ORIGINAL ARTICLE

William D. Brown · Laurent Keller

Resource supplements cause a change in colony sex-ratio specialization in the mound-building ant, *Formica exsecta*

Abstract We examine the role of food resources on split sex ratios in *Formica exsecta*. Models of resource-based sex allocation predict that greater resources will cause an increase in the production of reproductive females (gynes) and an increase in overall size of offspring. We experimentally increased food resources for a subset of colonies in a polygynous population with a very male-biased sex ratio. This increase in food availability caused colonies that were male specialists the prior year to switch to female production. Overall, a significantly greater proportion of food-supplemented colonies produced gynes, compared to control colonies. Moreover, food-supplemented colonies produced significantly larger workers and males (but not gynes), compared to those produced by control colonies. There was, however, no significant difference in the numerical productivity of food-supplemented and control colonies. We also measured the natural association between colony sex specialization and proximity to conifers, which typically harbor honeydew-bearing aphids (an important natural food source). In line with the view that resources play an important role for determining sex ratios in social insects, we found that female-producing colonies were significantly closer to conifers than were male-producing colonies.

Keywords Hymenoptera · Productivity · Resources · Sex allocation · Social insects

W. D. Brown (✉)
Department of Biology,
State University of New York at Fredonia,
Fredonia, NY 14063, USA
e-mail: William.Brown@fredonia.edu

L. Keller
Department of Ecology and Evolution, Biophore,
University of Lausanne,
Lausanne 1015, Switzerland

Introduction

Split sex ratios, i.e., an extreme specialization in the sex of reproductive offspring with some colonies producing mainly males and others mainly females within populations, are one of the most intriguing phenomena in ants and other social Hymenoptera. To date, split sex ratios have been mostly explained on the basis of colony-level variations in kin structure. Relatedness asymmetries cause colony members to have different inclusive fitness gains from rearing male vs female offspring, leading to queen-worker conflict over relative allocation of resources in the two sexes (Trivers and Hare 1976; Charnov 1978; Nonacs 1986a; Pamilo 1991). Because queens are equally related to both sexes of reproductives, their equilibrium investment is expected to equal a 1:1 ratio of the sexes but workers are expected to adjust the sex ratios depending on their relatedness to male vs female brood. When relatedness asymmetries within a colony exceed the population average, workers should specialize on reproductive females (gynes), but when relatedness asymmetries fall below this average, they should specialize on males (Boomsma and Grafen 1990, 1991; Boomsma 1991, 1993; Ratnieks 1991; Bourke and Chan 1994; Ratnieks and Boomsma 1997).

Support for relatedness-induced split sex ratios is mixed, and a growing number of studies suggest that ecological constraints (Deslippe and Savolainen 1995; Aron et al. 1999; Helms 1999; Ode and Rissing 2002; Bono and Herbers 2003; Foitzik et al. 2003) and queen control (Passera et al. 2001; Fournier et al. 2003; Helms et al. 2004; Helms et al. 2005; de Menten et al. 2005) may also play a fundamental role. To date, there have been few experimental tests of hypotheses for split sex ratios in social insects, but evidence supporting a role for food resources comes from a field study in which Deslippe and Savolainen (1995) provided additional food to colonies of the ant *Formica podzolica*. These colonies allocated a significantly greater proportion of their resources to gynes than did untreated colonies. Similarly, experimental supplements of seeds increased gyne production in the ant

Aphaenogaster rudis (Morales and Heithaus 1998). Bono and Herbers (2003) showed that *Myrmica brevispinosa* colonies produced more gynes in response to supplemental sugar but supplemental protein had no effect on sex ratio or productivity. In contrast, Aron et al. (2001) showed that supplemental protein increased proportional investment in sexuals vs workers in the Argentine ant (*Linepithema humile*), though it did not alter sex ratios. Herbers and Banschbach (1998) found that food supplements shifted sex ratios towards greater production of females in the ant *Temnothorax longispinosus*, although a previous study had shown the opposite pattern (Backus and Herbers 1992).

A positive relationship between food availability and gyne production is predicted by a pair of models of sex-ratio variation that focus on resources, rather than relatedness, as the causal variables of sex-ratio variation. First, the queen-replenishment hypothesis (Brown and Keller 2000; Brown et al. 2002) holds that gyne production depends on resources available per queen in species with polygynous (multiple-queen) colonies. According to the queen-replenishment hypothesis, related female offspring compete for opportunities to reproduce within the natal colony, a phenomenon known as local resource competition. However, the intensity of local resource competition within the natal colony will decrease as the abundance of resource grows and at some point colonies will benefit from gaining additional reproductive queens. Thus, only colonies with excess resources per queen will produce females. Colonies with a shortage of resources per queen will specialize on male production and we generally predict a male-biased population sex ratio. Second, the hypothesis of multifaceted parental investment (MFPI) (Rosenheim et al. 1996) also predicts that greater resources will spur female production. MFPI holds that, because gynes are large and especially costly to produce, their production may often be constrained by a lack of sufficient resources available to the colony. Therefore, when resources are scarce, diploid offspring are channeled into becoming workers rather than reproductives, while males still develop into sexual adults; when resources are abundant, colonies specialize on production of gynes (Nonacs 1986a,b; Rosenheim et al. 1996).

In this study, we provide an experimental test of the relationship between food availability and sex ratio by altering the pool of food resources available to individual colonies of polygynous *Formica exsecta* and measuring sex-ratio specialization. Although the vast majority of colonies produce only male sexuals in polygynous *F. exsecta* and the population sex ratio is typically very male biased (Brown and Keller 2000; Brown and Keller 2002; Liautard et al. 2003), we predict that food supplements will stimulate a switch from male production before feeding to female production afterwards. Because aphid honeydew is an important natural food resource for this species and many other *Formica* species, we also examine the relationship between colony sex specialization and proximity to potentially aphid-bearing conifers.

Materials and methods

We studied a population of polygynous *F. exsecta* located at Les Chenevières, a pasture at approximately 1,200 m in the commune of Le Vaud in the Jura Mountains of Switzerland. This population has been the subject of several previous studies (Brown and Keller 2000; Keller et al. 2001; Brown and Keller 2002; Brown et al. 2002; Liautard and Keller 2001; Brown et al. 2003). The study population contains more than 1,200 nests (Liautard et al. 2003) with high year-to-year survivorship and is characterized by a moderate level of polygyny, with a median value of about six queens per colony based on genetic measures of effective queen number (Brown and Keller 2000). These colonies had been previously mapped and marked with a unique alphanumerical code written onto a wooden stake that was driven into the ground immediately adjacent to the nest.

Food supplements

The experiments began when workers resumed foraging in spring, immediately after snow-melt (ca. April 1). From previous work, we had knowledge of the sex-ratio specialization of each colony during the earlier breeding season. We selected 39 previously male-producing colonies and 21 previously female-producing colonies. We included a greater number of male-producing colonies because they are much more numerous and because we were primarily testing the ability of food supplements to cause a shift from male to female production. We supplemented resources (food-plus treatment) for 30, randomly chosen colonies and left the remaining 30 colonies as unmanipulated controls. Food supplementation was conducted by placing tuna (a protein source) and honey (a sugar source) on or immediately adjacent to the nest every third day beginning in the spring and continuing until sexual brood became pupae (late June). Sugar and protein sources were distributed ad libitum and separately into 9-cm plastic Petri dishes. Approximately 100 g of honey and 30 g of tuna were provided once every 3 days. We estimate that an approximate total of 3 kg of honey and 1 kg of tuna were provided per treatment colony over the entire breeding season. Most, but not all, of the food supplements were usually consumed during this period, suggesting that we had satiated the colonies with these particular nutrients. Large *Formica aquilonia* colonies of about one million workers consume approximately 200 kg of sugar per season (Rosengren and Sundström 1987, 1991). Assuming that *F. exsecta* require similar amounts per worker and given that *F. exsecta* colonies contain between 5,000 and 25,000 workers (Brown et al. 2002), we estimated that colonies should require from 1 to 5 kg of sugar during the period of sexual production. Thus, our treatment should have come very close to meeting the maximum requirements of sugar and protein.

For each focal colony, we estimated the investment in males, gynes, and workers by using the mark-recapture method of Sundström ([1995]). The vast majority of sexuals are produced from the first eggs laid during the season. Once most larvae had entered the pupal stage, but before any had emerged as adults, nests were gently opened and between 20 and 3,980 pupae per colony were collected from just beneath the surface. A total of 63,309 pupae were individually marked with a dot of ink from a nontoxic, permanent red marker (Sharpie). Pupae were released back into the nest by gently opening the surface, returning the marked pupae, and closing the nest. Workers continuously move pupae within the nest (presumably to locations of optimum temperature and humidity) and effectively mix the brood. Two days later, we captured another sample of pupae and used the proportion of marked to unmarked pupae to estimate the total number of pupae within the colony.

Colony sex specialization and progeny production

We also collected 10–150 pupae per colony to estimate the ratio of workers, gynes, and males. Progeny sex and caste were estimated by moistening pupae in ethanol and observing the size, eye shape, and genitalia of late-stage pupa. Males of *F. exsecta* are size-dimorphic (Agosti and Hauschteck-Jungen [1987], Fortelius et al. [1987]) and pupae fall into three nearly discrete size categories corresponding to workers, small males, and the combination of large males and gynes. Male pupae were classified as large if their size was identical to that of the gynes. Otherwise, they were counted as small males. Large males are generally produced in female-producing colonies, whereas small males are produced within both male- and female-producing colonies. As in previous studies (Brown and Keller [2000]; Brown et al. [2002]; Liautard et al. [2003]), we classified colonies as male producing if they produced no gynes and female-producing if they produced gynes, usually along with large and small male progeny.

To determine dry weights, we collected adult males and gynes (up to 10 individuals per sex and morphotype per nest) before flight as they emerged from their nest. Young workers were obtained by collecting worker pupae from each colony and placing them in laboratory nests with ca. 50 adult workers and a small amount of nest material. New workers were easily identified as callow, tan-colored individuals and were collected within 24 h after eclosion from the pupae. All individuals were dried at 60°C for 24 h, and weighed on a MT5 Mettler balance accurate to 0.01 mg.

Colony size

We estimated the size of the worker force using the protocol for worker mark-recapture outlined by Sundström ([1995]) and Brown et al. ([2002]). Before brood emerged, 200 to 2,000 adult workers per colony were collected, counted, sprayed lightly with a leather and wood spray paint, and released back onto the nest. Approximately 24 h later, workers were recaptured on the nest and the total number of workers was estimated from the proportion of marked to unmarked ants.

Experimental analyses

Colony size and numerical production of progeny were normalized (Kolmogorov–Smirnov test, Lilliefors $P>0.05$) by ln transformation before analyses. Relative worker production was transformed by the arcsine of the square root. Means were backtransformed and are reported with backtransformed 95% confidence intervals.

Supplemental food may affect any of three components of overall brood production: (1) total number of progeny (numerical productivity), (2) caste ratios (including sex ratios), or (3) individual sizes within castes. Because MFPI and the queen-replenishment hypotheses make specific predictions about how resources will alter productivity, we tested each of these three effects separately. We used ANCOVA to analyze the effect of treatment on numerical brood production, using food supplementation vs control as a fixed factor and colony size as a covariate.

Next, we analyzed the consequences of food treatments on colony sex ratios using two analyses. First, we analyzed frequencies at which colonies switched their sex-ratio specialization in response to food supplements, predicting that food-supplemented colonies would be more likely to switch from male-producing to female-producing because of the added resources per queen. Second, we compared the proportion of female-producing colonies between treatment and control groups, using logistic regression with colony size (worker number) and productivity as covariates. We also tested the effect of food supplements on proportional allocation to workers. Four colonies (three controls and one treatment) produced no sexual brood and are excluded from sex-ratio analyses.

Finally, we analyzed the effect of treatment on the dry mass of individual progeny using a nested ANOVA, within individual dry mass as the dependent variable and colony identity as a factor nested within treatment.

Sex specialization and proximity to conifers

Because conifers tend to harbor aphids that produce honeydew, a major food source for *Formica* species, we tested the prediction that colonies situated closer to conifers would have a greater resource base and, thus, would be more likely to specialize on female sexual progeny. To test this prediction, we recorded sex specialization by opening nests and recording the presence or absence of gyne pupae and we then measured the distance from the edge of colony dome to the nearest conifer using a 50-m measuring tape. We collected these data for a total of 162 colonies in six populations within pastures in the Swiss Jura Mountains,

including Le Bois de Gaye, La Comb aux Rocs, Les Orgères, Le Pré de Joux, Le Pré Nouveau, and nonexperimental colonies in the population at Les Chenevières (see Liautard et al. 2003 for information about these populations).

Results

Effect of food supplements on sex specialization and worker production

Food supplements had a significant effect of the direction in which sex ratios changed between years. Specifically, supplemental feeding increased the rate at which colonies switched to female production if the colony was originally male-producing ($\chi^2=5.61$, $df=1$, $P<0.05$); 12 of 20 (60%) food-supplemented colonies switched to female production, compared to only 3 of 15 (20%) of control colonies. Supplemental feeding increased the rate at which colonies remained female-producing, though not significantly so (Fisher's exact test, $P>0.05$); four of seven (57%) food-supplemented colonies remained as female producing, compared to 4 of 14 (29%) control colonies.

Similarly, within the year of the experiment, food supplements resulted in a significantly greater proportion of female-producing colonies ($\chi^2=7.14$, $df=1$, $P<0.01$). Overall, 16 of 27 (59%) food-supplemented colonies produced females whereas only 7 of 29 (24%) control colonies produced females. Female-producing colonies were also significantly larger (Wald=5.59, $df=1$, $P=0.02$).

As we have shown previously (Brown et al. 2002), male-producing colonies produced significantly more workers than female-producing colonies ($F_{1,52}=22.28$, $P<0.0005$). However, there was no significant independent effect of food supplements on worker production ($F_{1,52}=2.06$, $P=0.16$). Only female-producing colonies produced large males, but within female-producing colonies, there was no effect of food supplements on numerical investment in large males ($t=0.95$, $df=19$, $P=0.10$).

Effect of food supplements on progeny number and size

Colony size had a strong positive effect on numerical productivity ($F_{1,52}=12.41$, $P<0.001$) but food supplements did not significantly affect the total number of progeny produced (ANOVA $F_{1,52}=0.05$, $P=0.82$). The average (backtransformed) numerical productivity was 14,052 (95% CI 6,495–30,387) brood in control colonies and 13,899 (95% CI 5,996–32,220) brood in treatment colonies.

Although total numbers of progeny were equivalent, colonies receiving food supplements tended to produce significantly larger progeny. As reported above, a higher proportion of females were gynes in food-supplemented colonies and gynes weighed more than 3.5 times workers (Table 1). Moreover, sizes of both workers and small males were significantly larger in food-supplemented colonies, compared to controls. By contrast, there was no significant effect of food supplementation on the weight of the large males and gynes.

Sex specialization and proximity to conifers

Across the 162 colonies in six populations in the Swiss Jura Mountains, female-producing colonies were significantly closer (mean 8.76 m; 95% CI 6.67–11.51 m) to a coniferous tree than were male-producing colonies (mean 20.01 m; 95% CI 17.71–22.62 m) ($F_{1,152}=41.62$, $P<0.0001$). However, this effect varied among populations as indicated by a significant interaction between population and sex-ratio specialization ($F_{4,152}=2.82$, $P=0.0002$). The effect was strongest in colonies with a low average distance to aphid-bearing conifers (including Les Chenevières, our main study population). Thus, it appears that when trees are nearby, they have a substantial impact on colony sex ratios. When these food sources are not in close proximity, the proportion of female-producing colonies is comparable but aphid honeydew is unlikely to explain sex ratios.

Discussion

Supplemental food significantly altered sex ratios, with colonies receiving additional sugar and protein being more likely to specialize on female sexual progeny. Moreover, colonies that had specialized on male production the previous year were more likely to switch to female production when given supplementary food. These results give strong experimental support to models of resource-based split sex ratios.

Table 1 Comparisons of individual, dry body mass for gynes, large males, small males, and workers produced by food supplemented and control colonies of *Formica exsecta*

	Food supplemented		Control		F	df	P
	Body mass (g)	95% CI	Body mass (g)	95% CI			
Gynes	4.34	4.26–4.42	4.49	4.38–4.60	2.40	1, 138	0.14
Large males	3.61	3.46–3.76	3.45	3.32–3.58	1.20	1, 81	0.28
Small males	1.87	1.82–1.92	1.79	1.74–1.84	4.27	1, 355	0.040
Workers	1.21	1.18–1.24	1.16	1.11–1.19	28.89	1, 365	<0.0005

Our results are in sharp contrast with those of Aron et al. (2001), who reported that protein supplementation in captive colonies of the Argentine ant, *Linepithema humile*, caused a numerical increase in brood production but did not alter sex ratios. In our study, supplemental food caused a shift in sex ratios but no significant change in numerical progeny production. Instead, there was a shift towards the production of larger castes (gynes and large males) and greater investment in individual workers and small males. Our results are more consistent with those of Deslippe and Savolainen (1995), Morales and Heithaus (1998), and Bono and Herbers (2003), each of which reported greater female-biased production under food supplements. However, in the ant *Aphaenogaster rudis,* the difference in sex ratio was apparently due to greater numerical production of gynes without any change in worker or male production (Morales and Heithaus 1998). In *Myrmica brevispinosa*, greater female production occurred in colonies receiving supplemental sucrose but not those receiving only supplemental protein (Bono and Herbers 2003), suggesting that the nutritional quality of the resource has an important effect on sex ratios.

The two models of resource-based sex ratios, queen-replenishment and multifaceted parental investment (MFPI), are not mutually exclusive and our results support general predictions of each model. Both suggest that a greater resource pool will simulate production of female sexual progeny. According to queen-replenishment hypothesis, this occurs because the colony can support more reproductive queens, and, thus, the colony produces females to bolster its cadre of related queens (Brown and Keller 2000). Our previous studies have provided particularly strong support of queen replenishment. Female progeny production corresponds to a low effective queen number and high per capita queen productivity (Brown and Keller 2000; Brown et al. 2002; Kümmerli et al. 2005). Daughters appear to be adopted back into their natal colonies (Liautard and Keller 2001) and female production is followed by an increase in effective queen number and a switch to specialization of males the following breeding season (Brown and Keller 2002).

However, our results also provide support for MFPI. According to MFPI, greater female production occurs when progeny numbers are constrained by something other than the immediate availability of resources required for progeny growth, and, thus, excess resources can be channeled into producing larger individual progeny (notably gynes) without much additional cost (Rosenheim et al. 1996). Gilboa and Nonacs (2006) supported MFPI in three ant species, *Formica hewitti*, *F. planipilis*, and *Pogonomyrmex salinus*, based on the body size distribution of male and female progeny. In our study, the overall increase in progeny production within food-supplemented colonies was mediated through changes in progeny size, including discrete changes in caste and increases in worker and small male mass, and not through changes in the number of total progeny. A lack of change in numerical productivity could arise for either of two reasons. First, numerical production may be constrained by another resource that we did not manipulate during the experiment (Rosenheim et al. 1996). Second, the initial investment that determined progeny numbers in the cohort that we censused may have been determined before the beginning of our food supplements. If so, additional resources could only be used to increase the sizes and developmental trajectories of a number of offspring that was fixed very early in the breeding season. Although we initiated the treatment as early as possible in the spring, it is possible that queens and workers utilize resources acquired before overwintering for initial investment in progeny. In contrast to our results, Herbers and Banschbach (1998) reported that greater gyne production in food-supplemented plots of *Temnothorax longispinosus* was associated with numerical increases in progeny production, including a 20-fold increase in gyne production, but no significant increase in dry mass of individual progeny. However, their food supplements covered two sequential breeding seasons, and, thus, they were certain to be providing resources before the onset of progeny production in the second year. Ode and Rissing (2002) showed that the timing of food supplementation has important consequences for sex allocation in *Messor pergandei*. Early food supplements while queens were laying reproductive brood increased the number of gynes, whereas later food supplements increased gyne size.

In our experiment, food supplements increased the sizes of worker and male brood, but not the size of gynes. Larger males have greater fitness in harvester ants due to greater mating success and greater sperm production (Abell et al. 1999; Wiernasz et al. 2001) and similar directional selection on male body size may occur in *F. exsecta*. Lack of an effect of food supplements on gyne size is surprising, given that larger queens might be expected to have greater success at becoming established as reproductives. For example, Wiernasz and Cole (2003) showed that larger queen *Pogonomrymex occidentalis* have greater success at colony founding. Perhaps directional selection on gyne size is reduced in species in polygynous species that reproduce by colony budding rather than independent colony founding, such as polygynous *F. exsecta*.

In addition to the effect of food supplements on sex ratios, we found a strong association between female-production and proximity to conifers, and by extension, proximity to aphid honeydew, a major natural food source for mound-building *Formica* ants. Boomsma (1993) suggested that ants in aphid-rich nest sites should specialize on gynes because the high carbohydrate availability (in the form of honeydew) will make gynes relatively cheap to produce. Average distance of female-producing colonies to conifers in *F. exsecta* was less than half that of male-producing colonies. These results match those of Deslippe and Savolainen (1995), who reported that sex ratios were more female-biased in colonies of *F. podzolica* along forest edges. In our study, the exception was a single population (Le Pré Nouveau) that was situated in a large and unusually open meadow with a very large average distance to conifers (30.38 m compared to between 6.92 and 24.38 m among the other populations). This population contained a remarkably high proportion of

female-producing colonies (12 of 23 surveyed (52%) for an ant that typically has strongly male-biased sex ratios (Brown and Keller 2000; Liautard et al. 2003). However, in this population, there was no difference in proximity of male- and female-producing colonies to conifers. We presume that progeny production at Pré Nouveau was based predominantly on resources other than honeydew from aphid-dwelling conifers.

F. exsecta is a model species for studies of sex-ratio evolution (Pamilo and Rosengren 1983; Sundström et al. 1996; Brown and Keller 2000; Brown et al. 2002; Liautard et al. 2003; Kümmerli et al. 2005). We have shown that sex ratios in wild populations correlate with proximity to natural food sources and are altered by experimental changes food availability. Our results demonstrate the important role of food resources in determining the sex ratios in this polygynous social insect.

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