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Colony age, neighborhood density and reproductive potential in harvester ants

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Abstract At about age 5 years, colonies of the harvester ant, *Pogonomyrmex barbatus*, begin to produce winged, sexual forms (alates) that mate in large annual aggregations. We examined how colony age and neighborhood density affect the numbers, body mass, and body fat of alates produced by 172 colonies ranging in age from 4 to 17 years. Over one-third (36%) of all colonies produced no alates. Failure to reproduce was independent of colony age. Of those colonies that did produce alates, older colonies produced more alates than younger colonies. Older colonies produced lighter female alates (in dry mass), but the total biomass of additional alates produced by older colonies far outweighed the reduced allocation to female alate body mass. Body fat content was much higher in female alates (36.0% on average) than in males (3.7% on average). Alate body fat content was not related to colony age. The fitness of female alates may be related to their fresh body mass; that of females captured after mating and reared in the laboratory was positively correlated with egg-laying rate, although not with the total number of eggs in the first brood. Neighborhood density was not related to alate number, mass, or fat content, in contrast to the results of a 1995 study at the site, in which alate numbers were negatively related to neighborhood density. Thus the influence of crowding on reproductive output appears to vary from year to year, perhaps in response to variation in rainfall and food supply. Alate output by individual colonies was correlated among years. These results suggest that a few, older colonies dominate the pool of reproductives year after year.

Key words Harvester ants · Life history · Intraspecific competition · Body mass · Body fat

Introduction

In most organisms, reproductive output changes over the lifetime of an individual (Harper and White 1974; Clutton-Brock 1988; Roach 1993). Age-specific patterns of reproduction, as well as other features of life history, may be influenced by ecological factors such as food supply and competition (reviewed by Stearns 1976; Roff 1992). Given the ecological importance of ants, surprisingly little is known of the life histories of ant colonies. It is not known for how long colonies of any ant species reproduce, whether reproductive output or quality change as colonies age, or how intraspecific competition affects age-specific patterns of reproduction. Here, we examine colony life history in a monogynous, seed-eating ant species (*Pogonomyrmex barbatus*) in which colonies live for 15–20 years (Gordon 1991), using a study population in which colonies have been censused since 1985.

Ant colonies are iteroparous: the queen continues to produce reproductives (winged sexual males and females, or alates) for many years. Each summer, mature colonies of *P. barbatus* send male and female alates to a mating aggregation. Colonies begin to reproduce, by contributing alates to that year's mating flight, when they are about 5 years old (Gordon 1995) and have reached a size of about 10,000–12,000 workers (Gordon 1992).

The quality, as well as the quantity, of alates may contribute to a colony's reproductive success. The body mass of a female alate may affect its survival and reproduction. Approximately 99% of newly-mated *P. barbatus* queens do not survive the first year (Gordon and Kulig 1996). A successful founding queen must dig a burrow, lay eggs, and rear the first brood of workers from her body stores. Until the first workers begin to forage, a queen has no source of food or water apart

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from soil moisture. Females with higher body fat may have greater access to energy stores and metabolic water. Large queens may also have an advantage in brood production; in some ant species, egg-laying rate is positively related to body mass (Keller 1988).

The neighborhood density of conspecifics can affect the reproductive output of a colony. Colonies compete with conspecific neighbors for foraging area. Behavioral interactions of neighbors change as colonies grow older and larger (Gordon 1992; Gordon and Kulig 1996), and so do the pressures exerted by competition with neighbors. Large neighbors diminish a founding colony's chances of survival (Gordon and Kulig 1996). Competition with large neighbors has little effect on the mortality of older, established colonies (Gordon and Kulig 1998), but can affect a colony's ability to produce alates. A previous study of colonies near the age when reproduction begins (5–7 years) showed that more crowded colonies produced fewer alates (Gordon and Wagner 1997). As resource availability fluctuates from year to year, the importance of density may vary as well.

We investigated the following questions. (1) What is the relationship between colony age, number of alates produced, and the mass and fat content of individual alates? We measured alate production of colonies ranging in age from 4 to at least 17 years. (2) What is the effect of colony density on reproductive output? We measured the effects of density on a wider range of colony ages than we had considered previously (Gordon and Wagner 1997). (3) Is there a correlation between numbers of alates produced in different years? For some of the colonies, we compared alate production in 1997 with measures from 1995.

Materials and methods

The study was conducted in a harvester ant population of about 350 colonies near Rodeo, New Mexico, USA, in July 1997. Colony age was known or estimated from censuses made each year since 1985 (Gordon and Kulig 1996). Of about 300 colonies that could have reached reproductive age (4 years or older), we measured alate production in 178 colonies, ranging from 4 to 17 years old and representing a range of neighborhood densities. Of the 178 colonies, there were 24 for which alate numbers had been counted in 1995.

Alates were collected with traps made of aluminum screening, consisting of a circular base about 8 cm high of wide screening, topped by a large inverted cone capped by a smaller cone, as in Gordon and Wagner (1997). Alates exit the bottom cone at its top, open end and become trapped in the upper, smaller cone. We attempted to release as many alates as possible, after counting, to join the mating flight. This population is the subject of a long-term study and we hoped to minimize disruption of its dynamics. Colonies appeared to forage normally while the traps were in place, because ants could move freely through the base of wide screening.

Traps were secured around the nest mounds in early July. There were two large mating flights, on 22 and 23 July, and a third smaller flight on 27 July. We counted alates from the first two flights only. A contingency table analysis of the presence or absence of alates in the first and second flights showed that patterns of alate production were consistent between the two flights; i.e., colonies that contributed no alates to the first flight were unlikely to contribute alates to the second. We therefore assumed that the relative contributions of different colonies to the reproductive pool could be characterized from counts made in the first two flights.

In 1995, we found that on the day of the flight, large aggregations of alates formed on the ground around some of the traps, making it impossible to determine whether the alates in the trap came from that colony. In 1997, similar aggregations formed around six traps. As before, these colonies were excluded from the data analysis, leaving 172 colonies.

During the mating flights we visited each trap, counted the alates, and released most of them so that they could join a mating aggregation. After all traps were visited once, we visited them again in the same order, counting and releasing the few, late-emerging alates. Alates were counted by four people, each adhering to a predetermined sequence which scrambled colonies with respect to local density. Collecting from 178 colonies (in 1997) rather than 45 (in 1995) took much longer; it took about an hour for four people to visit and count the alates from all 178 colonies. We had the impression that females were able to escape the traps, and did so more quickly than males. In colonies visited more than about 30 min after alates began to fly, we noticed a lower proportion of females, while in many of the colonies visited last there were still large numbers of males inside the traps. For the second mating flight, on 23 July, the numbers of males and females for the first 10 colonies visited by each observer in about the first 15 min of the flight differed significantly from the number we found for colonies visited later (for females: $t = -4.1$, $df = 171$, $P < 0.001$; for males: $t = -2.5$, $df = 171$, $P = 0.01$). The difference was most pronounced in older colonies, which also had more alates, perhaps because the jostling in a crowded trap increased the chances an alate would get back to the open end of the cone. The mean proportion of females in early counts on 23 July was 43.8% (SE = 6.1, $n = 34$ non-zero colony counts), while for the colonies visited more than 15 min later it was 27.8% (SE = 3.7, $n = 74$ non-zero counts). For data analysis we used numbers of males only, and checked whether including the females, or using only the counts from colonies visited early, led to consistent results.

We examined the effect of colony age and density on two related measures of colony reproduction. First, we used chi-square tests to examine the effect of age and density, grouped as categorical variables, on the failure to reproduce. Second, for those colonies that did produce alates, we used linear regression to examine how alate number, mass, and body fat depend on colony age and density. Alate numbers for each colony were the totals for both flights. As measures of density we used (1) distance to the seventh-nearest neighbor (the greater the distance, the lower the density) and (2) the number of colonies within a circle of 20 m radius. These measures were based on previous work showing that colonies are most likely to overlap in foraging range with neighbors up to their seventh-nearest, and that foraging ranges rarely overlap between colonies more than 20 m apart (Gordon and Kulig 1996).

In 25 colonies, we collected alates to measure body mass and body fat. In some of these colonies, only males or only females were present at the time of collection. A sample of 15 foraging workers was also collected from each of the 25 colonies, to compare worker and alate mass. Fresh masses were obtained immediately after collection; ants were then dried to constant mass at 60°C and reweighed. We measured fat content as a percentage of dry mass for three to ten alates of each sex per colony, using methods modified from Peakin (1972) and Keller and Passera (1989). Fat was extracted from dried, newly weighed alates by soaking alates individually in approximately 1.5 ml of ethyl ether for 24 h. The fluid was discarded and replaced, and the alates soaked for an additional 18 h. Alates were then dried for 24 h at 60°C and weighed. Fat content was calculated as: 100 × (total dry mass − fat-free dry mass)/total dry mass. All weights were made to the nearest microgram.

To determine how egg-laying rate is related to female body mass, we measured the fresh mass and egg-laying characteristics of 49 wingless females. Newly mated queens drop their wings after they fly away from the site of the mating aggregation. Several hours after the 23 July flight, we collected wingless females as they searched for places to dig a nest. We placed each female in a small petri dish with a damp cotton ball for moisture. Females were maintained in the laboratory in darkness, with the exception of about 30 min of light per day during which eggs were counted. Eggs were counted daily for 14 days, by which time egg-laying had largely ceased. The average maximum and minimum temperatures in the laboratory were 26.5°C (± 1.8 SD) and 19.1°C (± 2.0), respectively.

To examine the relationship between body mass and egg-laying rate, we first transformed the daily egg output for each individual queen as follows:

$$y_t = \ln[n_c/(m - n_c)]$$

where n_c = the cumulative number of eggs present at time t and m = the total number of eggs eventually laid by that queen. Thus y_t is the transformed number of eggs present at time t relative to the maximum number of eggs produced. We estimated each queen's rate of egg production as the slope of the regression of y_t for that individual against days since the mating flight.

Results

Alate numbers, body mass, and body fat

Many colonies (36.4%) produced no alates at all. In the 108 colonies that did produce alates, numbers of alates averaged 7.8 (±2.0 SE) for females and 16.9 (±2.7 SE) for males. In the first 10 traps visited by each observer ($n = 39$), the counts averaged 13.2 (±2.4 SE) for females and 15.0 (±3.1 SE) for males.

The number of alates per colony was not related to the mass or body fat of the alates. There was no significant relationship between the total number of males a colony made and the mean dry mass or fat content of either sex (females: $R^2 < 0.05$, $F_{1,9} < 5$, $P > 0.5$; males: $R^2 < 0.1$, $F_{1,19} < 0.2$, $P > 0.2$).

Average fresh masses were 49.8 mg (±0.4 SE, $n = 89$) for females and 24.4 mg (±0.2 SE, $n = 175$) for males. There was a significant correlation between wet and dry mass for both females ($R^2 = 0.94$, $F_{1,86} = 1292$, $P < 0.001$) and males ($R^2 = 0.93$, $F_{1,170} = 2349$, $P < 0.001$), but the sexes differed in the relationship between wet and dry mass. Water comprised 64.6% (±0.1 SE, $n = 172$) of the fresh mass of males but only 46.9% (±0.1 SE, $n = 88$) of females. Percent body water declined as female dry mass increased (Fig. 1a; regression coefficient = –0.21, $R^2 = 0.17$, $F_{1,86} = 17.9$, $P < 0.001$). In contrast, there was no relationship between percent water and dry mass in males (Fig. 1b; $R^2 = 0.002$, $F_{1,170} = 0.3$, $P = 0.6$). Fat comprised 36.0% of female dry mass (±0.4 SE, $n = 81$) and 3.7% of male dry mass (±0.1 SE, $n = 138$). Percent body fat was significantly related to dry mass in females (Fig. 1c; $F_{1,79} = 7.8$, $P = 0.007$), but not in males (Fig. 1d; $F_{1,136} = 2.6$, $P = 0.1$).

Colonies differed significantly in the mass and fat content of the alates they produced. The mean (± SE) dry mass of alates ranged among colonies from 23.4 (±1.4) to 28.1 (±0.4) mg for females and male dry mass from 7.4 (±0.2) to 10.0 (±0.1) (Kruskal-Wallis test, $\chi^2 > 33$, $df > 12$, $P < 0.001$ for both sexes). Mean (±SE) fat content ranged from 31.4% (±1.7) to 39.4% (±0.5) in females and from 1.5% (±0.1) to 6.1% (±0.4) in males (Kruskal-Wallis test, $\chi^2 > 42$, $df = 11$, $P < 0.001$ for both sexes). Colonies that produced

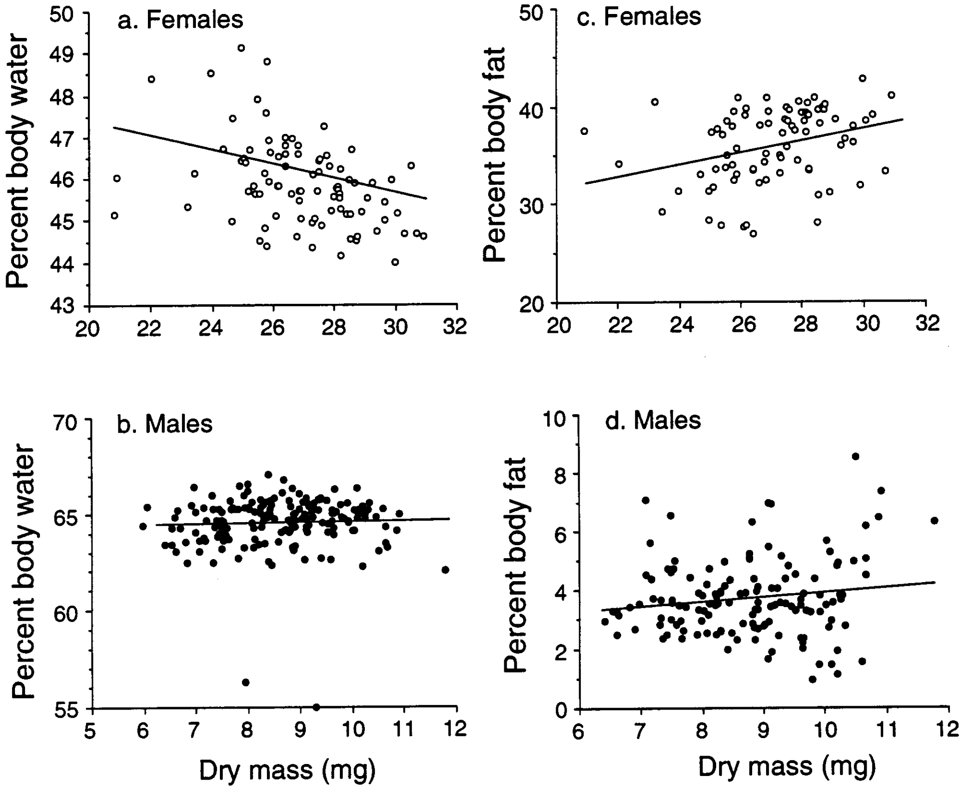

Fig. 1 Relationship between dry body mass of *Pogonomyrmex barbatus* alates and water content of females (**a**), water content of males (**b**), fat content of females (**c**), and fat content of males (**d**)

heavier female alates also produced heavier workers. Colonies differed in average worker dry mass [Kruskal-Wallis test, $\chi^2 = 103$, $df = 24$, $P < 0.0001$; range in colony averages 3.81 mg (± 0.17 SE) to 6.30 mg (± 0.27)], and average worker dry mass was positively related to average female alate dry mass (regression coefficient = 1.87, $R^2 = 0.3$, $F_{1,11} = 4.8$, $P = 0.05$). There was no relationship between worker dry mass and male dry mass ($R^2 = 0.01$, $F_{1,19} = 0.2$, $P = 0.7$).

Colony age and reproduction

Whether a colony produced alates was independent of colony age. We divided colonies into four age classes (4–5, 6–9, 10–13, 14–17 years) and found that all were equally likely to produce no alates ($\chi^2 = 0.15$, $df = 3$, $P > 0.9$).

Of the colonies that produced alates, older colonies produced more alates than younger colonies. There was considerable variation among colonies in alate production: most were produced by just a few, old colonies (Fig. 2). There was a significant positive relationship between total number of males and colony age (Fig. 2a; N males $= -2.3 + 2.1 \times$ age in years; $R^2 = 0.06$, $F_{1,106} = 6.6$, $P = 0.01$). Visual inspection of the data suggested that variance in number of males also increased with colony age (Fig. 2a); we therefore transformed alate number by taking the square root. Again, there was a significant positive relationship between the number of male alates and colony age ($R^2 = 0.04$, $F_{1,106} = 4.3$, $P = 0.04$). There was also a significant positive relationship of total number of alates, male and female, and colony age (Fig. 2b; N alates $= -5.0 + 3.2 \times$ age in years, $R^2 = 0.06$, $F_{1,106} = 6.8$, $P = 0.01$). In this case, when alate numbers were square root transformed, this relationship was only marginally significant ($R^2 = 0.03$, $F_{1,106} = 3.0$, $P = 0.08$).

Apparently, sampling error due to alates escaping from the traps did not cause the positive relationship between colony age and number of alates. The trend persisted when we examined total number of alates for the first 10 colonies counted on 23 July by each observer, when we believe our counts were accurate (N alates $= -106.2 + 17.7 \times$ age in years, $n = 26$ non-zero counts, $R^2 = 0.5$, $F_{1,24} = 25.6$, $P < 0.001$; square-root-transformed data: $R^2 = 0.4$, $F_{1,24} = 18.2$, $P < 0.001$).

The relationship between colony age and reproductive output was weak when all colonies, including those that produced zero alates, were included in the analysis. There was a significant, positive relationship between the number of males and colony age (N males $= 0.4 + 1.1 \times$ age in years, $R^2 = 0.02$, $F_{1,170} = 4.3$, $P = 0.04$), but when the number of males was square root transformed, the relationship was no longer statistically significant ($R^2 = 0.03$, $F_{1,170} = 1.4$, $P = 0.2$). This is not surprising, as the addition of zero counts considerably increased the variance at older ages.

Younger colonies produced heavier female alates than older colonies (Fig. 3; mean female dry mass $= 29.0 – 0.2 \times$ age in years, $R^2 = 0.4$, $F_{1,11} = 7.4$, $P = 0.02$), but there was no significant relationship between colony age and male dry mass (Fig. 3; $R^2 < 0.01$, $F_{1,20} = 0.2$, $P = 0.7$). There was no significant relationship between colony age and fat content for either female ($R^2 = 0.2$, $F_{1,9} = 2.4$, $P = 0.2$) or

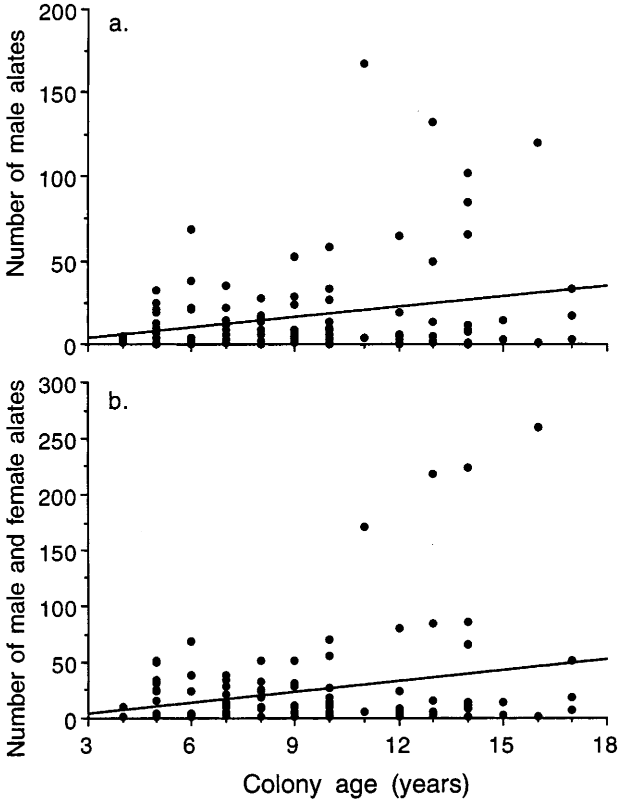

Fig. 2 Relationship between colony age and the number of male alates (**a**) and male and female alates (**b**) (n = 108 colonies). See text for regression statistics. About a third (32%) of the total number of alates produced came from 3–4% of the colonies

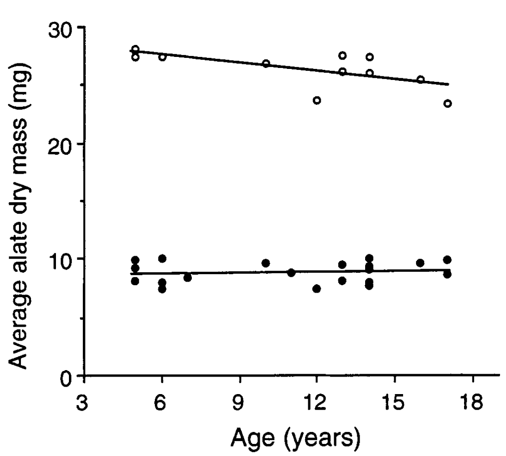

Fig. 3 Relationship of average female and male alate dry mass to colony age (*open symbols* females, *filled symbols* males)

male alates ($R^2 = 0.04$, $F_{1,19} = 0.8$, $P = 0.4$). Worker mass was positively but weakly related to colony age; the relationship was not statistically significant ($R^2 = 0.1$, $F_{1,22} = 2.5$, $P = 0.1$).

Neighborhood density and reproduction

Alate production was not related to colony density. First, colonies that differed in neighborhood density were equally likely to produce no alates ($\chi^2 = 6.9$, *df* = 5, $P = 0.3$; distance to seventh-nearest neighbor categorized as 10–15.9, 16–18.9, 19–21.9, 22–24.9, 25–27.9, 28 m and more). Second, for those colonies that did produce alates, colony density was not related to the total number of males trapped, with density measured as distance to the seventh-nearest neighbor ($R^2 < 0.01$, $F_{1,106} < 0.01$, $P = 0.9$) or number of colonies within 20 m ($R^2 < 0.01$, $F_{1,106} = 0.2$, $P = 0.7$). There was also no effect of density on the combined number of males and females trapped, with density measured as distance to the seventh-nearest neighbor ($R^2 < 0.01$, $F_{1,106} < 0.1$, $P = 0.9$) or number of colonies within 20 m ($R^2 < 0.01$, $F_{1,106} = 0.2$, $P = 0.6$). When colonies that produced no alates were included in the four regression analyses listed above, the outcome of each remained non-significant ($R^2 < 0.01$, $P > 0.5$ for all regression analyses). Using only the first 10 colonies counted on 23 July by each observer, there was again no effect of density on total alate number (distance to the seventh-nearest neighbor: $R^2 = 0.006$, $F_{1,37} = 0.2$, $P = 0.6$; number of colonies within 20 m: $R^2 = 0.03$, $F_{1,37} = 1.1$, $P = 0.3$).

In 1995, we found an effect of density on alate number in 39 colonies aged 5–7 years. For the 24 of those 39 colonies that were measured again in 1997, we found no relationship between density and total number of males trapped (distance to the seventh-nearest neighbor: $R^2 = 0.01$, $F_{1,22} = 0.3$, $P = 0.6$; number of colonies within 20 m: $R^2 = 0.01$, $F_{1,22} = 0.2$, $P = 0.6$). Considering only colonies aged 5–7 years in 1997, we also found no significant effect of density on the number of male alates (distance to the seventh-nearest neighbor: $R^2 = 0.003$, $F_{1,53} = 0.1$, $P = 0.7$; number of colonies within 20 m: $R^2 = 0.003$, $F_{1,53} = 0.2$, $P = 0.7$). Unusually large numbers of new colonies had appeared in 1996 and 1997, but these small colonies, aged 2 years or less, do not compete strongly with neighbors for foraging area (Gordon 1992; Gordon and Kulig 1996). We therefore tested for an effect of density on total number of males using only neighboring colonies 5 years or older. Again, we found no effect, either for density measured as distance to the seventh-nearest neighbor ($R^2 = 0.003$, $F_{1,170} = 0.4$, $P = 0.5$), or number of colonies within 20 m ($R^2 = 0.003$, $F_{1,170} = 0.6$, $P = 0.4$).

Neighborhood density and body mass were unrelated. Density had no significant effect on female dry mass (distance to seventh-nearest neighbor: $R^2 = 0.2$, $F_{1,11} = 2.9$, $P = 0.1$; colonies within 20 m: $R^2 = 0.07$, $F_{1,11} = 0.8$, $P = 0.4$), male dry mass (distance to seventh-nearest neighbor: $R^2 = 0.03$, $F_{1,20} = 0.6$, $P = 0.4$; colonies within 20 m: $R^2 = 0.07$, $F_{1,20} = 1.4$, $P = 0.2$), or worker dry mass (distance to seventh-nearest neighbor: $R^2 = 0.04$, $F_{1,24} = 1.2$, $P = 0.3$; colonies within 20 m: $R^2 = 0.01$, $F_{1,24} = 0.4$, $P = 0.5$). Density also had no effect on alate fat content (for both measures of density; females: $R^2 < 0.06$, $F_{1,11} < 0.7$, $P > 0.4$; males: $R^2 < 0.01$, $F_{1,20} = 0.05$, $P > 0.9$).

Comparison of colony reproduction in 1995 and 1997

A comparison of data from 1995 and 1997 showed colony-specific trends in alate production (Fig. 4). In the 24 colonies in which alates were counted in both years, the number of males produced in 1995 and 1997 was significantly and positively correlated ($r = 0.48$, *df* = 22, $P = 0.02$). Inspection of Fig. 4 indicates that the significance of this correlation rests heavily on the values for one or two colonies, so the trend should be interpreted with caution. The trend was not an artifact of a general, age-related increase in alate production by the 24 colonies over the 2 years; these colonies actually produced fewer alates on average in 1997 than they had 2 years earlier [1995: 9.6 ± 2.4 (SE) males and 12.7 ± 3.2 total alates; 1997: 4.9 ± 1.8 males and 7.0 ± 2.5 total alates].

There was no colony-specific tendency to fail to reproduce ($\chi^2 = 1.4$, *df* = 1, $P = 0.7$). Of the 24 colonies trapped in both 1995 and 1997, 9 colonies had no alates in 1995 and only 3 of those 9 colonies failed to produce any alates in 1997.

Queen mass and oviposition

Queens began to lay eggs 5–15 days after the flight, and ceased to lay eggs within 2 weeks (Fig. 5). Initial body mass had no significant effect on the onset of egg-laying ($R^2 = 0.002$, $F_{1,47} = 0.1$, $P = 0.7$). Ten of the 49 queens approached their maximum number of eggs too abruptly to estimate the slope ($n < 3$ days) and were

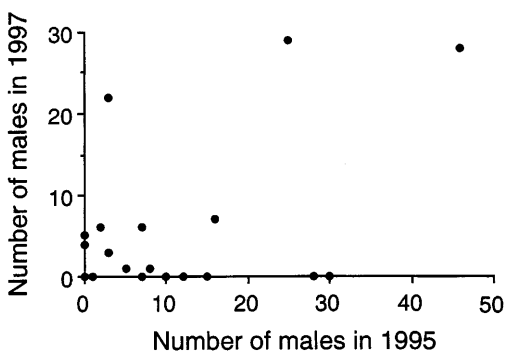

Fig. 4 Relationship between the number of males produced in 1995 and 1997 ($n = 26$ colonies)

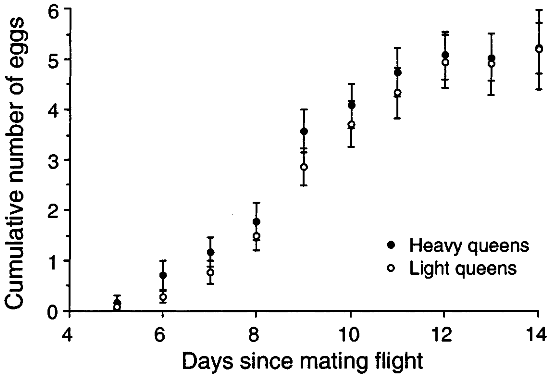

Fig. 5 Mean, cumulative egg production over time by *P. barbatus* females (*filled symbols* females with body masses greater than the median, *open symbols* females with body masses less than the median, *bars* SE)

excluded from the analysis; 7 of these queens were heavier than the mean body mass and 3 were lighter. Rate of egg production was significantly and positively correlated with body mass ($r = 0.37$, $df = 37$, $P = 0.03$). As a result, heavy queens reached their maximum egg number more quickly than lighter queens [time since flight to maximum egg number (days) = 32.4–0.4 × body mass (mg); $R^2 = 0.2$, $F_{1,47} = 9.1$, $P = 0.004$]. However, the maximum number of eggs laid was independent of body mass (Fig. 5; $r = 0.02$, $df = 47$, $P = 0.8$; mean maximum number of eggs = 8.4 (±0.4 SE).

Discussion

Harvester ant colonies continue to reproduce into old age; we found no evidence for reproductive senescence. Although fully one-third of the colonies we studied did not produce alates in 1997, the failure to reproduce was independent of colony age. Moreover, among colonies that did produce alates, older colonies made greater numbers of alates (males) than younger colonies (Fig. 2). The increased number of alates in older colonies detected here was probably not an effect of colony age on male production only. The trend persisted when we included counts of females, and when we considered only colonies checked just as the mating flight began, when we believe our counts of females as well as males were accurate. Variance, like alate number, also increased with colony age. A few, old colonies produced large numbers of reproductives, while most colonies produced few or none.

Older colonies produced smaller female alates, which suggests that there may be a trade-off between alate number and size as a colony ages. However, because colonies produce greater numbers of alates as they grow older, we estimate that older colonies allocate more biomass to reproduction than younger ones, even though each female alate from an older colony is smaller. Using the counts of the first 10 traps visited by each observer, we find that colonies produce about seven to eight additional alates per year, approximately three females and four males. The dry mass of female alates is approximately 0.2 mg lighter with each increasing year of colony age, but this small annual decrease in female alate mass is swamped by the additional 110–120 mg of dry alate mass per year allocated to extra alates (three females, each weighing about 27 mg dry mass, plus four males, each about 9 mg dry mass). Female alate mass is correlated with the mass of workers (sterile females) from the same colony, and average worker mass also declined marginally with age. Thus females, both sterile and reproductive, may decrease in mass with increasing colony age. We do not know the cause of this trend. Among insects there is a general pattern of decreasing egg size with increasing female age (reviewed in Roff 1992); however, the relationship between egg and adult alate size in ants is not known. Diminishing egg size would not account for the constancy of male mass as the colony ages.

The production of greater numbers of alates by older harvester ant colonies is not due to an increase in colony size. Worker number in *P. barbatus* colonies increases until the age of 5 years, and levels off at around 10,000 to 12,000 workers (Wildermuth and Davis 1931; MacKay 1981; Gordon 1992). Allocation to reproduction thus continues to increase after the number of workers available to gather and process food ceases to grow. Alate production may be related to the accumulation of stored food. Larger colonies seem to have larger stores of food; the largest colony excavated in a previous study (Gordon 1992) had over a liter of stored seeds (D. Gordon, personal observation).

We found some evidence that heavier females are at a reproductive advantage. Heavier females laid eggs at a higher rate than lighter ones, and therefore reached their maximum egg number more quickly (approximately 10 h earlier per milligram of initial body mass). Heavier females did not, however, lay more eggs overall. The rate of egg-laying could affect colony fitness. Nanitic workers have been observed foraging on the study site in October, approximately 10 weeks after the mating flight; developmental rates in the laboratory are similar. Colonies are rarely active aboveground from about November until March. Fast egg production could translate into a small but possibly important increase in the period of available foraging time between the emergence of the first workers and winter dormancy. If a large queen's high egg-laying rate continues as she ages, colonies with large queens might accumulate workers at a greater rate, thereby increasing the colony's ability to gather resources. Large body mass might also affect survivorship during the claustral stage. We found that, in general, heavier alates had disproportionately higher body fat than lighter ones (Fig. 1c). However, this relationship did not explain the colony-age-related differences we detected in female alate mass; female alates produced by young colonies were heavier overall but did not have a higher percent body fat than those produced by old colonies. If overall queen mass (not percent body fat) is correlated with fitness, our results suggest that older colonies produce less fit but more queens.

Female and male alates differed markedly in their free body water contents and in the relationship between water content and body mass. Females had much higher body fat (36% in females, 4% of dry mass in males) and lower body water (46% in females, 65% in males) than males. R.A. Johnson (unpublished data) also found higher water content in male relative to female alates of several desert ant species, including *P. barbatus*. Differences in water content between the sexes, as well as differences among large and small females, appear to reflect differences in the representation of water-poor adipose tissue (Fig. 1; see also MacKay 1985). Males do not require very large fat stores because, unlike females, they die shortly after the mating flight. However, variation in fat content among males (Fig. 1d) could affect mating success if it influences such characteristics as stamina or dispersal distance.

There was no effect of density on alate numbers when we considered the density of neighbors of all ages or that of large neighbors, 5 years or older, which would compete most strongly for foraging area (Gordon and Kulig 1996). This result contrasts with our earlier result from 1995, when crowded colonies produced fewer alates. It appears that the effect of neighborhood density on alate production varies from year to year. Effects of neighborhood density on colony mortality also vary from year to year (Gordon and Kulig 1998).

Neighborhood density may affect reproduction only when resources are scarce (e.g. Boag and Grant 1984). We measured alate production in 2 years, 1995 and 1997, and found an effect of density only in 1995. Observations of rainfall and numbers of new colonies both indicate that food was more abundant in 1997 than 1995. Rainfall is correlated with seed production in many desert species (e.g., Kadmon 1993). The year 1995 followed a series of dry years, while 1996 and 1997 had unusually heavy rains; 1996 was the first time, in observations made since 1981, that standing water covered large areas of the study site (D. Gordon, personal observation). The series of dry years before 1995 may have led to depleted colony food stores, and increased competitive pressure, in that year. Founding colony survival is probably correlated with food availability. Numbers of new colonies on the site were at their lowest since 1985 in 1994 and 1995, and at their highest in 1997 (see Gordon and Kulig 1998 for data through 1996; 45 new colonies in 1997).

The effects of fluctuations in food availability may depend on colony age. In 1995, we measured alate production only in 5–7 year old colonies. These younger colonies may have had smaller food stores, and may have been more affected by competition than were older colonies. In years when food is abundant, even younger colonies may find enough resources to produce alates.

For 24 colonies measured in both 1995 and 1997, alate production was weakly but significantly correlated across years. These results suggest that patterns of reproduction may be colony specific. Mortality of newly mated queens is very high (Gordon and Kulig 1996), so the chance that each female alate will successfully found a colony is slim. Only colonies that steadily produce large numbers of alates may have any offspring at all.

Harvester ant colonies vary greatly in alate production. A small number of old colonies dominate the mating pool by contributing large numbers of alates, while each year surprisingly large numbers of mature colonies do not reproduce at all (23% in 1995, 36% in 1997). The effect of neighborhood density on alate production varies from year to year, perhaps in response to changes in food availability. Long-term studies are needed to determine how age structure, spatial distributions, and fluctuating resources shape the life histories of ant colonies.

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Note added in Proof There are errors in Table 1 of Gordon and Wagner 1997 Oecologia 109:556–560. Please contact DM Gordon for the correct data.