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Relatedness within colonies of social Hymenoptera is often significantly lower than the outbred population maximum of 0.75. Several hypotheses address the widespread occurrence of low relatedness, but none have measured the covariation of colony fitness and relatedness. In a polyandrous harvester ant, *Pogonomyrmex occidentalis*, average within-colony relatedness in the population is low but highly variable among colonies, and relatedness is negatively correlated with colony growth rate. Differences in growth rate strongly influence survival and the onset of reproduction, leading to a 35-fold increase in fitness of fast-growing colonies. Benefits of a genetically diverse worker population may favor polyandry in this species.

The relation between genetic relatedness and altruism has dominated modern studies of social behavior, especially in the social Hymenoptera where asymmetries in relatedness among male and female offspring and among queens and workers shape interactions (*1*). Technical advances in the estimation of relatedness have allowed social insect biologists to study the relation between relatedness and many aspects of reproductive allocation and behavior (*2–4*).

Although high within-colony relatedness promotes the spread of altruistic traits and may favor many types of social behavior, the diversity of social systems among social insects (from singly mated, single queens to multiply mated, multiple queens) produces a corresponding diversity of relatedness values. To explain such diversity, a number of hypotheses have been proposed that identify potential advantages to low relatedness (*5*). Low relatedness that arises from polyandry (multiple mating by queens) is of particular interest, because polyandry is taxonomically widespread. Data from natural populations comparing relatedness to aspects of fitness are virtually absent (*6*, *7*).

We have studied the western harvester ant *Pogonomyrmex occidentalis*. Colonies of this species are founded by a single queen (*8*); variation in the mating frequency of queens produces variation in colony relatedness. We genotyped six workers from each of 1492 colonies (*9*) over a 4-year period at two variable loci, phosphoglucose isomerase (PGI) and amylase (AMY) (*10*). Within-colony relatedness was estimated individually from the combined electrophoretic data (*11*). The average relatedness in the population is 0.324 ± 0.017 (mean ± SE, $n = 1128$ colonies collected in 1993). We censused colonies annually between 1993 and 1998 and measured colony size (*12*) in 1993, 1994, 1997, and 1998 to determine survival and growth. Colony growth rate was correlated in all years with colony size: Small colonies grew more rapidly than large colonies (1993–1994: $r = -0.33$; 1994–1997: $r = -0.59$; 1997–1998: $r = -0.34$). We used the residuals of the regression of growth on size in a given time interval to estimate colony growth corrected for current size for that interval (*13*).

Relatedness and residual colony growth are negatively correlated for every time interval (1993–1994: Spearman rank correlation $r_s = -0.0908$, $n = 927$, $P = 0.0057$; 1994–1997: $r_s = -0.0789$, $n = 809$, $P = 0.025$; 1997–1998: $r_s = -0.0243$, $n = 791$, $P = 0.495$). Overall, the relation is strongly negative [combining these probabilities by using Fisher's method (*14*), $\chi^2 = 19.12$, df = 6, $P < 0.005$]. Total growth over the 5-year period 1993 to 1998 is also negatively correlated with colony relatedness ($r_s = -0.102$, $n = 646$, $P = 0.0095$) (Fig. 1). Although significant, the correlation between growth and relatedness is not very large. Our estimate of average colony relatedness for the entire population is accurate, but the estimates for individual colonies have large standard errors (*2*, *3*). On the assumption that the correlation between colony relatedness and growth is due to a correlation between the actual growth and actual

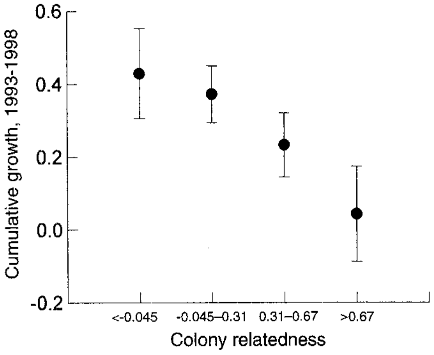

Fig. 1. The relation between colony growth and colony relatedness. Colony growth is the residual growth over the 5-year period 1993 to 1998. Colonies are categorized by their within-colony relatedness as being more than 1 SD (SD = 0.356) below the mean individual relatedness (0.315), within 1 SD below the mean, within 1 SD above the mean, and more than 1 SD above the mean.

Fig. 2. The path analysis estimate of the relation between colony growth and colony relatedness. The correlation between actual growth and measured growth is based on the correlation between colony size and our measure of colony size (*8*), and the correlation between estimated and actual relatedness for individual colonies is estimated from simulations (*14*). The correlation between measured growth and estimated relatedness is the correlation with growth over a 5-year period.

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relatedness, we used path analysis (*15*) to estimate that the true correlation is at least five times greater (Fig. 2).

Our data include several cohorts (colonies that were 1-year-old in 1992, 1993, 1994, or 1995, and which were older than 1 year in 1992). To address the possibility that the patterns described are driven mainly by one cohort, we analyzed the five cohorts separately. In 9 of 11 pairs (fast versus slow growing) of relatedness estimates for the three growth intervals (*16*), colonies categorized as fast growing had lower relatedness (Fig. 3) (Wilcoxon signed rank test, $z = 2.49$, $P = 0.0128$).

Rapidly growing colonies survive longer than slowly growing colonies and they attain reproductive maturity at younger ages. The cohort of colonies initially discovered in 1993 is most informative in this regard. Mortality was substantially lower in fast-growing colonies (12/35 died) compared with slow-growing colonies (28/42 died, $\chi^2 = 8.02$, df = 1, $P < 0.001$). Rapidly growing survivors also were significantly larger than slow-growing survivors [10.16 ± 0.46 (95% confidence limits) versus 8.76 ± 0.60], a difference that corresponds to a 50% increase in worker number (*9*). About 65% (15/23) of the fast-growing survivors had reached the minimum size for reproduction in contrast to only 1 of the 14 slow-growing survivors ($\chi^2 = 11.96$, df = 1, $P < 0.001$).

These effects could arise either from an advantage of low relatedness or a disadvantage of high relatedness. High relatedness could be disadvantageous owing to genetic incompatibility between mates; females who mate with several males suffer lower average costs than females who mate with a single incompatible male (*17*, *18*). Genetic incompatibility in ants can result from the sex determination system. Females must be heterozygous at the sex-determining locus (*19*, *20*). Males are typically haploid, but diploid males result when a queen mates with a male that shares a sex-determining allele. Diploid males are sterile, reduce worker production, and represent a cost to the colony. The cost is a function of the queen's mating frequency and the number of sex-determining alleles in the population (*20*, *21*). We simulated the effect of diploid male production on colony growth and conclude that it is unlikely to generate the correlation between relatedness and colony growth (*22*). If queens are more likely to mate first inside the nest and then mate multiply, increased inbreeding will be associated with lower mating frequency. Inbreeding depression is consistent with the results that we observe. Although inbreeding equivalent to 28% sib mating has been reported in this population (*10*), we found no heterozygote deficiency in the present data.

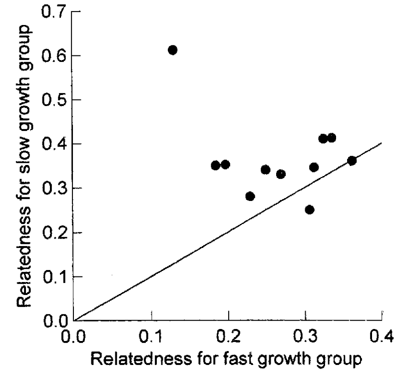

Fig. 3. Relatedness for the fast- and slow-growth groups for specific cohorts of colonies in specific years (*16*). The line shows equal relatedness in the two groups.

Large numbers of matings also reduce the asymmetries in relatedness between queens and workers and can reduce the potential for conflicts of interest over reproductive allocation (*23*). Because the effects we observe occur several years before the colony is capable of reproduction, this mechanism is unlikely to explain our findings.

The fitness advantage of colonies with low relatedness in *P. occidentalis* may be due to their increased genetic diversity. If a diversity of worker genotypes confers resistance to pathogens, then higher relatedness (low genetic diversity) may slow colony growth (*24*). Empirical support for this hypothesis has been found in bumblebees (*25*). This may be particularly important in a species such as *P. occidentalis*, which has a colony life-span of 40 years or more (*9*, *26*). Alternatively, increased genetic diversity may produce workers with varying thresholds for different behavior and thus more efficient performance (*27*). Empirical support for this hypothesis has been found in honeybees (*28*).

Regardless of the mechanism, there is a substantial fitness advantage to polyandry in this natural population. Survival is twice as great in the fast-growing colonies, and the average fast-growing survivor was 18 times more likely to reproduce (*29*). Recent theoretical work (*6*) has suggested that queens can increase their inclusive fitness by 1.33- to 3-fold by modifying sex ratios to their advantage. In *P. occidentalis*, the estimated 35-fold selective advantage of increased growth associated with lower relatedness must overwhelm any fitness effects that derive from modifying allocation ratios.

References and Notes

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8. In over 1000 observations of nest-founding queens, we have seen one instance of two queens in the same burrow. The two queens fought and both were found dead the next day.
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11. We modified the method of Queller and Goodnight (*3*) to accommodate our data set.
12. Nest cone volume [the natural logarithm of the product of the length (in centimeters) of the north-south axis, the length of the east-west axis, and the height + 1 cm] is highly correlated to the natural logarithm of the number of foragers in the colony ($r = 0.89$) (9). Colony size is estimated as ln(workers) = 3.22 + 0.31(ln nest size).
13. Colonies classifed as fast growth had growth residuals of more than 0.5 size units, and slow-growth colonies had residuals of less than −0.5 for a given time interval. This corresponds to growing 1.6 times or 0.6 times faster than expected.
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15. We used path analysis [C. Li, *Path Analysis: a Primer* (Boxwood, Pacific Grove, CA, 1975)] to estimate the strength of the correlation between real growth and real relatedness, because we know or can estimate the correlation between each of the other quantities: (estimated correlation of growth and relatedness) = (observed correlation)/(correlation of estimated and actual growth)(correlation of estimated and actual relatedness). The correlation between real colony growth and estimated growth is the square of the correlation between worker numbers and nest size measurements (9). We used simulations to estimate the correlation between measured and actual relatedness of individual colonies. On the basis of average relatedness, the effective number of equivalent matings is 3.75. The average colony relatedness is a function of the harmonic mean number of matings [D. C. Queller, in *Queen Number and Sociality in Insects*, L Keller, Ed. (Oxford Univ. Press, Oxford, 1993), pp. 132–152; M. J. Wade, *J. Theor. Biol.* **112**, 109 (1985)]. A zero-truncated Poisson with parameter 4.855 gives a harmonic mean of 3.75 matings and generates variation in female mating frequency. We constructed random data sets from known allele frequencies, selecting the queen's number of mates randomly from the mating distribution and randomly choosing six offspring. We assumed that each male contributed equally to the potential offspring, although in any colony there will be variation in the number of offspring from a given father. Real relatedness in the simulated colonies is $1/4 + (1/2)^n$ where n is the number of matings by that female. Estimated relatedness, by the Queller-Goodnight method, can range from -1 to $+1$. The correlation of actual with estimated relatedness was estimated from 1000 colonies, and replicated 1000 times to estimate the standard errors of the correlation coefficients (SE = 0.0315).
16. We obtained three pairs of relatedness estimates from 1993–1994, and four each from 1994–1997 and 1997–1998. In 1993, only three cohorts were present. In 1994–1997 and 1997–1998, the 1992 cohort did not have enough colonies for a valid test, although they were both in the appropriate direction. Of 11 estimates, 2 show a reversed pattern (in 1997–1998 the 1994 cohort: r for slow-growth colonies = 0.25, r for fast-growth colonies = 0.307; in 1997 the colonies older than 1 year in 1992: r for slow growth = 0.360, r for fast growth = 0.362).

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22. We assumed an inverse rank correlation between colony growth and the fraction of workers lost to diploid males. We assumed a zero-truncated Poisson distribution of matings per female (*15*), and that for any simulation that there were *n* sex-determining alleles that were each at the equilibrium frequency of 1/*n* in the population (*17*). The average sample size in our cohorts was 178 colonies with, on average, 60 slow-growing and 78 fast-growing colonies. We randomly assembled a population of 178 colonies, produced by queens that mated a variable number of times with males whose alleles at the sex-determining locus were randomly derived from the population; queens were necessarily heterozygous. For each colony, we calculated the proportion of diploid males produced and ranked the decrement in colony growth. After ranking the colonies by growth rate, we took that slowest growing and fastest growing subset (60 and 78 colonies, respectively) and calculated relatedness based on the number of matings by each queen. We calculated the difference in relatedness for each of 1000 replicates for populations that had from 3 to 20 sex-determining alleles in the population. We estimated the 95% confidence intervals of this difference from the simulated distribution of differences. Because all colonies are assumed to survive, even those that lose 50% of their worker force to diploid males (and they are more likely to have the highest relatedness), the differences that we obtain in simulations are likely to be larger than differences that will occur in nature. Colony mortality will censor the extreme data. The upper 95% confidence interval does not overlap the average relatedness difference.
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30. We thank X. Ren, C. Heymann, J. Vilinski, J. Yencharis, K. Miller, and the Bureau of Land Management in Grand Junction, CO, for assistance and J. Strassmann, D. Queller, I. Billick, and T. McGlynn for valuable comments. We acknowledge the support of NSF grants DEB-9509312 and IBN-9507470 (B.J.C. and D.C.W.), NSF grant BSR-9108034 (D.C.W.), the University of Houston Coastal Center, and a University of Houston Limited Grant-in-Aid of Research.

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