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Colony Budding and its Effects on Food Allocation in the Highly Polygynous Ant, *Monomorium pharaonis*

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Abstract

To advance our understanding of the causes and the consequences of budding (colony multiplication by fragmentation of main nests), we investigated nest movement in the facultatively polydomous Pharaoh ant, *Monomorium pharaonis*. Demographic data revealed that Pharaoh ants are highly polygynous and have a relatively low worker to queen ratio of 12.86. Budding experiments demonstrated that the number of available bud nests has a significant effect on colony fragmentation and increasing the number of bud nests resulted in smaller colony fragments. The overall distribution among bud nests was uneven, even though there was no evidence that the different life stages and castes partitioned unevenly among the bud nests and the analysis of individual colonies revealed no evidence of an uneven split in any of the colonies. This demonstrates that Pharaoh ants have the ability to exert social control over colony size and caste proportions during budding, which may contribute to their success as an invasive ant. The intensity of nest disturbance had a significant effect on whether or not the ants migrated into bud nests. Major disturbance resulted in the ants abandoning the source nest and migrating to bud nests and minor disturbance did not stimulate the ants to abandon the source nest. The results of the successive budding experiment which allowed the ants the opportunity to bud into progressively smaller nest fragments demonstrate that Pharaoh ants maintain a preferred minimum group size of 469 ± 28 individuals. Food allocation experiments utilizing protein marking revealed that nest fragmentation in Pharaoh ants has no negative impact on intracolony food distribution. Overall, our results suggest that nest units in the Pharaoh ant behave like cooperative, rather than competitive, entities. Such cooperation is most likely facilitated by the fact that individuals in all bud nests are genetically related, remain in close proximity to each other, and may continue to exchange individuals after budding.

Introduction

The movement of animals is a fundamental feature of both solitary and social organisms and a crucial component of almost all ecological and evolutionary process. Social organisms, such as ants and bees, are well known to relocate (Franks et al. 2002) and movement often entails the relocation of whole colonies. In fact, it appears that periodic nest relocation is an integral part of the life history of many social organisms and vital to the colony's survival, growth, and reproduction. Ant colonies have been traditionally viewed as static; however, it is becoming increasingly apparent that they are not spatially fixed and are subject to frequent movement (Smallwood & Culver 1979; Tsuji 1988; Gordon 1992;

Banschbach & Herbers 1999; Gibb & Hochuli 2003; McGlynn et al. 2004; Heller & Gordon 2006). Nest relocation is not a spurious event, but a highly coordinated process involving complex decisions made at the colony level (Hölldobler & Wilson 1990; Mallon et al. 2001; Pratt et al. 2002). In many ant species, nest movement is mediated by stereotyped techniques of communication and transportation that may be linked to chemical (Droual 1983) or behavioral signals (Pratt et al. 2002).

Nest movement is a disruptive and costly strategy and involves a balance between the potential costs and benefits of relocation (Tsuji 1988). Costs may include loss of foraging time, energy expended locating and constructing a new nest site, competition for space and food resources with local species (Traniello & Levings 1986; McGlynn et al. 2004), and exposure to predation during migration (Brown 1999; Pezon et al. 2005). Despite the costs, nest movement is often necessary for the survival of the colony. In many cases, nest movement functions as a reproductive strategy (Hölldobler & Wilson 1990; Pedersen & Boomsma 1999). In other cases, ants move their nests to avoid predation (Droual 1984; Yamaguchi 1992; McGlynn et al. 2004; Dahbi et al. 2008), to escape from unfavorable environmental conditions (Yamaguchi 1992; Gibb & Hochuli 2003), to increase access to food (McGlynn et al. 2004), to maximize foraging efficiency (Holway & Case 2000), or to avoid overcrowding (Gobin et al. 1998). In other cases, nest movement may be a seasonal phenomenon, where the colony undergoes an annual fission–fusion cycle (i.e. seasonal polydomy; Herbers 1986; Traniello & Levings 1986; Heller & Gordon 2006; Buczkowski & Bennett 2008).

Nest movement is frequently observed in highly polygynous and polydomous tramp ants, especially those that make little investment in nest construction (e.g. Argentine ants, Holway & Case 2000; Heller & Gordon 2006; odorous house ants, Smallwood & Culver 1979; Buczkowski & Bennett 2006, 2008; and Pharaoh ants, Edwards 1986). Such species are characterized by highly fluid colony structure and high propensity to bud whereby a reproductively competent colony fragment migrates to a new location to establish a new nest. Newly budded nests often retain contact with the natal nest and form large polydomous colonies composed of numerous nests (Traniello & Levings 1986; Heller & Gordon 2006). Budding may serve both as a reproductive strategy or simply a response to environmental stress. As a reproductive strategy, budding is a highly effective form of local dispersal that dramatically increases the probability of successful colony founding because new colonies are created independently of gyne production and may be initiated at any time. Budding may also be a response to environmental stress and colony fragmentation may occur due to a wide range of biotic and abiotic factors; however, only limited information exists on the factors responsible for inducing the budding behavior. Possible factors include overcrowding, seasonal changes in weather, physical disturbance, dietary change (depletion or discovery of new resource), or chemical disturbance (Buczkowski et al. 2005).

To advance our understanding of the causes and the consequences of budding we assessed social fragmentation in the facultatively polydomous Pharaoh ant, *Monomorium pharaonis* (L.). The Pharaoh ant is a ubiquitous introduced invasive species that exhibits several tramp ant characteristics such as generalist diet, extreme polygyny, extensive polydomy, unicoloniality, colony reproduction by budding, and close association with humans (Passera 1994). In their introduced range, especially temperate climates, Pharaoh ants are synanthropic and dependent on humans for food and shelter. Nests are exclusively indoors and are frequently established in and around household items (e.g. between sheets of paper, under objects) and are repeatedly subjected to physical disturbance by humans – a factor that promotes budding and is thought to facilitate the spread of Pharaoh ants.

We present two experiments designed to investigate nest movement in Pharaoh ants. Our first objective was to examine budding from a single source nest into multiple bud nests and to determine the effect of increasing the number of bud nests on the fragmentation pattern and the resulting colony social structure. In ants, colony fractionation can result in queenless or queenright nests (Herbers 1990; Snyder & Herbers 1991) which may have important consequences for colony reproductive dynamics and social evolution (Trivers & Hare 1976). The specific questions we sought to answer were: (1) will all, or only some, available nests be occupied, (2) will individuals distribute themselves evenly or unevenly among the available bud nests, and (3) will the original (i.e. source nest) egg:larva:pupa:worker:queen ratios be maintained during migration? Second, we used protein marking to test for possible changes in food allocation resulting from budding events by comparing the pattern of food distribution in intact nests (i.e. before budding) vs. fragmented nests (i.e. after budding).

Materials and Methods

Stock Colonies and Experimental Arenas

Stock colonies of Pharaoh ants, *M. pharaonis*, that originated from USDA–ARS in Gainesville, Florida, USA, were maintained at constant temperature and humidity in an environmentally controlled rearing and testing room (25 ± 1°C, 65% ± 10% RH) for several years. Colonies were reared in 38 × 50 cm Fluon™-coated trays (DuPont Polymers, Wilmington, DE, USA) on a regular diet of 10% sucrose, crickets, peanut oil, boiled egg yolk, and artificial diet (Bhatkar & Whitcomb 1970). Each colony was provided with six nests composed of plastic petri dishes (64 cm^2) filled with plaster. The outside of the nests was spray painted black to provide darkness preferred by the ants. The Pharaoh ant is a unicolonial species (Passera 1994) and we detected no aggression between any of the colonies.

Experimental arenas consisted of 100 × 100 × 5 cm high plastic, Fluon™-coated trays. Each experimental arena was provisioned with empty bud nests for colonization by the migrating ants. Budding from a single source nest into two, three, or four empty bud nests was examined. All bud nests were made exactly the same to make them equally attractive, were identical in size and construction to the source nests, and were not previously occupied by ants and thus did not contain any species- and/or colony-specific chemicals that might be attractive to the ants. All source and buds nests were kept unmoistened throughout the test to rule out nesting preferences due to variations in humidity. A glass vial containing drinking water was placed next to each empty nest. The empty nests were always arranged equidistant from each other and from the source nest in the center of the tray. Thus, two nests were placed in opposite corners of the tray, three nests in the corners of an equilateral triangle fitted within the tray, and four nests in the corners of the tray. In addition, each test arena was provisioned with 10% sugar water placed in the center of the tray. For all experiments, source nests were randomly selected from larger stock colonies.

Nest Demographics

The Pharaoh ant is a widespread invasive pest species, yet no information exists on the demographics of Pharaoh ant colonies, an essential prerequisite for understanding colony ergonomics, population dynamics, and social evolution. To address this gap we censused all life stages and castes including eggs, larvae (all instars), pupae (worker and sexual), workers, and queens (alate and dealate) at the nest level. No males have ever been observed in our colonies. We report demographic data from all nests utilized in this study (n = 31). All nests were randomly selected from stock colonies raised according to a standard protocol (see above).

Effect of Nest Number and Disturbance Intensity on Social Fragmentation

Budding from a single source nest into two, three, or four bud nests was examined using the experimental set-up and methods described above. Briefly, the source nest was placed in the center of the experimental arena and surrounded by bud nests. The nest covering was removed from the source nest to stimulate migration. Removing the nest covering simulates a disturbance that Pharaoh ants might typically experience in the urban environment due to their close association with humans and opportunistic nesting habits. The resulting colonization pattern was examined 24 h later and all life stages and castes were counted in all occupied nests. Preliminary experiments indicated that 24 h allowed sufficient time for the ants to settle down into the chosen bud nests and little ant exchange was observed among the nests after the initial 24 h. Five replications were performed for each test.

The second objective was to examine the effect of intensity of disturbance on the extent of social fragmentation. Budding from a single source nest into four empty nests was examined following minor or major disturbance. Minor disturbance consisted of removing the source nest from its familiar territory (stock colony) and placing it in a new, unfamiliar territory (experimental arena) without removing the nest lid. Minor disturbance simulates a scenario where colony fragments are inadvertently transported by humans to new locations. Indeed, human-mediated long-distance jump dispersal is thought to be a key factor in the dispersal of Pharaoh ants and other invasive ant species (e.g. invasive Argentine ants, Suarez et al. 2000). The objective was to determine whether the presence of empty nests and the novelty of unfamiliar territory alone were sufficient to cause social fragmentation. Major disturbance consisted of placing the nest in the test arena and removing the nest lid which immediately stimulated the ants to seek a more suitable refuge. In all tests, the ants were allowed 24 h to explore the arena and colonize the empty nests. Subsequently, all life stages and castes were counted in the source and bud nests. Five replications were performed for each level of disturbance.

Successive Budding and Colony Social Structure

We hypothesized that budding in Pharaoh ants might stop once the source nest divides into fragments of some preferred minimum size. The objective was to determine a point at which nests stop budding and remain as a single cohesive social unit. In a two-part experiment, we examined the extent to which social fragmentation may continue when the colony is given the opportunity to undergo successive budding events. We first examined budding from a single source nest to four bud nests as described above (n = 5). Subsequently, each nest fragment was again given the opportunity to bud by placing it in a new arena with four empty nests. The nests were once again disturbed by removing the nest covering and the resulting colonization pattern was examined 24 h later.

Food Distribution between Nests in Intact and Budded Colonies

To test for possible changes in food allocation resulting from budding events we compared the pattern of food distribution in intact nests (i.e. before budding) vs. fragmented nests (i.e. after budding). Intact nests were selected at random from stock colonies and fragmented nests were fragments of source nests that were first allowed to bud into four nests (as above). To track the distribution of food to the various castes and developmental stages (larvae, workers, and queens) we utilized protein marking and double-antibody sandwich enzyme-linked immunosorbent assay (DAS–ELISA). In both tests, the ants were starved for 24 h and were subsequently fed 10% sucrose:water solution containing 0.5 mg technical grade rabbit immunoglobulin (IgG) protein (Sigma Chemical Co., St. Louis, MO, USA) for 1 h. We randomly sampled 100 workers, 20 queens, and 20 larvae from intact nests or 25 workers, 10 queens, and 10 larvae from each of the four bud nests 24 h later to determine the amount of protein marker acquired by the ants in each nest. All individuals were frozen in individual tubes and later analyzed by DAS–ELISA. Three replicates were performed for each test. DAS–ELISA was performed on individual ant samples using previously described techniques (Buczkowski & Bennett 2006).

Statistical Analysis

All data analyses were performed using SAS 8.1 statistical software (SAS Institute 2002). For budding experiments, we created a mixed model (PROC GLM) with caste nested within subunit (bud nest) as fixed effects and colony and subunit nested within colony as random effects. This tested the null hypothesis that the ants split evenly among the bud nests. For immunomarking experiments, the samples were scored positive for the presence of the protein marker if the ELISA optical density value exceeded the mean negative control value by three standard deviations (Hagler 1997). Based on results of preliminary tests, the value for the positive-negative optical density threshold was determined to be 0.10. The percentage of samples testing positive for the IgG protein was tabulated by first calculating the percent of individuals testing positive within a replicate and then averaging across replicates. Percentage data were arcsine transformed to stabilize the variance. ANOVA tests were conducted to determine the significance of nest fragmentation on the spread of the marker. This was accomplished by using the PROC GLM procedure.

Results

Nest Demographics

A census of 31 nests revealed an average of 421 ± 15 eggs (range 307–613), 175 ± 9 larvae (range 115–304), 329 ± 18 pupae (range 154–513), 2185 ± 49 workers (range 1605–2717), and 170 ± 8 queens (range 105–251). On average, each nest contained a total of 3280 ± 66 individuals (range 2537–3958). The ratio of eggs:larvae:pupae:workers:queens (standardized to the number of queens) was 2.48:1.03:1.94:12.86:1.00. On average, a nest comprised 12.8% eggs, 5.3% larvae, 10.0% pupae, 66.6% workers, and 5.2% queens.

Effect of Nest Number and Disturbance Intensity on Social Fragmentation

Pharaoh ants readily migrated from disturbed source nests and colonized nearby undisturbed bud nests. The ants always completely vacated the source nests and colonized all available bud nests (Fig. 1a–c). When the ants migrated from a single source nest into two bud nests (Fig. 1a), the overall distribution among the bud nests was uneven (df = 4, F = 3.17, p = 0.027; analysis of subunit nested within the

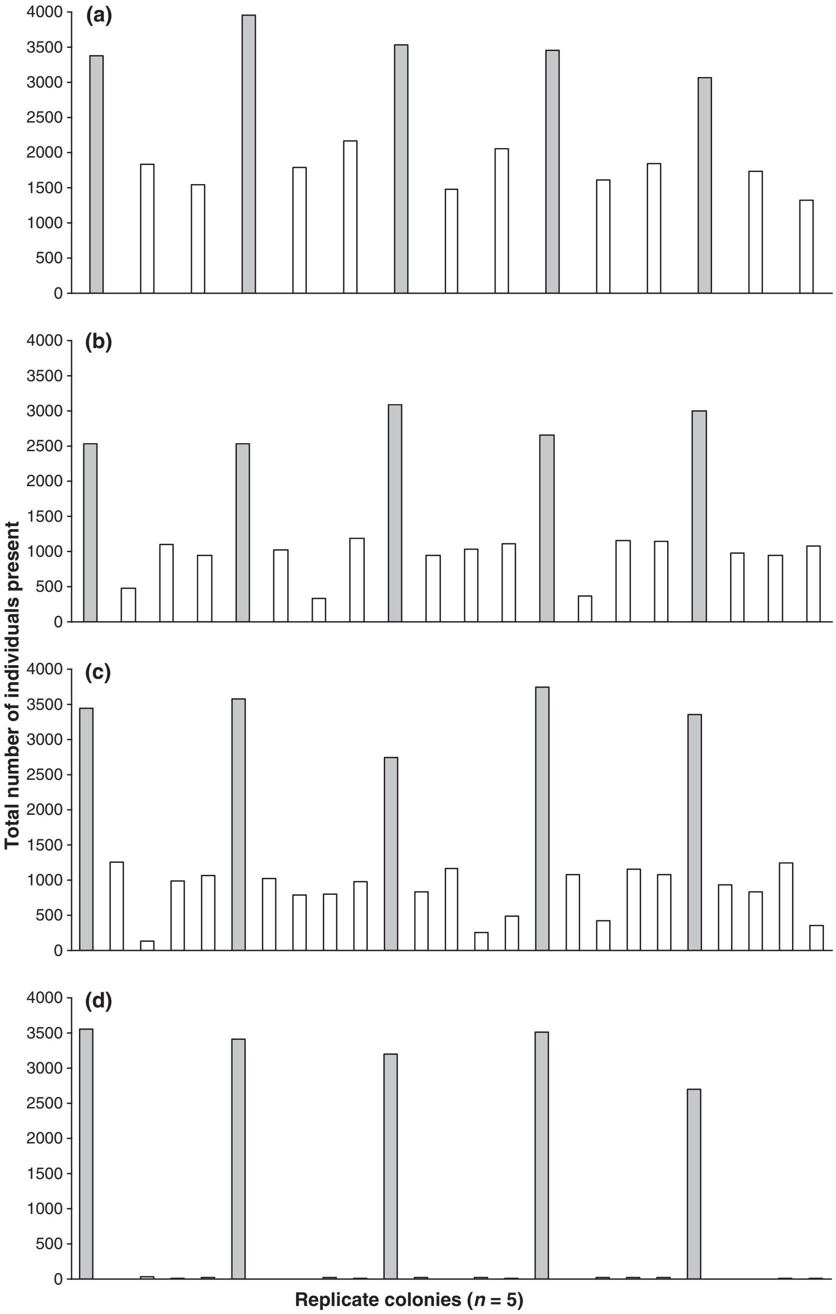

Fig. 1: Effect of nest number, nest spatial position, and disturbance intensity on social fragmentation in Pharaoh ants. The results of budding from a single source nest into (a) two bud nests, (b) three bud nests, (c) four bud nests (major disturbance), and (d) four bud nests (minor disturbance) are presented as the total number of ants. Shaded bars indicate the total number of individuals (summed over castes) in source colonies (n = 5) and open bars indicate the total number of individuals in bud nests.

colony). However, our analysis also indicated no evidence that the castes partitioned unevenly among the bud nests (df = 8, F = 0.88, p = 0.484) and the analysis of individual colonies revealed no evidence of an uneven split in any of the colonies when each colony was modeled separately with caste as a fixed effect and subunit as a random effect. The individual models did not reject the null hypothesis of an even split. This is due to limited power: with a sample size of 5 for each level of subunit and a standard deviation of around 250, the power is only 50% to detect a 400 size difference. Furthermore, budding was approximately even in all five colonies with the colonies splitting in the following percentage ratios: 46/54, 55/45, 58/42, 53/47, and 43/57. When the ants were offered three bud nests (Fig. 1b), the overall distribution among the bud nests was again uneven (df = 8, F = 3.37, p = 0.0038). As with two bud nests, our analysis indicated no evidence that the castes partitioned unevenly among the bud nests (df = 8, F = 1.55, p = 0.164) and the analysis of individual colonies revealed no evidence of an uneven split. None of the individual models rejected the null hypothesis of an even split (due to limited power) and the split among the bud nests was relatively even in two out of five colonies (31/34/36 and 32/33/36). When four bud nests were available (Fig. 1c), the overall distribution was again uneven (df = 12, F = 4.44, $p < 0.0001$). Once again, our analysis indicated no evidence that the castes partitioned unevenly among the bud nests (df = 12, F = 0.70, p = 0.749) and the analysis of individual colonies revealed no evidence of an uneven split.

The intensity of nest disturbance had a significant effect on whether or not the ants abandoned the source nest and migrated into bud nests (Fig. 1c, d). Major disturbance resulted in the ants abandoning the source nest and migrating to bud nests (Fig. 1c). The ants completely vacated the source nest and colonized all four bud nests. Minor disturbance, however, did not stimulate the ants to abandon the source nest and a great majority of individuals remained in the source nest (Fig. 1d). Of the 3295 ± 165 individuals that initially occupied the source nests, only 7.8 ± 2.1 (0.4%) workers were found in bud nests, perhaps as scouts, rather than permanent residents. All brood and queens remained in the source nests.

Successive Budding and Colony Social Structure

The source nests contained an average of 3374 ± 170 individuals (n = 5). During initial budding (i.e. a single source nest provided with four bud nests) each of the five source nests fragmented into four bud nests.

During successive budding, each fragment of the source nest was again provided with four bud nests, yet each fragment only split into an average of 1.8 ± 0.1 nests and the ants colonized 36 of 80 (45%) of available bud nests. During successive budding 30% of the colony fragments remained as a single colony fragment, 60% split into two bud nests, and 10% split into three bud nests. The size of the colony fragment had a significant effect on the probability of any subsequent budding (df = 4, t = 2.03, p = 0.012) with smaller colony fragments remaining intact and larger colony fragments being more likely to undergo subsequent budding. The results of the successive budding experiment suggest that the preferred minimum colony size for Pharaoh ants is 469 ± 28 individuals, which included 61 ± 5 eggs, 29 ± 3 larvae, 53 ± 6 pupae, 296 ± 19 workers, and 29 ± 3 queens. This is equivalent to 13.0% eggs, 6.2% larvae, 11.03% pupae, 63.2% workers, and 6.2% queens.

Food Distribution in Intact and Fragmented Colonies

Nest fragmentation had no negative impact on intracolony food distribution to larvae, workers, or queens. In fact, the percentage of ants testing positive for the protein marker was often higher in bud nests relative to intact nests. Intact nests contained 213 ± 32 larvae, 2198 ± 114 workers, and 184 ± 32 queens. Eight hours after feeding on protein-marked sucrose, 67 ± 4% of larvae, 76 ± 4% of workers, and 83 ± 4% of queens in intact nests tested positive for the marker. Bud nests contained 40 ± 4 larvae, 72 ± 4% of which tested positive. The percentage of larvae testing positive in intact nests was not significantly different from the percentage of larvae testing positive in bud nests (df = 4, t = −0.84, p = 0.449). Bud nest also contained 579 ± 11 workers, 94 ± 3% of which tested positive and 50 ± 5 queens, 88 ± 7% of which tested positive. The percentage of workers testing positive in bud nests was significantly higher than the percentage of workers testing positive in intact nests (df = 4, t = −4.65, p = 0.010), but the percentage of queens was not (df = 4, t = −0.84, p = 0.448).

Discussion

In this study, Pharaoh ant nests were highly polygynous with an average of 170 ± 8 queens per nest and the queens comprised 5.2% of all individuals at the nest level. The nests also contained 2185 ± 49 workers or 66.6% of all individuals. Consequently, the nests had a relatively low worker to queen ratio of 12.86. In social insect societies, high queen number is often associated with major changes in life-history traits, including the loss of mating flights and nest formation via budding (Keller 1995). Indeed, Pharaoh ant colonies proliferate by budding without mating flights and such traits characterize most invasive, unicolonial tramp ants (Passera 1994).

The Pharaoh ant is an invasive cosmopolitan pest species and in temperate regions is exclusively restricted to living in human-built structures. As a result, the close association with humans and dependence on humans for food and nesting sites may drive the evolution of Pharaoh ant colony social structure (i.e. high degree of polygyny) and spatial structure (i.e. high degree of polydomy). Specifically, nest site limitation, frequent nest site disturbance, and fluctuations in food availability may have a strong effect on the evolution of social and/or spatial structure. Empirical studies of intraspecific variation in colony queen number have linked nest site limitation, high nest density, and resource limitation (primarily food) to high queen numbers (Seppä et al. 1995; Ross et al. 1996; Pedersen & Boomsma 1999). Experimental studies of polygynous ant populations have also demonstrated plasticity in queen number in response to habitat saturation (Herbers 1986) and food availability (Herbers & Banschbach 1999). Further, flexibility in queen number and social structure may facilitate the invasion of new habitats, especially when small propagules are transported by human-mediated jump dispersal into uninvaded areas (Hee et al. 2000; Eow et al. 2004). Comparisons among free-living field colonies, free-living indoor colonies, and other captive laboratory colonies will be necessary to determine whether the observed worker to queen ratio and the high degree of polygyny are representative of all Pharaoh ant populations and the degree to which environmental factors imposed by humans dictate social colony structure in Pharaoh ants.

A notable characteristic of tramp species is colony reproduction by budding. In our study, Pharaoh ants were forced to migrate by disturbing the physical integrity of the nests. The number of available bud nests had a significant effect on colony fragmentation and increasing the number of bud nests resulted in smaller colony fragments. While the results of statistical tests indicate that the overall distribution among the bud nests was uneven (for two, three, or four bud nests), the data presented in Fig. 1 indicate that colony budding was fairly even in many replicates. Further, our analysis also indicated no evidence that the castes partitioned unevenly among the bud nests and the analysis of individual colonies revealed no evidence of an uneven split in any of the colonies. Such discrepancy indicates that the practical importance of the statistical conclusion regarding the evenness of budding may be low and true biologic meaning may be subject to individual interpretation.

The intensity of nest disturbance had a significant effect on whether or not the ants abandoned the source nest and migrated into bud nests. Minor disturbance did not stimulate the ants to abandon the nest and a great majority of individuals remained in the nest. This suggests that the presence of empty nests and the novelty of unfamiliar territory alone are not sufficient to induce budding and also suggests lack of overcrowding in the source nests. The ants explored the test arena and the empty nests, possibly to mark the novel area with species- and/or colony-specific pheromones, but did not colonize bud nests, suggesting high nest fidelity in the absence of disturbance. In contrast, major disturbance resulted in the ants abandoning the source nest and migrating to bud nests. Immediately following disturbance, the ants established pheromone trails from the source nest to the bud nests as well as among the bud nests and continued to exchange individuals among the nests until the source nest was completely vacant. This activity was especially intense during the first 1–3 h when the brood was being relocated by the workers. Subsequently, ant activity tapered off and little movement was observed after the initial 24 h, suggesting that the ants had settled into their chosen nests. These results suggest that physical nest disturbance may be a major factor driving budding in Pharaoh ants.

The results of the successive budding experiment which allowed the ants the opportunity to bud into progressively smaller nest fragments demonstrate that Pharaoh ants maintain a preferred minimum group size and stop budding once that size is reached. Our data suggest that the preferred minimum group size for Pharaoh ants is 469 ± 28 individuals, which includes approx. 300 workers and 30 queens (10:1 ratio). Ants maintain an optimal colony size for a number of reasons including improved defense against predators (Holway & Case 2001; Walters & Mackay 2005), increased foraging success (Holway & Case 2001; Buczkowski & Bennett 2008), greater likelihood of successful colony establishment (Hee et al. 2000), and increased productivity of new workers and reproductives (Walin et al. 2001; Sorvari & Hakkarainen 2007). Future experiments should focus on whether the preferred group size reported here is indeed optimal for colony survival, productivity, and foraging success by comparing it to smaller propagules.

The polydomous colony structure that results from social fragmentation due to nest budding normally provides the colony with a number of ecological and evolutionary advantages (reviewed in Debout et al. 2007); however, budding also creates a new level of complexity (i.e. a substantial increase in polydomy) and thus creates additional challenges for the colony. One major challenge is food allocation among spatially separated nests, and in extreme cases, resource competition between the mother nest and the bud nests (Walin et al. 2001; Buczkowski & Bennett 2006). Budding entails partitioning of the worker force which may result in uneven food distribution among the nests depending on the social composition of nests and the spatial arrangement of nests relative to the food source. In the current study, however, we detected no major disproportion in food allocation among the spatially separated nests. In fact, budding resulted in enhanced food distribution, suggesting that food distribution may be more rapid and more complete in smaller colonies. Previous studies reported similar results with respect to reproductive allocation in ants, whereby nest productivity increased with nest density, due to local resource enhancement (Walin et al. 2001; Denis et al. 2007). Results of the food distribution experiment suggest that nest units in polydomous colonies of *M. pharaonis* behave like cooperative, rather than competitive, entities. Such cooperation is most likely facilitated by the fact that individuals in all bud nests are genetically related, remain in close proximity to each other, and may continue to exchange individuals after budding (Elias et al. 2005). What remains to be tested is the degree to which individuals are exchanged among nests after budding and factors that promote such exchange, nest fidelity of individual workers to determine whether workers consistently deliver harvested resources to their own nests or other bud nests, and the effect of food distribution on the spatial pattern of nests and vice versa.

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