect size of studies on queen replacement by daughter ($r = 0.552$) and variation in mate number ($r = 0.368$; randomized ANOVA, $n = 7$, $P = 0.54$). However, the number of species studied was small and the trend was in the direction predicted by the information constraints, which are higher for mate number variation than queen replacement.

The effect sizes were highly variable but seemed to be uniformly distributed and showed no sign of a publication bias (Figure 1). The trim and fill analysis did not detect missing studies ($n = 7$, number of missing studies $L_0 = 0$), and there was no significant correlation between effect size and sample size (Spearman rank correlation test, $n = 7$, $r_s = -0.036$, $P = 0.94$). The fail-safe number was small ($X = 15$, quantitative criterion = 45), but the criterion is extremely hard to meet with small sample sizes (Rosenberg et al. 2000).

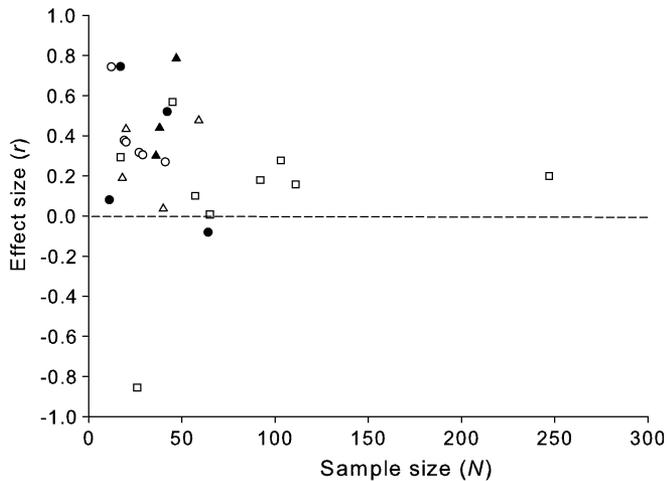


Figure 1

Relationship between effect size and sample size for studies on queen replacement by daughter (filled triangles), variation in mate number (filled circles), comparison between monogynous and polygynous colonies (open squares), queen number variation inferred from the count of queens in polygynous colonies (open triangles), and queen number variation inferred from relatedness (open circles). Each point corresponds to 1 species.

Queen number variation

We found 16 studies examining sex allocation adjustment and queen number variation among colonies (Appendix). There were data on sex allocation in monogynous and polygynous colonies for 8 ant and 1 wasp species, data on the correlation between sex allocation and counts of queens in polygynous colonies for 4 ant species, and data on sex allocation with respect to queen number inferred from relatedness variation for 1 ant and 5 wasp species.

Overall, sex allocation was significantly correlated with queen number variation, in the predicted direction that colonies with higher queen numbers produced more males (Table 1, $r = 0.22$). Hence, changes in queen number explained on average 5% of the variance in sex allocation. This value is conservative because 6 out of the 15 effect sizes had to be calculated from P value thresholds or without applying OH test, resulting in slightly underestimated effect sizes (see Appendix).

The impact of queen number variation on sex allocation did not depend on the group of study. The mean effect size of the comparison between monogynous and polygynous colonies, queen number variation in polygynous colonies, and queen number variation inferred from relatedness were not significantly different (randomized ANOVA, $n = 19$, $P = 0.263$). It is possible that the comparison between monogynous and polygynous colonies had a lower and nonsignificant effect size because polygynous colonies can occasionally be headed by unrelated queens and thus have high relatedness asymmetries (e.g. Fournier et al. 2003). However, interpreting the differences is delicate as there was overall no significant difference between the mean effect sizes of relatedness asymmetry variation and queen number variation (randomized ANOVA, $n = 22$, $P = 0.20$).

The mean effect size became nonsignificantly different from 0 when carrying out a trim and fill analysis ($n = 15$, number of missing studies $L_0 = 5$, adjusted mean $r = 0.132$, 95% CI: 0.08–0.253, $P > 0.05$). This small, adjusted mean effect size might be partly due to the 6 studies for which the effect size was slightly underestimated (see Appendix). Otherwise, there was no significant correlation between sample size

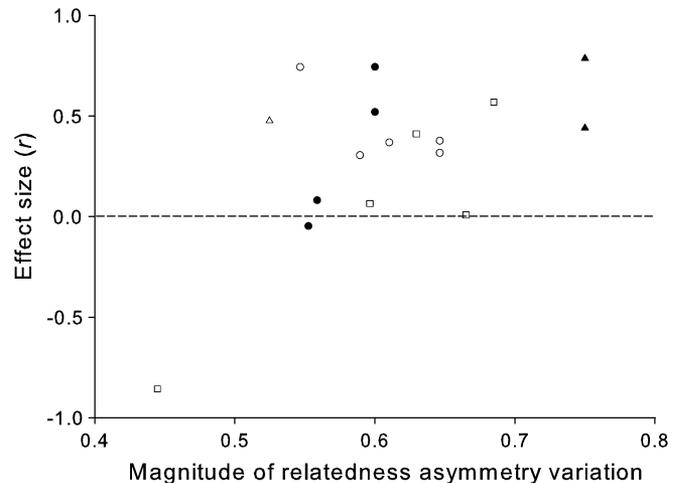


Figure 2

Relationship between effect size and magnitude of relatedness asymmetry variation for studies on queen replacement by daughter (filled triangles), variation in mate number (filled circles), comparison between monogynous and polygynous colonies (open squares), queen number variation inferred from count of queen in polygynous colonies (open triangle), and queen number variation inferred from relatedness (open circles).

and effect size (Spearman rank correlation test, $n = 15$, $r_s = -0.357$, $P = 0.19$) and the fail-safe number was large ($X = 78$, quantitative criterion = 115).

Effect size and magnitude of relatedness asymmetry variation

The magnitude of variation in relatedness asymmetry among the most differing classes of colonies could be measured for 17 studies (Appendix). Overall, it was not significantly correlated with effect size (Figure 2, Spearman rank correlation test, $n = 17$, $r_s = 0.331$, $P = 0.20$). This nonsignificant pattern held when analyses were restricted to studies on queen replacement and mate number variation (Spearman rank correlation test, $n = 6$, $r_s = 0.736$, $P = 0.10$) or queen number variation (Spearman rank correlation test, $n = 11$, $r_s = 0.10$, $P = 0.77$). It should, however, be noted that these analyses are based on small data sets and that the correlations tend to be positive, particularly in the case of queen replacement and mate number variation.

Competitive interactions among relatives

We found 12 studies on 10 species examining how competitive interactions among relatives influence sex allocation in the social Hymenoptera. These involved 7 studies on LRC and 6 studies on LMC, in 10 ant species. Overall, sex allocation shows a significant correlation with the extent of competitive interactions between relatives, with a mean effect size of $r = 0.501$ (Table 1). Hence, competitive interactions among relatives explain 25.1% of the variance in sex allocation. This did not depend on the group of study—the mean effect size of the LRC ($r = 0.496$) and the mean effect size of the LMC ($r = 0.473$) were not significantly different (randomized ANOVA, $n = 9$, $P = 0.92$).

The effect sizes were highly variable but seemed to be uniformly distributed and showed no sign of publication bias. The trim and fill analysis did not detect missing studies ($n = 10$, number of missing studies $L_0 = 0$), we did not detect a lack

of studies with both nonsignificant result and small sample size (Spearman rank correlation test, $n = 10$, $r_s = -0.195$, $P = 0.59$), and the fail-safe number was large and above the quantitative criterion ($X = 155$, quantitative criterion = 60), which strongly suggests that there was no significant publication bias.

There was no significant difference between the mean effect sizes of competitive interactions, relatedness asymmetry variation, and queen number variation (randomized ANOVA, $n = 32$, $P = 0.15$).

DISCUSSION

Overall, this meta-analysis reveals that workers of social Hymenoptera bias colony sex allocation in their favor when relatedness asymmetry varies among colonies, as predicted by split sex ratio theory. When the queen was replaced by a daughter or mated with more than one male, variation in relatedness asymmetry explained 20.9% of the variance in sex allocation among colonies. This value is considerably higher than the average (3.6%) amount of variance explained in ecological and evolutionary studies (Møller and Jennions 2002) and hence provides a quantification of the success of split sex ratio theory.

While confirming the significant and pronounced impact of workers on colony sex allocation, the meta-analysis also reveals that worker control is far from complete as approximately 80% of the variance in sex allocation among colonies remains unexplained. Many uncontrolled stochastic factors can affect the sex ratio of field colonies, and a large amount of the variance in the data set might be due to such noise. However, part of the variance might also come from yet unrecognized adaptive predictors of sex allocation. One such potential source of variation among colonies that deserves further investigation is that queens might prevent worker manipulation by providing male-destined haploid eggs in some colonies and female-destined diploid eggs in other colonies (Passera et al. 2001; Roisin and Aron 2003; de Menten, Fournier, et al. 2005b; Rosset and Chapuisat 2006).

A somewhat surprising result of our survey was that very few studies contained quantitative data on both sex allocation and relatedness asymmetry variation. This contrasts with recent reviews that listed numerous qualitative results (Queller and Strassmann 1998; Bourke 2005) and suggests that further studies documenting quantitative variation are still needed to permit a more detailed analysis of the factors influencing the degree of sex ratio adjustment by workers.

One important aspect of the meta-analysis is that despite the small sample size, there was little sign of publication bias.

In particular, there was no lack of studies on relatedness asymmetry variation that had small sample sizes and small effect sizes. Hence, the conclusion that workers bias colony sex allocation in their favor is unlikely to be due to the nonpublication of studies with negative results.

Queen number variation explained 5% of the variance, a value that is also significantly greater than 0. This result is consistent with worker control as relatedness asymmetry generally decreases when queen number increases. It is, however, difficult to evaluate the precise degree of adaptive sex allocation manipulation by workers because queen number variation is a variable of a different order that generally correlates with variation not only in relatedness asymmetry but also in LRC, life histories, and ecological factors (Ross and Keller 1995; Chapuisat and Keller 1999; Rosset and Chapuisat 2007).

The degree of worker control did not differ significantly among studies with different sources of variation in relatedness asymmetry (queen replacement, mate number, queen number). Hence, we found no support for the hypothesis that workers have more control when relatedness asymmetry is easier to assess (e.g., queen replacement versus mate number). Similarly, the degree of sex ratio adjustment by workers did not correlate significantly with the magnitude of the variation in relatedness asymmetry among colonies, suggesting that workers were not more likely to bias the sex ratio in their favor when differences in relatedness asymmetry among colonies were large. This contrasts with several previous analyses which have suggested that the strength of selection and information constraints may limit the extent of sex allocation adjustment in both vertebrates and invertebrates (Herre 1987; West and Sheldon 2002; Boomsma et al. 2003; Schino 2004; Sheldon and West 2004; Griffin et al. 2005). However, both analyses in this study suffer from a lack of power due to the very small and heterogeneous data set, and there were trends in the predicted direction, which stresses the importance of obtaining data from a greater range of species.

Overall, split sex ratio theory explained approximately 20% of the variance in sex allocation among social Hymenoptera colonies exhibiting variation in relatedness asymmetry, which is close to the 25% explained by LMC and LRC in the few species of social Hymenoptera where relatives compete. These values are very high compared to many ecological and evolutionary studies and confirm the remarkable predictive power of sex allocation theory (West et al. 2005). Moreover, worker control of sex ratio, LMC, and LRC are 3 processes based on kin selection. Hence, kin selection proves central and very successful at explaining sex allocation variation in social animals.

APPENDIX

Studies used in the meta-analysis. The “factor” indicates the source of variation being tested in each class of study, the “effect size” is the correlation between colony sex allocation and the relevant factor, and the “magnitude of relatedness asymmetry variation” is a measure of the proportion of variation in relatedness asymmetry among colonies in the population, estimated as $\frac{RA_{high}}{RA_{high} + RA_{low}}$ in which RA_{high} and RA_{low} are mean relatedness asymmetries in the highest and lowest relatedness asymmetry classes, respectively.

Species	Factor	Effect size (<i>r</i>)	Magnitude of relatedness asymmetry variation	Sample size	Reference
(a) Studies on relatedness asymmetry variation					
Ants					
<i>Formica exsecta</i>	Mate number	0.520 ¹	0.60	42	Sundström et al. (1996)
<i>Formica truncorum</i>	Mate number	0.745 ²	0.60	17	Sundström and Ratnieks (1998)
<i>Lasius niger</i>	Mate number	-0.047 ³	0.55	64	Fjerdingstad et al. (2002)
Bees					
<i>Augochlorella striata</i>	Queen replacement	0.440 ⁴	0.75	38	Mueller (1991)
<i>Bombus hypnorum</i>	Mate number	0.081 ⁵	0.56	11	Paxton et al. (2001)
<i>Halictus rubicundus</i>	Queen replacement	0.786 ⁶	0.75	47	Yanega (1989), Boomsma (1991)
<i>Lasioglossum laevisimum</i>	Queen replacement	0.300 ⁷	NA	36	Packer and Owen (1994)
(b) Studies on queen number variation					
Ants					
<i>F. exsecta</i>	Queen number inferred from relatedness	0.270 ⁸	NA	41	Kümmerli R, personal communication
<i>F. exsecta</i>	Count of queens in polygyne colonies	0.476 ⁹	0.52	59	Brown and Keller (2000)
<i>F. exsecta</i> (mean of the 2 above studies)		0.386		50	
<i>Formica podzolica</i>	Monogyne versus polygyne colonies	0.180 ¹⁰	NA	84	Deslippe and Savolainen (1995)
<i>Formica selysi</i>	Monogyne versus polygyne colonies	0.008 ¹¹	0.67	65	Rosset and Chapuisat (2006)
<i>Leptothorax acervorum</i>	Monogyne versus polygyne colonies	0.411 ¹²	0.63	116	Hammond et al. (2002)
<i>L. acervorum</i>	Monogyne versus polygyne colonies	0.068 ¹³	NA	80	Chan et al. (1999)
<i>L. acervorum</i>	Monogyne versus polygyne colonies	0.065 ¹⁴	0.60	51	Heinze et al. (2001)
<i>L. acervorum</i> (mean of the 3 above studies)		0.200		247	
<i>Leptothorax longispinosus</i>	Monogyne versus polygyne colonies	0.278 ¹⁵	NA	103	Herbers (1984)
<i>Myrmica ruginodis</i>	Monogyne versus polygyne colonies	0.569 ¹⁶	0.68	45	Walín and Seppä (2001)
<i>M. ruginodis</i>	Count of queens in polygyne colonies	0.434 ¹⁷	NA	20	Walín and Seppä (2001)
<i>M. ruginodis</i> (mean of the 2 above studies)		0.533		33	
<i>Myrmica tahoensis</i>	Monogyne versus polygyne colonies	0.159 ¹⁸	NA	111	Evans (1995)
<i>Pheidole pallidula</i>	Monogyne versus polygyne colonies	-0.856 ¹⁹	0.45	26	Fournier et al. (2003)
<i>P. pallidula</i>	Count of queens in polygyne colonies	0.190 ²⁰	NA	18	Helms et al. (2004)
<i>P. pallidula</i> (mean of the 2 above studies)		-0.501		22	
<i>Stenamma debile</i>	Monogyne versus polygyne colonies	0.101 ²¹	NA	57	Buschinger and Heinze (2001)
<i>S. debile</i>	Count of queens in polygyne colonies	0.037 ²²	NA	40	Buschinger and Heinze (2001)
<i>S. debile</i> (mean of the 2 above studies)		0.075		49	
Wasps					
<i>Brachygastra mellifica</i>	Queen number inferred from relatedness	0.744 ²³	0.55	12	Hastings et al. (1998)
<i>Parachartergus colobopterus</i>	Queen number inferred from relatedness	0.377 ²⁴	0.65	19	Queller et al. (1993)
<i>Polistes fuscatus</i>	Monogyne versus polygyne colonies	0.294 ²⁵	NA	17	Noonan (1978)
<i>Polybia emaciata</i>	Queen number inferred from relatedness	0.368 ²⁴	0.61	20	Queller et al. (1993)
<i>Polybia occidentalis</i>	Queen number inferred from relatedness	0.317 ²⁴	0.65	27	Queller et al. (1993)
<i>Protolybia exigua</i>	Queen number inferred from relatedness	0.305 ²⁴	0.59	29	Queller et al. (1993)
(c) Recent studies on competitive interactions among relatives that complement the data set of West et al. (2005)					
Ants					
<i>Cardiocondyla minutior</i>	LMC	0.225 ²⁶		37	Heinze et al. (2004)
<i>Cardiocondyla obscurior</i>	LMC	0.593 ²⁷		14	de Menten, Cremer, et al. (2005)
<i>Cataglyphis cursor</i>	LRC	0.089 ²⁸		14	Pearcy and Aron (2006)

Notes on the calculation of effect sizes and magnitudes of relatedness asymmetry variation in Appendix (tables refer to each article).

¹ Proportion of females produced by single-mated queen versus multiple-mated queen colonies, $P_{1994} = 0.006$, $P_{1995} = 0.0001$. The relatedness asymmetry was inferred to be 3:1 and 2:1 in single-mated queen and multiple-mated queen colonies, respectively.
² Proportion of females produced by single-mated queen versus multiple-mated queen colonies, $F_{1,14} = 12.7$ for 1989–1991 and $F_{1,16} = 25.9$ for 1992–1995. The relatedness asymmetry was inferred to be 3:1 and 2:1 in single-mated queen and multiple-mated queen colonies, respectively.
³ Sex investment ratio in single-mated queen versus multiple-mated queen colonies, Lausanne $Z_{(1997)} = -0.25$ and $Z_{(1998)} = -1.16$, Uppsala $Z = -0.19$. We calculated a weighted average from the relatedness asymmetries in Table 5, which were measured with 2 microsatellite markers.
⁴ Sex investment ratio in eusocial (queen present) versus parasocial (queen replaced by a daughter) colonies, $t = 2.08$. The relatedness asymmetry was inferred to be 3:1 and 1:1 in eusocial and parasocial colonies, respectively.

Appendix footnotes, continued

- ⁵ Sex investment ratio in single-mated queen versus multiple-mated queen colonies, data from Table 2, excluding the 3 colonies that produced fewer than 5 individuals, 1-tailed Wilcoxon rank-sum test, $P = 0.394$. The relatedness asymmetry, measured with 4 microsatellite markers, was 3:1 and 2.37:1 for single-mated queen and multiple-mated queen colonies, respectively.
- ⁶ Proportion of females produced by eusocial (queen present) versus parasocial (queen replaced by a daughter) colonies, chi-squared test, $\chi^2 = 29.02$. The relatedness asymmetry was inferred to be 3:1 and 1:1 in eusocial and parasocial colonies, respectively.
- ⁷ Correlation between sex investment ratio and relatedness asymmetry, $r_s = 0.30$. The relatedness values between classes of nest mates indicate that queen replacement is the most likely source of relatedness asymmetry variation among colonies.
- ⁸ Correlation between sex investment ratio (proportion or resources allocated to females) and worker-brood relatedness in polygyne colonies, unpublished data, $r_s = 0.270$.
- ⁹ Genetic effective queen number in female- versus male-producing polygyne colonies, $F_{1,39} = 11.43$. We calculated the relatedness asymmetry in polygyne colonies as described in Methods, using effective queen number of 2.7 and worker relatedness of 0.087 in female-producing colonies and effective queen number of 6.7 and worker relatedness of 0.062 in male-producing colonies.
- ¹⁰ Proportion of males produced by polygyne versus monogyne colonies, $F_{2,78} = 1.16$, $P = 0.03$. The OH test on these statistics gave $r_s = 1$, $P_c = 0.70$, and final $P = 0.05$.
- ¹¹ Sex investment ratio in monogyne versus polygyne colonies, $Z_{(2001)} = -0.11$ and $Z_{(2002)} = -0.01$. The relatedness asymmetry, measured with 9 microsatellite markers, was 2.76:1 and 1.39:1 in monogyne and polygyne colonies, respectively.
- ¹² Sex investment ratio in monogyne versus polygyne colonies, $F_{1,110} = 22.3$. The relatedness asymmetry, measured with 5 microsatellite markers, was 3.4:1 and 2.0:1 for monogyne and polygyne colonies, respectively.
- ¹³ Sex investment ratio in monogyne versus polygyne colonies, excluding data from the Santon population which were presented in Hammond et al. (2002), Aberfoyle $F_{1,29} = 0.02$ and Roydon $F_{1,23} = 0.39$.
- ¹⁴ Sex investment ratio in monogyne versus polygyne colonies, $P = 0.64$. The relatedness asymmetry in monogyne colonies was inferred to be 3:1. We calculated the relatedness asymmetry in polygyne colonies as described in Methods, using the median queen number of 3 and worker relatedness of 0.493.
- ¹⁵ Proportion of males produced by polygyne versus monogyne colonies, $P = 0.07$. The OH test on these statistics gave $r_s = 1$, $P_c = 0.93$, and final $P = 0.0024$.
- ¹⁶ Sex investment ratio in monogyne versus polygyne colonies, Leimann $P = 0.031$ and Täktom $P = 0.002$. The relatedness asymmetry was measured with 4 allozyme loci. In the Leimann population, it was 2.71:1 and 1.55:1 for monogyne and polygyne colonies, respectively. In the Täktom population, it was 2.68:1 and 0.92:1 for monogyne and polygyne colonies, respectively.
- ¹⁷ Correlation between sex investment ratio and queen number in polygyne colonies, from the data in Appendix, Leimann $r_s = -0.457$ and Täktom $r_s = -0.395$.
- ¹⁸ Sex investment ratio in queenless monogyne and polygyne colonies, $\chi^2_{(2)} = 2.79$. The data set was not amenable to OH test, so the effect size for monogyne versus polygyne colonies is conservative.
- ¹⁹ Sex investment ratio in monogyne versus polygyne colonies, $F_{1,22} = 60.13$. The relatedness asymmetry, measured with 4 microsatellite markers, was 2.66:1 and 3.32:1 for monogyne and polygyne colonies, respectively. These values do not differ significantly, and the magnitude of relatedness asymmetry variation was estimated with the relatedness asymmetry of monogyne colonies in the numerator.
- ²⁰ Correlation between proportion of females and queen number in polygyne colonies, $r_s = -0.19$.
- ²¹ Proportion of females produced by monogyne versus polygyne colonies, data from Tables 2–4, excluding queenless colonies, 1-tailed Wilcoxon rank-sum test, $W = 369$, $P = 0.223$.
- ²² Correlation between sex investment ratio and queen number in polygyne colonies, data from Tables 2–4, excluding queenless colonies, Spearman rank correlation test, $r_s = -0.037$.
- ²³ Relatedness among females in female-producing colonies versus relatedness among workers in male-producing colonies, 1-tailed t -test, $P < 0.005$. The effect size is conservative because it had to be calculated from the P value threshold. We calculated the relatedness asymmetry as described in Methods, estimating queen number from worker relatedness given in Table 1.
- ²⁴ Relatedness among females in female-producing colonies versus relatedness among workers in male-producing colonies, t -test, $P < 0.05$ for each of the 4 species. Effect sizes are conservative because they had to be calculated from the P value thresholds. We calculated the relatedness asymmetry as described in Methods, using relatedness among queens and relatedness among workers in female- and male-producing nests, respectively.
- ²⁵ Sex investment ratio in colonies founded by one versus several queens, data from Table 1, Wilcoxon rank-sum test, $W = 41.5$, $P = 0.113$.
- ²⁶ Proportion of haploid eggs in polygyne versus monogyne colonies, $\chi^2_{(4)} = 2.161$. The OH test on these statistics gave $P = 0.086$.
- ²⁷ Proportion of ergatoid males in polygyne versus monogyne colonies, $\chi^2 = 4.93$.
- ²⁸ Correlation between proportional investment in females and total sexual productivity, $Z = -0.334$.

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