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# QUEEN SIZE MEDIATES QUEEN SURVIVAL AND COLONY FITNESS IN HARVESTER ANTS

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*Abstract.*—We examined the effect of queen size on the probability of new colony establishment in the ant *Pogonomyrmex occidentalis*. Large queens are significantly more likely to survive than small queens through the initial stages of colony founding. These differences in individual fitness correlates have corresponding effects on colony fitness. In species in which individual queens vary in fitness, sexual allocation ratios should incorporate the individual fitness functions.

*Key words.*—Ants, colony fitness, *Pogonomyrmex*, reproductive allocation, selection.

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Large size is frequently associated with higher fitness in females. Larger females may have higher survival probabilities, reproduce more often, and have more and/or larger offspring (Clutton-Brock 1988; Roff 1992; Stearns 1992). In many species of insects, fecundity and female size are strongly correlated (e.g., McLain and Marsh 1990; Robb et al. 1992; Nunney 1996; Oberhauser 1997; Carvalho et al. 1998).

In social insects, especially ants, new colonies are frequently begun by a single queen, who rears the first brood of workers alone (Wilson 1971; Hölldobler and Wilson 1990). The queen can expend a significant amount of protein and lipid reserves stored in her body until the first worker brood has matured (Wheeler and Buck 1996). Among ants, queens which found colonies singly are significantly larger than those which found new colonies as part of a group (Herbers 1984; McInnes and Tschinkel 1995; Kikuchi et al. 1999; Ruppell and Heinze 1999), have much larger fat stores (Keller and Passera 1989), and are relatively large compared to workers (higher queen-worker thoracic volume ratios; Stille 1996). In harvester ants, large queens have higher fat content than small queens (Wagner and Gordon 1999), and queens that forage during colony-founding are smaller than queens that do not forage (Johnson 2002). Size also may affect desiccation rate in ants; queens, which are larger than workers, lose water at a significantly lower rate (Lighton and Feener 1989; Lighton et al. 1993; for an alternate explanation see Johnson 2000), and species with larger queens occupy more xeric environments (Kaspari 1993; Johnson 1998).

These relationships suggest that queen size may be subject to natural selection. Although intraspecific variation in queen size has now been widely documented in ants (Buschinger and Heinze 1992; Heinze et al. 1992; Ruppell et al. 1998; Kikuchi et al. 1999; Ruppell and Heinze 1999; Wagner and Gordon 1999; Ode and Rissing 2002), the consequences of variation in queen size for correlates of queen fitness have not been addressed. If queen survival is influenced by queen size, then colony fitness may be affected not only by the number of queens produced, but their size. Colonies investing equally in queens, in terms of the female biomass produced, may not have equal fitness if they differ in average queen size. Here, we determine the role of queen size in mediating queen survival through the initial stages of colony founding in the western harvester ant, *Pogonomyrmex occidentalis*.

In western Colorado, queens of *P. occidentalis* mate in large hilltop swarms. Mating begins in midafternoon (around 1500 MDT) and continues until early evening (around 1800) (Wiernasz et al. 1995; Abell et al. 1999). Queens then fly back to the desert floor and begin digging individual nest burrows, which they continue to excavate for several days after the mating flight. Colony founding in this species is invariably by single queens (Cole and Wiernasz 2000a), but queens continue to forage while they raise the first brood of workers. Size may affect survival in several ways: (1) large queens may be less susceptible to desiccation; (2) they may be less prone to predation and more adept at intraspecific competition; or (3) they may be able to mature the first brood of workers more rapidly.

## Materials and Methods

This study was carried out in an area approximately 150 m x 100 m that is located within a large permanently marked population of *P. occidentalis* (for a complete description of the site see Wiernasz and Cole 1995). After the 3 August 1997 mating flight, we searched for actively digging queens by walking slowly through the area, and videotaped all foundresses that we observed. A millimeter rule was used as a scale measurement. The burrows of videotaped queens were marked with orange 37.5 cm survey flags placed 2 cm north of the entrance. Queens were not individually marked because marking would require capture and destruction of the burrow. Because digging queens are very wary, they were recorded from a distance of over a meter, and from as directly overhead as possible. For two weeks after the flight, the marked burrows were checked twice daily and scored as open, closed, or queen (if the queen was observed); burrows were scored once more on 21 August. Frequent rainfall in August simplified burrow scoring—queens were judged alive if their burrow showed signs of activity after a rainfall. Although this may have created some false negatives, it is likely to have eliminated false positives. Unusually heavy rain in September prevented continued burrow checks. In mid-October,

TABLE 1. Summary statistics for the size distribution of measured queens before and after selection (mean ± SD [sample size]), and the estimated distribution before selection based on an actual survival rate of 0.290 to 17 days.

| | Head Width (mm) | Thorax Width (mm) | Gaster Width (mm) |
|---|---|---|---|
| Estimated mean before selection (SD) | 2.144 ± 0.195 | 1.926 ± 0.206 | 2.541 ± 0.214 |
| Survivors to 17 days | 2.220 ± 0.215 (106) | 2.005 ± 0.239 (102) | 2.555 ± 0.206 (104) |
| Dead by 17 days | 2.112 ± 0.176 (139) | 1.893 ± 0.182 (134) | 2.535 ± 0.217 (140) |
| Survivors to 73 days | 2.236 ± 0.185 (29) | 2.010 ± 0.176 (29) | 2.574 ± 0.194 (29) |
| Dead by 73 days | 2.214 ± 0.225 (77) | 2.003 ± 0.261 (73) | 2.548 ± 0.211 (75) |

all marked nests were checked twice in a three day period. Maturation of the first brood of workers takes approximately five weeks (Johnson 1998; personal observations), so this census represents survival through the initial stages of colony founding. Queens were scored as alive if the burrow showed signs of activity. In late May 1998, all marked nests were checked a final time as part of the annual census of the entire study site (see Wiernasz and Cole 1995).

Queen size was quantified by three morphometric measurements using Optimus 5.2 imaging software (Media Cybernetics, Carlsbad, CA). We measured head width (across the eyes), thorax width (at the widest point), and gaster width (at the widest point) on all queens. We compared the size of queens that were still alive on 21 August to those that had died by that time using both univariate tests of individual morphometric characters and principal components analysis. We compared the size of queens that were alive on 21 August with those still alive on 18 October to determine when during colony founding selection on size was acting. We determined the standardized selection coefficient (estimated as [size after selection − size before selection]/standard deviation prior to selection) by estimating the mean and standard deviation of queen size before and after selection. We used the size of surviving individuals to generate the size distribution after selection, and used the size of all individuals that had usable images to estimate the distribution before selection (of the 611 queens we video recorded, 249 produced usable images). The mean size before selection is the average size of survivors and nonsurvivors weighted by the true survival probability of 29% (based on observations of activity at all marked burrows). The variance in size before selection is the weighted mean square deviation of survivors and nonsurvivors from the mean before selection. To visualize selection, we estimated fitness functions using the cubic spline of survival on the trait with 500 bootstrap iterates to establish 95% confidence intervals (Schluter 1988).

We could not measure the dry weight of digging queens without disturbance that would influence survival. Instead, we used measurements of head, thorax and gaster width, and dry weight from an independent sample of 259 queens collected in 1994 at a large mating swarm (see Abell et al. 1999). This sample consisted of mainly winged queens (wings contribute negligibly to estimates of dry mass: less than 0.1 mg) that were measured using an ocular micrometer. We used the relationship between morphometric size and dry weight in this sample to estimate the weight of founding queens.

We used the relationship between queen size and survival to calculate the colony fitness function for investment in individual queens. Colony fitness was the payoff per unit of investment in queens of different sizes. The colony fitness gradient was the derivative of the colony fitness function (the additional fitness gained by the colony for making incrementally larger females). Measurements of average queen size obtained from colonies that have been monitored for reproductive output (Cole and Wiernasz 2000b) were used to evaluate colony performance in this population.

## RESULTS

We recorded 611 foundress queens in the act of digging nest burrows; 177 of these (29.0%) were known to be alive on 21 August. In the October census, 40 of these (7.0%) were still alive. None of the queens were alive during the May census, thus our analysis of selection is confined to the period when the queen is rearing brood alone. Queens that had survived the initial period of colony founding had significantly larger head ($t_{243} = -4.31$, $P < 0.0001$) and thorax ($t_{234} = -4.09$, $P < 0.001$) widths than queens that had died; gaster width did not differ between groups ($t_{242} = -0.74$, $P > 0.4$; Table 1). The first principal component was overall size, with all morphological measurements loading positively (PC 1 loadings = 0.85, 0.85, 0.80, for head, thorax, and gaster, respectively). The second PC contrasted head and thorax width (both loadings = 0.28) with gaster width (−0.61). The third PC contrasted head width with thorax width (loadings = 0.44 and −0.44, respectively) with gaster width contributing negligibly (loading < 0.001). Surviving queens had significantly higher scores for both overall size PC 1 ($t_{231} = -3.30$, $P < 0.002$) and PC 2 ($t_{231} = -3.53$, $P < 0.001$), but not PC 3 ($t_{231} = 0.32$, $P > 0.75$). There is significant selection on both PC 1 ($s^* = 0.322$) and PC 2 ($s^* = 0.317$), but not PC 3 ($s^* = 0.025$). Strong directional selection favors large queens (Fig. 1). The queen size distribution was not significantly different between the 17 day and the 73 day sample, whether we use univariate or multivariate measures (*t*-tests for all 6 comparisons, $P > 0.4$).

We estimated the relationship between dry weight and morphometric size to estimate the dry weight of videotaped queens. $\text{Dry weight (mg)} = -19.32 + 6.967^*(\text{HW}) + 2.031^*(\text{TW}) + 4.940^*(\text{GW})$ ($n = 259$, $r^2 = 0.85$). We then determined the effect of estimated dry weight on survival to estimate colony fitness. $\text{Survival} = -0.0874 + 0.0419 \times (\text{Dry Wt})$. The payoff to colonies, in terms of increased queen survival per unit of investment, was as follows: $\text{Survival/Dry Wt} = .0419 - (.0874/\text{Wt})$. The payoff to a colony in terms of the expected number of daughter colonies produced per unit of investment increased with increasing size of each queen (Fig. 2A), although at a declining rate. The average size of queens produced by colonies is clustered, and localized to the region of the colony fitness gradient where small

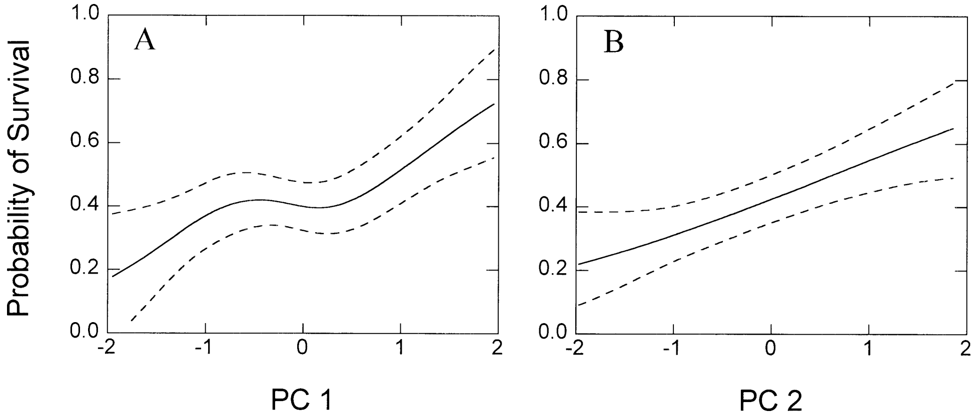

FIG. 1. Individual fitness functions showing queen survival (±95% confidence intervals) as a function of (A) overall size (PC 1) and (B) relative size of the head and thorax (PC 2). Both functions reveal significant directional selection favoring larger size.

changes in queen size result in small marginal changes in the fitness per unit of investment (Fig. 2B).

## DISCUSSION

In *P. occidentalis*, large queens are significantly more likely to survive the initial stages of colony founding than small queens. In a laboratory study, oviposition rate was found to be positively correlated with queen weight in *Pogonomyrmex barbatus* (Wagner and Gordon 1999). In *P. occidentalis*, selection on size acts very early, within the first three weeks, during the colony founding period, suggesting that there is a fitness advantage of large queens due to survival apart from any difference due to more rapid brood production.

Queen mortality in this population of *P. occidentalis* is extremely high, so any advantage to survival is likely to be important. Low queen survival typifies single foundress species (Hölldobler and Wilson 1990). Sources of this high mortality are largely unknown, although intense predation has been documented for some species (Nichols and Sites 1991; Gordon 1999). Size may affect survival in several ways. Foundresses must quickly dig a burrow that is deep enough to avoid high surface temperatures. Queens with relatively large heads (and thus large mandibles) and thoraxes may be able to dig faster or longer. Large queens also may be less prone to death by desiccation either during the initial burrow digging or during foraging trips they make while raising the first brood (Lighton et al. 1993).

Because queens could not be individually marked, the survival of individual queens could not be tracked with absolute certainty. A foundress could move elsewhere or be supplanted by another foundress. We did not observe movement or burrow supplanting, but such changes in foundress identity would not be detected by our study and may represent sources of error. A supplanting would result in a false positive; this is random error when one queen's probability of taking over another's burrow is independent of their relative sizes. If, as would seem reasonable, large queens are more likely to supplant small queens, then small queens would have a higher apparent survival probability, biasing against our results. A queen that moved elsewhere and survived is a false negative. If movement and subsequent survival is independent of body size, this is an additional source of random error. Only if small queens are more likely to move successfully than large queens, would we overestimate the strength of selection on

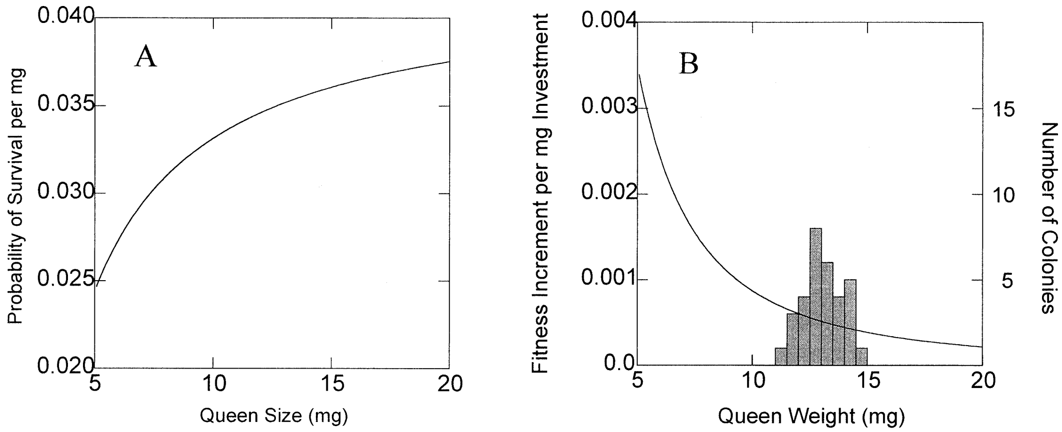

FIG. 2. The fitness of colonies as a function of the average size of the queens that they produce. (A) The incremental fitness gain (payoff per unit of investment) as a function of average queen size. (B) The additional fitness advantage to the colony for making incrementally larger queens. The histogram shows the frequency distribution of average queen sizes from colonies in 1994.

size. In some species of *Pogonomyrmex* established colonies move frequently (*P. badius* [W. R. Tschinkel, pers. comm.]; *P. barbatus* [Gordon 1992]), but in *P. occidentalis*, movement rates are quite low (~2.5% of colonies annually, unpubl. data). The degree to which foundresses in this genus move during the initial period of colony establishment is not known for any species. In our population, the behavior of established colonies suggests that the outcome of most moves to be a reduced probability of survival.

Selection at both the individual and the colony level favors increasing size. Selection on individual queens strongly favors increased body size (the strength of selection, $s^* = 0.32$) because the individual payoff to queens continues to increase with body size. Colonies also benefit from producing larger females because these females are more likely to survive. Whether the colony point of view is that of the colony queen or that of the workers, the colony benefits when all reproductives are as large as possible. Colonies appear to respond to this selection by producing large queens, although colonies still differ significantly in queen size (D. Wiernasz and B. Cole, unpubl. ms).

Because the individual fitness of queens, and the colonies that produce them, vary as a function of queen size, it is not sufficient to characterize fitness gain through female function by the total investment in females (e.g., Charnov 1982). Colonies which distribute a given amount of female biomass among fewer large queens will have a higher probability establishing new colonies than those which divide it into a larger number of small queens. In this species, both intra- and inter-colony variation in queen size is substantial. In most other species, the amount of variation in body size is largely unknown. It will be important to incorporate measurements of fitness as a function of size to measure sexual allocation accurately. Several species of ants produce queens that are highly variable or dimorphic in size (Buschinger and Heinze 1992; Ruppell et al. 1998; Kikuchi et al. 1999; Ruppell and Heinze 1999; Wagner and Gordon 1999). Particularly for such species, one can modify the sex allocation measures using the Shaw-Mohler equations (1953), to incorporate fitness differences within and between the sexes (Crozier and Pamilo 1996).

Given the apparent advantage to large queens, why are queens not even larger? Two factors may explain the upper limit on queen size. First, although large queens may be better defended against solitary arthropod predators, it is probably not possible for a queen to be large enough to defeat a group of workers from an established colony or a vertebrate predator (Gordon 1999). Foundresses of *Messor semirufus* avoid digging burrows in soil marked by conspecific workers, perhaps to reduce encounters with established colonies (Kawecki 1992). Second, queen size may have biomechanical constraints. Queens have significantly higher wing loading than males (A. Abell, B. Cole, D. Wiernasz, unpubl. data). Very large queens may have difficulty flying to the mating swarm or subsequently dispersing. If individual selection on queen size is stabilizing rather than directional, then the selective pressure on individual queens and the colony will coincide, provided individual queens are built to near their optimum size.

By contrast, in males of this species, there is considerable size variation both within and among colonies (Wiernasz et al. 2001; Wiernasz and Cole submitted). Although there is strong sexual selection on male body size (the strength of selection is as large, $s^* = 0.33$ [Abell et al. 1999; Wiernasz et al. 2001]), male size is not consistent among colonies. The coefficient of variation in body size of males (across colonies) is 0.119 (Wiernasz et al. 2001), for queens it is 0.065. This variability has consequences for colony fitness. A colony that produces males of average size has more than a 20% fitness loss compared to the colony that produces the largest males, whereas a colony that produces queens of average size has only 3% lower fitness than the colony that produces the largest queens. We suggest that selection on queen body size has contributed to the reduction of variability of queen size relative to male size in *P. occidentalis*. As a result colonies differ more with respect to male size than queen size.

These results have implications for the analysis of sexual investment ratios. Differences in the pattern of selection on queens and males mean that the shape of the colony fitness function will differ between the sexes (e.g., Campbell 2000). Fitness gain through male function (for a given amount of investment) will be greater than the gain through female function. As a consequence, understanding the pattern of sex allocation differences among colonies requires information about how selection operates on males and females at both the individual and colony level.

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