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Research article

Variation in queen size across a behavioral transition zone in the ant *Messor pergandei*

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Summary. Ant colonies should be selected to optimally allocate resources to individual reproductive offspring so as to balance production costs with offspring fitness gains. Different modes of colony founding have different size-dependent fitness functions, and should thus lead to different optimal queen sizes. We tested whether a behavioral transition from solitary colony founding (haplometrosis) to group colony founding (pleometrosis) across the range of the ant *Messor pergandei* was associated with a difference in queen size or condition. Both winged gynes and founding queens were significantly smaller and lighter at pleometrotic than at haplometrotic sites, with an abrupt shift in these characters across the 8.5 km-wide behavioral transition zone. Both the mutualistic advantages of grouping and among-queen competition within associations are likely to be important in selecting for smaller queen size in pleometrotic populations.

Key words: Haplometrosis, pleometrosis, body size, colony founding.

Introduction

The most vulnerable period in the life cycle of social insect colonies is that of colony founding, when a young queen leaves the parent nest to initiate her own colony. Daughter queens, or gynes, are relatively expensive to produce, and adult colonies should be selected to optimize allocation of resources to each individual offspring so as to balance the total number of offspring that can be produced with the fitness benefit each gyne would gain from additional energetic investment (Backus, 1993). Different types of colony founding vary in their energetic and behavioral requirements,

which can alter the optimal queen phenotype. For example, queens which disperse with nestmate workers (dependent colony foundation) are generally small and have few fat reserves, while independently founding queens are larger and fatter in order to provision the first worker offspring (Porter et al., 1988; Keller and Passera, 1989).

Independent colony founding itself encompasses two alternate strategies, haplometrosis and pleometrosis. Haplometrotic queens establish colonies alone and aggressively exclude conspecifics from the nest. In contrast, pleometrotic queens aggregate in groups to found joint colonies (Rissing and Pollock, 1988). Although it is likely that the selective pressures facing haplometrotic and pleometrotic queens differ (Rissing and Pollock, 1988), little research has addressed how independent founding strategy affects optimal queen body size. Selection should favor larger haplometrotic queens because they are more likely to survive colony founding (Wiernasz and Cole, 2003) and to produce an earlier and/or larger initial workforce (Wagner and Gordon, 1999; Liu et al., 2001). It is less clear how pleometrosis should influence body size. Queens in groups lose less weight per individual during founding than when alone (Rissing and Pollock, 1991), suggesting that smaller queens could be produced under pleometrosis, but grouping also promotes intracolony foundress competition which may select for larger or heavier foundresses (Nonacs, 1989; Reeve and Ratnieks, 1993; Bernasconi and Keller, 1998). Mintzer (1990) noted that group colony founding species in the genus *Atta* were significantly smaller than solitary founding species and suggested a functional link between social strategy and body size, but quantitative comparisons of haplometrotic and pleometrotic queen sizes have not been made.

The desert seed-harvester ant *Messor pergandei* shows an abrupt shift in colony founding strategy across its range in southwestern North America (Cahan et al., 1998), making it

an ideal system with which to examine the effect of founding strategy on body size. In western populations, queens are exclusively haplometrotic and intolerant of conspecifics. In eastern populations, queens are highly pleometrotic, with average numbers of queens per nest ranging from 2.5 to 7.39 (Pollock and Rissing, 1985; Ryti, 1988; Cahan et al., 1998). These two behavioral regions are connected by an 8.5 km-wide transition zone, across which founding strategy shifts abruptly. The two populations do not appear to differ phenotypically other than in colony founding behavior and are not significantly genetically differentiated (Cahan, 1999), suggesting that they are either fully conspecific or recently diverged and ecologically equivalent cryptic species. In this study, we assessed whether differences in colony founding strategy are associated with morphological differences in gyne body size and/or condition by measuring these variables over two years across the geographic transition between haplometrotic and pleometrotic populations.

Methods

Winged gynes were collected from adult colonies in January and February of 1997 and 1998 at 12 sites across southern California and Arizona (Fig. 1). Four sites, WW, DC, SS and UFC, were within the haplometrotic region. Two sites were within the behavioral transition zone, A and PW. The remaining six sites were in the pleometrotic region: FR, SW, MV, EM, FDL, and EH (full site names in Table 1).

Nest mounds were excavated lightly with a trowel and five gynes were collected. If fewer than five were seen in the top 5 cm of soil, the nest was considered not to have enough mature gynes and was not included in the study. The number of colonies sampled varied across sites and years and are presented in Table 1.

Gynes were killed by immersion in 70% ethanol (1997) or freezing (1998). Because ethanol dissolves body lipids, 1997 samples could not be used to determine queen dry mass. Samples from 1998 were dried individually at 55°C for 72 hours and weighed to the nearest 0.01 mg. Head widths of samples from both years were measured across the base of the eyes with a stereoscope fitted with an ocular micro-meter.

In addition to sampling gynes, newly-mated queens from the same sites were collected from starting colonies to examine the relationship

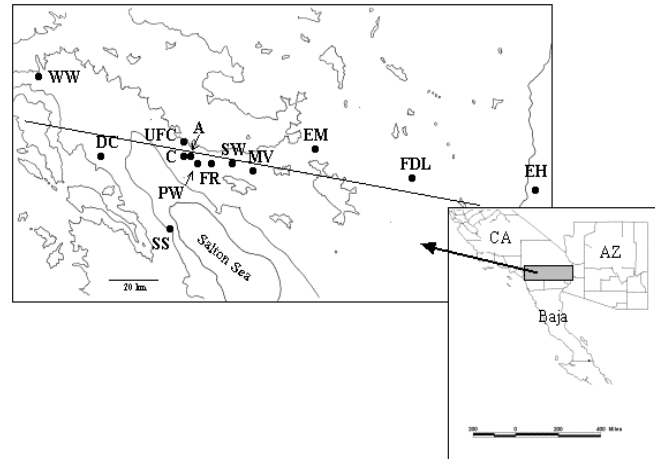


Figure 1. Map of collection sites in Riverside County, California. Contour lines indicate topography at 2,500 ft. (762.2 m) intervals. The solid line indicates a transect line (100° SE) bisecting the behavioral transition zone (see Cahan et al. 1998)

between body size and colony-founding strategy. Sites were examined every one to two days and all starting nests were excavated. All queens within the nests were collected and maintained for ≥ 8 hours in individual tubes with a moist piece of paper towel to fully rehydrate and then weighed to the nearest 0.01 mg.

Morphological variables were compared with nested ANOVAs in which colonies were nested within sites, which were nested within behavioral regions (haplometrotic, transition zone and pleometrotic). Year was included as a main effect. When overall significant effects were found, post-hoc pairwise comparisons were analyzed with the Bonferroni method. Relationships between body size variables in 1998 were assessed by an ANCOVA on dry mass with head width included as the covariate, with the same nested factors as the ANOVAs. Within sites, the relationship between queen size and founding strategy was tested in two ways. First, we compared live weights of queens found alone versus those found in groups with an unequal-variance t-test. For sites in which groups of varying sizes were collected, we also regressed live weight against the size of the group from which each queen was collected.

Table 1. Sample sizes per site for gyne and queen collection over the two years. Five gynes were sampled from each listed colony

Site	Type	Gynes (# of Colonies)		Queens		Average group size*
		1997	1998	1997	1998	
WW	Haplometric	10	10	53	151	1.02
SS	Haplometric	–	10	–	1	1
DC	Haplometric	10	8	82	16	1
UFC	Haplometric	7	3	4	4	1
A	Transition Zone	2	9	16	48	1.29
PW	Transition Zone	11	5	24	23	2.02
FR	Pleometrotic	12	9	37	97	2.83
SW	Pleometrotic	–	–	–	213	3.48
MV	Pleometrotic	3	9	–	18	2.33
EM	Pleometrotic	–	3	–	–	–
FDL	Pleometrotic	–	4	–	1	1
EH	Pleometrotic	–	5	–	18	2.17

* Group size average includes single-queen colonies and was pooled over the two collection years.

Results

Gynes were available at fewer sites in 1997 than 1998, particularly in the pleometrotic region, probably due to low winter rainfall in 1997 (Helms Cahan, 2001a). Only the haplometrotic and transition zone sites produced alates in both 1997 and 1998; gynes were significantly larger in size in 1997 than in 1998 ($F_{1,455} = 6.56, P < 0.05$), although the magnitude of this effect was less than variation across sites in 1998 (Fig. 2b). In both years, head widths of gynes showed a sharp decrease across the behavioral transition zone (Fig. 2a,b). Head widths varied between behavioral regions ($F_{2,455} = 42.49, P < 0.0001$), among individual sites within regions ($F_{9,455} = 18.88, P < 0.0001$), and among nests within sites ($F_{72,455} = 3.17, P < 0.0005$). Dry weight per unit body size also varied significantly at all of these levels (Type: $F_2 = 366.40, P < 0.001$; Site: $F_9 = 50.72, P < 0.001$; Nest:

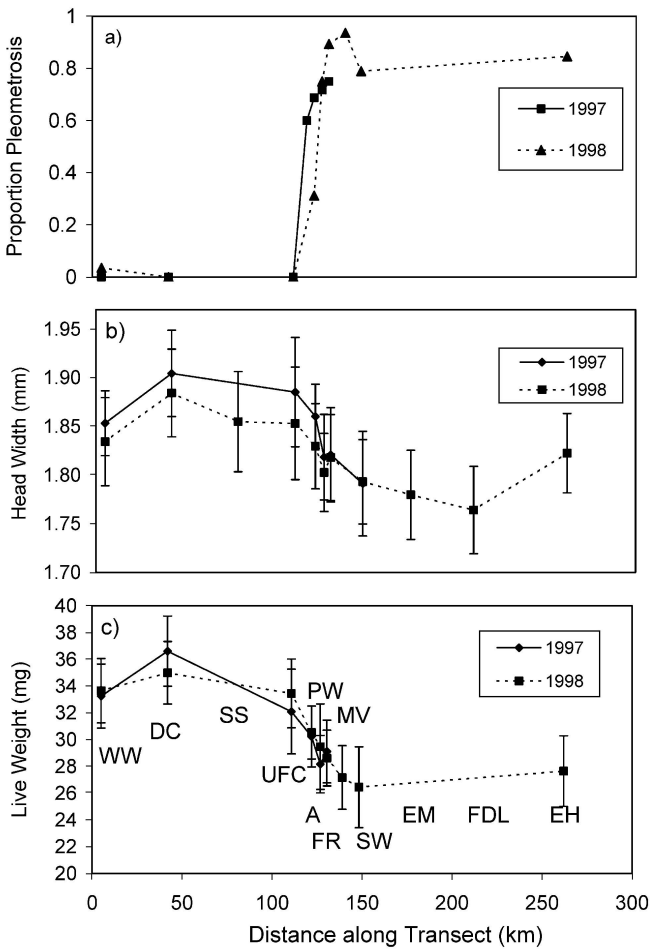


Figure 2. Geographical distributions of a) pleometrosis (data from Helms Cahan, 2001), b) gyne head width (\pm st. dev.), and c) queen live weight (\pm st. dev.) over the two-year study period. The geographical distribution of sites was linearized by assigning each site the distance from the western edge of the transect to the point at which a perpendicular line from the site crosses the transect line. The pleometrosis estimate for site MV in 1997 (0%, from Helms Cahan, 2001) was omitted from figure (a) because the estimate was based on only a single nest

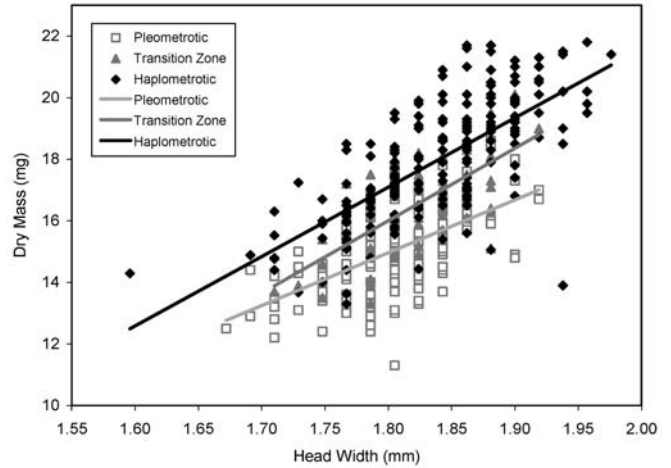


Figure 3. Relationship between dry mass and head width for gynes from the haplometrotic (black diamonds), transition zone (gray triangles), and pleometrotic regions (white squares). Lines indicate the best-fit linear regression lines for each set

$F_{73} = 3.78, P < 0.001$). Haplometrotic gynes were heavier per unit body size than transition zone gynes (Bonferroni Pairwise Comparisons, $P < 0.001$), which were heavier than those from the pleometrotic region ($P < 0.001$) (Fig. 3). The slopes of the relationship between dry mass and head width did not differ significantly among the three regions ($F_2 = 2.32, P = 0.1$).

Results for newly mated queens were similar to those for gynes. At sites for which two years of data exist, year did not have an overall effect on live weight (ANOVA, $F_1 = 0.35, P = 0.55$); although there was a significant interaction effect between year and site ($F_5 = 2.56, P < 0.03$), none of the sites differed significantly from year to year when considered individually. Queen live weight shifted abruptly across the behavioral transition zone, from heavier queens in the haplometrotic region to lighter queens in the pleometrotic region (Fig. 2c). Both behavioral region and individual site had a significant effect on queen live weight (ANOVA, Region: $F_2 = 32.33, P < 0.001$; Site: $F_8 = 4.759, P < 0.001$). When considered as pairs within regions, however, only a single pair, FR and MV within the pleometrotic region, were significantly different (Bonferroni pairwise comparisons, $P < 0.03$).

The live weights of queens found alone versus in groups were compared for all sites where at least one group nest was found (sites WW in 1998 only, A, PW, FR, SW, MV, EH). Data from each year were analyzed separately. Live weight was significantly associated with group membership in two sites: WW, in which queens found in groups were heavier ($t_{7,5} = -4.46, P < 0.005$; Fig. 4a), and PW in 1998 (but not in 1997), in which grouped queens were lighter than queens found alone ($t = 2.51, P < 0.03$). In the remaining sites there was no relationship between live weight and group membership. The same results were obtained when live weight was regressed against group size. The only significant correlation was for site PW in 1998, in live weight width and group size were negatively correlated ($F_{1,21} = 7.52, P < 0.02$; Fig. 4b).

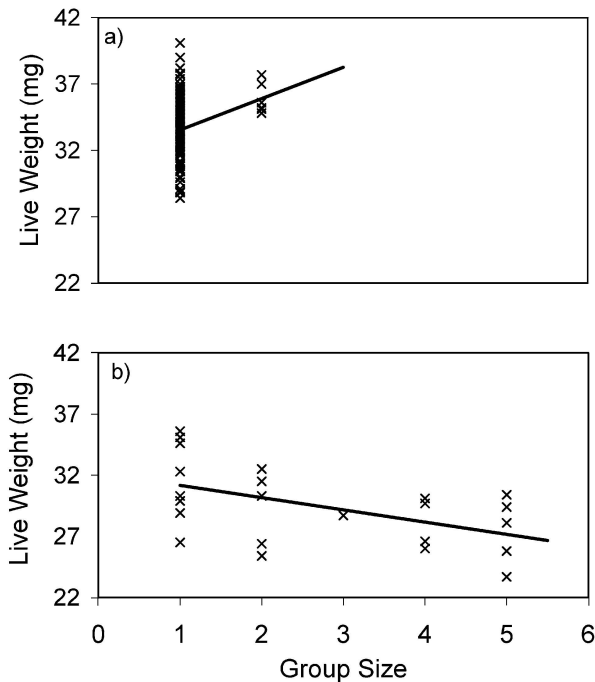


Figure 4. Relationship between live weight and group size at a) WW, a primarily haplometrotic site, and b) PW, a transition zone site

Discussion

The results of this study indicate a consistent, significant difference in queen size between haplometrotic and pleometrotic behavioral regions. Haplometrotic *Messor pergandei* gynes and mated queens were almost 20% heavier than their pleometrotic counterparts, while transition zone queens were intermediate (Fig. 2). This is attributable to differences both in size and relative condition. The morphological differences observed are unlikely to be due to regional variation in nutritional status of adult colonies. Although haplometrotic and pleometrotic regions differ in resource availability (Helms Cahan et al., 2001a), clines in average precipitation and resource abundance across the range of *M. pergandei* share neither the abruptness nor geographic location of the shifts in both founding behavior and body size (Helms Cahan, 2001a). In addition, although *M. pergandei* queen weight is affected by resource levels, overall body size does not change with the nutritional status of the colony (Ode and Rissing, 2003). It is more likely, therefore, that size and weight differences indicate a reduction in per-queen investment allocation associated with pleometrotic colony founding.

Two selective forces may contribute to the evolution of reduced body size in pleometrotic populations. First, parent colonies may benefit from reducing investment into individual gynes and redirecting the surplus into a larger number of offspring if reduced mass does not lower fitness returns. This could indeed be the case in pleometrotic associations in *M. pergandei*. Group colony founding requires fewer resources on average per queen than solitary founding because nest excavation and brood care responsibilities are shared, reducing the per capita energetic investment needed to permit

queens to found a colony successfully. Reduced weight loss per queen when in groups has been demonstrated in a number of ant species, including *M. pergandei* (Waloff, 1957; Bartz and Hölldobler, 1982; Tschinkel and Howard, 1983; Rissing and Pollock, 1991). It should be noted, however, that the size of individual gynes may not be equivalent to units of “offspring” from the perspective of a parent colony if sisters jointly found colonies. In this case, its investment into a single daughter colony would be the cost of two or more gynes rather than one, canceling out the benefit of smaller body size. The average relatedness of naturally cofounding queens is not significantly different from zero (Hagen et al., 1988), suggesting that the frequency of sibling associations is low and thus individual body size is a reasonable approximation of parental investment, but more detailed investigation of cofoundress genetic relationships would be needed to determine the precise frequency with which sibling associations occur.

A straightforward benefit to producing smaller queens may also be amplified by the potential for exploiting the investment of unrelated cofoundresses, a strategy only available when queens cohabit nests. Experiments forcing normally haplometrotic and normally pleometrotic *M. pergandei* queens to cofound colonies in the laboratory have shown that pleometrotic queens are highly adapted for intragroup competition, investing significantly less energy into the founding colony and consuming excess eggs laid by cofoundresses (Helms Cahan, 2001b). Importantly, large body size is not significantly associated with winning post-founding fights between queens in *M. pergandei* (Rissing and Pollock, 1987), so there may be few constraints on reducing queen body size in this species. This is not true for some other pleometrotic species (Nonacs 1992; Bernasconi and Keller, 1999), for which reduction in queen size or mass may not be selectively favored.

In addition to regional differences, queen body size also varied significantly within each region, both among sites and nests. However, outside of the transition zone this variation did not appear to be functionally related to queen grouping propensity. At all pleometrotic sites, there was no relationship between queen mass and group size. This is consistent with behavioral data reported in Cahan et al. (1998) suggesting that queens from pleometrotic sites found alone were fully pleometrotic in their behavioral preference but had failed to find a cofoundress while searching for a nest site. Only one haplometrotic site, WW, showed any variation in queen number across nests, with a total of two queen pairs found across both years. Unlike the trend across regions, grouped queens at this site were significantly larger than those found in solitary nests (Fig. 4a). Queens at WW are virtually always haplometrotic and it is likely that the observed grouping resulted from territorial “stalemates” between particularly large, aggressive queens rather than from active aggregation.

At site PW, the center of the transition zone between haplometrotic and pleometrotic regions, body size was significantly negatively related to group size in one of the two years. Three processes could lead to such an association. First, the two behaviorally distinct populations described as *Messor pergandei* could in fact be two cryptic species interspersed in transitional sites but genetically isolated from one another.

Preliminary estimates of gene flow between haplometrotic and pleometrotic populations suggest that this is not the case (Cahan, 1999), but additional genetic data are required before this hypothesis can be conclusively rejected. If gene flow does occur, recombination within the transition zone should decouple body size and founding behavior traits. However, many of the queens founding colonies at site PW may be immigrants from behaviorally “pure” sites on either side of the transition zone, producing linkage disequilibria between traits. This is especially likely because the transition is located in an area of low adult nest density relative to adjacent populations on either side (Helms Cahan, 2001a), decreasing the relative contribution of recombinant transition-zone colonies to the founding queen population. Alternatively, body size and founding strategy may both be influenced by the same gene or set of genes. Similar pleiotropic effects have been ascribed to the *Gp-9* gene (or gene complex) in the red imported fire ant, *Solenopsis invicta*; queens homozygous for the BB allele both found colonies independently and store large amounts of fat, while heterozygous queens (Bb) are recruited into adult nests and are significantly thinner than homozygous queens (DeHeer et al., 1999). More detailed morphological and genetic comparisons of gynes and founding queens collected within the transition zone may enable us to distinguish between these factors.

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