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The relationship between the distribution of worker sizes and new worker production in the ant *Formica neorufibarbis*

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Abstract While it is commonly assumed that variation in worker sizes within a single ant colony increases colony efficiency, there is little causal evidence of a link between worker size variation and colony performance. I tested whether the range of worker sizes within colonies of the ant species *Formica neorufibarbis* affected new worker production. Removing large workers from colonies lowered the rate of new worker production. A study of unmanipulated colonies indicated that colonies did not maintain a full range of worker sizes; mean worker head widths varied from 0.89–1.24 mm. Colonies naturally missing large workers did not have lower rates of worker production, suggesting that the relative size, not the absolute size, of workers within colonies was important. These are the first results to directly link the range of worker sizes to a component of colony fitness in a natural setting.

Keywords *Formica neorufibarbis* · Worker size · New worker production

Introduction

Cooperation between individuals can lead to division of labor. The increased efficiencies associated with such division of labor promote integrated, cooperative relationships that can lead to higher levels of organization, such as has apparently occurred with multi-cellular organisms and the eukaryotic cell (Smith and Szthmary 1995). Understanding how divisions of labor can lead to increased efficiency and fitness is important to understanding when higher levels of organization will occur. Worker polymorphism in eusocial organisms, where individuals within a colony display variation in size and form, is a commonly cited example of how the benefits of specialization and division of labor can promote higher levels of organization (e.g. Bonner 1988; Smith and Szathmary 1995).

Understanding worker polymorphism is one of the principle endeavors in the study of insect societies (Oster and Wilson 1978; Holldobler and Wilson 1990; Traniello and Rosengaus 1997). Perhaps because intra-colony variation in size and form is such a ubiquitous feature of many eusocial organisms, particularly ants, it has long been assumed that worker polymorphism is related to colony efficiency (e.g. Wheeler 1910; Wilson 1953). Unfortunately the relationship between worker polymorphism and colony fitness is poorly understood (Schmid-Hempel 1992).

Much of the evidence for the functional nature of worker polymorphism in ant colonies relies upon behavioral studies. There is a considerable body of empirical work indicating that worker behavior is related to size and/or form (e.g. Bernstein 1976; Wilson 1976a, b, 1980a, 1984; Brandao 1978; Espadaler et al 1990; Hasegawa 1993a; Beshers and Traniello 1996; Cerda and Retana 1997). Studies that link this behavioral specialization to some measure of worker efficiency (e.g. Wilson 1980b) are rare and even those studies do not link increased efficiencies to colony performance.

Ideally, studies should examine if the range of worker sizes within a colony, known as the caste distribution function (CDF), affects some meaningful measure of colony fitness or performance. Several studies (Walker and Stamps 1986; Beshers and Traniello 1994) demonstrated a correlation between the CDF and a component of colony fitness in the field. Such correlative evidence is equivocal, however. The CDF is commonly correlated with colony size (Brian 1957; Elmes 1974; Wilson 1983a; Fowler 1986; Tschinkel 1988; Gibson 1989; Hasegawa 1993a; Kaspari and Byrne 1995) and worker number is often an important predictor of colony fitness (Odum and Pontin 1961; Michener 1964; Fowler 1986; Nonacs 1986; Porter and Tschinkel 1986; Savolainen et

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al 1996). Thus, a correlation between the CDF and colony fitness could simply be a result of greater productivity in larger colonies. Experimental studies have relied on manipulating the CDF in a laboratory setting (Porter and Tschinkel 1985, 1986) or on using artificial colonies in a field setting (Hasegawa 1993b). Empirical evidence of a cause and effect relationship in a natural setting is still lacking.

In this paper I directly test whether the CDF affects colony performance in the weakly polymorphic ant species *Formica neorufibarbis*. Weakly polymorphic species do not have well-defined worker castes. Instead, they have a continuous range of worker sizes. In *F. neorufibarbis* larger workers are lighter in color than smaller workers and workers of different sizes and colors forage under different environmental conditions (Bernstein 1976). Bernstein (1976) suggested that colonies maintain a range of worker sizes to enable the colony to forage over a wide range of environmental conditions. I examined this hypothesis in two ways. First, I tested the general hypothesis that the range of worker sizes within colonies affects colony performance by manipulating the worker sizes within colonies and measuring new worker production. I also used an observational approach to test for a relationship between the CDF and new worker production. Secondly, I examined whether colonies maintained a full range of worker sizes as suggested by Bernstein (1976).

Materials and methods

Study organism and site

F. neorufibarbis is common above the treeline in the Rocky Mountain Region. The study sites were in the Virginia Basin (3,700–4,000 m in elevation) of the Gunnison National Forest, adjacent to the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado. Colonies often contain multiple queens and reproduce both by single queen founding and budding, where queens establish new nests in conjunction with workers from the parental nest. Colonies nest under rocks and occasionally use several rocks. There is little mixing between groups as indicated by observation of marked workers, generally little overlap in worker sizes between adjacent colonies, and consistent colony sizes over several years. Additionally, workers of different colonies are aggressive towards one another. Nests were assigned to colonies by marking workers in adjacent nests with different colors using an acrylic paint pen. A colony was defined as the set of nests within which workers mixed over a 24-h period. Previous work indicated that most mixing among nests was apparent within 24 h (Billick 1997).

Median colony size is approximately 150 workers, with a log-normal distribution (Billick 1997). New worker production is a linear function of colony size over the full range of colony sizes (Billick 2001). Less than 5% of colonies with mature queens produce queens or males in any given year. When colonies do reproduce, larger colonies produce more reproductives (Billick 1997). On warm days the brood, along with most of the workers, can be found at the rock-soil interface. Queens lay a single brood consisting of worker and alate larvae (if present) approximately a week after colonies emerge from the snow. Workers emerge from cocoons approximately 2 months later. Their diet consists primarily of dead insects, pollen and nectar from plants, and the honeydew of root aphids (Bernstein 1976; Wheeler and Wheeler 1986).

Intra-colony variation in the CDF and new worker production

I tested whether altering the distribution of worker sizes affected new worker production. I haphazardly collected 45 workers from each of 52 nests shortly before queens laid eggs. Nests were located in areas of low to moderate density to reduce measurement error due to incorrect assignment of nests to colonies. Nests in the study were at least 15 m apart and spread over an area of several square kilometers. Workers were assigned to size classes based on head widths in 0.02-mm intervals by using a 10× hand lens to compare workers to dead, previously measured specimens glued to cardboard cards. This method was sufficient to rank workers in terms of relative size; this method produced relative sizes very similar to measurements made with an ocular micrometer at 25× (r^2=0.79, P <0.0001, n =49). The distribution of worker sizes within colonies was roughly normal with a skew towards larger workers. Consequently, it was easier to reduce the variance in the distribution of worker sizes by removing the larger workers. One half of the nests were randomly assigned to an experimental treatment in which I removed the 15 largest workers from the sample and returned the remaining workers to the colony. The remaining colonies were assigned to the control treatment in which I removed 15 workers proportionately from all size classes leaving the distribution of worker sizes relatively unchanged. On average, 15 workers represented 7% of the colony, with a range of 1–22%.

Once larvae spun cocoons, approximately 35 days after worker size variation was manipulated, I used a mark/recapture protocol to estimate the number of cocoons produced, as well as the number of workers in the colony. I performed the mark/recapture census by overturning nest rocks and aspirating as many workers and cocoons as possible from the nests. Workers were marked with a Painters paint pen and cocoons with a permanent ink pen. Different colors were used on adjacent nests. Twenty-four hours later the nests were aspirated and workers collected. I counted the percentage of workers and cocoons that were marked to estimate total numbers of workers and cocoons. If any mixing between colors of adjacent nest rocks was observed the nest rocks were considered to be part of the same colony. This mark/recapture method yields similar estimates to counts of excavated colonies (Billick 1999). The procedure is more fully described in Billick (1999).

Occasionally the mark/recapture was performed when not all of the brood were in the cocoon stage; either some larvae had not entered cocoons or new workers had already emerged from cocoons. New workers were usually easily identifiable because they lacked pigmentation. The percentage of total new workers that these larvae or unpigmented workers represented was recorded at both the capture and recapture. I used the larger of these two values to estimate the percentage of new workers not in cocoons. This number was then added to the estimated number of cocoons to determine the number of new workers produced. If the colony was recaptured too late to distinguish new workers from old, the colony was not included in the analysis.

To estimate new worker biomass of colonies I measured the dry masses of five sets of eight workers and cocoons haphazardly collected from each colony. I calculated standing dry biomass by multiplying the number of workers by average worker dry mass. I calculated dry biomass production by multiplying the number of cocoons (pupae) by the average cocoon dry mass. Because worker biomass strongly affects cocoon biomass production (Billick 2001) I regressed total cocoon dry mass on worker biomass. Both variables were log-transformed to normalize the residuals. I then used ANOVA to determine whether removing large workers affected the residuals from cocoon-worker dry mass regression. This approach allowed me to detect whether there was an overall effect of removing large workers on cocoon production. A one-tailed test was applied because I was testing the hypothesis that removing large workers reduced colony productivity. Reproductive colonies were excluded from the analysis because worker production drops sharply when colonies produce either queens or males.

To determine whether removing large workers reduced cocoon production by either reducing the size or number of cocoons produced, I conducted two additional analyses. To test the effect of

the manipulation on cocoon number, I conducted a one-tailed ANOVA on the residuals of the regression of log cocoon number on log worker number. I used worker number instead of worker biomass to keep the units of both variables the same and to avoid scaling problems. To test the effect of the manipulation on average cocoon dry mass, I conducted a one-tailed ANOVA on the residuals of the regression of average cocoon dry mass on average worker dry mass.

Inter-colony variation in the CDF and new worker production

Using estimates of worker size and cocoon production from 52 colonies in which worker size was not manipulated I applied multiple regression to determine whether the average size of workers or the standard deviation of sizes affected cocoon production. These colonies were part of a separate, unrelated study (Billick 2001) in which half of the colonies received food supplementation. Because colonies were randomly assigned to the food treatment, and more importantly, because food supplementation had no effect on cocoon production (Billick 2001), the supplementation treatment was ignored in the following statistical analysis of cocoon production. I examined the standard deviation, as did Beshers and Traniello (1994), rather than the coefficient of variation because Bernstein's (1976) hypothesis suggests that the absolute range of worker size, and not the relative range of worker sizes should affect colony performance. Worker number was included as a covariate in the multiple regression and worker number and cocoon number were log-transformed to stabilize the variance.

Analysis of variance was used to quantify the degree of internest variation in worker sizes. I estimated the mean worker head width, standard deviation in head width, skew, and kurtosis in these colonies based on a sample of 35 workers haphazardly collected from each colony to avoid biasing estimates due to differing sample sizes (Sokal and Rohlf 1981). Worker and cocoon number were estimated using the mark/recapture method. I used a one group *t*-test to determine if the mean value of the skew and kurtosis were different than zero. Correlations among these components of the CDF and worker number were also calculated. Colonies were only included in the correlational analysis if 35 workers from each colony were measured.

Results

Of the initial 52 colonies in the worker removal experiment, 4 colonies were excluded from the analysis because they produced reproductives, 14 colonies disappeared before the mark/recapture, and I failed to get recapture data for 11 colonies. Estimates of worker size and cocoon size were made in 4 colonies for which I failed to get accurate estimates of worker number. These colonies are included in the analysis of cocoon size. Colonies with larger workers removed produced significantly less cocoon dry mass when compared to the colonies with workers removed from all size classes (Fig. 1A, $F_{1,\ 21}$= 4.3, P =0.025). Including the percentage of biomass removed as a covariate does not change this result [treatment: $F_{1,\ 19}$=5.4, P=0.015 (one-tailed); percentage biomass removed: $F_{1,19}$=0.20, P=0.67; interaction: $F_{1,\ 19}$= 2.2, P =0.16]. The magnitude of this effect can be estimated by comparing the productivity of the treatment colonies to the control colonies; colonies with large workers removed produced only 50% of the cocoon dry mass per gram of worker dry mass when compared to the colonies with workers removed from all size classes. The difference between treatments was mainly attributable to a decrease in the number of cocoons produced per worker (Fig. 1B; $F_{1,\ 21}$=3.6, P = 0.04), rather than a change in the size of individual cocoons (Fig. 1C; $F_{1,\ 25}$=0.29, P =0.30).

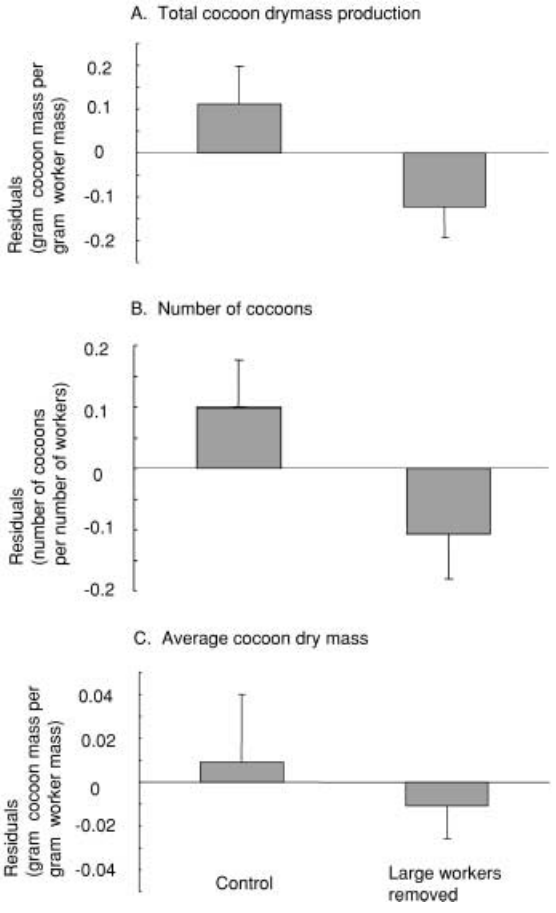

Fig. 1A–C The effect of removing large workers on cocoon production. **A** The effect of the treatment on cocoon production, as measured by total dry mass of cocoons. *Residuals* refers to the residuals from biomass production regressed on total worker biomass in the colony. **B** The effect of the treatment, as measured by the number of cocoons produced by colonies. *Residuals* refers to the residuals of the number of cocoons regressed on the number of workers. **C** The effect of the treatment, as measured by the average dry mass of the cocoons. *Residuals* refers to the residuals of average cocoon dry mass regressed on average worker dry mass. Figures are shown with one standard error bar

Variation between colonies explained 47% of the total variation in worker size in the unmanipulated colonies ($F_{49,\ 1860}$=35, P <0.0001; Fig. 2). Average head width size ranged from 0.89–1.24 mm. Overall worker head widths varied from 0.80–1.45 mm. The range of worker sizes within a colony was relatively small (average standard deviation =0.076, n =42); consequently different colonies often had considerably different distributions of worker sizes. Colonies had unimodal distributions. The mean kurtosis value was 0.08±0.14 SE, which was indistinguishable from zero (t_{42}=–0.60, 0.9> P >0.5). Worker size distributions were skewed towards larger workers within colonies (mean skew =0.324, t_{42}=4.31, P

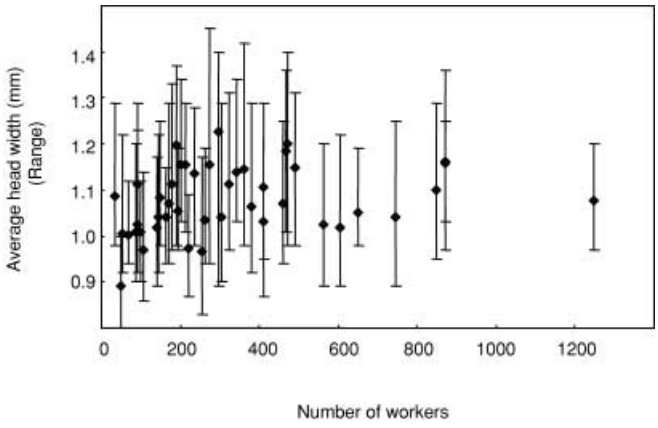

Fig. 2 The relationship between mean worker head width and worker number. Mean head widths are shown along with the maximum and minimum worker head widths

Table 1 Correlations between components of the caste distribution function and worker number (n =36 colonies). Estimates of the caste distribution function are based upon 35 workers per colony

	Mean head width	Standard deviation	Skew	Kurtosis
Log (worker number)	0.38*	0.26	–0.30	–0.36*
Mean head width		0.45*	–0.65**	–0.27
Standard deviation			–0.32	–0.21
Skew				0.54**

* significant at P <0.05 and ** P <0.05 after a Bonferonni correction

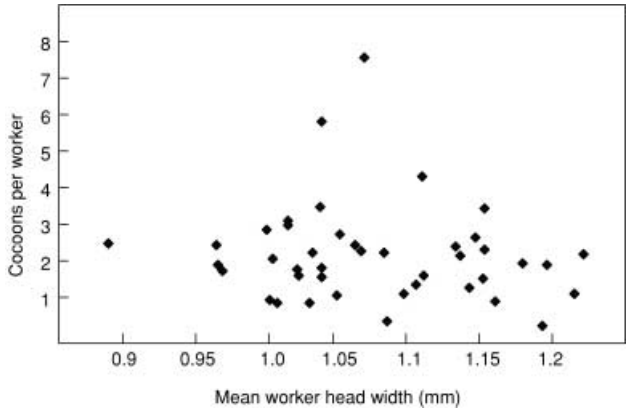

Fig. 3 The relationship between mean head width and the number of cocoons produced per worker

=0.0001). Average worker size increased slightly with increased worker number (Fig. 2; r^2=0.10, P =0.04, n =42). After applying a Bonferonni correction only mean head width and skew, and skew and kurtosis were significantly correlated (Table 1). Neither average worker size (Fig. 3, $F_{1, 37}$=1.1, P =0.30) nor the standard deviation of worker size ($F_{1,37}$=0.02, P =0.90) affected cocoon production, though the logarithm of worker number entered both models ($F_{1, 37}$=74, P =0.0001; $F_{1, 37}$=81, P =0.0001, respectively; reproductive colonies were excluded from the analysis). There was no evidence that mean worker size affected new worker production.

Discussion

To date there has been limited evidence that variation in worker sizes within ant colonies is adaptive. By manipulating worker sizes in a field setting, this study clearly demonstrates that the CDF affects new worker production in *F. neorufibarbis*. Additionally, reproductive potential in *F. neorufibarbis* (Billick 1997), as in many other colonial organisms, is primarily a function of worker number (Odum and Pontin 1961; Michener 1964; Fowler 1986; Nonacs 1986; Porter and Tschinkel 1986; Savolainen et al 1996). Consequently, the manipulation of the CDF affected colony performance in a manner linked to colony fitness.

Colonies with large workers removed did have a larger percentage of their biomass removed. The differences between treatments were small however (6.8% versus 5.4% in the control colonies), compared to the 50% decline in new worker biomass. Consequently, the decrease in new worker production was not due to the loss of the biomass of larger workers in any simple way.

While the CDF affected new worker production, the results were inconsistent with Bernstein's (1976) hypothesis that colonies retain a range of worker sizes to maximize foraging times. Bernstein (1976) suggests colonies maintain workers of different colors and sizes. Clearly that was not the case in this population (Fig. 2). The average worker size varied considerably between colonies. At the extreme there was little or no overlap in worker size between colonies.

This amount of variability in worker size between colonies is unusual. While intercolony variability in the CDF is common (e.g. Brian 1957; Wood and Tschinkel 1981; Wilson 1983b; Walker and Stamps 1986; Fowler 1986; Gibson 1989; Espadaler et al 1990; Beshers and Traniello 1994; Kaspari and Byrne 1995), mature colonies generally have a full range of worker sizes (Fowler 1986; Tschinkel 1988; Gibson 1989; Espadaler et al 1990; Beshers and Traniello 1994). The degree of variation between colonies in worker sizes suggests that *F. neorufibarbis* lacks tightly controlled mechanisms to regulate worker sizes within colonies. Indeed, the fact that colonies did not produce larger cocoons in response to the loss of large workers indicates that at least in the short term, *F. neorufibarbis* colonies lack the ability to respond to fluctuations in worker sizes within colonies. This stands in contrast to a number of other species in which the CDF is controlled by homeostatic mechanisms (Wilson 1983a; Johnston and Wilson 1985; Porter and Tschinkel 1985; Schmid-Hempel 1992).

In many species with distinct worker castes the distributions of worker sizes within colonies display a well-defined relationship to colony size (Wilson 1983a; Fowler 1986; Tschinkel 1988; Gibson 1989; Hasegawa 1993a; Kaspari and Byrne 1995). In *F. neorufibarbis*, however, the relationship between average head width was only

loosely correlated with colony size (Fig. 2), as it was in at least one other population of a weakly polymorphic species, *Trachymyrmex septentrionalis* (Beshers and Traniello 1994). The life history of *F. neorufibarbis* might explain the weak relationship between average worker size and worker number. Because colonies reproduce by colony budding, worker number at a single point in time is only loosely correlated with either colony age or worker number in previous growing seasons. Workers in small colonies may have been part of large, old colonies in previous growing seasons. Thus colony budding may largely disrupt and obscure any tendency for larger workers to be found in large, old colonies.

The finding that removing large workers decreased new worker production suggests that this large intercolony variation in worker size should translate into lower rates of new worker production for colonies that naturally have smaller workers. This was not the case; there was no relationship between components of the CDF and new worker production (Table 1, Fig. 3). One explanation is that colonies might be locally adapted to their microclimates. The apparent lack of homeostatic mechanisms controlling worker sizes makes this explanation unlikely. Additionally, microclimates above the treeline are largely dominated by aspect and time of emergence from snowmelt. Consequently microclimate tends to vary along predictable gradients. In contrast variation between colonies in average worker sizes displays no obvious patterns, with colonies of very different mean worker sizes directly adjacent to one another.

An alternative explanation for the lack of a relationship between the CDF and colony performance is that the relative size of workers is important, not their absolute size. Previous studies that have manipulated the CDF in an artificial setting have focused on the absolute size of workers. In *Colobopsis nipponicus* large workers defended their nests by plugging entrances (Hasegawa 1993a, b). Small workers are necessary to brood production in *Solenopsis invicta*, presumably because large workers are inefficient at handling brood (Porter and Tschinkel 1985, 1986).

On the other hand, there is some limited behavioral evidence that relative size can be important. Large workers store food in a number of species (Wilson 1974; Espadaler et al 1990; Hasegawa 1993a) and in at least one ant species, specialization for food storage is based on relative rather than absolute size (Rissing 1984). Consequently, removal of large *F. neorufibarbis* workers may have negatively affected either food stores within colonies, or food storage capacity. Ultimately, however, the manner in which worker size and behavior translates into colony productivity is poorly understood. Consequently this explanation for why removing large workers decreased new worker production is speculative.

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