LETTER

The rewards of restraint in the collective regulation of foraging by harvester ant colonies

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Collective behaviour, arising from local interactions[1], allows groups to respond to changing conditions. Long-term studies have shown that the traits of individual mammals and birds are associated with their reproductive success[2–6], but little is known about the evolutionary ecology of collective behaviour in natural populations. An ant colony operates without central control, regulating its activity through a network of local interactions[7]. This work shows that variation among harvester ant (*Pogonomyrmex barbatus*) colonies in collective response to changing conditions[8] is related to variation in colony lifetime reproductive success in the production of offspring colonies. Desiccation costs are high for harvester ants foraging in the desert[9,10]. More successful colonies tend to forage less when conditions are dry, and show relatively stable foraging activity when conditions are more humid. Restraint from foraging does not compromise a colony's long-term survival; colonies that fail to forage at all on many days survive as long, over the colony's 20–30-year lifespan, as those that forage more regularly. Sensitivity to conditions in which to reduce foraging activity may be transmissible from parent to offspring colony. These results indicate that natural selection is shaping the collective behaviour that regulates foraging activity, and that the selection pressure, related to climate, may grow stronger if the current drought in their habitat persists.

In ant populations, the colony is the reproductive individual, producing offspring colonies. The study was conducted with a population of about 300 colonies of the red harvester ant, *Pogonomyrmex barbatus*, at a site near Rodeo, New Mexico, USA that has been censused each year since 1985, so the ages of all colonies are known[11]. A colony is founded by a single queen and lives for about 25 years[12–14]. When the colony is about 5 years old, it reaches a stable size of about 10,000 workers[15] and begins to produce reproductives[16], males and gynes, that mate polyandrously. Newly mated gynes found offspring colonies. In a recent study we used microsatellite variation to identify the offspring colonies founded by daughter gynes of parent colonies, and thus to estimate the female component of colony lifetime reproductive success, in the number of offspring colonies founded by daughter gynes[14]. We did not estimate the contribution of males to colony reproductive success. In only about 25% of colonies, daughter gynes successfully founded new colonies, ranging from 1 to 6 offspring colonies per parent colony.

Harvester ant colonies forage for seeds in the desert, where foraging carries a high cost of ant desiccation. Previous work shows that colonies adjust foraging activity to food availability, using interactions between returning and outgoing foragers[17,18], and that colonies vary in the regulation of foraging[12,18]. Foraging activity changes from day to day[17] in response to food supply and humidity, and other conditions such as the number of larvae requiring food. Ants lose water when foraging, and obtain most of their water from metabolizing the fats in the seeds they eat[9,10]. Foraging is regulated using a simple positive feedback system in which outgoing foragers are stimulated to leave the nest when they interact with returning foragers carrying food into the nest[19]. The rate of forager return reflects current food supply

because each forager searches until it finds a seed[20], so foragers return more quickly the more food is available. Harvester ant colonies vary in the regulation of foraging activity, by varying in the response to the rate of forager return[17,18]. Colonies show characteristic foraging behaviour from year to year[12], reflecting colony-specific behavioural reaction norms[8] for the relation between foraging activity and current conditions.

How a colony regulates its foraging behaviour is associated with its lifetime reproductive success. In poor conditions when humidity is low, foraging activity reflects reproductive success more strongly than when humidity is high. Foraging activity in colonies with and without offspring colonies differed overall on dry days (Cochran-Mantel-Haenszel test, $M^2 = 10.96$, d.f. = 2, $P = 0.004$) but not on humid days (Cochran-Mantel-Haenszel test, $M^2 = 0.27$, d.f. = 2, $P = 0.87$) (Fig. 1). Of the colonies that foraged at all on dry days, more colonies with than without offspring colonies tended to show low rather than high foraging activity (Fig. 1), although the difference between colonies with and without offspring colonies was not significant (Mantel-Haenszel chi-squared test, NS).
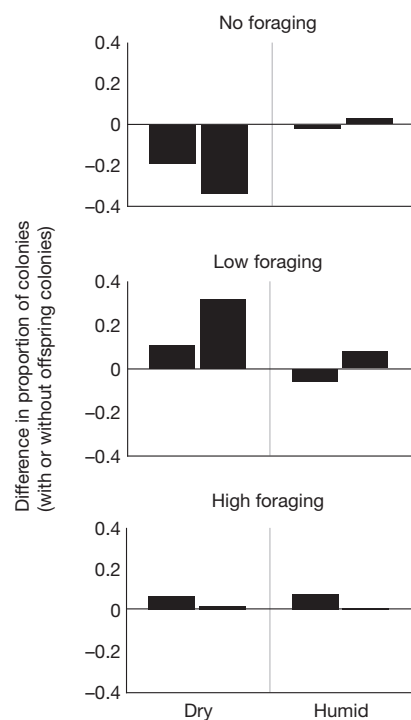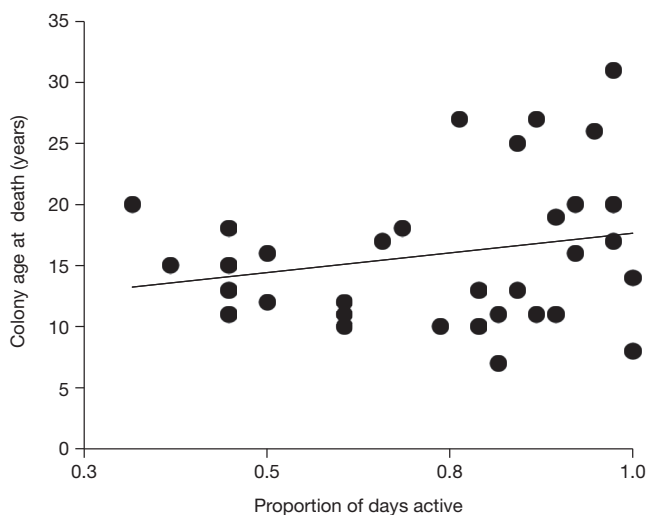

Figure 1 | Foraging activity on dry days is associated with reproductive success. Each bar shows foraging activity on one day, for two dry and two humid days in 2012 (weather data are in Supplementary Table 1). Each bar shows the difference obtained by subtracting the proportions of colonies with and without offspring colonies, showing foraging activity in the indicated category: none, low, or high. The difference shown is the proportion of 37 colonies with offspring colonies, minus the proportion of 24 colonies without offspring colonies.

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Stability in foraging activity, in good conditions, is associated with high reproductive success. Colonies with offspring colonies fluctuated less in foraging activity over 5 humid days in 2011 than those without offspring colonies, showing a higher ratio of smallest to highest foraging rate (colonies with offspring colonies, mean ratio = 0.51 (s.d. = 0.17); colonies without offspring colonies, mean ratio = 0.36 (s.d. = 0.17); $t = 2.09$; $P < 0.049$, two-tailed t-test). The standard deviation of a colony's foraging rate, in numbers of returning foragers per 30 s, over 5 humid days, was lower for colonies with offspring colonies ($n = 21$) than for colonies without offspring colonies ($n = 21$) ($t = 2.60$, $P < 0.01$, two-tailed t-test). The mean and sum of foraging rate over 5 days was not significantly different (colonies with offspring colonies, mean = 32.7 (s.d. = 16.5) ants returning per 30 s, colonies without offspring colonies, mean = 34.5 (s.d. = 22.7) ants returning per 30 s, $t = 0.29$, NS; colonies with offspring colonies, mean sum foraging = 163.7 (s.d. = 82.2) ants returning per 30 s, colonies without offspring colonies, mean sum foraging = 172.6 (s.d = 113.5) ants returning per 30 s, $t = 0.3$, NS).

There was no survival cost of not foraging (Fig. 2). Previous work has demonstrated that a colony does not forage every day, and the proportion of days that it forages actively is a colony-specific trait that persists from year to year[12]. The proportion of days a colony foraged ranged from 0.32 to 1.0 in 1986 and from 0.35 to 1.0 in 1987, and colony age at death ranged from 7 to 30 years. There was no relation between the proportion of days that a colony foraged in 1986 or 1987 and its age at its death sometime in the subsequent 25 years (1986, $z = -1.227$, d.f. = 32, $P = 0.21$; 1987, $z = 0.77$, d.f. = 35, $P = 0.4$, Spearman's rank correlation). It appears that colonies can collect sufficient food on good days to desist from foraging on poor days without risking starvation. Although colonies compete with neighbours for foraging area[21], and food is apparently a limiting resource for desert granivores[22], colonies can store seeds for long periods, up to many months[23].

There is some evidence that the regulation of foraging may be transmissible from parent queens to their daughter queens. Because daughter queens do not tend to found colonies near their parents[14], there is no contact between parent and offspring colonies that could lead to cultural transmission of collective behaviour. The 42 offspring colonies of 17 parent colonies resembled their parents in the choice of days in which to reduce foraging activity. In the course of 5 days in 2011, 11 of 17 parent colonies reduced foraging activity on the same day, and the offspring colonies of 5 of these did so as well. All 6 of the parent colonies that chose an uncommon day to reduce foraging had offspring colonies that also chose an uncommon day. This produced a significant association between parents and offspring colonies in the choice of day on which foraging was most reduced (Fisher's exact test, $P = 0.04$). This indicates that offspring colonies may resemble their parent colonies in the reaction norm that links particular conditions, characteristic of a certain day, to the reduction of foraging activity. However, there was no correlation between parents and offspring in the sum ($z = -0.83$, d.f. = 15, $P = 0.4$) or standard deviation ($z = -0.63$, d.f. = 15, $P = 0.5$) of foraging over 5 days. Many factors probably produce variation among colonies in foraging activity, such as variation in the amount of stored food and in the number of brood to feed[24]. If there is heritable variation among colonies in sensitivity to day-to-day changes in weather conditions, data from many colonies on many days that differ greatly in weather conditions might be needed to discern a correlation in the foraging behaviour of parent and offspring colonies.

That some aspect of foraging behaviour may be transmissible from queens to daughter queens is consistent with previous work indicating that foraging behaviour is transmissible from queens to daughter workers. A queen of *P. barbatus* can live for about 25 years, whereas workers, her daughters, live at most about a year[25]. Thus colony-specific foraging behaviour that persists from year to year is due to characteristics that appear in successive years in distinct, successive cohorts of workers, all of which are daughters of the same queen, though not of the same fathers. Variation in the foraging and circadian genes whose expression is associated with foraging activity in this species[26] may lead to the transmissibility of foraging activity.

It may seem surprising that high reproductive success is not associated with high foraging activity. In much of foraging theory, the amount of food collected is assumed to be correlated with reproductive success. In studies of social insects, the assumption that more food means more offspring arises from a chain of inference: the more workers, the more food is collected; the more food, the more reproductives can be produced; and the higher the reproductive output, the greater the realized reproductive success of the colony in offspring colonies. Both the measures of the variables and the chain of inference itself require testing. Here, because we can estimate colony lifetime reproductive success, it was possible to test directly whether in fact reproductive success, in offspring colonies founded by daughter queens, is correlated with foraging activity. Colonies that forage actively on more days do not live longer; colonies with or without offspring colonies differ most in poor conditions, when colonies with high reproductive success tend to show low foraging activity. Although it is clear that a colony with inadequate food could not survive or make reproductives at all, it seems that once some minimum threshold of food supply is reached, other factors, including perhaps the cost of desiccation, have a stronger impact on colony reproductive success than persistently high foraging activity. Like many animal species that store food, for example in fat reserves, harvester ant colonies store seeds for many months[23]. Harvester ant colonies that conserve more water may be able to produce more, or better-hydrated female reproductives that can survive longer during the founding stage[27]. In other conditions, such as in tropical forests where the cost of foraging is low, other constraints, such as interspecific competition, probably create different evolutionary pressures on the collective foraging behaviour of ant colonies.

METHODS SUMMARY

Foraging behaviour was observed in a population of about 300 colonies of *P. barbatus* at a site near Rodeo, New Mexico, USA in which the ages of all colonies have been determined, and the female component of lifetime reproductive success has been estimated for most mature colonies[14]. To test the relation of foraging activity and survival, correlations were examined between the foraging activity of 34 colonies on 38 days in 1986 and 37 colonies on 34 days in 1987, and the number of years the colony survived. To compare foraging activity of colonies with and without offspring colonies, foraging activity was compared for 21 colonies that had

Figure 2 | No survival cost of not foraging. Each point shows the proportion of days out of 38 days in 1986 that a colony foraged actively and the age of the colony at death. The line shows the least-squares fit; colony age at death and proportion of days active were not significantly correlated.

offspring colonies and 21 that did not on 5 humid days in 2011, and for 37 colonies with and 24 colonies without offspring colonies on 2 dry and 2 humid days in 2012. The transmissibility of foraging behaviour from parent to offspring colonies was evaluated by examining the association between 17 parent and 42 offspring colonies in sensitivity to conditions in which to reduce foraging, and for the same 17 parent and 42 offspring colonies, the correlation over 5 days in 2011 of mean parent and offspring colony values for foraging rate and standard deviation of foraging rate.

Full Methods and any associated references are available in the online version of the paper.

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METHODS

Number of days foraging and colony survival. A harvester ant colony does not forage actively every day, and the extent of a colony's tendency to forage actively persists from year to year[12]. The survival cost of not foraging was examined using the correlation between number of days active and colony survival over the subsequent 25 years. We recorded for 34 colonies in 1986 whether the colony was foraging actively on each of 38 days (between 24 Jun to 6 Aug 1986), and for 37 colonies in 1987 whether it was foraging actively on each of 34 days (between 5 July to 19 Aug 1987). Foraging activity was recorded in 23 of these colonies in both years. All but 3 of the colonies had died by the 2011 census. The number of years the colony lived was the number of years from the year the colony was founded until the year it was determined to be dead. The oldest colonies were determined to be at least 5 when the census began in 1985, but may have been older. The relation between foraging activity and colony survival was examined by using Spearman's rank correlation to test for a correlation between the proportion of days (out of 38 in 1986 and out of 34 in 1987) that a colony foraged actively, and the number of years it lived.

General methods for measures of foraging activity. Supplementary Table 1 shows temperature, dew point and relative humidity for the days on which foraging was measured.

For measurement of foraging activity, Supplementary Table 2 lists which colonies were observed in each year and the colony age in 2010. There is no evidence of reproductive senescence in this species[14], and age-specific fecundity is approximately the same from age 5 years onward[14]. Only colonies aged 10 years or older in 2010, when parent–offspring colony pairs were identified[14], were used in comparisons of colonies with and without offspring colonies, so all colonies had at least 5 years (from ages 5 to 10 years) in which to produce offspring colonies.

Foraging rate in humid conditions. In 2011, foraging rate was measured as the number of ants returning to the nest in 30 s, on 5 humid days in August (Supplementary Table 1) in 42 colonies aged 12 years or older, of which 21 had offspring colonies and 21 had no offspring colonies. To test whether foraging rate is associated with reproductive success, I determined for each colony: (1) the sum of the foraging rates over the 5 days; (2) the mean foraging rate over the 5 days; (3) the standard deviation in foraging rate over the 5 days; and (4) a measure of the extent to which the colony ever decreased its foraging rate. Of the 42 colonies observed, 12 colonies with offspring colonies and 11 colonies without offspring colonies foraged actively on all 5 days. For each of these 23 colonies, the smallest normalized foraging rate was calculated, representing the lowest proportion observed to forage in the course of the 5 days. Foraging rate was normalized for differences among colonies in colony size by dividing each day's foraging rate by the largest rate observed in that colony in the course of the 5 days. For these 4 measures, two-tailed t-tests were used to compare colonies with and without offspring colonies.

2012 comparison of foraging rate in dry and wet days. In August 2012, during a time of severe drought, foraging activity was measured on two dry days (12 August and 13 August) and two humid days (23 August and 24 August) in 24 colonies that had no offspring colonies, and 37 colonies with offspring colonies, with ages 10 to 30 years. Foraging activity was ranked, based on the range of foraging rates previously observed[18,19], as none, low (1 to 4 returning foragers per 5 s), or high (5 or more returning foragers per 5 s). Cochran-Mantel-Haenszel tests were used to test for a difference between the two dry and the two humid days in the proportions of colonies with and without offspring colonies showing each foraging rate (none, low or high). Then Mantel-Haenszel chi-squared tests were used to test separately for a difference in the proportions of colonies with and without offspring colonies showing none, low or high foraging, stratified by dry or wet days.

Transmissibility of colony foraging behaviour. In Aug 2011, foraging rate was measured as described in comparison of foraging rate in dry and wet days for the same 5 days in an additional 19 colonies for a total of 61 colonies. Of these colonies, 17 were parent colonies, ranging in age from 10 to 30 years old, and 44 colonies, ranging in age from 3 to 29 years old, were one of 1 to 5 offspring colonies founded by a daughter queen of one of the parent colonies. To evaluate the transmissibility of foraging behaviour from parent to offspring colony, Spearman's rank correlation tests were used to examine the correlation, between the value for the parent colony and the mean value for all of that parent colony's offspring colonies, of the sum over the 5 days of foraging rate and of the standard deviation over the 5 days of foraging rate.

I also examined the similarity of parent and offspring colonies in the choice of day in which it most reduced foraging activity. Although all 5 days were fairly humid (Supplementary Table 1), conditions and foraging activity all differed from day to day. I found for each colony that was active on all 5 days (17 parents and 42 offspring colonies), the day or days on which the foraging rate was lowest; any day with a foraging rate within 1 ant per second of the lowest day's foraging rate was also considered a day on which foraging rate was lowest. Foraging activity was lowest on August 11 for 65% of parent colonies and 31% of offspring colonies. Each parent colony was classified as having its lowest foraging rate either on August 11 or on some other days (including another day as well as August 11). For each parent colony, the lowest foraging rate of half or more of its offspring colonies was determined to be August 11 or on some other day. A Fisher's exact test was used to determine whether parent colonies that had lowest foraging rates on a day other than the most common day were likely to have offspring colonies that also had lowest foraging rates on a day other than the most common day.