Journal of Arid Environments xxx (2017) 1–6

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Colony size and foraging strategies in desert seed harvester ants

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ARTICLE INFO

Article history:
Received 10 January 2017
Received in revised form
19 April 2017
Accepted 28 April 2017
Available online xxx

Keywords:
Formicidae
Harvester ant
Ant size
Colony size
Foraging type

ABSTRACT

We summarized the literature on foraging strategies, colony sizes, and body sizes of seed harvesting ants to test hypotheses about the relationship between colony size and foraging strategy, and body size and foraging strategy. We used a Wilcoxon-Mann-Whitney test to test hypotheses about body size, colony size, and foraging strategy with the following results: (1) The maximum length of a worker ant in trunk trail foraging ant species or group foraging ant species is significantly smaller than in individual foraging ants except in the North American genus *Pogonomyrmex*; and (2) the maximum number of worker ants per nest in trunk trail foraging ant species or group foraging ant species is significantly larger than in individual foraging ants. While most seed harvesting ants can forage as individuals, only seed harvesters with large colonies develop group or trunk-trail foraging strategies. Flexibility in foraging strategy is important in desert seed harvesters because of the unpredictability of food resources among years.

1. Introduction

Harvester ants are among the most important insects inhabiting arid and semi-arid environments. Seed harvester ants are species of ants that collect seeds that are stored in nest granaries and consumed by members of the colony. Because harvester ants collect and store seeds in their nests, they directly affect the spatial distribution and population size of plants, particularly species whose seeds are preferred by the ants (Whitford, 1978a). Species of seed-harvesting ants utilize three types of foraging strategies: individual foragers, group foragers, and trunk-trail foragers (Bernstein, 1975; Holldobler, 1976; Holldobler and Wilson, 1990). In ants using an individual foraging strategy, a worker leaves the nest and when that worker returns with a food item, it does not recruit other workers to the location where the food item was found. Tandem running occurs when one ant leads another to a chosen location by tactile or chemical signals, frequently following the leader's own trail. Column foraging and trunk trail foraging involves recruiting a number of workers to follow an odor trail. Column foraging involves short-lived odor trails, and trunk trails involve mass recruitment to odor trails that persist for days to weeks (Plowes et al., 2013). Most species of seed-harvesting ants are capable of foraging as individuals but not all species group forage (columns) or utilize trunk trails. Indeed, the most common foraging strategy of seed-harvesting ants is a mixture of individual and group foraging (Holldobler and Wilson, 1990). Foraging behavior of a colony depends on the success of scouts. If scouts leave a nest, return with only one seed, and do not lay down a pheromone trail, colonies do not establish trunk trails. However if a scout returns to the nest with one seed after laying down a pheromone trail, the colony sends many workers on the trail to exploit the rich food patch identified by the scout (Holldobler and Wilson, 1990).

In some deserts, there may be several species of seed-harvesting ants with overlapping foraging territories and, in these situations, there is generally only one species that utilizes group or trunk-trail foraging (Brown et al., 1979; Whitford and Ettershank, 1975). Group foraging ants recruit to a scent trail and move along the trail in columns to an area with a concentration of seeds. These ants return to the colony along the same route, resulting in two-way traffic on the pheromone-marked trail. The columns in which group foraging ants leave the nest are in different directions every day and are defined as rotating columns. This type of foraging is found in *Messor pergandei* (Holldobler and Wilson, 1990). Some group foraging trails can be trunk trails from which some of the vegetation is removed by the ants.

Studies using tuna fish or ground beef as bait documented that *Pogonomyrmex* spp. recruit large numbers of foragers to high-protein bait, and continue to transport bits of meat to the colony for more than one hour after colonies foraging on seeds ceased

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http://dx.doi.org/10.1016/j.jaridenv.2017.04.016
0140-1963/

above-ground activity (Whitford et al., 1980) (Whitford, unpublished data). Most seed-harvesting ants will take insect carrion or live insects like termites whenever they find these scarce resources, and may not behave as the central place foraging theory suggests (Whitford, 1978a; Whitford and Jackson, 2007).

Pogonomyrmex rugosus seed harvester ants, which utilized trunk trails when foraging for seeds, foraged as individuals when colonies switched from seeds to emerging grass cicadas (Whitford and Jackson, 2007). While species of seed harvesting ants such as *Pogonomyrmex rugosus* utilize trunk trails to exploit rich seed patches, they retain the flexibility to forage as individuals when collecting a scattered resource such as emerging grass cicadas.

While most seed-harvester ants use an individual foraging strategy when seed resources are sparse and dispersed, only a few species appear to use group foraging strategies when seed resources are abundant and clumped (Whitford and Bryant, 1979). Why don't all seed harvesters switch to group foraging when seeds are abundant? Several studies of foraging behavior in *Pogonomyrmex* spp. have focused on the central place foraging theory to explain food choice and foraging behavior. The central place foraging theory has mixed success when applied to seed selection in harvester ants (Morehead and Feener, 1998). While colonies of ants forage from a central place, smaller colonies need a smaller area to meet colony needs but larger colonies travel further but expend less time and effort because trunk trails locate rich resources (Dornhaus et al., 2012). In order to test these ideas, we collected data on colony sizes, worker sizes, and foraging strategies from the published literature. We hypothesize that colony size may be the factor that determines the foraging strategies that might be employed by a seed harvesting species. In addition, foraging strategy may, in part, be determined by the size range of worker-foragers. Here we review the published literature on foraging behaviors in seed harvesting ants and test hypotheses concerning colony size, body size, and dominant foraging strategy.

2. Methods

Data on worker ant size, colony size, and main foraging type in desert harvester ants were collected from the literature. Two dimensions of worker ant size were analyzed, the maximum length of a worker ant and its average or mid-range length. The worker ant mid-range length was calculated from the worker ant size range, and was used in data analysis when the worker ant average length was missing. The measure of colony size was taken as the maximum number of worker ants per nest because most ants within a colony are worker ants. Seed-harvesting ants included in Table 1 were so classified by Bolton (1995). Table 1 contains records on ants for which data on the main foraging type and on at least one additional parameter exist, i.e., worker ant size and/or colony size.

We examined the relationship in species of harvester ants between worker ant size and foraging type, or between colony size and foraging type using Wilcoxon-Mann-Whitney tests (Siegel and Castellan, 1988). The parameters used in these tests were: n_T - the number of species of trunk trail foraging ants or group foraging ants in the sample; W_T - the sum of ranks of species of trunk trail foraging ants or group foraging ants in the sample; n_I - the number of species of individual foraging ants in the sample; W_I - the sum of ranks of species of individual foraging ants in the sample; and N - the total number of ant species in the sample. In the case of the sample of ants from all genera mentioned in Table 1, tests were performed for large samples, in which the Z value was calculated according to the equation:

$$Z = \frac{W_T \pm 0.5 - \left[\frac{n_T(N+1)}{2}\right]}{\sqrt{n_T\, n_I\, (N+1)/12}}$$

The p-values were obtained from a Z table. The value of W_I is not mentioned in the computation of the Z value, since this Z test checks certain parameters of trunk-trail foraging ants or group foraging ants. In the case of separate samples of ants from different specific genera, the following was done: for ants of the genera *Aphaenogaster*, *Messor*, *Monomorium*, and *Pheidole*, the samples did not contain enough data to carry out this test, and therefore, no such test was performed. For ants of the genus *Pogonomyrmex*, tests for large samples were performed as described above. In order to determine whether any correlation exists between each of the above measurements of ant size and the above measurement of colony size, Spearman's rank correlation tests were performed (Siegel and Castellan, 1988).

3. Results

The following results were obtained by the Wilcoxon-Mann-Whitney tests for ants from all genera mentioned in Table 1: The maximum length of a worker ant in a trunk trail foraging ant species or group foraging ant species is significantly smaller than that of individual foraging ants ($n_T = 15$; $W_T = 250.5$; $n_I = 26$; $W_I = 643$; $N_I = 41$; $Z = -1.759$; $p < 0.040$). The average or mid-range length of a worker ant in trunk trail foraging ant species or group foraging ant species is very significantly smaller than in individual foraging ants ($n_T = 17$; $W_T = 249$; $n_I = 30$; $W_I = 879$; $N = 47$; $Z = -3.531$; $p < 0.001$). The maximum number of worker ants per nest in trunk trail foraging ants or group foraging ants is very significantly larger than in individual foraging ants ($n_T = l\,1$; $W_T = 320$; $n_I = 24$; $W_I = 310$; $N = 35$; $Z = 4.317$; $p < 0.001$).

The Wilcoxon-Mann-Whitney tests for ants of the genus *Pogonomyrmex* revealed that the maximum length of a worker ant in trunk-trail foraging ant species is significantly larger than in individual foraging ant species ($n_T = 2$; $W_T = l\,1$; $n_I = 21$; $WI = 235$; $N = 23$; $Z = l\,0.800$; $p = 0.03$). The average or mid-range length of a worker ant in trunk trail foraging ant species is also significantly larger than in individual foraging ant species ($n_T = 2$; $W_T = 49$; $n_I = 24$; $W_I = 302$; $N = 26$; $Z = 2.165$; $p < 0.0154$). Furthermore, the maximum number of worker ants per nest in trunk-trail foraging ant species is significantly larger than in individual foraging ant species ($n_T = 2$; $W_T = 41$; $n_I = 19$; $W_I = 190$; $N = 21$; $Z = 2.336$; $p < 0.01$).

A Spearman rank correlation test for a possible relation between the maximal length of a worker ant and the number of worker ants per nest demonstrated that there is no correlation between these parameters ($N = 30$; $\Sigma\ d^2_i = 4021$; $r_s = 0.1054$; $\alpha > 0.25$). A Spearman rank correlation test for a possible relation between the average or mid-range length of a worker ant and the number of worker ants per nest demonstrated that there is no correlation between these parameters ($N = 33$; $\Sigma\ d^2_i = 6287.5$; $rs = -0.0507$; $\alpha > 0.25$).

4. Discussion

Theoretical models that examined the relationship between colony size and recruitment strategies in ants concluded that ant colonies of a certain size should use only one recruitment method and always the same method, rather than a mixture of two or more (Planque et al., 2010). Desert seed harvester ants evolved in unpredictable environments where seed resources may vary greatly among years. Desert seed harvesting ants need flexible recruitment