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Colony size and reproduction in the western harvester ant, *Pogonomyrmex occidentalis*

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Summary. We report data from a four-year field study on the relationship between colony size and reproduction in the western harvester ant, *Pogonomyrmex occidentalis*. In all years, the likelihood of reproduction significantly increased with increasing size in both field censuses during naturally-occurring mating flights and experimentally-watered colonies whose entire reproductive output was collected. However, the total amount of reproductive biomass was unrelated to colony size. We describe the size threshold for reproduction in *P. occidentalis* and show that it varies across years. Once colonies become reproductively mature, they reproduce consistently although not in every year. We describe a method for collecting the entire reproductive output for desert ants whose reproductive flights are cued by rainfall.

Key words: Reproduction, size-based demography, size thresholds, mating flights, *Pogonomyrmex*

Introduction

In organisms that are long-lived and reproduce repeatedly, the schedules of reproduction and mortality are important for understanding the evolution of any tradeoffs between reproduction, growth and maintenance or the patterns of reproductive allocation. Frequently in organisms that have indeterminate growth, such as ant colonies, increased reproduction may accompany increased size. Although considerable data and theory exist on sex ratio allocation in ants, as well as data from a number of species on the relation of reproduction to colony size, there is little long-term information on the pattern of reproduction. The probability of reproduction in an ant colony is presumed to increase with colony size (Oster and Wilson, 1979; Hölldobler and Wilson, 1990), but actual data are available for surprisingly few species. Several studies have found no relationship between colony size and reproductive output (e.g., *Tetramorium caespitum* in some years, Brian and Elmes, 1974; *Pogonomyrmex montanus*, MacKay, 1981; *Lasius niger* for some comparisons, Boomsma et al., 1982; *Myrmica scabrinodis*, Elmes and Wardlaw, 1982; *Trachymyrmex septentrionalis*, Beshers and Traniello, 1994; *Pheidole "nigricula"* and *P. "specularis"*, Kaspari and Byrne, 1995).

The form of the relationship between colony size and the probability of reproducing may have significant consequences. The probability of reproduction may increase gradually with size (which appears to be true in *Myrmica sulcinodis*, Elmes, 1986; *Camponotus pennsylvanicus* and *C. ferrugineus*, Fowler, 1986; *Formica podzolica*, Savolainen et al., 1996), or there may be a threshold size above which reproduction is inevitable (*Pheidole dentata*, Johnston and Wilson, 1985; *Solenopsis invicta*, Tschinkel, 1993). In some species, such as *Pogonomyrmex barbatus* (Gordon, 1995) there may be an age threshold for reproduction. Depending on the form of this function, we may make very different predictions about how a colony should balance current growth against future reproduction, and how this tradeoff changes with size. For most species the data are not currently available to describe how size affects the probability of reproduction although it would be valuable to have information about as many species as possible.

One can ask at least two slightly different questions about the relationship between colony size and reproduction: (1) how does colony size affect the probability of reproduction? and (2) what is the relationship between colony size and the amount of reproduction? These questions have not usually been separated, but need to be in order to distinguish both components affecting life history evolution in particular species as well as factors determining population dynamics. It is important to understand the relation between colony size and the probability of reproducing. For example, in modeling the relation of size to reproduction, one might then treat reproduction as a size-related phenomenon, but the amount of reproduction as a random variable, once reproductive size has been achieved.

In this paper, we will present data both on the relationship between colony size and the probability of reproduction and on the relationship between colony size and the total amount of reproduction. We shall show that size strongly influences the probability of reproduction in *P. occidentalis* over four years of field data, that the size threshold for reproduction varies annually, and that colony size and the total amount of reproduction by a colony are not related. We also describe a technique for measuring reproduction in desert ants.

Materials and methods

Pogonomyrmex occidentalis is widely distributed in western North America in desert grasslands. Our study site of 29 ha in western Colorado consists of a large population of permanently mapped and tagged colonies (about 1300 colonies alive in any year). The vegetation at the study site is characterized as adobe badlands, dominated by woody chenopods (*Atriplex* spp.), native perennial grasses, and woody composites. The details of the study site and the population can be found in Wiernasz and Cole (1995).

Pogonomyrmex occidentalis reproduces in large mating swarms. Alates emerge from the nest and fly to hilltop leks (Nagel and Rettenmeyer, 1973; Wiernasz et al., 1995; Abell et al., 1999) where they mate. Reproductive flights typically occur in late afternoon from mid-July onwards, on the first sunny day after substantial rainfall. We have observed reproductive flights as early as 26 June and as late as 15 August. New colonies are founded by single, multiply-mated queens, and secondary polygyny is unknown in the genus (Cole and Wiernasz, 1997; 1999).

We obtained data on colony reproduction in two ways: by surveying colonies that are producing alates during the natural mating flight, and by collecting the reproductive output of entire colonies by stimulating their reproductive flights. Survey data are from scan samples of approximately 15 s per colony during the natural mating flight. In each mating flight from 1994–97, we surveyed as many colonies as possible ($n = 162$ to 324), recording whether the colony was producing reproductives.

We induced reproductive flights by watering colonies. This procedure works when the reproductives are mature and ready to fly, and before rainfall causes the population mating flight. We used local temperature data to approximate when reproductives are mature, and then opened the nest cones of several large, non-experimental colonies to confirm that alates were ready. Six to eight L of water, depending on colony size, were applied to the surface of the nest mound with a backpack-mounted sprayer in mid to late afternoon. This amount is equivalent to a rainfall of 15–20 mm. Although mating flights can be initiated after as little as one mm of rain (in late summer), because we were inducing colonies before the natural mating flight has occurred we provided a large stimulus for the mating flight. The following day, at 1400–1500 h, reproductives began exiting and entering the nest entrance, and continued to emerge from watered colonies until 1700–1800 h. We captured reproductives by placing a trap over each colony. This is an aluminum screen cone one meter high that is riveted to a 15 cm wide circular strip of galvanized steel flashing one meter in diameter. Over a hole in the top of the cone, we attached a screen collection chamber, using Velcro® for easy removal. The trap was placed over as much of the nest cone as possible including the nest entrance; the steel flashing was shoved into the ground so that ants could not avoid the trap. When reproductives emerged from the nest, they flew or crawled up the sides of the cone, entered the collection chamber and remained there until they were collected. The entire collection bag was placed in a 8 L Ziploc® bag and placed in a cooler. Workers were often collected with the reproductives; these were separated and later returned to the colony. If reproductives continued to emerge from the colony after the collection chamber was removed, they were collected by hand as they emerged. We watered 20 colonies per day and monitored the reproductive output of 200 colonies annually. Reproductives were killed by freezing at −20 °C, and placed individually in separate wells of a tissue culture plate, and dried at 60 °C in a drying oven for at least five days. Individual dry weight did not change after four days. Weights were obtained within one hour following removal from the drying oven.

The watering method extracted the entire reproductive output from a colony. As a check on the method, we censussed previously watered colonies during the natural reproductive flight. Colonies which failed to produce reproductives after watering, did not reproduce during the mating flight. Similarly, colonies that did produce reproductives after watering, did not reproduce further during the population flight. In 1996 there was an unusually early rainfall (26 June) and a partial flight of reproductives. Because this early flight occurred before any colonies were watered, the data from 1996 are distorted by an unknown amount. The survey data for 1996 are from the much larger flight that occurred on 17 July.

The size of colonies was estimated from the size of the nest cone as: $\mathrm{Ln}\,[\mathrm{Length} \times \mathrm{Width} \times (\mathrm{Height} + 1\ \mathrm{cm})]$. This measure is very highly correlated to estimates of worker population (Wiernasz and Cole 1995). We measured the size of all experimentally watered colonies before we began watering. We measured the size of all colonies on the study site during 1994 and 1997, but only 20% of the colonies in 1995–96. For surveyed colonies that were not measured directly in 1995–96, we estimated size using a linear interpolation of size change in those colonies from 1994 to 1997. Because our data consisted of colonies that either did or did not reproduce, we used logistic regression for statistical analyses. In order to compare several years simultaneously we visualized the relationship between size and reproduction by calculating the expected values from the logistic regressions.

In 1997, we began a food supplementation experiment with the watered colonies. In that year, we only used data from colonies that did not receive a cracked wheat supplement, since we found that this treatment influenced the probability and the amount of reproduction.

Results

Colony size significantly affected the probability of reproduction for both surveyed and watered colonies in every year of the study (Fig. 1). Logistic regressions of colony reproduction on colony size indicate a significant, positive effect of size for both survey data (1994: 1.11 (0.26) (regression coefficient [standard error]), $n = 162$ (sample size), $p < 0.001$; 1995: 0.706 (0.17), $n = 219$, $p < 0.001$; 1996; 1.01 (0.22), $n = 158$, $p < 0.001$; 1997: 1.13 (0.19) $n = 324$, $p < 0.001$) and for watered colonies (1994: 1.50 (0.41), $n = 71$, $p < 0.001$; 1995: 2.13 (0.49), $n = 89$, $p < 0.001$; 1996: 0.63 (0.21), $n = 157$, $p < 0.001$; 1997: 1.06 (0.35), $n = 99$, $p < 0.003$).

Although years differ in the exact relation between reproduction and colony size, a consistent feature is the relation between colony size and the proportion of colonies that reproduce. Nests below a size class of approximately 10 are quite unlikely to reproduce. In no year do more than 25% of

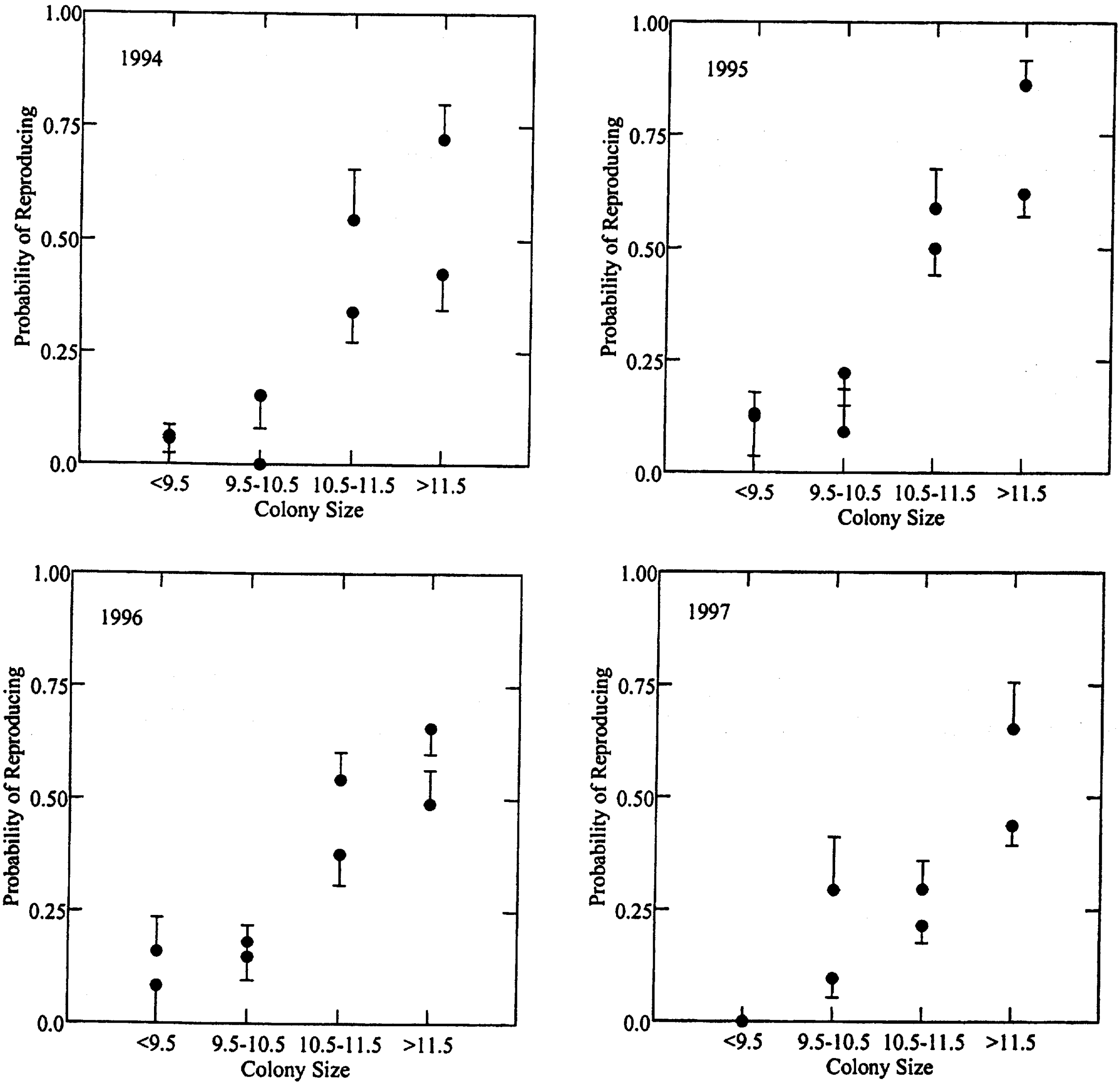

Figure 1. The probability of colonies that reproduced for each of four years (1994–1997) as a function of colony size estimated from the volume of the nest cone. The proportion of colonies reproducing, and the standard error, in each size range is shown for surveyed colonies (error bar below the point) and watered colonies (error bar above the point).

colonies smaller than this size reproduce; typically 10% or less reproduce. The probability of reproducing changes rapidly above the size, suggesting that there is a threshold size that permits reproduction. Eight‸colonies were initially small (size class < 10.5) in order to monitor the ontogeny of reproduction, and only 24 of these have reproduced during the course of the study. However, colonies larger than the reproductive threshold do not reproduce every year. The probability of reproducing is substantially less than one for all size classes greater than 10, indicating that reproductively mature colonies do not reproduce every year. In part, this is a consequence of some colonies never reproducing; 15 large colonies (size class > 11) have never reproduced. Sixty-nine colonies reproduced initially in either 1994 or 1995. Two of these died, of the remainder, 16 (24%) reproduced every year, 26 (39%) reproduced in all but one year, and 19 (28%) reproduced once. Reaching a threshold size does not guarantee reproduction, it just makes it more probable.

Eighty y‸

Unlike the effect of colony size on the probability of reproduction, the amount of reproduction (total dry mass of reproductives) was unrelated to colony size in all years of the study (Fig. 3). The consistent lack of a correlation indicates that other factors, perhaps local resource availability, are the primary determinants of reproductive effort.

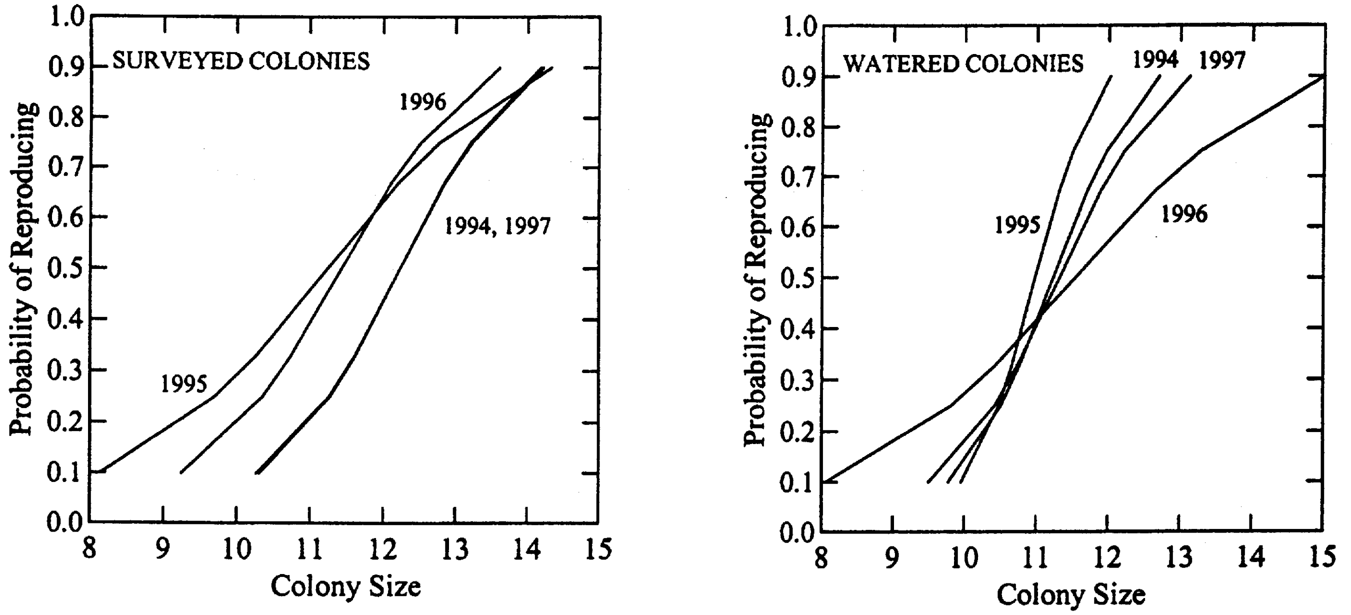

Figure 2. Reproductive curves for surveyed and watered colonies illustrated by estimates from the logistic regressions to facilitate comparisons among years. In each case we plot only the range of estimates of probability of reproduction between 0.1 and 0.9 since estimates outside this range have very large uncertainty.

The nest surveys underestimate reproduction in comparison to watering the colonies. This is most easily seen in 1994, 1995 and 1997, where the probability that larger colonies reproduce does not overlap between surveyed colonies and watered colonies (Fig. 2). In 1996 the differences between watered and surveyed colonies were not as great. Since the early, partial reproductive flight in 1996 occurred before colonies could be watered, this is may be responsible for anomalies in the data from the watered colonies in 1996. This can be seen by comparing the expected values for the logistic regression for all survey data and all data from watered colonies. For the data from watered colonies each of the curves has a similar shape, the major difference is that they are shifted to the right (1994, 1997) or to the left (1995); the curve for 1996 has a much shallower slope and includes smaller size classes (Fig. 2). We have used the logistic regression to calculate the size at which 50% of the colonies are predicted to be reproducing (Table 1). This reproductive size (RS50) is significantly different between watered and surveyed colonies in 1994, 1995, and 1997, supporting the interpretation that the survey data underestimate reproduction.

We examined the possibility that scan samples may miss small numbers of reproductives and only detect reproduction in colonies that produce large numbers of reproductives. We compared the size distribution of watered and surveyed colonies that reproduced in 1997, the year for which we have the most data (Table 2). The watered colonies have a significantly smaller mean size and a significantly higher likelihood of reproducing, especially in the smaller size classes (using a t-test and the Kolmogorov-Smirnov two-sample test, respectively), unless the watered colonies are restricted to those that produce at least 50 total reproductives. Although sample sizes

Table 1. The size of colonies at which 50% are reproducing (RS50)

	RS50	95% confidence limits
1994 Survey	12.24	11.85–13.03
Watered	11.23	10.72–11.61
1995 Survey	11.25	10.82–12.25
Watered	10.98	10.60–11.23
1996 Survey	11.43	11.07–11.82
Watered	11.54	11.02–12.73
1997 Survey	12.24	11.97–12.67
Watered	11.64	11.22–12.66

Table 2. Size distribution of colonies that reproduce in surveys and after watering, 1997

	Mean colony size	Probability that watered ~~surveyed~~ colonies are the same size as surveyed colonies	
		Using t Test	Using KS Test
All surveyed colonies that reproduced	11.72	–	–
All watered colonies that reproduced	11.36	0.012	0.009
Colonies that produced more than 50 reproductives	11.42	0.082	0.09

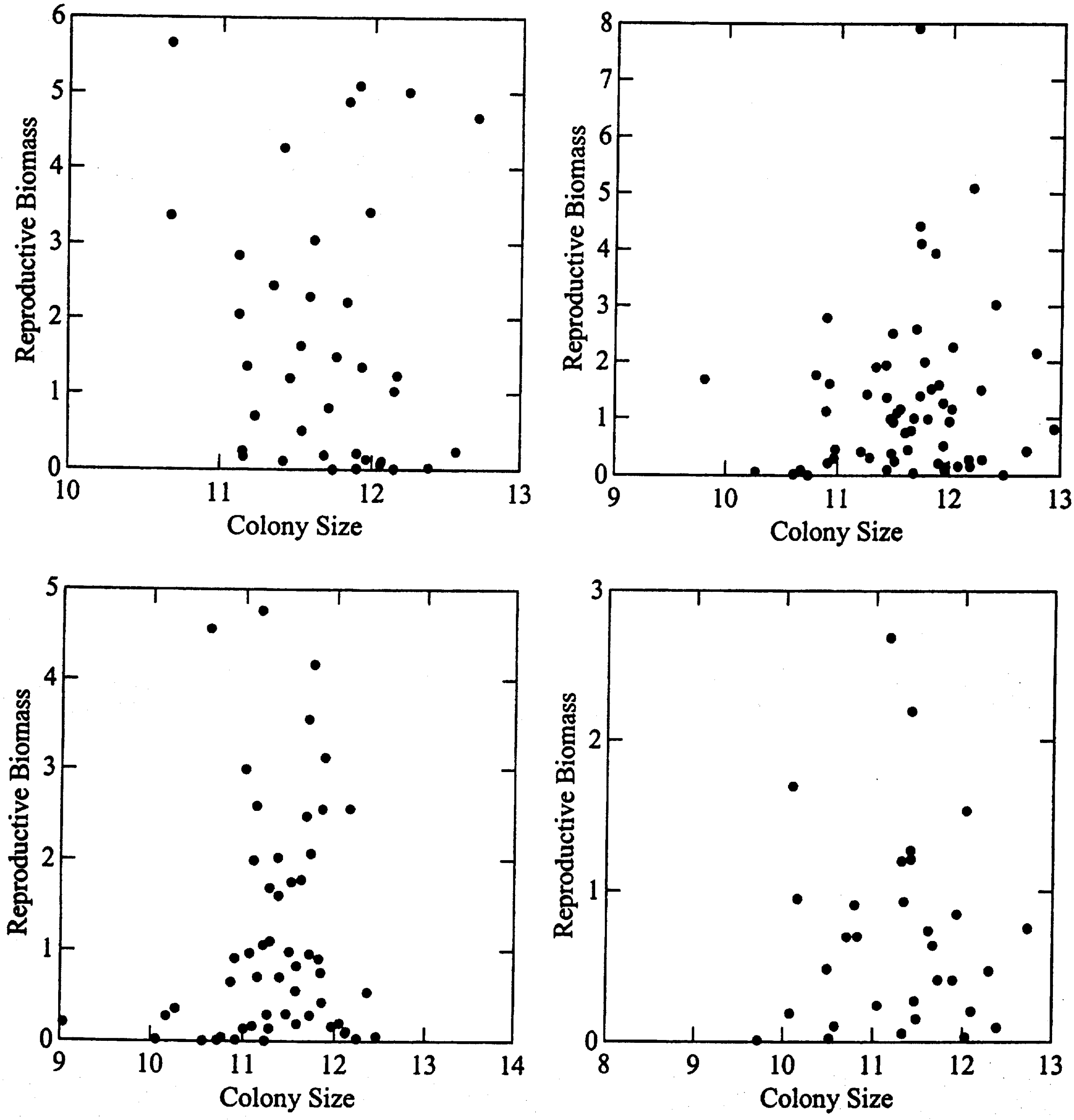

Figure 3. The total reproductive biomass for colonies that produced reproductives as a function of colony size for 1994–1997. In each year there is no significant regression of reproductive biomass on colony size.

are lower when we exclude colonies that produce fewer than 50 reproductives, which may account for some of the reduction in the p-values shown in Table 2, the mean colony size for surveyed and watered colonies becomes nearly identical.

Discussion

The control of reproduction in *P. occidentalis* is well explained by size-based demography (Caswell, 1989). In this respect, its demography resembles that of many plants rather than that of many large animals. The consequences of this observation may be important for the regulation of population density and for the evolution of other life history characteristics. A population of harvester ants approaches a stable size distribution of colonies, rather than a stable age distribution. If annual variation in the reproductive threshold occurs, the size distribution will not reach equilibrium, but will be a random variable whose distribution is a function of the environmental variability (Caswell, 1989).

Although age is correlated with size (especially in young colonies), by the time that a colony reaches reproductive size, the correlation between age and size is weak, because growth slows as a function of size (Cole and Wiernasz 1999). Colonies also may decrease in size in successive years; due to damage from rodents and for unknown reasons. It is possible for an individual colony to repeatedly cross the reproductive threshold. This will influence the probability that a colony will reproduce in any given year as well as its lifetime reproductive success.

It seems sensible that scan surveys would be inherently less able to detect reproduction than alate collection. If a colony is only producing a few reproductives, it would be easy to miss them while monitoring the colony for a short period, and this is reflected by the offset in the watered and surveyed size distributions in 1994 and 1997. The comparison of size distributions in surveyed colonies and watered colonies that produced more than 50 reproductives suggests that we are subsampling the fraction of colonies whose average production is more than 50 reproductives. In 1995 and 1996 the distributions of surveyed and watered colonies overlap in different ways. 1995 was an abnormally cold (based on degree day data from March–July) and wet (based on spring precipitation) year. Although watering of colonies was delayed in 1995, it may not have been delayed long enough for all alates to mature. Data from 1996 are the most different, with a marked reduction in the probability of reproduction among large size classes (Fig. 1). 1996 had near normal spring rainfall, but was warmer than average; an early reproductive flight changed the alate distribution in unknown ways. Larger colonies may have been more likely to have mature alates at the time of the first flight, and these were lost to the watering experiment, thus underestimating reproduction.

We find no evidence whatever that the size of a colony influences the amount of reproduction, once the colony has decided to reproduce. Investigators often assume that ants have a size based demography. This assumption underlies most general models for caste evolution in ants (Oster and Wilson, 1978), and is applied rather generally both to the threshold for beginning reproduction and to the relation between size and reproductive output. In *P. occidentalis* colony size affects the relationships independently. Although size influences the probability of reproduction, the amount of reproduction may be determined by the nutritional state of the colony which may determined more by local resources than by colony size.

Few studies contain the data that allow a direct test of the adequacy of age versus size based demography in ants. In one of the best studied cases, that ~~a~~ of *Pogonomyrmex barbatus* (Gordon, 1995), the age of a colony appears to determine reproductive maturity. Colonies reach reproductive maturity at about 5 years and reproduce annually thereafter. Although many species show a graded increase in the probability of reproduction with colony size, (e.g. *Myrmica sulcinodis*, Elmes, 1986; *Camponotus pennsylvanicus* and *C. ferrugineus*, Fowler, 1986; *Formica podzolica*, Savolainen et al., 1996; *P. occidentalis*, this study), they may do so because colonies reach the age of reproductive maturity at different colony sizes. Even for species which show a positive correlation between colony size and measures of colony reproduction (*Tetramorium caespitum* Brian and Elmes, 1974; *Myrmica sabuleti*, Elmes and Wardlaw, 1982; *M. sulcinodis* Elmes, 1987; *Harpagoxenus sublaevis* Bourke et al., 1988; *Lasius niger*, for some measures, Boomsma et al., 1982; *Trachymyrmex septentrionalis*, Beshers and Traniello, 1994; *Pheidole "multispina," P. "rugiceps,"* Kaspari and Byrne, 1995; *Formica podzolica*, Savolainen et al., 1996), this does not exclude the possibility that the onset of reproduction is geared to colony age.

The comparative data do not support the generalization that all ant demography is size-based. Although colony size influences whether a colony reproduces in *P. occidentalis*, neither *P. occidentalis* nor *P. montana* (MacKay, 1981) show a correlation between colony size and reproductive output. Some species, especially those with deterministic colony growth where a maximum is achieved rather rapidly, may have age-based patterns of reproduction. Other species, particularly those which have indeterminate colony growth, may be characterized by size based patterns of demography. Finally, it is possible that some aspects of reproduction, such as the onset of reproduction, may be based on one set of factors while the amount of reproduction may be based on a different mechanism.

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