

Competitive Advantages of Earlier Onset of Foraging in *Pogonomyrmex occidentalis* (Hymenoptera: Formicidae)

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ABSTRACT Colonies of the western harvester ant (*Pogonomyrmex occidentalis* Cresson) with greater genetic diversity begin foraging earlier, forage for longer durations, and collect more food than those with less genetic diversity. In this study we tested whether earlier onset of foraging improved the foraging success of colonies at baits placed midway between neighbors. Colonies that began foraging earlier in the morning were more likely to be the first to discover the food and to monopolize the food source. Colony size was also important with larger nests monopolizing significantly more baits than smaller nests. These results show that early foraging by colonies can provide an intraspecific foraging advantage at a clumped food resource. This advantage adds more evidence to a growing body of work showing how polyandry, genetic diversity, and colony-level performance are interrelated in *P. occidentalis* colonies.

KEY WORDS foraging, intraspecific competition, western harvester ant, polyandry

The western harvester ant is an important ecological component of North American arid grasslands and deserts (MacMahon et al. 2000, Johnson 2001). These ants affect soil composition (Wagner et al. 1997, 2004; Wagner and Jones 2006), hydrology (James et al. 2008), and the distribution, abundance, and recruitment of desert plants (Davidson et al. 1984, 1985; Rissing 1986; Wolff and Debussche 1999; Nicolai and Boeken 2012). A number of studies have focused on the foraging dynamics and food choice of western harvester ants (Morehead and Feener 1998; Whitford and Steinberger 2009; Crist and MacMahon 1991a,b, 1992) because of their importance in seed predation and dispersal.

The regulation of foraging by harvester ant colonies has been extensively studied as a model of how social activity is modulated by interactions among workers. The onset of foraging activity follows a characteristic pattern that begins with the earliest workers to become active (patrollers). Interactions between patrollers and other workers determine whether and where the colony will forage (Gordon 1991; Greene and Gordon 2007a, b). The maintenance of foraging depends on interactions between returning foragers and workers who are potential foragers (Fewell 1990, Gordon 2002, Schafer et al. 2006, Gordon et al. 2008, Beverly et al. 2009). Variations in foraging pattern are generated by variation among colonies in the leaving rate of patrollers (Gordon et al. 2011).

Finally, foraging patterns in western harvester ants are important in understanding the evolution of multiple mating in social insects. *Pogonomyrmex occidentalis* Cresson colonies are headed by a single queen that mates with an average of six males (Wiernasz et al. 2004). Colony growth rate is positively correlated with the number of times a queen has mated (Cole and Wiernasz 1999, Wiernasz et al. 2004) and foraging activity is influenced by within-colony genetic diversity (Cole et al. 2008, Wiernasz et al. 2008). Genetically diverse colonies begin foraging earlier in the day than less diverse colonies and this increases the total amount of time a colony spends foraging. During the summer season *P. occidentalis* foraging occurs in discrete morning and afternoon–evening foraging periods (Crist and MacMahon 1991a, Cole et al. 2010). The characteristics of the morning and afternoon–evening foraging periods are correlated; colonies that begin foraging earlier in the morning also forage later in the evening. Colonies that forage for longer periods conduct more foraging trips and retrieve more food. Colonies that collect more food realize a net energy gain, as foraging returns are known to be much greater than the costs in this species (Fewell 1988a, Morehead and Feener 1998). Increased genetic diversity in a *P. occidentalis* nest allows colonies to acquire more food resources than less diverse colonies.

The value of early foraging may be due solely to the expansion of the time available for foraging. In this case, the SD in the onset foraging time (20–25 min depending on data set; Wiernasz et al. 2008) will govern the variation in food collection. However, this estimate is based on the assumption that the relative success of food collection is consistent across foraging time. There are at least two factors that may alter this

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estimate. First, the type of food collected early in the morning might differ from what is retrieved later in the morning. Seeds or insects that become available overnight may be preferentially collected by colonies that begin foraging earlier in the morning. Second, the ability of colonies to retrieve food that is closer to neighboring colonies may be facilitated by activity that occurs earlier in the morning. Differences in the onset of foraging may give early foraging colonies a greater advantage than is apparent from the differences in foraging duration, especially for food that exists as high density patches. Food resources can occur in patchy distributions at a scale that is relevant to individual *P. occidentalis* colonies (Price and Reichman 1987, Fewell 1988b).

If colonies that begin foraging early are more likely to discover food, recruit nestmates to such food sources and monopolize a food source that would have been equally accessible to a later foraging neighbor, a consequence of earlier onset of foraging would be that larger foraging areas can be effectively controlled by early foraging colonies. Differences in the timing of foraging would translate into differences in space use by colonies and influence the pattern of territoriality. Alternatively, early foraging may have no effect on the ability of colonies to monopolize peripheral food sources. Early foraging would increase foraging duration, but a colony's foragers remain concentrated in the central portion of its territory, and do not affect foraging on territorial margins. If there is some mechanism that compensates colonies that begin to forage later, for example, increased speed of foragers, later foraging colonies may actually be able to monopolize resources that are at the periphery of their foraging territory.

In this article, we use a field experiment to test the prediction that early foraging colonies gain a disproportionate advantage over their later foraging neighbors because they can monopolize food sources for which they may be in competition.

Materials and Methods

The western harvester ant is a central place forager that is common in arid habitats of the southwestern United States (Gregg 1963, Cole 1968). A large proportion of this species' diet is composed of seeds (Cole 1968; Crist and MacMahon 1991b, 1992; Cole et al. 2008). *P. occidentalis* build extensive subterranean nests that are topped with a pebble and soil mound that contains the sole nest entrance (Cole 1994). Nest mounds are overdispersed across the landscape (Wiernasz and Cole 1995). This pattern of nest distribution is indicative of a territorial species that competes intraspecifically for foraging space, which is typical for many *Pogonomyrmex* species (De Vita 1979, Rytí and Case 1986, Johnson 2001). Foraging territories are variable in shape and interlock like puzzle pieces with the abutting boundaries of their neighbors (Hölldobler 1974, Gordon 1991).

The study site was located on Bureau of Land Management land in western Colorado, ≈10 km northwest

of Fruita (Mesa Co.). This site is ~1 km east of a similarly situated long-term study population of *P. occidentalis*. Cole and Wiernasz (2002) and Wiernasz and Cole (1995) provide detailed locality and habitat information for the long-term study site. The experiment was conducted from 13 June to 3 July 2006 on mornings that were either sunny and clear or partially cloudy for a brief period of time.

Baiting trials involved pairs of colonies that were selected, and their bait locations marked, at least 1 d before their use. The colonies for each day of baiting trials were chosen to be spatially arranged so the nests and baits could be observed by walking a circuit. The first colony of each baiting-trial pair was a randomly chosen mature colony that was subsequently found, based on visual observations, to have a neighbor with a similar-sized nest cone. Every colony had numerous neighbors. Immature colonies, that is, nests with small cones, were not considered for testing. The relative number of foragers in a colony was later estimated as the $\ln(\text{length} \times \text{width} \times \text{height})$ of the nest cone using measurements taken after the bait trials were completed. This metric is highly correlated ($r = 0.9$) with the size of a colony's foraging force (see Wiernasz and Cole 1995).

The distance between each pair of nest entrances was measured to the nearest tenth of a meter. The midpoint of this distance was marked with flagging, placed on the ground, and subsequently used as the location for the baiting trail. Before the baiting trails we had no knowledge of and collected no information about colony start-up times, trunk trails or foraging-area use. We also had no a priori reason to suspect early or late start up colonies were more likely to have exclusive use of, previous experience in or have trunk trails leading to the area where we placed our baits.

The bait consisted of chopped pearl barley dyed with food coloring. Foragers vigorously collect from and recruit nestmates to barley and the dye has no influence on foraging behavior (D.C. Wiernasz, unpublished observations). The combination of sparse vegetative ground cover, the bright color of the grain and the pale colored soil allowed an observer to easily track foragers carrying dyed grain. Successful *P. occidentalis* foragers run quickly back to their nest along a fairly straight-line return route. The resident colony of a forager visiting a pile of dyed grain can easily be determined by tracking an individual leaving the grain pile back to its nest entrance. Each day of sampling began at ≈7 a.m. MDT and before any above ground ant activity. Approximately 10 g of dyed grain was placed at the midpoint between each set of paired colonies. The food was spread along the ground to form a line of grain one meter in length. This created a line of grain perpendicular to the midpoint of the shortest linear distance between the two nest entrances. Five bait trails were observed on most days; on two occasions four baits were observed. During the first four mornings some colonies were tested against more than one colony by using different baits with additional neighbors. Subsequent baiting samples

were conducted by testing each colony against only one other colony during a single morning of sampling.

The nests and baits were visited in the same order during each circuit of a morning's baiting trails. Each colony or bait was watched for a maximum of a few minutes during each observation. All observations were made while standing a few meters away from the nest or the bait. The time between observations of the same nest or any single bait ranged from 7 to 15 min. The onset of foraging was recorded as the time, to the nearest minute, that a forager was observed leaving the area surrounding the nest mound. This corresponds to the measure of the onset time of foraging used in previous studies (Wiernasz et al. 2008, Cole et al. 2010). Once foraging onset was recorded for a colony its nest mound was not routinely revisited during subsequent rounds of observation.

The first forager observed at a bait was followed back to its nest to determine its colony of origin. Subsequent foragers at that bait followed the same path back to the nest and could be assigned to that colony by their use of the same return route. Any subsequent foragers at a bait not using a known return route were followed to determine their colony of origin. For each observation at a bait that was being foraged upon we recorded the time the observation began, to the nearest minute, and the number of foragers observed at the bait from each nest. Baits that were being actively foraged upon were typically watched for a few minutes. Each morning sampling period ended ~2 h after the last colony began foraging. Earlier test samples had shown observations taken past this time revealed no new discoveries of baits by any colonies. Foraging intensity was also found to remain the same or was beginning to decline at this time. This reflects the fact that rising temperatures in mid to late morning on hot summer days lead to a waning foraging effort that eventually ceases altogether during the intense heat of mid-day (Cole et al. 2010).

The time to bait discovery was calculated as the number of minutes from foraging onset until the first forager from a colony was observed at a bait. Colonies were classified according to their foraging onset time relative to their neighbor (the same, early, or late). For a pair of colonies it was not always possible to obtain all measurements, such as cases where only one colony foraged from the bait.

Each colony was categorized as monopolizing or not monopolizing a bait. Monopolization was characterized by a bait discovery period, where one or a few foragers initially gathered seed from the grain pile, followed by a recruitment response that led to sustained foraging involving numerous workers. These colonies then either continued to collect from the grain pile until all the grain was removed or, more typically, for the remainder of the observation period. The ability to find, recruit nestmates to, and sustain foraging at a grain pile were important in determining whether a colony monopolized a bait. A colony was categorized as not monopolizing a bait if they never had more than two foragers at a bait for any obser-

Table 1. Logistic regression statistics for the model that includes ln of forager no. and early vs late foraging to predict bait monopolization

Intercept	Estimate	SE	<i>t</i> -ratio	<i>P</i>	Odds ratio
Constant	-15.448	6.658	-2.320	0.02	
Early onset	1.038	0.443	2.342	0.02	2.82
ln of colony size	2.104	0.958	2.196	0.03	8.20

vation period, if their foraging intensity was inconsistent through time or if a colony never foraged at the bait. Win and loss are used interchangeably with monopolization and nonmonopolization in the remainder of the text.

Logistic regression (Minitab 2010) was used to assess if the number of foragers in a colony (the ln estimate), distance to the bait, early versus late foraging, and baiting-with-one versus baiting-with-more-than-one bait per morning influenced bait monopolization. Models were evaluated using various combinations of these variables. Time variables, such as time to food discovery and the difference in start-up times between colonies, were undefined in some cases (e.g., no foraging from the bait by a colony) and were not used in the logistic regression analysis. We also examined differences between early and late foraging colonies, and winning and losing colonies, using χ^2 and *t*-tests.

Results

Eighty-one colonies were observed at 68 bait samples on 12 mornings. Eight of these baits had no ant visits or one of the paired colonies was inactive. These trials were removed from our analyses. Fifteen of the remaining 60 baits were tested with a colony that was presented with multiple baits, placed between different neighbors, during a single morning. The results from these samples did not differ from the single bait samples (see logistic regression results in the next section). Two of the 60 baits were cases where both colonies recruited to and successfully foraged from the bait. Both colonies at these baits were categorized as winners.

Components of Foraging Success. The goal of the logistic regression analysis was to identify variables that influenced bait monopolization. Eliminating baits that were inadequate for this question (i.e., nine cases where both colonies started foraging at the same time and three instances where a third colony foraged from a bait) reduced the number of baiting trials from 60 to 48. This provided 96 colonies for analysis. For the two baits where both colonies effectively foraged from the bait each colony was treated as monopolizing the bait. The selected best fit logistic regression model ($\chi^2 = 12.60$, *df* = 2, *P* < 0.01; Table 1) included two significant variables, earlier onset of foraging and the ln estimate of forager number. Models with distance to bait and/or the number of baits presented to a colony always yielded coefficient estimates with *P* > 0.05 for these variables.

Early colonies began foraging an average of 25.4 min (SD = 20.5; $n = 60$) sooner than their paired neighbors. In the logistic regression model the coefficient estimate for the early/late parameter was (1.04). The antilog of this value (2.82) is the multiplicative change in the predicted odds and thus represents a 182% increase in the predicted odds of monopolizing a bait for colonies that are the first to forage. For the ln estimate of a colony's workforce, winning colonies (7.01; SD = 0.23; $n = 41$) were significantly larger ($t = -2.64$; $df = 94$; $P = 0.01$) than losing colonies (6.88; SD = 0.25; $n = 55$).

Onset of Activity, Food Discovery, and Monopolization. Colonies that began foraging earlier in the morning were more likely to discover baits before later-to-forage neighbors. For the 48 baiting trials examined in the logistic regression analysis significantly more baits were first discovered by the early onset colony (35 early, 13 late; $\chi^2 = 10.1$; $P < 0.01$). Colonies that were the first to discover the bait were far more likely to monopolize the bait. For the 37 of the 48 baits where there was a clear winner and loser (9 of the 48 baits were not monopolized by either colony and two were effectively foraged upon by both colonies), 35 were monopolized by the colony that first found the bait ($\chi^2 = 29.4$; $P > 0.01$). Twenty-five of these 37 colonies were the early onset colony (25 early, 12 late; $\chi^2 = 4.57$; $P = 0.033$). Along with the results of the logistic regression analysis, these outcomes demonstrate that early foraging can be important in establishing precedence of food discovery and the eventual monopolization of newly discovered food resources.

At the 37 baits with a winner and loser, early onset colonies started foraging an average of 32 min (SD = 19.1) before late onset colonies. For paired colonies where the late onset colonies won the bait, the average time difference (24.1 min; SD = 14.6; $n = 12$) was less than the average for early onset winners (35.1 min; SD = 20.2; $n = 25$) but this difference was not significant ($t = -1.69$; $df = 35$; $P = 0.10$). Late onset colonies that monopolized baits were not successful relative to unsuccessful late onset colonies because they were beginning their foraging significantly closer to the time when their early neighbors began foraging.

Later onset colonies that monopolized baits did not discover baits (time from first foraging activity to bait discovery: 42.3 min, SD = 26.2, $n = 12$) any faster than early onset colonies that monopolized baits (49.7 min, SD = 29.9, $n = 25$, $t = -0.74$, $df = 35$, $P = 0.47$; Fig. 1). However, colonies that monopolized a bait had significantly shorter discovery times (mean discovery time = 47.3 min; SD = 28.6; $n = 37$) than colonies that discovered but did not win the bait (105.4 min to discovery; SD = 33.1 $n = 14$, 23 of the 37 losing colonies did not discover the bait; $t = -6.20$; $df = 49$; $P < 0.01$; Fig. 1).

Early Versus Late Winners. Early onset colonies did not always succeed in monopolizing the bait. We used a statistical approach that compares the onset times of winning colonies to determine whether early onset colonies lost baits more often than expected. The onset times of colonies in this study were previously

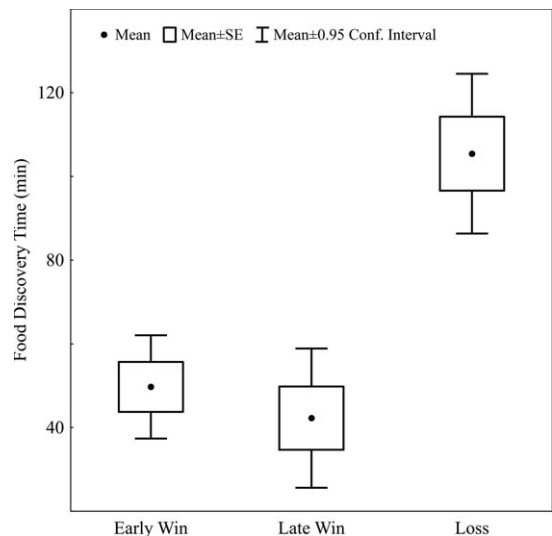


Fig. 1. Mean food discovery time for colonies that monopolized the bait, grouped separately by early and late foraging onset, and those that lost the bait.

unknown. The average starting time difference between pairs of colonies was 25.4 min. Under the reasonable assumption that these two colonies represent two random samples from a normal distribution of colony onset times (Wiernasz et al. 2008), we can use the difference between the earlier and later colony to estimate the SD of the distribution of colony onset times. The average difference between a pair of samples is 1.12 SDs. This allows us to estimate that the SD of onset times in the population is ≈ 23 min ($25.4/1.12$). This value is in accord with previous estimates, from an earlier study (Wiernasz et al. 2008), of 20–25 min.

The average early onset colony had a head start of 25 min, which translates to discovery of a bait ≈ 48 min (with a SD of 31.4 min) after becoming active. The average later onset colony discovers food on average 73 min (with a SD of 37 min) after the early onset colony becomes active. Because the time for food discovery is independent of colony onset time, we assume that these two time periods are independent. Late onset colonies are expected to find food before early onset colonies when a random sample taken from a normal distribution with a mean and SD of 73 and 37, is less than a random sample taken from another distribution with a mean of 48 and a SD of 31. We simulated this process and found that the late colonies should discover the food earlier than the early colonies 30% of the time. This compares well with our data (12 of 37 = 32% late colonies monopolized the bait), and is consistent with the observation that when late colonies win the bait, they are not as late as typical.

Discussion

Early foraging starts a chain of events that significantly increases the probability that a colony will

monopolize a food resource. Colonies that begin to forage earlier in the morning are more likely to discover potentially contestable food first. Once food has been discovered it is virtually certain to be monopolized by the discovering colony. However, the timing of foraging was not the sole factor that determined the outcome of intraspecific food competition in *P. occidentalis*. Having a larger forager force improved the odds of winning and, overall, winning colonies were larger than losers. Being an early, large colony is better than being a late, small colony, but late, larger nests can be good competitors.

These results add to our understanding of how colony level performance can be influenced by polyandry in *P. occidentalis* through the genetic task specialization model (Fuchs and Moritz 1998, Graham et al. 2006, Oldroyd and Fewell 2007). Polyandry is favored in social insect colonies when increases in colony-level genetic diversity significantly improve colony performance (Crozier and Page 1985, Sherman et al. 1988, Crozier and Fjerdingstad 2001). The model operates when multiply mated queens produce a diverse worker population that performs tasks with greater efficiency than less diverse colonies.

Previous work with *P. occidentalis* has shown that the genetic diversity of a colony's worker force can influence correlates of colony fitness (Cole and Wiernasz 1999, Wiernasz et al. 2004). One mechanism by which genetic diversity leads to increased fitness is through changes in the temporal pattern of foraging activity. Foraging earlier leads to an increase in the total amount of time spent foraging during each day (Wiernasz et al. 2008, Cole et al. 2010), which in turn leads to taking in more food (Cole et al. 2008). In this study we show that earlier-foraging colonies are also more likely to discover and monopolize food resources for which they may be contending with neighbors.

Being active outside the nest before a neighbor can also provide advantages when competing for foraging space. *P. occidentalis* colonies rarely engage in large scale battles (Clark and Comanor 1973). Contact between nonnestmates in areas distant from the nest mound typically results in both workers retreating rapidly toward their respective nests. Actively occupying space can be an important component of territorial defense, that is, *Pogonomyrmex barbatus* (F. Smith) workers from neighboring nests use contact with nonnestmates as one cue for assessing territory boundaries (Gordon 1991). The earliest foragers are potentially able to reach and find themselves unopposed by other ants at their territory boundaries. Earlier-to-forage workers can thus encroach upon and gather food from a neighbor's territory with impunity and, if nestmates are recruited to a food rich area at the boundary edge, may push their territory boundary into a resource rich area simply by being present in force before their neighbors (e.g., Gordon 1992, Gordon and Kulig 1996).

Close to the nest entrance mature colonies have an unassailable advantage over their neighbors. It is virtually impossible for another colony to successfully

recruit to food or for a new colony to be founded successfully in the close vicinity of an established colony. However, this advantage declines as one moves further from the nest. Halfway between nests, where the numerical advantage of similar sized colonies is lower, the timing advantage of the early foraging colony is at its greatest. A contestable patch of vegetation near a boundary that produces a seasonal burst of desirable seeds could more easily be monopolized by the colony with foragers that first arrive at the food, which we have shown is more likely to be the early onset colony. This early arrival strategy is also supported by our finding that winning colonies discovered their baits significantly faster than losing colonies. One important aspect of this potential advantage we need more information about is the relative importance of naturally occurring food resources that are similar to our baits. The probability of a colony encountering clumped food resources and the potential contribution of such resources to the overall diet of *P. occidentalis* is currently unknown.

A foraging territory is a resource in and of itself. The same mechanisms that can be used to expand a territory boundary into a food rich area can also be used as a general means of territory establishment and change (Adams 2001, 2003). Moving territory boundaries to exchange less productive for more productive foraging space could be easier for early onset colonies, as would establishing and holding foraging space when colonies are reemerging from their winter foraging hiatus. Early onset colonies, when compared with later-to-forage neighbors within the milieu of a western harvester ant population with contiguous territory boundaries, may be more adept at expanding and moving their territories as their colonies grow, more easily adjust their territory when food resources change and potentially have larger territories.

Later onset colonies that monopolized baits were less common in our samples but are of interest. These late onset winners appear to neither succeed by very quickly finding a bait soon after they begin foraging (late winners did not exhibit significantly shorter bait discovery times than early onset winners) nor by starting foraging closer in time to when their early onset neighbor begins foraging (late winners did not lessen the time difference between foraging start up times and reduce the early onset colonies' start-up time advantage). Instead it appears that late onset winners by chance find the bait before early onset neighbors and this alone allows them to monopolize a bait. Regardless, it may prove fruitful to examine late onset winning colonies in greater detail in future studies. This should include examining all the neighbors of a focal early and late nest pair. It may be that successful late colonies are predominantly surrounded by nests, other than their focal early foraging neighbor, that are smaller or do not forage very early. In *P. barbatus*, interactions between colonies vary as a function of colony size (Gordon and Kulig 1996). Alternatively some early colonies, seemingly less competitive relative to a late neighboring colony that monopolized a bait, may be habitually exploiting more productive

foraging areas that are located away from their larger, late onset neighbor. Studies of both *P. occidentalis* (Fewell 1988a) and *P. barbatus* (Gordon 1991, 1992, 1995; Gordon 2002; Beverly et al. 2009) have shown that colonies do not use all possible directions of foraging equally, but rather persist foraging in certain directions based on recent experience.

Our work shows that a temporal shift in foraging, via a behavioral mechanism linked to polyandry, can influence intraspecific competition between ant colonies. This study also suggests different ways that competitive differences can arise from time-of-foraging differences between *P. occidentalis* colonies. Further research is needed to explicitly examine the influence of early versus late foraging in regard to natural food resources, how foraging duration advantages may vary through the foraging season, and how important the putative behavioral advantages suggested by our data are in determining foraging boundaries.

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