

Local resource competition and sex ratio in the ant *Cataglyphis cursor*

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The local resource competition (LRC) hypothesis predicts that wherever philopatric offspring compete for resources with their mothers, offspring sex ratios should be biased in favor of the dispersing sex. In ants, LRC is typically found in polygynous (multiple queen) species where foundation of new nests occurs by budding, which results in a strong population structure and a male-biased population-wide sex ratio. However, under polygyny, the effect of LRC on sex allocation is often blurred by the effect of lowered relatedness asymmetries among colony members. Moreover, environmental factors, such as the availability of resources, have also been shown to deeply influence sex ratio in ants. We investigated sex allocation in the monogynous (single queen) ant *Cataglyphis cursor*, a species where colonies reproduce by budding and both male and female sexuals are produced through parthenogenesis, so that between-colony variations in relatedness asymmetries should be reduced. Our results show that sex allocation in *C. cursor* is highly male biased both at the colony and population levels. Genetic analyses indicate a significant isolation-by-distance in the study population, consistent with limited dispersal of females. As expected from asexual reproduction, only weak variations in relatedness asymmetry of workers toward sexual offspring occur across colonies, and they are not associated with colony sex ratio. Inconsistent with the predictions of the resource availability hypothesis, the male bias significantly increases with colony size, and investment in males, but not in females, is positively correlated with total investment in sexuals. Overall, our results are consistent with the predictions of the LRC hypothesis to account for sex ratio variation in this species. *Key words*: dispersal, *Formicidae*, relatedness, sex allocation, thelytoky. [*Behav Ecol* 17:569–574 (2006)]

Social Hymenoptera have been the focus of much empirical and theoretical work for testing the predictions of sex ratio (Fisher 1930) and kin selection (Hamilton 1964) theories. So far, most studies emphasized the effect of relatedness asymmetries and resource abundance on sex allocation (Bourke and Franks 1995; Crozier and Pamilo 1996; Chapuisat and Keller 1999; Sundström and Boomsma 2001; Heinze 2004). Asymmetry in relatedness of females and males toward the workers that raise them arise from the haplodiploid sex-determining system of Hymenoptera, which causes full sisters to be 3 times more related to each other ($r = 0.75$) than they are to their brothers ($r = 0.25$). Fisherian sex ratio selection should thus result in a 3:1 female bias, when workers (which are always females) raise full siblings and control sex allocation (Trivers and Hare 1976). Female bias is expected to decrease concomitantly with a decrease in relatedness asymmetries, both at the population and colony levels. The most important factors reducing relatedness asymmetries are the presence of more than one reproductive queen per colony (polygyny) when queens are related, multiple mating by queens (polyandry), and worker reproduction (Trivers and Hare 1976; Boomsma and Grafen 1991; Bourke and Franks 1995; Crozier and Pamilo 1996). Cross-species analyses over a large range of Hymenoptera show that colonies with high relatedness asymmetries tend to produce more females than colonies with lower relatedness asymmetries, consistent with workers controlling sex allocation (Sundström 1994; Sundström et al. 1996; Queller and Strassmann 1998; Chapuisat and Keller 1999).

Resource availability may also cause sex ratio variation among colonies. Two models examine explicitly resource-dependent sex investment ratios. First, resource abundance

directly affects caste determination among the diploid brood, that is, whether a diploid egg will develop into a sterile worker or a winged queen. Food-constrained colonies should produce workers rather than winged females, while their haploid brood will still develop into adult males, promoting a male-biased sex ratio. On the other hand, well-fed colonies can convert a large proportion of the diploid brood into reproductive females; they should rear both males and females, with a relative overinvestment in winged females (Nonacs 1986; Crozier and Pamilo 1993). Second, the multifaceted parental investment hypothesis (MPIH; Rosenheim et al. 1996) proposes that resource-limited colonies specialize on the production of the cheaper sex, usually males, whereas colonies with sufficient resources but limited by the rate of brood production specialize on the production of the most costly sex, that is, winged females. Thus, predictions of the resource abundance and MPIH hypotheses are similar in that both predict an association between productivity and sex allocation, with more productive colonies investing proportionally more in queen production (Nonacs 1986; Crozier and Pamilo 1993; Rosenheim et al. 1996). Several studies have shown a positive association between reproductive output and relative investment in females ants (Deslippe and Savolainen 1995; Banschbach and Herbers 1996; Morales and Heithaus 1998; Ode and Rissing 2002; but see e.g., Backus and Herbers 1992; Herbers and Banschbach 1999; Aron et al. 2001 for different results).

A key factor that has received relatively little attention is the influence of dispersal strategies of both sexes on sex allocation. When distance of dispersal varies between the sexes, the fitness return from investing into the less dispersing sex is a diminishing function of the total investment in sexuals, that is, the less dispersing sex becomes devaluated. Under local mate competition (LMC; Hamilton 1967), competition among sons for mates lowers the reproductive value of males with increased investment in sexuals. When LMC exists, the constant male hypothesis predicts that colonies should produce males up to some threshold and then invest all remaining

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resources in female reproductives, resulting in a female-biased sex ratio at the population level (Frank 1987). Conversely, under local resource competition (LRC; Clark 1978), dispersal of females is limited and related queens compete for access to resources (nest sites, food), so that the fitness return through females decreases with increased investment relative to the fitness return through males. Thus, LRC predicts an association between productivity and sex allocation, with more productive colonies investing proportionally more in male production. Under LRC, the constant female hypothesis predicts that colonies should invest the same amount of resources in females and all remaining resources in males. With increasing access to resources, investment in males is expected to increase while investment in females should remain constant (Frank 1987). In ants, LRC is typically found in polygynous species where foundation of new colonies occurs by budding (Keller 1991), that is, young mated queens leave the colony with adult workers to initiate new colonies nearby, which results in a strong population structure and a male-biased population-wide sex ratio (Pamilo and Rosengren 1983; Ward 1983; Sundström 1993, 1995; Chan and Bourke 1994; Walin and Seppä 2001). In such species, however, the effect of LRC on sex allocation is often blurred by the effect of lowered relatedness asymmetries due to polygyny.

We investigated sex allocation in the monogynous (single-queen colonies) ant *Cataglyphis cursor*. In this species, queens mate multiply (Pearcy et al. 2004b), which should lower relatedness asymmetries. Nevertheless, a recent study showed that queens use sexual reproduction for workers and thelytokous parthenogenesis for new queens production (Pearcy et al. 2004b). Males arise from unfertilized eggs, as is usually the case in Hymenoptera. Because both male and female sexuals are produced asexually, asymmetries in relatedness are not affected by queen mating frequency and, hence, no between-colony variation in relatedness asymmetries is expected. Unmated workers of *C. cursor* can produce males by arrhenotokous parthenogenesis and females by thelytokous parthenogenesis (Cagniant 1973). However, behavioral studies suggested that workers never reproduce in queenright colonies (Cagniant 1979); this requires confirmation through genetic analyses. An interesting feature of the species is that, while strictly monogynous, colonies reproduce by budding (Lenoir et al. 1988; Clémencet et al. 2005). LRC is therefore likely to affect colony sex ratios in *C. cursor*. We tested the effects of relatedness asymmetries, resource availability, and LRC on colony sex ratio.

MATERIALS AND METHODS

Field collection and sampling

Cataglyphis cursor is found in the stretches of steppe and Mediterranean forest up to dry forest and is discontinuously distributed from central Spain to Mongolia (Agosti 1990). Nests of *C. cursor* possess a single entrance and usually one vertical gallery leading to rooms located up to 1 m deep. In this species, there is no overwintering brood (Cagniant 1976). Production of sexuals and workers is separate in time; sexuals emerge on mid-May from the very first eggs laid at the end of the winter, while workers are produced later on, in summer. Mating occurs in or close to the nest in early June and is followed 1–3 weeks later by colony budding (Lenoir et al. 1988). Transfer of workers and brood between the mother and daughter nests can last for a few weeks, after which colonies remain isolated from each other.

Fifty-seven nests of *C. cursor* were completely excavated in the end of April/early May in 2001, 2002, and 2003 at St-Hyppolite (southern France; 42.82°N, 2.99°E), before the

emergence of the first sexuals. Colonies whose entrances were located less than 1 m apart were not collected so as to prevent mixing individuals from different nests (personal observation). All adults (queens and workers) as well as brood at various stages (eggs, larvae, and sexual pupae) were collected and brought into the laboratory. The number of workers per colony was counted (mean colony size \pm SD = 752.4 \pm 602.4; range: 78–2658), and a sample of workers from each nest was immediately stored at -80°C for subsequent genetic analyses. Colonies were housed in artificial nests. They were maintained under laboratory conditions ($26 \pm 2^{\circ}\text{C}$ and 12:12 h light:dark) and were fed on cockroaches, sugar water, and grapes. Colonies were censused twice a week, and all sexuals emerging from the pupae were collected and deep frozen.

DNA extraction and microsatellite analysis

To assess the kin structure of the colonies, a sample of workers ($\bar{X} \pm \text{SD} = 16.07 \pm 6.04$; range: 7–28), the queen and up to 32 sexuals taken from 35 colonies were genotyped at 4 polymorphic microsatellite loci (*Ccur11*, *Ccur46*, *Ccur58*, and *Ccur63b*; Pearcy et al. 2004a). Individual ant DNA was extracted by homogenization in a digestive solution (100 mM NaCl, 50 mM Tris, 1 mM ethylenediaminetetraacetic acid, 0.5% sodium dodecyl sulfate, and 200 $\mu\text{g}/\text{ml}$ proteinase K [Biogene, Cambridge, UK]) and incubated for 2 h at 55°C . Genomic DNA was purified by phenol/chloroform and precipitated with ethanol following standard protocols and then suspended in 100 μl . Amplifications were carried out in a 10- μl volume using the standard $10\times$ buffer and *Taq* from QIAGEN polymerase kit (Pearcy et al. 2004a). Amplified fluorescent fragments were visualized using an automated ABI Prism 310 sequencer.

Population and colony genetic structure

A total of 12–30 workers ($\bar{X} \pm \text{SD} = 15.3 \pm 5.8$; $n = 535$) and the queen ($n = 33$; 2 queens died before genetic analyses) were typed from a sample of 35 nests. Relatedness coefficients were estimated using the program RELATEDNESS 4.2c according to the method described by Queller and Goodnight (1989). Colonies were weighted equally and standard errors (SEs) were obtained by jackknifing over colonies. Isolation-by-distance was investigated by plotting [$F_{st}/(1 - F_{st})$] coefficients between pairs of colonies against the log of geographical distance (Slatkin 1993). Significance of correlation coefficient between genetic differentiation and geographical distance was assessed with Mantel test using GENEPOP 3.2a (Raymond and Rousset 1995) with 10 000 permutations. In addition, we investigated whether adjacent colonies (i.e., nearest neighboring nest) had nonzero interrelatedness by using RELATEDNESS 4.2c. Life-for-life relatednesses are used throughout.

The possibility of worker reproduction was assessed by comparing the genotype of the males with the queen's genotype; worker reproduction was assessed from males genotype only because worker-produced females are not genetically distinguishable from the queen's own diploid offspring. Seventy-one males were typed from 9 colonies ($\bar{X} \pm \text{SD} = 7.9 \pm 4.3$). Sons of queens must carry a queen-derived allele at all loci and, as a group, they should not display more than 2 alleles at a single locus. Sons of workers may carry with equal probability either an allele derived from the mother or the father of the worker. Any male that carry a nonqueen allele is a worker's son. However, because sons of workers may carry queen alleles at all loci by chance, this probability of nondetection was estimated following Foster et al. (2001),

$$P_{\text{nondetect}} = \sum_i^n p_i(0.5^i),$$

where n is the number of patriline in the nest, p_i is the proportional contribution of the i th father to the brood, and l_i is the number of informative loci analyzed at the i th patriline. An informative locus is one where the queen and her mate have different alleles so that the workers carry an allele that the queen does not.

Sex ratio analysis

Investment ratio was expressed as the proportional investment in females among sexuals. Reproductives of both sexes were dried for 48 h at 55°C and then weighted at the nearest 0.01 mg. Sexual dimorphism is weak in the species; the average dry weight of mature females was $D_f = 4.08 \pm 0.69$ mg, not significantly different from the males dry weight $D_m = 3.33 \pm 0.49$ mg (two-tailed t -test, $t = 0.13$, $df = 8$, $P = 0.89$). Investment ratios were calculated by multiplying each colony male and female numbers with their respective dry weight. Data were corrected by using Boomsma's (1989) energetic cost ratio $(D_f/D_m)^{0.7}$. Colonies producing less than 5 sexuals ($n = 6$ colonies) were not considered in our analysis because low sexual production increases the probability of extreme sex ratios.

Statistical analyses

To explore the effect of relatedness asymmetries, colony size and total sexual productivity on colony sex ratios, a logistic binomial regression model was carried out using the procedure GLM in the software R (Ihaka and Gentleman 1996). This model assumes that the dependent variable is a probability that follows a binomial distribution and can account for variation in sample size. Spearman rank correlations were used to test for an association between colony size or investment in each sex and total sexual productivity using the software GRAPHPAD INSTAT®.

RESULTS

Population genetic structure

There was a significant correlation between genetic differentiation between pairs of colonies and the geographical distance (Mantel test: $P = 0.028$), indicating low but notable isolation-by-distance pattern in the study population. Genetic viscosity was also supported by the significant nonzero relatedness between adjacent nests ($r = 0.23$; $SE_{\text{jackknife}} = 0.02$, $n = 35$ nests; two-tailed t -test, $P < 0.001$).

The mean population-wide genetic relatedness among workers was $r = 0.42$ ($SE_{\text{jackknife}} = 0.02$, $n = 35$ nests), consistent with queens being mated with 4–8 males in the study population (Pearcy et al. 2004b). None of the 71 males ($n = 9$ colonies) examined carried nonqueen alleles. The average probability of nondetection of worker-produced males was low and equal to 0.13. This indicates that worker reproduction is rare or even absent in queenright colonies of *C. cursor*.

Colony sex ratios

From the 57 colonies sampled, 20 (35%) produced sexuals. There was a positive association between colony size and sexual production (Spearman rank correlation, $r_s = 0.50$, $n = 57$, $P < 0.001$; Figure 1a). Only 14 colonies (26%) raised more than 5 sexuals: 9 produced females and all 14 produced males (Figure 2). From these colonies, we collected 59 females and 231 males, resulting in a male-biased population-wide numerical sex ratio (proportion of females among sexuals) of 0.20. The population-wide sex investment ratio in females was 0.24, giving a 1:3.2 female to male investment ratio.

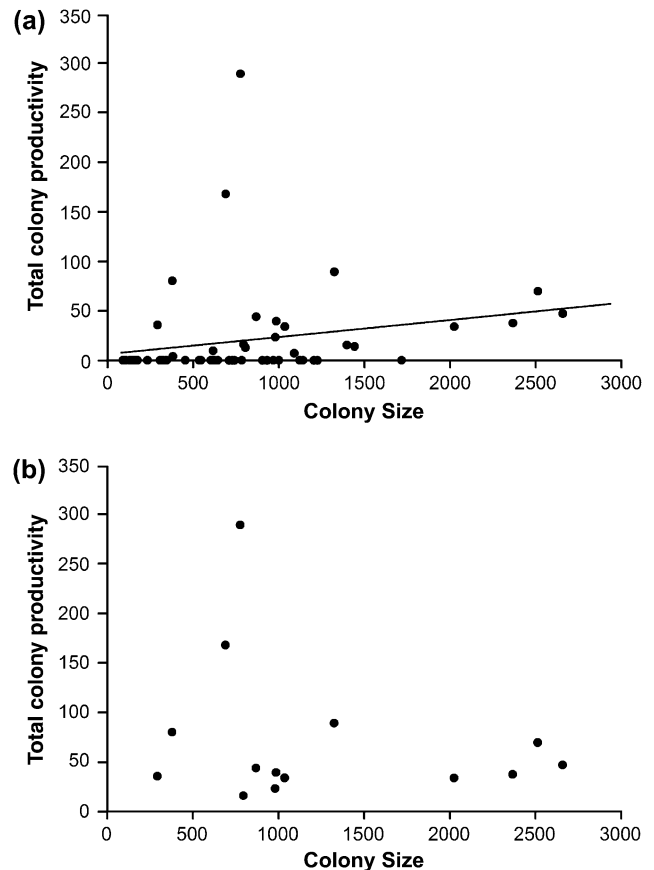


Figure 1
Total colony sexuals production as a function of colony size for all colonies ($n = 57$) (a) and for colonies producing at least 5 sexuals ($n = 14$) (b).

Relatedness asymmetries and sex ratio

As expected from the production of winged females through thelytokous parthenogenesis, relatedness between the queen and their sexual daughters was close to 1 and twice the relatedness between the queen and their sons (Table 1). By contrast, the mean relatedness of workers, who are sexually produced, to reproductive females was not different from 0.5 (two-tailed t -test, $t = 1.63$, $P = 0.14$). The life-for-life

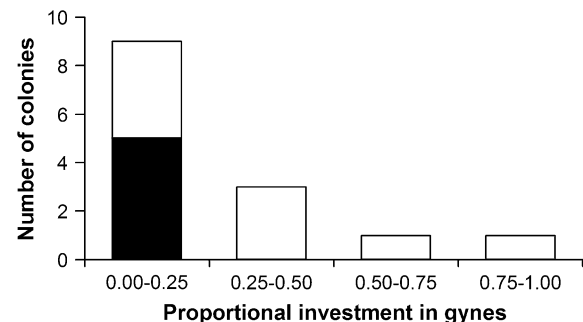


Figure 2
Distribution of the proportional investment in females (investment sex ratio corrected for sex-specific differences in energetic cost) produced by individual colonies of *Cataglyphis cursor*. Black area represents colonies producing exclusively males; no colony produced only females.

Table 1
Life-for-life relatedness estimates (\pm SE) of queens and workers to sexual male and female offspring in *Cataglyphis cursor*

	Queen	Worker
Sexual females	0.99 \pm 0.01	0.62 \pm 0.07
Males	0.49 \pm 0.01	0.32 \pm 0.08

relatedness of workers to males was also not significantly different from 0.25 expected in colonies headed by a single queen, independently of queen mating frequency (two-tailed *t*-test, $t = 1.76$, $P = 0.12$). The SEs (jackknife) associated with these relatedness values are low, indicating limited variations between colonies in their kin structure. Relatedness asymmetry of workers toward females and males ranged from 1.6 to 2.4 across colonies and was on average 1.98:1. Colony sex ratio was not correlated with variations in relatedness asymmetry (logistic regression, $n = 9$, $P = 0.14$; Figure 3a).

Resource availability and sex ratio

Among the 14 colonies producing sexuals, there was no association between colony size and total sexual productivity (Spearman rank correlation, $r_s = -0.11$, $n = 14$, $P = 0.71$; Figure 1b). However, sex allocation was significantly negatively correlated with colony size, with larger colonies investing proportionally more in male production (logistic regression, $n = 14$, $P < 0.001$; Figure 3b). In addition, there was a negative, albeit nonsignificant association between the proportional investment in females and total sexual productivity (logistic regression, $P = 0.75$, $n = 14$; Figure 3c).

LRC and sex ratio

Consistent with the predictions of LRC, the slope of the regression line of investment in males was significantly higher than that of investment in females (analysis of covariance, $P < 0.001$; Figure 4). Moreover, investment in males increased significantly with total sexual productivity (Spearman rank correlation, $r_s = 0.83$, $n = 14$, $P < 0.001$), whereas investment in females did not ($r_s = 0.48$, $P = 0.08$; Figure 4). These trends are robust, and significance remained unchanged even when the extreme values of total sexual productivity (productivity values of 293 and 170) were removed from the analysis (investment in males and females for $n = 13$: $r_s = 0.79$, $P = 0.001$ and $r_s = 0.35$, $P = 0.24$, respectively; for $n = 12$: $r_s = 0.73$, $P = 0.009$ and $r_s = 0.17$, $P = 0.60$).

DISCUSSION

Our results show that sex ratio in *C. cursor* is male-biased both at the colony and population levels and that male bias significantly increases with colony size. More importantly, investment in males, but not in females, is positively correlated with total investment in sexuals. These results are consistent with the predictions of the LRC between related females to account for sex ratio variation in this species. LRC is also supported by the positive correlation between genetic and geographic distances (see also Clémencet et al. 2005 for similar results), suggesting that related colonies experience competition for access to food sources and/or nest sites. In dependent-founding species, worker production must be regarded as an investment in females because they support young queens to successfully establish new nests (Hamilton 1975; Macevicz 1979; Pamilo 1991). Estimating investment in females for a col-

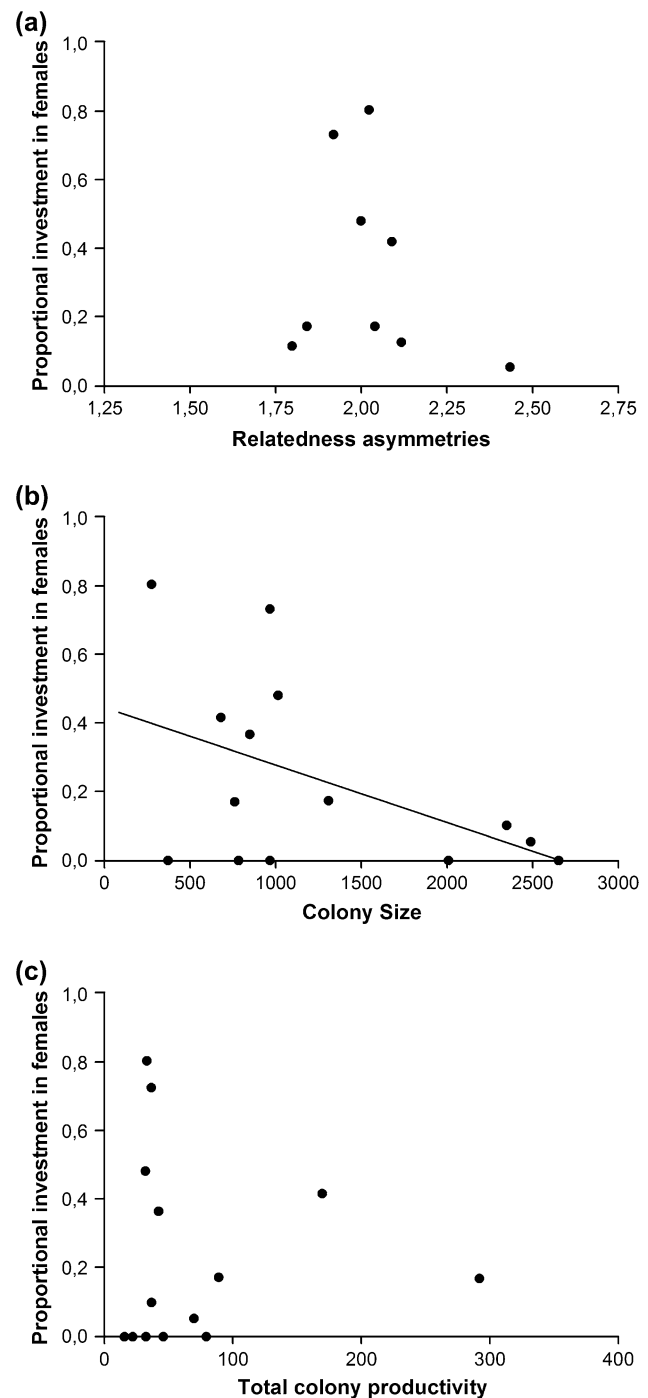


Figure 3
Proportional investment in females as a function of relatedness asymmetries (a), colony size (b), and total sexual productivity (c).

ony may prove complex because the number and composition of the buds are variable so that it is difficult to assess the number of workers involved in the budding process and, thus, the proportional investment in workers that should be counted as investment in the female sex. In *C. cursor*, workers emerge after colony budding. Sexual production, mating, and budding occur successively until the end of spring, while workers are produced after budding, in summer. The cost associated with departure of old workers from the mother nest is therefore reduced. Moreover, there is no direct competition for allocation of resources between sexuals and workers (Pamilo 1991);

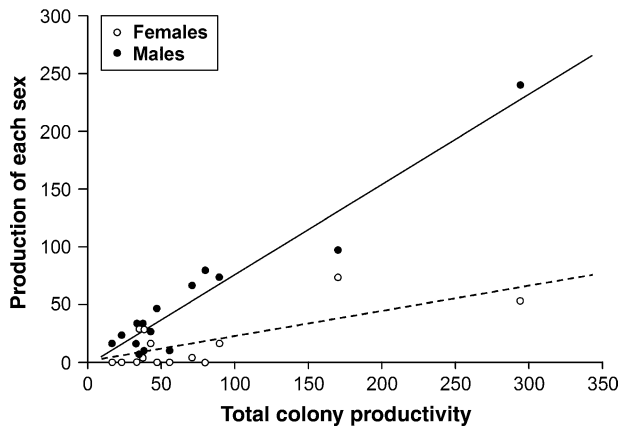


Figure 4
Total investment in males (plain line) and in female reproductives (dotted line) as a function of total sexual productivity. Tendency lines are given for both males and females, yet nonsignificant for the latter.

resources that are not spent into sexual production are not simply channeled into worker production. As a result, the male-biased sex investment ratio reported here in *C. cursor* should not be considerably overestimated.

Neither relatedness asymmetry nor resource availability or worker reproduction explains sex ratio variations across colonies in *C. cursor*. Relatedness asymmetries toward reproductives indicate that queens' and workers' interests converge because both are on average twice as much related to female sexuals than to males. This stems from the unusual mating system of this species, whereby reproductives of both sexes are produced through parthenogenesis while workers arise from fertilized eggs. Consistent with the parthenogenetic production of sexuals, our data show that asymmetries of relatedness are stable across colonies and fail to justify between colony sex ratio variations in *C. cursor*. The resource availability hypothesis seems also unlikely to explain sex ratio variations in the population studied. According to this hypothesis, small colonies should favor male production, whereas large and well-fed colonies should favor females. Although we did not test experimentally the influence of resource availability over sex ratio, our results do not fit the predictions of the hypothesis. They show that sex ratio is significantly more male biased in large colonies than in small ones and that colonies producing few sexuals tend to produce proportionally more females than colonies with high sexual output. Finally, our genetic analyses revealed no worker-produced male, consistent with the absence of worker reproduction in queenright colonies (Cagniant 1979).

Under LRC, the constant female hypothesis (CFH) predicts the production of a constant amount of females before investing additional resources into males, resulting in a negative association between proportional investment in females and total sexual production (Frank 1987). Although our data support a clear effect of LRC on population-level sex allocation in *C. cursor*, they are not fully consistent with the CFH. First, 5 out of the 14 colonies sampled did not rear females at all. Large variation in female production is also direct evidence against CFH, which predicts low variation in female production across colonies. Female production varied from 0 to 18 but remained still less variable than male production (0–72). Second, our data show a negative, though not significant, association between proportional investment in females and total sexual productivity. However, the fact that few colonies produce sexuals in this species greatly limited our sampling and, hence, does not allow an unambiguous test of this hypothesis.

In ants, a male-biased sex ratio at the population level is usually found in polygynous species. One reason is that the presence of multiple reproductive queens reduces the worker's relatedness asymmetries (Trivers and Hare 1976). Another is that, while monogynous ant species usually reproduce by emitting dispersing sexuals (new queens and males), polygynous ants often exhibit colony budding (Keller 1991). This results in LRC among daughter queens, which predicts male-biased sex ratio at the population level (Clark 1978; Pamilo 1991). The ant *C. cursor* is remarkable in that this strictly monogynous species reproduces by budding. In addition, both male and female sexuals are produced by parthenogenesis (respectively, arrhenotoky and thelytoky), so that relatedness asymmetries do not vary between colonies. Our current findings therefore strongly support LRC as the primary factor affecting sex ratio in this species.

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