Does Foraging Activity Affect Foraging Success in the Western Harvester Ant (Hymenoptera: Formicidae)?

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Ann. Entomol. Soc. Am. 101(1): 272–276 (2008)

ABSTRACT Foraging behavior has been extensively studied in harvester ants (Hymenoptera: Formicidae); however, there is little information about the determinants of foraging success. We developed a path analysis model to quantify the functional relationships among the components of foraging at the colony level (onset, duration, number of foragers) and foraging success. Variation in the onset of foraging among colonies directly influences the amount of time a colony has available for foraging, and contributes substantially to the total biomass of food retrieved. This difference in foraging effort provides a causal explanation for previously observed differences in colony growth rates.

KEY WORDS *Pogonomyrmex occidentalis*, foraging, foraging effort, foraging success, activity

How multiple mating by queens translates to colony fitness has been the source of questions about the evolution of multiple mating in the social Hymenoptera. A variety of hypotheses have been proposed that may generate advantages for multiple mating in social insects. These advantages have been reviewed by several authors, most recently by Crozier and Fjerdingstad (2001). Essentially, the possibilities include advantages that decrease the negative effects of genetic incompatibility (including diploid males), increase the ability of colonies to cope with diseases, or increase the efficiency of division of labor. Although each set of hypotheses has received some support, there is still little evidence concerning the relative importance of these effects in natural systems.

Data showing that colonies differ in fitness components as a function of the queen's mating frequency do not discriminate among the possible explanations for the adaptive significance of multiple mating. For example, in harvester ants it has been shown that colonies that have greater genetic diversity have increased growth rates (Cole and Wiernasz 1999, Wiernasz et al. 2004). Increased colony growth could result from any of the potential explanations for genetic diversity. However, evidence of a relationship between foraging patterns and genetic diversity would provide more support for hypotheses based on division of labor than on diploid male production or disease resistance.

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In the western harvester ant, *Pogonomyrmex occidentalis* (Cresson) (Hymenoptera: Formicidae), colonies with greater genetic diversity in the worker force begin foraging earlier in the morning, and for longer periods (Wiernasz et al. 2008). An intuitive extension of this pattern is that increasing the time available for foraging increases foraging activity, food collection and finally, colony growth. Although multiple mating affects colony foraging activity, the relationship between foraging duration and foraging success is unknown.

Foraging behavior in harvester ants has been the subject of considerable study. The use of trails and landmarks in orientation and navigation has been studied in a variety of species. Trunk trail use is related to the degree of interspecific territoriality (Hölldobler 1976). The energetic and dietary considerations involved in seed choice as part of a foraging strategy (Davidson 1978; Fewell 1988; Crist and MacMahon 1991, 1992), have illustrated that the foragers make decisions about seed choice on the basis of size, caloric payoffs, and the relative proportions of other nutrients in the seeds. The effects that seed foraging have on community structure have been studied both with respect to interactions among harvester ants and the effects of ants on plant community structure (Bernstein 1975; Whitford 1978; Davidson 1977a,b, 1978, 1980, 1985; Crist and Wiens 1996). Among harvester ants, the effect of interactions is equivocal, some studies implicate competitive interactions among species (Brown and Davidson 1977), whereas others indicate that the effect that harvester ants have on plant communities is probably greater through their effects on soil than their effects on seed removal (for reviews, see MacMahon et al., 2000 and Johnson 2001). The behavioral roles of patrolling, foraging, and nest maintenance and the factors that regulate the behavior of individuals have been studied by Gordon (1986, 1991, 1995), Gordon and Kulig 1996, and Brown and Gordon 2000. These studies have emphasized the behavior of individual workers (orientation, behavioral role, or seed preferences) or the role that species play in the community or ecosystem. We lack information about foraging of harvester ants at the colony level.

It is not known how colonies differ in the time they spend foraging and whether differences in the time for foraging, particularly earlier foraging, have any effect on food collection. For example, does the earlier onset of foraging lead to more foraging activity? Although this seems reasonable, if colonies simply shift the entire foraging schedule earlier or later, there may be no correlation between starting time and total foraging activity. Does more time for foraging translate into more food collected? Again, this is reasonable, but colonies might retrieve equivalent amounts of food in a variety of ways—some increasing the effort per unit time, some extending the time of foraging. Even if more effort is expended in foraging (i.e., even if more foragers are sent from colonies), this will not necessarily result in the retrieval of more food. Colonies that send out larger numbers of foragers might be less efficient at foraging. Although increased genetic diversity is associated with an increased amount of time spent in foraging activity, without direct measurement of the correlation between foraging duration, the number of foragers and the amount of food retrieved, it is impossible to evaluate whether increased duration of activity represents an advantage. These questions have not been studied in harvester ants, nor in other ant species.

The purpose of this study is to measure the degree to which changes in the onset of foraging activity increase foraging success in a colony. We begin with the hypothesis that earlier foraging activity causes more time to be spent on foraging, which increases the food obtained by the colony. This hypothesis proposes a causal link between increased genetic diversity and increased colony growth through its effect on advancing the time that colonies begin activity. Our study bears directly on the hypothesis that the relationship between increased growth and higher genetic diversity can be explained by increased foraging by colonies with greater genetic diversity.

Materials and Methods

Our study site in western Colorado consists of a large population of permanently mapped and tagged colonies of the western harvester ant (for the site description, see Wiernasz and Cole 1995, Cole and Wiernasz 2002). We quantified foraging activity and measured food intake in 20 colonies (two blocks of 10 colonies each, located ≈400 m apart). Enclosures were constructed after the design of MacKay (1981) and Crist and MacMahon (1991) from 30-cm aluminum flashing riveted into a ring and custom-fitted to extend ≈2 m beyond the nest in all directions. Four pairs of entrance and exit slits measuring 1 by 4 cm were cut 8 cm from the top of each enclosure at 90° around the circumference. When installing enclosures, we attempted to align entrances and exits with preexisting foraging trails, but this could not always be accomplished. The enclosures were inserted ≈5 cm into the ground and sealed around the bottom with a layer of soil. We formed soil ramps leading up to entrance and exit slits and sprayed them with water to stabilize them. Colonies were habituated to the enclosures for several days before beginning data collection.

Four researchers collected foraging data from two colonies per person per day for 20 d between 11 June and 5 July 2004. At this time of year, *P. occidentalis* typically begin foraging within an hour after sunrise. They stop foraging during the hottest part of the day, with an additional period of foraging in the late afternoon and evening. We quantified food intake only during the morning. Sampling was initiated 15 min after a colony began foraging in the morning (often by 7:15 MDT). Covered plastic cups were placed inside the entrance slits to serve as pitfall traps for returning foragers and any solid food they carried. Traps were opened for 4-min sampling periods at 20–25-min intervals until foraging ended (typically by 11:30 MDT, but considerably later on overcast days). After each sampling period, trapped ants were transferred to a cooler with an ice pack for 15 min to facilitate sorting and food retrieval. We placed food items from each sample into labeled 1.5-ml microcentrifuge tubes and released ants near the nest entrance. To compensate for the removal of food from the colony, we added an equivalent quantity of sunflower seeds to the surface of the nest mound. Collections were frozen to preserve contents before being shipped to the University of Houston for analysis. Samples were weighed to the nearest 0.1 microgram. Single food samples from nine colonies were lost before processing.

Onset time is the time of the first foraging sample (15 min after foragers leave the nest enclosure). Foraging duration is the difference between the time of the first and last foraging sample. The total workers is the number collected from each colony during the foraging period. Because sampling occurred during four of every 20 min, we assumed that ≈20% of the total foragers were captured. We used the total mass of the food retrieved (total food) as a measure of foraging success. It is possible to use caloric values, but these values conflate accessible and nonaccessible calories. Nutrient analysis also depends on understanding the importance of particular nutrients to the diet of specific colonies. With these limitations in mind, we elected simply to use the total mass.

Because four people collected data, we first tested for an observer effect. For both the total number of workers collected ($F_{3,124} = 1.49$; $P > 0.2$) and the total mass of food retrieved ($F_{3,106} = 1.60$; $P = 0.19$), the observer effect was not significant. We did not include observer in further analyses. Colony size was measured using the size of the external nest cone. Colony size is measured as the natural log-transformed product of the dimensions (in centimeters) of the nest

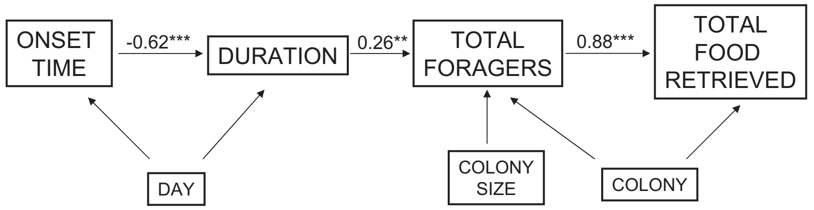

Fig. 1. Path diagram for the components of foraging activity in harvester ants. The variables along the upper row are residuals formed by removing the covariates shown as the variables below. **, $P < 0.01$; ***, $P < 0.001$.

cone on the north-south axis, the east-west axis, and the height. This measure has been shown to be highly correlated with the forager force of a colony (Wiernasz and Cole 1995).

We tested for direct effects between onset time, duration, total foragers, and the total food retrieved (see path diagram, Fig. 1). Because days differed in temperature, we assumed that this might affect the time that activity began or the total amount of time that the colony foraged. Colony identity and colony size were hypothesized to influence the total number of foragers, whereas colony identity was hypothesized to influence the total food retrieved. Colony identity may affect food retrieval because colonies at different locations may have microgeographic difference in the amount of available food or in temperature; this would be observed as a colony effect. To analyze each of the direct effects, we used residuals in all analyses. Thus, we used onset time after the effect of day was removed as the independent variable in a regression of duration for which the effect of day also had been removed. The total food retrieved, after colony identity was removed, was regressed on total foragers after the combined effects of colony size and colony identity were removed. The standardized regression coefficients (values expressed in standard deviation units) are then the path coefficients of the model (Li 1975).

To estimate the average effect of earlier foraging onset on food collection, we regressed the estimated total food retrieved on the time that a colony began foraging. The estimated total food retrieved was calculated as 5 times the total food collected because food was collected only for four of every 20 min. When the interval between food collections was slightly longer than 20 min, we adjusted the multiplicative factor. The potential gain in additional food from earlier onset of foraging was estimated by regression (which is predicted to be negative if earlier onset of foraging increases food intake). To estimate the average foraging load of a worker, we regressed the total food retrieved on the number of foragers, for each day that data were collected. The slope of the line was the average foraging load of a returning worker. The estimate of colony onset time was obtained using a least square estimate of colony starting time after the effect of day was removed.

Results

Data were collected from 20 colonies for a total of 138 colony-days. During this period, 59,184 workers were captured, an average of 428 ± 376 (SD) workers per colony per day. Because returning foragers were collected for 4 min every 20–25 min, the average number of total foraging trips per colony per day was estimated as 2,140. Earlier onset of foraging significantly increased the amount of food retrieved, by 13.20 mg/min (regression of total food on onset time, 95% CL = 5.3–21.1 mg/min, $P = 0.001$). For each minute that one colony begins foraging earlier an additional 13.2 mg of food is returned to the colony compared with another colony. The average foraging load of a worker (the regression of food retrieval on the number of foragers) was 0.748 mg per worker (95% CL = 0.69–0.80 mg per worker) when the regression is forced through 0 and 0.629 mg per worker (95% CL = 0.55–0.71) when the regression is not forced through zero. The average foraging load for a colony did not depend on the onset of foraging (regression of average load on onset time, df = 113, $P > 0.75$). The standard deviation in the onset of foraging among colonies was 24.8 min.

The day of data collection had a significant effect on both onset time ($F_{19,\ 118} = 4.39$; $r^2 = 0.41$; $P < 0.001$) and the duration of foraging ($F_{19,\ 118} = 6.53$; $r^2 = 0.51$; $P < 0.001$). Further analyses using time variables were based on the residuals after the effect of day was removed. Colony identity had a significant effect on the total workers collected during a morning ($F_{19,\ 118} = 2.73$; $P < 0.001$), although colony size was not significant ($F_{1,\ 127} = 2.12$; $P > 0.1$; r^2 for the complete model = 0.34). The total food retrieved was also influenced by colony identity ($F_{19,\ 95} = 2.52$; $r^2 = 0.34$; $P < 0.01$). Further analyses were performed on the total workers and total food retrieved after these external factors were removed.

The path coefficients (the standardized regression coefficients) were highly significant between all of the hypothesized variables (Fig. 1). Colonies with earlier onset times foraged for significantly longer periods than those with later ones ($r = -0.62$, $P < 0.001$; Fig. 2a). A longer foraging duration led to significantly greater number of workers being sent out to forage ($r = 0.26$, $P < 0.01$; Fig. 2b), which in turn significantly increased the total food retrieved ($r = 0.88$, $P < 0.001$; Fig. 2c).

Discussion

We found a direct relationship between foraging success, in terms of biomass of food retrieved, and foraging effort. Earlier onset of foraging increases food

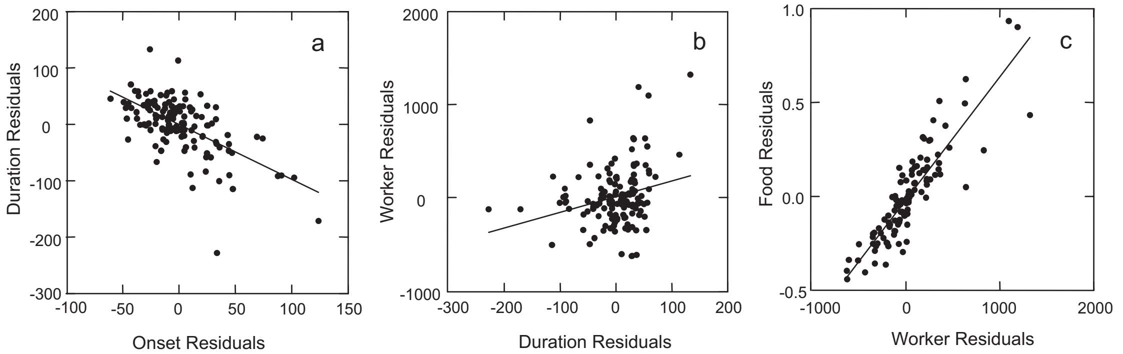

Fig. 2. Pairwise relationships between the factors in the path diagram (see Fig. 1). Each point represents the residual estimate of the variable after the effects of the covariates have been removed. The regression coefficients and significance levels are given in the text. (a) The relation of the onset of foraging and duration of foraging. (b) The relation of the duration of foraging and the number of foragers captured. (c) The relation of the number of foragers captured and the amount of food retrieved.

retrieval by increasing the time available for foraging and therefore the total number of foragers released by the colony. The average foraging success of a worker did not depend on when the colony started foraging; instead, colonies differed in the total effort devoted to food collection. Although weather conditions affected the foraging behavior of all colonies (differences among days), and microgeographic variation in vegetation may have affected food availability, when these variables are accounted for statistically, there is a direct causal path between onset of foraging and food retrieval. We found no effect of colony size. This does not mean that colony size is unrelated to the number of foragers, only that when the effect of colony identity is simultaneously estimated, we could detect no remaining effect of size on the number of foragers produced. Early onset of foraging may lead to greater foraging success through a variety of mechanisms. Colonies that begin foraging early may be more likely to discover concentrations of food, be better able to recruit to and thus monopolize concentrated resources, or carry out more productive foraging trips than colonies that become active later.

We found no evidence of compensation among the components of foraging. For example, if foraging duration and intensity had been negatively correlated, there would not have been a significant effect of foraging duration on forager number. Indeed, one might have predicted that colonies which forage for greater time send out fewer foragers per time interval. Colonies that had low foraging efficiency per worker may have compensated by sending out more foragers. The strength of the correlation between the number of foragers and the amount of food collected (Fig. 2c), suggests that the efficiency of single workers is nearly constant—greater foraging success is due to greater effort. Compensation could still occur if colonies that foraged more actively during the morning (the subject of this study), foraged less effectively in the evening. We have found that the duration of colony foraging in the morning and evening is significantly positively correlated (unpublished data), although we have not quantified food retrieval, suggesting that compensation is unlikely.

We can use the relationship between foraging onset and food intake to estimate whether the expected increase in food collection for a colony that begins foraging early is important. On average, each minute that a colony begins foraging earlier gains the colony 13.2 mg of food. The average load of a worker is 0.63–0.75 mg (depending on whether the regression is forced through zero). This means that for each minute gained in onset time, a colony will retrieve food equal to the load of an additional 17.6–21 workers. Comparing colonies that begin foraging 1 SD earlier than the population mean (24.8 min) to an average colony suggests that earlier colonies will collect an additional 327 mg of food per morning. This is equivalent to the amount collected by 436–520 additional average foragers. This amounts to an increase of 17% in food collection per day compared with the population mean. Earlier onset of foraging thus produces a substantial increase in food intake that is likely to affect colony growth and survival. Increased food availability also increases reproductive success in *P. occidentalis,* a result common to many species of ants (for review, see Bono and Herbers 2003).

Colonies that began foraging earlier in the morning have greater genetic diversity (Wiernasz et al. 2008), and they also had greater foraging success. Colonies with higher genetic diversity also have higher growth rates (Cole and Wiernasz 1999; Wiernasz et al. 2004). Our results strongly suggest that differences in genetic diversity among colonies produces variation in the onset of foraging, which leads to greater foraging effort and food retrieval, and ultimately faster growth and larger size. In *P. occidentalis,* the benefits of multiple mating are consistent with mechanisms of increased colony performance through more efficient division of labor (Crozier and Fjerdingstad 2001; Beshers and Fewell 2001).

Acknowledgments

We thank Alexander Dixson for help with data collection and Ian Billick, David Lubertazzi, and Brittany Davis for helpful comments. This study was supported by National Science Foundation grant NSF-IBN-0344896.

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Received 24 May 2007; accepted 18 September 2007.