

Foraging Behavior of *Pogonomyrmex owyhee* in Southeast Idaho¹

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ABSTRACT

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Foraging behavior of *Pogonomyrmex owyhee* Cole was studied from 1977 to 1979 in Raft River Valley, Idaho. Average foraging distances were positively correlated with the estimated number of foragers per colony. Foraging trips took an average of 11.3 min, with 64% of this time spent in transit and 36% searching. Of the foragers, 75% returned with food, 21% with rock or debris, and 4% without a payload. Foraging ranges of individual colonies seldom overlapped, and aggressive encounters between ants of neighboring colonies were not observed. Concepts of territoriality may be unnecessary to explain space and resource partitioning among adjacent colonies of *P. owyhee*.

Foraging behavior is determined substantially by the fitness alternatives included within optimal foraging strategies. Oster and Wilson (1978) provided a comprehensive discussion related to foraging strategies of social insects, including ants. They partitioned group foraging into four substrategies: recruitment, trunk trail, preying en masse, and group hunting, all exhibiting different foraging behaviors. Davidson (1977b) introduced cost-benefit analyses to studies of foraging *Pogonomyrmex* species and provided valuable insights into the alternative strategies of group-foraging versus individual-foraging species. According to Porter and Jorgensen (unpublished data), *Pogonomyrmex owyhee* satisfies Davidson's (1977b) criteria for group foraging and Oster and Wilson's (1978) criteria for trunk trail group foraging.

Territoriality, a phenomenon specifically related to foraging, is a behavior used by numerous species of ants, including *Pogonomyrmex* species (Hölldobler 1976), to establish home ranges. Optimization models by Davidson (1977b) and Oster and Wilson (1978) suggest that territorial behavior will diminish when the costs of maintaining a territory exceed the benefits, or when the food resources are much reduced, or both. This theoretical breakdown in territorial behavior is not likely in species of desert-dwelling *Pogonomyrmex*, since seed reserves seem to be present in sufficient supply to provide cost-effective home ranges during most years (Bernstein 1974, 1975, Tevis 1958). The cost of maintaining home ranges by ants has been projected by Hölldobler (1976) to result from intercolony aggression and sometimes the transfer of a colony to another location, rather than the original specific spacing of colonies by founding queens or territorial aggression between them.

Cost-effective foraging is a function of energy expended and obtained while gathering food, including distance to the food, size of food, time to forage, distribution of food, abundance of food, and foraging for nonfood items (De Vita 1979, Hansen

1978, Davidson 1977b, Bernstein 1974, 1975, Whitford and Ettershank 1975, Whitford 1973, 1976, Tevis 1958). These factors, along with costs to maintain home ranges, must be compensated for while foraging to provide optimal benefits for the colony at large. The purpose of our research was to describe foraging behavior of *P. owyhee* as it relates to the potential interactions of foragers from adjacent colonies and partitioning of the food resources.

Materials and Methods

Our studies were conducted in Raft River Valley, Idaho, where sagebrush-greasewood, *Artemisia tridentata*-*Sarcobatus vermiculatus*, plant communities were extensive. Overstory plant cover (>30 cm) for the study site was 4.81% *A. tridentata* and 19.22% *S. vermiculatus*. Understory plant cover (<30 cm) was 2.91% *A. tridentata*, 1.89% *Descurainia richardsonii*, 0.03% *Halogeton glomeratus*, 0.91% *Lepidium perfoliatum*, 2.66% *Opuntia polyacantha*, 0.39% *S. vermiculatus*, and 5.01% *Sitanion hystrix*. Total combined percent cover was 37.90%, including some species too few to mention.

Foraging ranges were determined for nine rather closely spaced colonies, ranging from small to large. Distances, time, and searching behavior were first noted by recording exit, search, and return times along with distances traveled for 57 foragers that were individually observed for their complete foraging trips. Measurements of time were recorded to assist the assessments of tempo and foraging efficiency. After this preliminary examination, 355 foragers were tracked until they left the trunk trail and began search behavior. Time and distances were recorded. Forager populations for eight of the nine colonies were estimated by using the Lincoln index (Porter and Jorgensen 1980) to determine if colony size (and perhaps age) could be correlated with tempo and foraging distance.

Individual foraging trips for 412 ants were plotted on a foraging map (Fig. 1). This map was used to compare the positions of trunk trails among adjacent colonies and also to establish areas where home ranges and foraging ranges overlap. Comparative home range sizes were approximated by computing

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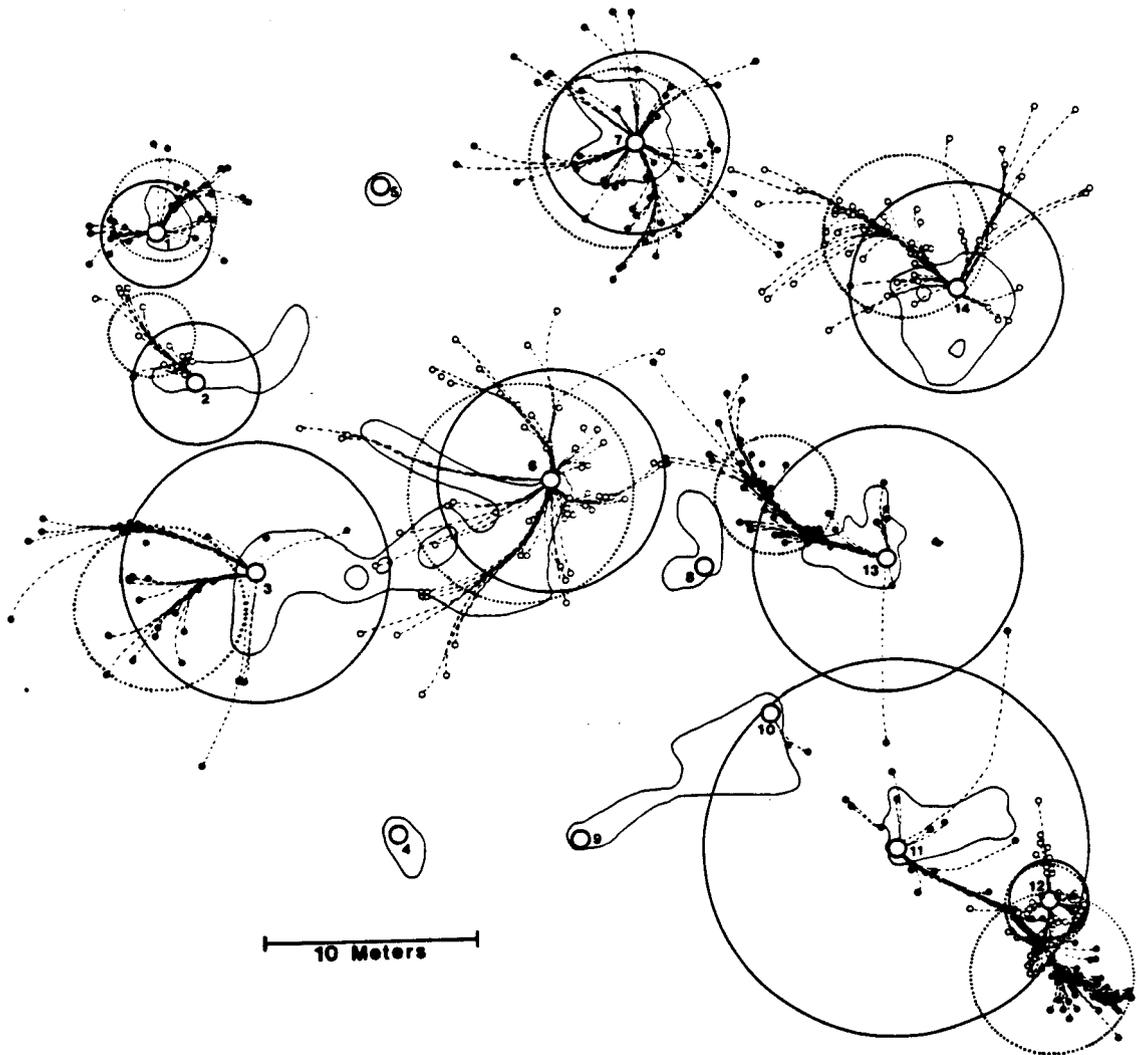


FIG. 1.—Map of foraging (July 1978) *P. owyheeii* ants from nine active colonies, demonstrating home ranges (solid circles), foraging ranges (dotted circles), and trunk trails (dashed lines). Clearings around mounds are illustrated with a fine solid line.

a circular area around each mound, using the average distance from the mound to where forage items were obtained and returned as the radius. These estimates of home range size were used only to compare mounds of different sizes and develop an approximate area around the mound within which ants might be expected to forage. Foraging ranges and their respective centers were also computed to assess possible competition for food at a given time. The center is simply the geometric center of the foraging points, and the ranges were computed by using the average distance from the geometric center to the foraging points as the radius. Aggressive behavior was searched for in the overlapping areas of home ranges and foraging ranges.

Foraging efficiencies were estimated by determining the item and weight of material (payloads) returning to the mound. Samples of 25 to 75 ants from

each of five colonies were collected five times between June and July. Payloads were classified as seeds, animal materials, plant debris, and rocks.

Results and Discussion

Calculations of foraging efficiencies and tempos require rather accurate measurements of individual time and energy for each behavior (Oster and Wilson 1978). By accumulating these functions for foragers and their returned payloads, it is possible to compute colony foraging efficiencies. An extension of these analyses provides the basis for describing optimal foraging behavior (Taylor 1978). Although we do not have the data complete enough to analyze foraging efficiencies, time per foraging trip and the likelihood of returning with a food item can be used to measure efficiency.

We observed 1,450 *P. owyheeii* returning to the

mound an average of 73% of the time with seeds, 2% with insects of dung, 12% with plant detritus, 9% with rocks, and 4% without an observable payload. An average of 34.8 mg of seeds, 4.7 mg of insects and dung, 18.4 mg of detritus, and 110 mg of rocks were returned per 100 foraging trips. Although insects were included in only 2% of the foraging trips, they accounted for 12% of the food weight per unit trip. Seeds were distributed at 73% *Descurania pinata* (1.0 by 0.6 mm in size; 20% by weight), 18% *Sitanion hystrix* (7.0 by 1.0 mm; 62% by weight) 7% *Descurania perfoliatum* (2.0 by 1.3 mm; 15% by weight) and 2% other assorted species. Care must be taken to avoid assigning a negative value to nonfood items, since these materials are apparently essential to nest and mound construction (Lavigne 1969).

We also determined an average trip for 57 foragers to be 11.3 ± 1.5 min (3–55 min), and they traveled an average of 8.0 ± 0.9 m (3.0–13.3 m). We found that 11.3 min per trip broke down into 4.1 min searching, 3.5 min traveling to the resource, and 3.6 min returning to the mound. Transit speed is then 2.2 m/min. Transit speed is considered a measure of tempo (Oster and Wilson 1978), although its importance to the foraging strategies is not clear. The mean transit speed and the estimated size of forager populations was not significantly correlated ($P > 0.05$, $n = 6$) among the colonies, even though there was a tendency for the speed to increase some as the colonies increased in size.

The foraging map (Fig. 1) illustrates the observed variation in home range sizes and foraging distances. The average foraging distance per mound was 5.2 m, with individual ants ranging from 0.6 to 15.6 m. There was a positive correlation between foraging distances from the mound and the estimated forager population sizes (Fig. 2). These relationships are not surprising, since small colonies require less energy to provide for their growth and comparatively less

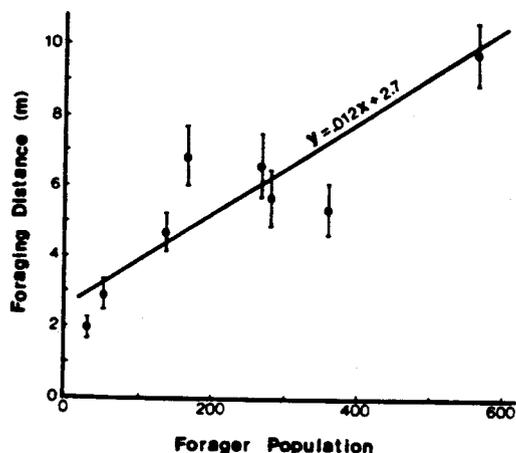


FIG. 2.—Correlation between the average foraging distances and the estimated forager population sizes (July 1978) of eight colonies: 95% confidence intervals for foraging distances are illustrated for each colony.

space from which to collect it. Longer foraging trips required longer foraging times ($P < 0.001$); thus, increased predation would be expected, with more energy per trip expended and fewer trips made per day. Larger home ranges require more energy to maintain, possibly taxing the foraging process beyond its ability to provide. One might logically conclude that forager efficiency will decline as colony size increases, suggesting an optimal size and that cost inefficiency may establish an upper limit on colony growth.

Models have been reported for other *Pogonomyrmex* spp. that were useful in understanding *P. owyhee* foraging and territorial behavior: *Pogonomyrmex rugosus*, *Pogonomyrmex barbatus*, and *Pogonomyrmex desertorum* (Davidson 1977a), and *Pogonomyrmex maricopa*, *P. rugosus*, and *P. desertorum* (Hansen 1978). Davidson (1978) discussed another important foraging strategy—selection of optimum sized seeds while foraging furthest from the mound. As greater energy is expended in foraging, the ants apparently become more selective of their payloads.

Hölldobler (1976) reported home ranges for *P. barbatus*, *P. maricopa* and *P. rugosus* as well as ranges for several other genera. Although most of his studies discussed orientation phenomena, he conducted some field experiments that indicated that trunk trails of these three *Pogonomyrmex* species never cross, and that foraging ants of different intraspecific colonies often fight fiercely when they encounter one another at the perimeters of their adjacent home ranges. However, Whitford (1976) reported a general lack of aggressive interactions among individuals from adjacent colonies when their foraging trails crossed. Figure 1 demonstrates that home ranges of *P. owyhee* seldom overlap; thus, both distance between adjacent colonies and trunk trail orientation can possibly serve to relieve intraspecific confrontations and reduce the potential need to use large amounts of energy for territorial behavior while foraging. Methods used by *P. owyhee* to keep home ranges and foraging ranges from overlapping are still not known. Recognition of home ranges and foraging ranges must occur among neighboring colonies, but it is not clear that aggressive territorial behavior is responsible. Perhaps frequent passive encounters and subsequent adjustments are sufficient to provide the recognition required to sense ranges of adjacent colonies.

The use of trunk trails and foraging recruitment leave territory and home range concepts a little untidy and somewhat difficult to interpret. If trunk trails are rotated or moved as reported by Bernstein (1975), and foraging ants avoid crossing trunk trails of other colonies (Hölldobler (1976)), there is little need to develop territorial concepts to interpret space used by ants while foraging. Fighting while foraging would be limited to individual confrontations that would likely be avoided for prolonged periods as trunk trails move. Such fighting may be avoided altogether, resulting in passive confrontations or perhaps indifference. In fact, many hours

of observations failed to find a single pair of foraging *P. owyheeii* fighting. It seems that territorial confrontations resulting in fighting were not compelling space and resource partitioning factors among adjacent *P. owyheeii* colonies at the time we studied them. Perhaps the concept of aggressive territorial behavior is not especially useful in understanding their foraging behavior, although home ranges and foraging ranges may be maintained by less aggressive encounters.

Colonies 11 and 12 pose the most interesting potential for interactions, since mound 12 lies within the presumed home range of mound 11 (Fig. 1). This resulted in a foraging overlap that was almost complete, even though the most intensive foraging by each colony was seemingly not in the same areas. Also, extensive crossing of trunk trails was evident. Foraging ants from these two colonies were in frequent contact, but fighting was not observed. Colony 11 was no longer active in 1979, suggesting that it either died or transferred to another location to avoid the cost of maintaining a colony with too frequent contact with ants from colony 12. The location may simply have been cost ineffective because of competition or frequent possessive interactions, resulting in altered foraging behavior rather than territorial behavior. Willard and Crowell (1965) reported several colony transfers of *P. owyheeii* in Oregon, and we observed two in Idaho. Although a few transfers have been reported, they are less common than transfers reported for other *Pogonomyrmex* species, especially *Pogonomyrmex badius* (Carlson and Gentry 1973).

Perhaps the strategy for avoiding interactions of *P. owyheeii* foragers in the field would be to rotate their trunk trails and resultant foraging ranges around the mound sites (Fig. 1). This would give some relief from forager competition, provided that the trails are moved among all of the colonies so as to avoid overlapping the foraging ranges. We expect that trunk trails may move to avoid extensive interactions, although we have no historical data to demonstrate it. Also, it seems logical to think that colonies isolated from others would not even find trunk trails necessary when food resources abound; then territoriality has more meaning, because possible intercolony interactions could increase as the use of resources within the home range is more diffuse or a new colony is established nearby.

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