Insectes Sociaux

RESEARCH ARTICLE

Sex allocation in the ant *Camponotus (Colobopsis) nipponicus* (Wheeler): II. The effect of resource availability on sex-ratio variability

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Abstract Sex-ratio studies have played a prominent role in tests of kin selection theory in the eusocial Hymenoptera. The winner in sex-ratio conflict between queens and workers must control the ratio through proximate mechanisms. To determine how a colony adjusts its sex ratio, the mechanism of sex-ratio determination was analyzed in the field in colonies of the ant *Camponotus (Colobopsis) nipponicus*. A path model including five colony characteristics showed that the resource availability of the colony (quantified as the amount of stored fat in the bodies of the workers) has a large positive effect on the proportion of new queens in the female larvae, but has little effect on male production. The results indicated that a colony adjusts the sex ratio by altering the proportion of new queens obtained from a diploid brood in response to resource availability rather than by eliminating male larvae.

Keywords Ants · Sex ratio · Resource availability · Hymenoptera

Introduction

Since Trivers and Hare (1976) proposed that the queens and workers in eusocial Hymenoptera have conflicting interests over sex allocation, sex-ratio studies have played a prominent role in tests of kin selection theory. Many empirical results and theoretical formulations have been presented (Taylor, 1981; Pamilo and Rosengren, 1983; Ward, 1983; Herbers, 1984, 1990; Nonacs, 1986a,b; Bourke et al., 1988; Boomsma, 1989; Pamilo, 1991; Hasegawa, 1994; Helms, 1999; Fournier et al., 2003; Helms et al., 2004). Although queens and workers have conflicting interests in sex allocation at the population level (Trivers and Hare, 1976; Pamilo, 1991; Crozier and Pamilo, 1993; Mehdiabadi et al., 2003; Helms et al., 2005; Rosset and Chapuisat, 2006; Helanterä and Ratnieks, 2009), the sex ratios in individual colonies have been shown to vary considerably. Shaw and Mohler (1953) showed that if the population sex ratio is at equilibrium, all sex ratios in a colony, from all males to all females, are equally fit because the return per unit investment becomes equal for both sexes. Thus, factors affecting sex allocation in colonies must be considered separately from factors affecting the population sex ratio.

The power to manipulate the sex ratio is crucial for optimizing the sex ratio in accordance with one's own interest (Rosset and Chapuisat, 2006; Helanterä and Ratnieks, 2009). From this viewpoint, the proximate mechanisms for manipulating the sex ratio are important determinants of the winner of this conflict. The ultimate factors affecting sex-ratio variation among colonies have been reviewed by Kümmerli and Keller (2009), but the two possible proximate mechanisms of sex-ratio manipulation by workers are male elimination (Chapuisat et al., 1997) and manipulation of female development (Hammond et al., 2002).

The winner in the conflict over sex allocation differs on a case-by-case basis (Hasegawa 1994; Chapuisat et al., 1997; Helms, 1999; Passera et al., 2001; Hammond et al., 2002; Fournier et al., 2003), but the outcome of the conflict is determined by the relative abilities of the conflicting parties

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to perform sex-ratio manipulation. Thus, we need to know how a colony adjusts its sex ratio if we are to examine the balance of power between the queens and the workers. The effects of experimental and natural variation in the food supply on sex ratios have been examined in several ant species (Boomsma et al., 1982; Backus and Herbers, 1992; Deslippe and Savolainen, 1995; Morales and Heithaus, 1998; Brown and Keller, 2006; Kümmerli and Keller, 2009), but additional data are still needed to evaluate the relationship between the manipulation mechanism and the identity of the winner. I examined the effect of resource availability on the sex ratio in the field in colonies of the ant *Camponotus (Colobopsis) nipponicus*. A colony of *C. nipponicus* includes sterile workers with a singly mated queen, and the sex ratio is optimized for the workers, i.e., 0.250 ± 0.027 to females (Hasegawa, 1992, 1994). The sex-ratio distributions are unimodal and do not show a split sex-ratio pattern (Hasegawa, 1994). The *C. nipponicus* workers accumulate energy reserves as fat bodies in their gaster, and the amount of stored fat in the workers is correlated with the food supply to the colony (Hasegawa, 1993). Using this trait, I test whether food supply/fat body impacts into gynes in this ant. The results will show sex-ratio adjustment through female development and not through male killing.

Materials and methods

Study organism

Camponotus nipponicus is an arboreal, nocturnal ant that nests in the hollows of dead twigs in warm regions of Japan (Hasegawa, 1992). This ant is monogynous and has dimorphic worker subcastes (major and minor), both of which can store resources as fat bodies in their gaster (Hasegawa, 1992, 1993). Adult workers overwinter with larvae that will pupate as adults by early summer. The overwintered larvae grow rapidly after late March, and the destination (queen, male, major and minor workers) of the overwintered larvae can be distinguished after May by their body shape (Hasegawa, 1992). The queen does not lay eggs during the winter. Male-destined eggs are laid predominantly in July and August (Hasegawa, 1992, 1994), meaning that males arose from the overwintered larvae. Thus, the small larvae found in early summer are the brood produced by eggs laid after hibernation. Nuptial flights occur after early August. In each sex, an individual has a single mate. There is no sign of inbreeding or population subdivision (Hasegawa, 1994).

Sampling and colony characteristics

The study site was a coastal forest at Amatsukominato, Chiba, Japan. Samples were collected in early July in 1990 and in late June in 1991 and 1992. In these 3 years, 17, 17 and 8 trees, respectively, were selected randomly within the study site, and all dead twigs attached to these trees were collected. Only twigs with *C. nipponicus* nests were brought to the laboratory, and they were broken open to collect the nest members. A total of 45, 53 and 32 colonies were collected in 1990, 1991 and 1992, respectively. All nest members were counted to identify their physical caste, and the larvae were further classified into three size categories: (1) small larvae, <1.60 mm in length, the category representing larvae produced after hibernation; (2) sexual larvae, the larvae that will pupate as alate females or males and whose larger size and body shape at maturity enables them to be distinguished by sex from worker-destined larvae (Hasegawa, 1992); and (3) worker-destined larvae, those larvae (1.60–3.50 mm in length) that do not fall into either of the preceding two categories and can be considered to represent overwintered and worker-destined individuals. These categorizations enabled me to determine the numbers of males, new queens, and workers in the overwintered larvae, in addition to the number of individuals in the new brood produced after hibernation. Because *C. nipponicus* is nocturnal, daytime collection allowed me to collect all nest members.

Because *C. nipponicus* has two distinct worker subcastes, the total dry weight of workers was used as an index of colony size. For each colony, the total weight of workers was estimated from the pupal dry weights of each subcaste to avoid the overestimation that would result from using the dry weight of the adult workers (the adult weight includes additional nutrition acquired after eclosion). To estimate the amount of stored fat in each nest, ten individuals were selected randomly for each subcaste, and fat was extracted by preservation in acetone (for details, see Hasegawa, 1993). The fat content of each subcaste was calculated by subtracting the dry weight of the body from the dry weight before fat extraction. The total amount of stored fat was calculated from these values and was used as an index of resource availability for the field colonies. The colony boundaries were determined by testing the behavioral interactions of workers from adjacent nests (for the behavioral test, see Hasegawa, 1992). The sex allocation ratio in each colony was estimated from the average dry weights of the adult alates (for females, 2.721 mg; for males, 0.456 mg; see Hasegawa, 1994).

Path analysis

Six colony characteristics [colony size (CS), total amount of colony fat; FAT, number of males; NM, number of overwintered female larvae (queen-destined females + worker-destined females, both of which are >1.60 mm in size at the time of collection); NF, number of small larvae (<1.60 mm); SBR, proportion of new queens in overwintered female

larvae; PQ, sex allocation ratio (male/(male + female)), R] were used to analyze the mechanism determining the sex allocation ratio in a colony. The determinants of sex allocation in the colonies were investigated with a path analysis (Wright, 1921). Path analysis estimates the sign and magnitude of directional relationships in interaction networks (=path diagram) (for details, see Li, 1975; Sokal and Rohlf, 1994; Crespi and Bookstein, 1989; Crespi, 1990; Herbers, 1990).

Construction of the path diagram

A path diagram was constructed to represent the biology of *C. nipponicus*. During the winter, the brood in a *C. nipponicus* nest consists solely of larvae. Male eggs are produced during the previous summer (Hasegawa, 1992). From the spring to the early summer, a colony accumulates resources in the form of fat bodies in the workers (FAT), and the queen produces new eggs that develop into small brood (SBR). The proportion of queens in the overwintered females (PQ) is determined in the spring. A path diagram was constructed from this information. The diagram shows that interactions among CS, NM and NF affect FAT and SBR, that all of these factors affect PQ, and that R is determined as a result (Fig. 1a). In the diagram, causal relationships are represented by one-headed arrows, and the double-headed arrows in the diagram represent the correlations between pairs of variables. Because males and females show differential rates of energy consumption during their development (Boomsma and Isaaks, 1985), I treated NM and NF as two separate variables in the diagram.

Evaluation of the path model

A path model predicts a correlation between two variables connected by a double-headed arrow (Herbers, 1990; Sokal and Rohlf, 1994). The internal consistency of the path diagram can be evaluated by comparing the correlations expected from the diagram with the observed correlations. To test the consistency of the path diagram used in this study, the correlation between FAT and SBR expected from the path diagram was compared with the observed value.

The three data sets obtained during each sampling year (1990–1992) were analyzed separately, and the sign and magnitude of the path coefficients were compared among the data sets to identify the factors that showed consistent effects on the other variables. The factors that showed consistent effects were interpreted as important factors (Herbers, 1990). To normalize the data distributions, all proportional data were standardized with an arcsine transformation (Sokal and Rohlf, 1994). For the path analysis, all data were standardized by their mean and standard deviation. The path coefficients were calculated as the partial
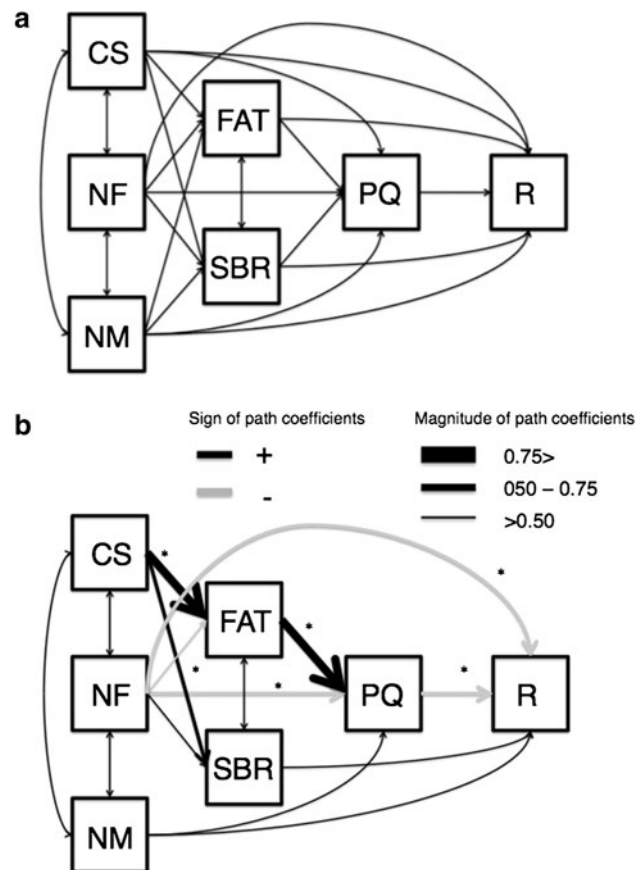

Fig. 1 a The path diagram for examination of the mechanism of sex-ratio determination within a colony. A *double-headed arrow* shows correlation between variables, and a *single-headed arrow* represents the causal relationship between a causal variable and the response variable. **b** The results of the path analysis based on 3 years of data. The *black single-headed arrows* represent consistently positive effects over 3 years, and the *gray single-headed arrows* represent consistently negative effects. The *thickness* of the *arrow* represents the magnitude of the path coefficient. Causal relationships are presented only if they showed a consistent sign over 3 years. The *asterisks* show the effects in which at least a path coefficient is statistically significant

regression coefficients of the dependent variables on the independent variables in a path diagram (Herbers, 1990). Only paths showing consistent signs across the data sets were viewed as indications of robust relationships. For those paths, the average magnitude was used to represent the strength of the effect (Fig. 1b).

Results

Relationship between colony productivity
and investment in each sex

Figure 2 shows the relationships between the total number of brood in a colony (as an index of colony productivity) and the investment in each sex. The investment in each sex
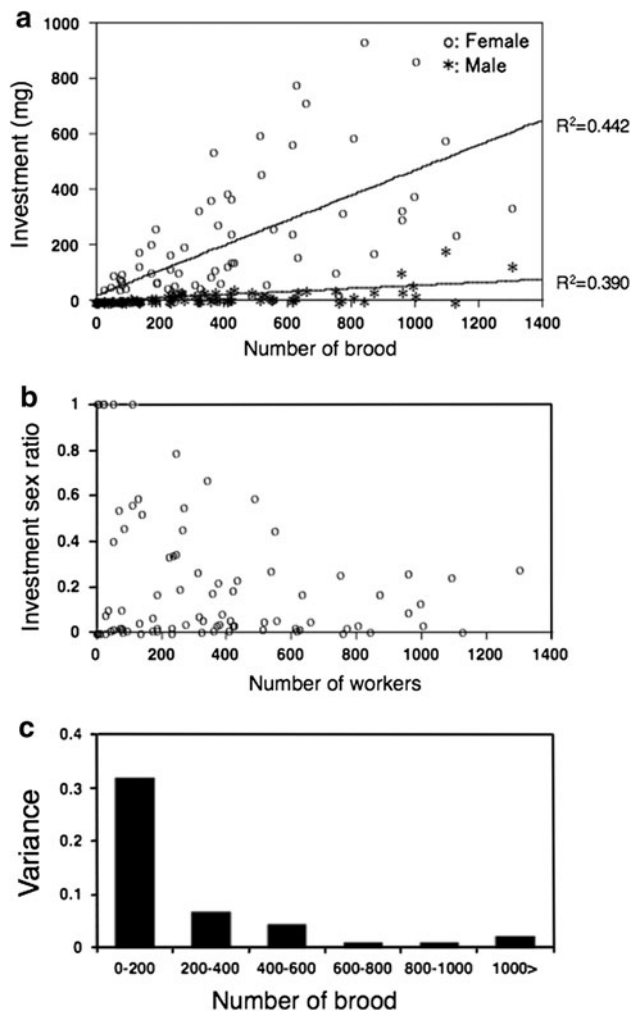
Fig. 2 **a** The relationship between the total number of brood in a colony (as an index of colony productivity) and the number of reproductive females (*open circle*) or males (*asterisks*). The regression line is shown for each sex. **b** The relationship between the total number of workers (as an index of colony size) and the investment sex ratio. **c** The value of the variance in the sex investment ratio for each class of colony productivity. Colony productivity is represented by the total number of brood in a colony, and the productivity is divided into five classes

Table 1 Evaluation of the constant sex hypothesis

Year (n)	Observed correlation between IF and IM	Proportion of variance in TSI explained by	
		IF	IM
1990 (31)	0.736*	0.503*	0.126*
1991 (27)	0.643*	0.724*	0.045*
1992 (17)	0.780*	0.686*	0.044*

TSI, IF and IM represent total sexual investment, investment in sexual females, and investment in males, respectively

* $p < 0.001$

Table 2 Observed and expected correlation (r) between the amount of stored fat in workers' body (FAT) and the number of small larvae (SBR)

Years	Observed r	Expected r	Explained proportion of variance in	
			FAT	SBR
1990	0.689	0.604	0.945	0.546
1991	0.767	0.786	0.896	0.906
1992	0.947	0.912	0.988	0.908

The expected correlations were estimated from the path diagram (Fig. 1a). The proportions of the total variance explained in each variable are also shown

Results of the path analysis

Table 2 shows the expected and the observed correlations between the fat reserve and the number of small brood and the proportion of variance explained by the model. In all 3 years, the observed correlations were close to the expected values. Thus, the internal consistency of the path diagram was high. Figure 1b shows the results of the path analysis. Among the path coefficients that showed consistent signs over the 3 years, the colony size had a positive effect on the fat reserve (0.92 ± 0.09; mean ± SE) and the number of small brood (0.57 ± 0.24). The fat reserve had a strong positive effect on the proportion of queens in the diploid larvae (1.51 ± 0.58). The number of females had negative direct effects on the proportion of queens in the diploid larvae (−0.63 ± 0.13) and the investment sex ratio (−0.69 ± 0.05). The number of females also had a positive effect on the number of small brood (0.55 ± 0.19). The number of males had a positive direct effect on both the proportion of queens (0.17 ± 0.13) and the investment sex ratio (0.23 ± 0.08), and the proportion of queens had a negative direct effect on the investment sex ratio (−0.65 ± 0.10). The signs of the path coefficient of the other causal relationships changed over the years and were, thus, not robust.

increased with colony productivity, but the investment in females was widely distributed around the regression line. This result showed that much of the variance in the total sexual investment was explained by the investment in females. A different analysis also supported this view. The investment in reproductive females explained large proportions of the variance in the total sexual investment (50.3, 72.4 and 68.6 % in 1990, 1991 and 1992, respectively; Table 1), whereas the investment in males explained far less of the variance in the TSI (12.6, 4.5 and 4.4 % in 1990, 1991 and 1992, respectively; Table 1).

Among the coefficients discussed above, the effect of the fat reserve on the proportion of queens in the diploid larvae is important. Thus, the robustness of this relationship was examined further. Because the structure of a path diagram may have substantial effects on the path coefficients, I removed the number of females (NF), the number of males (NM) and the number of small brood (SBR) and the possible combinations of these variables from the original diagram and recalculated the path coefficient linking the fat reserve to the proportion of queens for each simplified diagram. The three data sets resulted in additional 21 path coefficients. All but one of these 21 coefficients had positive signs. Thus, the observed positive effect is robust to possible changes in the path diagram. These results indicate that the resource availability of a colony controlled the proportion of new queens in the female larvae in *C. nipponicus*.

Examination of the male elimination hypothesis

In *C. nipponicus*, the fat content of the workers increased rapidly after hibernation (Hasegawa, unpubl.), and most female larvae do not attain the queen-destined size during the spring (Hasegawa, 1992). Therefore, if the sex ratio is regulated by eliminating excess males rather than by controlling the proportion of new queens (Aron et al., 1994, 1995), the number of males will be controlled in response to the number of new queens. In this case, a large proportion of the variance in the male proportion of the total brood would be explained by the variance of the proportion of queens in the female larvae. However, only 1.5 % of the variance in the male proportion was explained by the proportion of queens (regression analysis, $F = 1.118$, n.s.).

Discussion

In social ants without worker reproduction, only queens can manipulate primary sex ratio by additional production of male-destined eggs; whereas workers can bias secondary sex ratio by male eliminations (Chapuisat et al., 1997) or a developmental manipulation for female larvae (Hammond et al., 2002). If ants control male numbers in response to the availability of resources to their colony, two possible ways of achieving such regulation are possible: (1) the elimination of male-destined larvae or (2) the laying of additional male-destined eggs. Aron et al. (1994, 1995) demonstrated that workers of *Iridomyrmex humilis* and *Solenopsis invicta* removed a portion of the male-destined eggs from their colony. Queens from monogynous *Pheidole pallidula* colonies produced a more highly male-biased primary sex ratio than queens from polygynous colonies (de Menten et al., 2005). In *C. nipponicus*, even male-destined eggs produced in early summer cannot develop into adults by the mating

season of the same year (see Hasegawa, 1992). Accordingly, a possible alternative mechanism for sex-ratio regulation through male number is the elimination of male larvae. If workers regulate the colony sex ratio by male elimination, the excess male number should be adjusted in response to the number of new queens. If this is the case, a large part of the variance in the proportion of males in the sexual larvae should be explained by the variance in the proportion of new queens in the females. However, such a relationship was not detected. Male elimination is not the case in *C. nipponicus*.

In *C. nipponicus*, most female larvae do not attain the queen-destined size during the spring (Hasegawa, 1992). Low food availabilities seem to switch queen production to major worker production from large overwintered larvae (Hasegawa, unpubl.). These facts suggest that fate of a larva is determined after hibernation. The observed large effect in contrast to the species in which male elimination occurs, *C. nipponicus* appears to regulate the sex ratio through the proportion of new queens in the diploid larvae. In the path analysis, two major colony characteristics, the colony size and the fat reserve, showed no consistent direct effect on the investment sex ratio in the colony (Fig. 1b). However, the fat reserve showed strong, positive direct effects on the proportion of queens in the diploid larvae, and this positive effect was robust to the change made in the structure of the path diagram. Although the colony size did not have a direct effect on the proportion of queens, this variable showed an indirect positive effect on the proportion of queens through a direct effect on the fat reserve. Note that a path coefficient between two variables is a value that controls the effects of the other variables (Sokal and Rohlf, 1994). In addition, the pupal dry weight was used to estimate colony size to avoid the overestimation that would result from the use of adult weight due to nutrition acquired after eclosion. These results showed that the fat reserve primarily regulates the proportion of queens irrespective of colony size. Thus, resource availability is a primary determinant of the sex ratio within a colony of *C. nipponicus*.

Several ant species have been shown to alter the sex ratio in response to the availability of an additional food supply (Boomsma et al., 1982; Backus and Herbers, 1992; Deslippe and Savolainen, 1995; Morales and Heithaus, 1998; Brown and Keller, 2006; Pearcy and Aron, 2006; Kümmerli and Keller, 2009). Thus, sex-ratio regulation through queen development depending on resource availability may be common in ants. The way that a colony adjusts the sex ratio affects the outcome of sex-ratio conflict between queens and workers (Rosset and Chapuisat, 2006; Helanterä and Ratnieks, 2009). In *C. nipponicus*, the manipulation of larval development may favor the workers in conflict with the queen over the sex ratio. Hasegawa (1994) has demonstrated that the population sex ratio is optimized for the

workers in this species. Ant workers actually engage in brood rearing and can thus control the development of larvae in response to the resources available to the colony. The queens would have only a limited way (e.g., production of male-destined eggs) to counter against the workers. In ants, the winner in queen–worker conflict situations depends on the particular situation in question (Hasegawa, 1994; Chapuisat et al., 1997; Helms, 1999; Passera et al., 2001; Hammond et al., 2002; Fournier et al., 2003). It is interesting to consider the identity of the winning party in the light of the proximate mechanism for sex-ratio regulation. Additional studies on such proximate mechanisms will be useful for this purpose.

C. nipponicus is an obligate monogynous ant. In this species, a colony contains a singly mated queen (Hasegawa, 1994). Because the colony queen produces only males, there is no variation in relatedness asymmetry among colonies (Hasegawa, 1994). The population sex ratio is at the workers' optimum. This finding suggests that the workers are the winners of the conflict over sex allocation (Hasegawa, 1994). In *C. nipponicus*, the workers would control the sex ratio in the colony by altering the proportion of queens in the female larvae. Ant queens can oppose worker control by producing a male-biased primary sex ratio (de Menten et al., 2005), but an extremely male-biased ratio in the eggs will decrease colony growth. In addition, the workers cannot convert new workers to new queens without restrictions because a colony must ensure the production of the minimum number of workers required for the next season. Thus, the way that a colony adjusts the sex ratio is a question of life-history evolution. Therefore, it is of interest to examine the relationship between colony growth and the sex-ratio pattern from the perspective of life-history evolution in eusocial Hymenoptera.

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