Behav Ecol Sociobiol (1992) 31:417–427

Behavioral Ecology and Sociobiology

How colony growth affects forager intrusion between neighboring harvester ant colonies

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Received September 26, 1991 / Accepted July 8, 1992

Summary. Colonies of the harvester ant, *Pogonomyrmex barbatus*, adjust the direction and length of foraging trails in response to the foraging behavior of their conspecific neighbors. In the absence of any interaction with its neighbor, a mature colony expands its foraging range at a rate of 0.85 ± 0.15 m per day. Exclusion experiments show that if a colony is prevented from using its foraging trails, the neighbors of that colony will enter its foraging range within 10 days. Exclusion experiments were performed with three age classes of colonies: young (1 year old), intermediate (3–4 years old), and old (5 years old or more). Colonies 3–4 years old are most likely to expand foraging ranges, and to retain newly-gained areas. To examine the relation of colony age (in years) and colony size (in numbers of workers), colonies of known age were excavated. Colonies increase greatly in size in years 3 and 4. Foraging area may be of greater current or prospective value for younger, smaller, quickly growing colonies than for older, larger ones of stable size.

Introduction

In many animals, spacing patterns are continually adjusted by the behavioral interactions of neighbors. Two distinct, though not exclusive, factors may determine the outcome of territorial conflict. The first is the ability of each participant to defend territory, or "resource holding potential" (Maynard Smith and Parker 1976; Petrie 1984; Reichert 1978). The second is differences between participants in the value of contested resources, or "value asymmetry" (Beletsky and Orians 1987, 1989).

Colonies of ants interact at territory boundaries (Greenslade 1971; Majer 1976; Hölldobler 1976, 1978, 1981; Traniello and Levings 1986), which may be marked by colony-specific chemicals (Traniello 1989). Some studies of ants show that in contests between colonies of different size, the larger or more threatening one tends to win, indicating the importance of resource holding potential (Adams 1990; Hölldobler 1981). Theoretical work and reviews of ant territoriality tend to emphasize the role of resource holding potential (e.g. Hölldobler 1983; Hölldobler and Lumsden 1980).

Here I investigate how colony size affects the interactions of foragers of neighboring harvester ant colonies. Colony growth may affect a colony's need for food (e.g. Engen and Stenseth 1989). Hölldobler (1978) suggested that in the ant *Oecophylla longinoda*, younger, growing colonies recruited more ants to contested foraging areas than did older, larger colonies. In many species of ants, territories are held for years (Hölldobler and Lumsden 1980), and foraging areas may be valued prospectively as well as in the immediate short term (Stamps and Tollestrup 1984). A foraging area may be more valuable for young, growing colonies, when a colony may obtain a foraging area to be used for many years, than for older colonies with more stable territories.

The foraging area of a harvester ant colony is a star-shaped region (Fig. 1). Foragers travel to and from the nest on foraging trails up to 40 m long. Foraging distances vary, depending in part on food availability (Rissing 1988). *Pogonomyrmex barbatus* colonies sometimes establish "trunk trails", permanent, cleared tracks in the vegetation leading from the nest to the foraging area (Hölldobler 1976), as well as other habitual trails, across bare soil, which are not apparent when not in use by foragers (Gordon 1991). Each day a colony chooses which of its habitual tracks will be used to channel foragers out to the area in which they will search for food (Gordon 1991). Encounters between neighboring colonies are likely to occur at ends of trails. Ants distinguish workers of neighboring colonies from those of more distant ones (Gordon 1989a); it appears that foragers learn the colony-specific odor of their neighbors.

Previous work on *P. barbatus* shows that the behavior of foragers in young, small colonies differs from that of foragers in old, large ones. A colony may live 15–20

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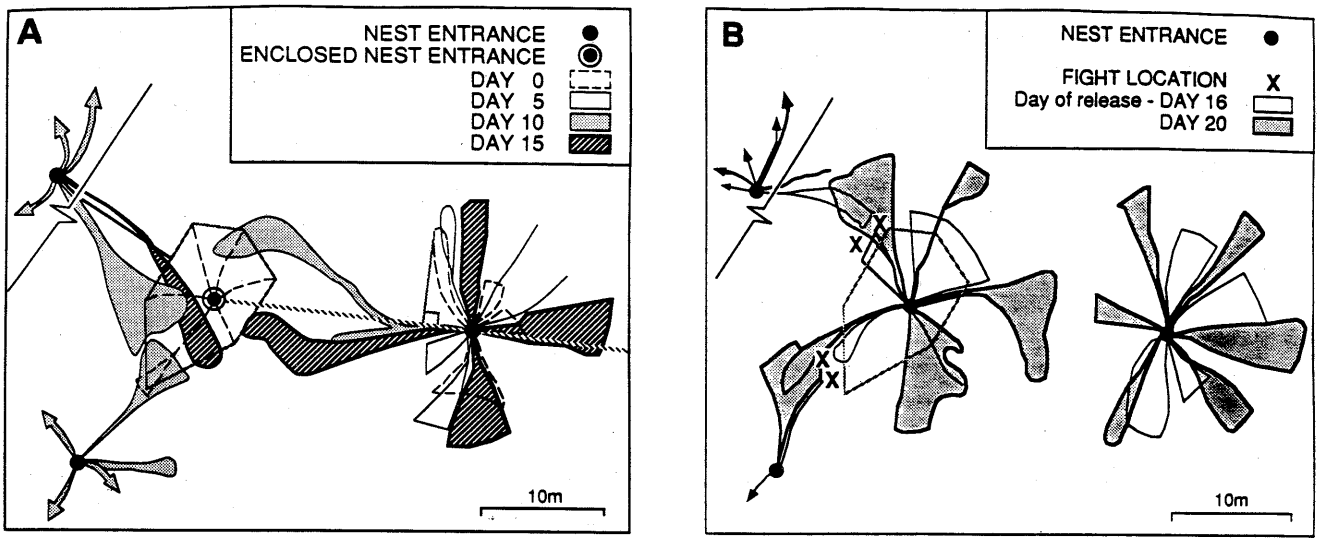

Fig. 1 A, B. Neighboring colonies forage toward an enclosed one. **A** The nest entrances and foraging trails of one enclosed colony and three neighboring ones, on day 0, the day before enclosure, and on days 5, 10 and 15 after enclosure. The enclosure, about 1 m in diameter, is shown as a *circle* surrounding the *nest entrance*. All the foraging trails of the enclosed colony on day 0 are shown surrounded by a large *polygon* connecting the endpoints of each trail; this polygon defines the foraging range of the enclosed colony. The projection of each trail onto the *line* connecting the nest entrance of one colony with that of its neighbor was used to derive a measure of encroachment; the sum of the base-lengths for triangles formed as shown for all trails was used as an index of encroachment (see text for details). On day 0, only the enclosed colony and its neighbor to the right were active. The *jagged line* at the upper left indicates that the neighboring colony at the upper left is further away from the enclosed one than shown. An *arrow* at the end of a foraging trail indicates that the trail continued further than shown. **B** The foraging trails of the same colonies on the day the enclosed colony was released (day 16) and 5 days later (day 20). Symbols as in Fig. 1 A unless indicated otherwise. The enclosure was removed, so the nest entrance of the enclosed colony is not surrounded by a circle. The *polygon* indicates the initial foraging range, as shown in Fig. 1 A. Fights were observed on day 16 only

years (Gordon 1991), as long as the queen survives to produce more workers. Both foraging behavior, and the boundaries of foraging ranges, appear to be more stable in colonies 5 years or older, than in younger ones (Gordon 1987, 1989 b). Which trails are used on a given day depends in part on previous interactions with conspecific neighbors (Gordon 1991). Foragers from 3 to 4-year-old colonies will repeatedly use trails that intersect with those of a neighbor if food is present at the point of intersection, even if this entails fighting. Foragers from old colonies (5 years old or more) only do so when food is more abundant. In the absence of abundant food, old colonies tend to avoid the use of trails that intersected those of an old neighbor on the previous day.

The finding that colonies over 5 are likely to avoid conflict with conspecific neighbors of the same age (Gordon 1991), raises the question whether any territorial pressure is exerted by an old colony on a neighbor of the same age. Are non-overlapping foraging areas maintained by encounters between neighboring colonies, and how frequently must interaction occur to be effective? To address these questions, harvester ant colonies were excluded from their foraging areas by enclosures that prevented foragers from leaving the colony or meeting neighboring colonies. In the first exclusion experiment, both enclosed colonies and their neighbors were at least 5 years old. To investigate variation among colonies, each replicate involved several neighbors of one enclosed colony. In other ant species (Adams 1990), as well as other insects (Alexander 1961; Davies 1978), the current occupant of a territory holds an advantage in a contest. To test whether this is true of *P. barbatus*, enclosures were removed and encounters between neighbors were allowed to resume.

The second exclusion experiment involved asymmetric contests between two colonies of different age, chosen from three age classes: young colonies (1 year old); intermediate (3–4 years old); and old colonies (more than 5 years old). If resource holding potential fully determines the outcome of territorial conflict, larger colonies should be more likely than smaller ones to gain and retain foraging areas.

Little is known about the relation of colony age (in years) and colony size (in total numbers of ants) in natural ant populations. Here, to measure how quickly young colonies increase in numbers of workers from one year to the next, colonies of known age were excavated.

Methods

The study was conducted near Rodeo, New Mexico, during the summers of 1989, 1990, and 1991, on an 8-ha study site containing about 250 colonies of *P. barbatus*.

Measures of colony age

Ages of colonies were determined from yearly maps and censuses of the study site (described in Gordon 1987, 1991). All *P. barbatus* colonies at the study site have been mapped each summer since 1985; records include deaths, relocations [which tend to occur during the summer (Gordon 1992)], and newly founded colonies. All colonies are labelled with an identifying number which persists in the same location from one year to the next. For all colonies less than 5 years old used in the foraging experiments, the colony had been mapped the first year it appeared as a small, apparently 1st year colony, and had been noted in the same place every year subsequently. All older colonies had been first noted as large, older colonies in 1985 and had been noted in the same place every year subsequently.

Enclosures

Colonies were prevented from foraging using enclosures made of aluminum flashing, about 2 m long and 1 m wide, buried at a depth of about 10 cm around the outer edge of the nest mounds. Joints were sealed with duct tape. This formed a more or less circular corral, about 0.8 m high and about 1 m in diameter, around each enclosed nest. When ants managed to dig out from under the enclosure, their nests were always re-enclosed by us the next day before foraging began. Enclosed colonies were fed 3–4 g mixed birdseed inside the enclosure on alternate days. Harvester ants store food inside the nest, and often there is no foraging activity for several days after an experiment in which a colony has been fed abundantly (pers. obs.). The amount fed to enclosed colonies was an estimate of the amount that would avert severe food deprivation, but not reduce the activity of enclosed colonies after they were released.

Maps of foraging trails

Maps of foraging trails were made using a grid of markers at 6.2-m intervals surrounding each enclosed colony and its neighbors. All nest entrances and foraging trails were mapped in the course of two visits per day to the region surrounding each enclosed colony, during the peak time of foraging. Trails were mapped by following the stream of foragers from the nest mound, and using graph paper marked with the location of the grid markers, the observer placed a line on the map corresponding to the path of the ants. A trail shown at any point on the map means that five or more ants were observed passing the corresponding point on the ground within 20 s. The end of the trail was recorded on the map indicating the place where no further ants were visible within 1 m during 10 s. Thus "foraging trail" as used here refers not to a cleared pathway on the ground, but to the area along which ants were observed to forage on a given day.

In 1990 (the third study of foraging behavior described below), foraging activity was generally low (possibly due to drought conditions), especially in 1-year-old colonies. Trails with insufficient foragers to meet the requirement that a trail contain at least five foragers passing any point on the trail in 20 s, but where there was a visible line of foragers travelling to and from the nest mound, were marked on the maps and included in the analysis of the foraging data for 1990.

Measures of foraging behavior

The extent to which one colony's trails were directed toward another colony was measured using an index of encroachment that includes both length and direction of foraging trails. To measure, for example, encroachment of colony A on colony B on a given day, I did the following. On that day's foraging trail map, I drew a straight line segment connecting the nest entrances of colony A and B. I then dropped a perpendicular line from the endpoint of each of colony A's foraging trails to the connecting line, forming a triangle (see Fig. 1 A). The base of the triangle is a vector projection of the trail; the hypotenuse is the trail itself. I found the length of the base, or projection, for each trail of colony A that was headed toward colony B. The longer the trail, or the more directly it heads toward colony B, the longer the projection. The index of encroachment for colony A on that day is the sum of the lengths of these projections for all trails headed toward colony B.

For the enclosure experiment using colonies of different age (study 3, below) two additional measures were used to measure how one colony directed its foraging toward another. The three measures were: (1) Index of encroachment, as above. (2) The proportion of trail length directed toward the neighbor. This proportion is a ratio; the numerator is the index of encroachment as above. The denominator is the sum of foraging directed toward the other colony, and foraging directed away from the other colony. The first component of the sum in the denominator is the index of encroachment, as above. The second is the same index, but of trails in the opposite direction: trails headed away from the other colony were projected onto an extension of the imaginary line connecting the nest entrances of the two colonies (shown extending from the colony on the right in Fig. 1 A), and these projections for all trails were summed. The proportion is thus Toward/Toward + Away. (3) Total length of foraging trails, the sum of the linear distances from the nest entrance to the endpoint of each foraging trail.

Studies of foraging behavior

1. Actively foraging neighbors (at least 5 years old). I mapped the foraging trails of seven pairs of neighboring, undisturbed colonies. All colonies were at least 5 years old. These maps were made in the course of another study (Gordon 1991). The purpose was to compare encroachment by one older colony on an older, active neighbor, with encroachment by an older colony on a neighbor that was experimentally enclosed; this is a control for experiment 2 described below. So as not to exaggerate the effects of enclosure, I sought to measure a situation when encroachment on an active colony seemed likely. To do this, I used unevenly paired colonies. One of the pair had larger numbers of foragers and foraged greater distances (details in Gordon 1991, pp 396–399). All seven pairs were mapped on day 1; I then compared the foraging behavior of each pair on this day with that of the same pair on another day, either 16 or 18 days later. I measured encroachment by the colony with greater numbers of foragers, toward that of the colony with smaller numbers of foragers.

2. Interactions of older neighbors: enclosure experiments. This enclosure experiment, done in 1989, involved 5 groups of colonies. Each group consisted of three or four neighboring colonies (nest entrances of adjacent colonies within 18 m), a total of 18 colonies. All but three were at least 5 years old; the remaining three were all unusually large 4-year-old colonies. In each group, one colony, located approximately in the center of the group, was enclosed. The trails of all colonies were mapped on the day before the enclosure was set up (day 0); on days 5, 10 and 15 during the period of enclosure; on the day of release (day 16) and on day 20. During the period of enclosure, of course, enclosed colonies had no foraging trails and were not mapped.

I measured the extent to which neighbors foraged toward enclosed colonies on days 0, 5, 10 and 15 using the index of encroachment described above. These 52 measures (13 neighbor colonies, 4 days) were used in the analysis. To examine variation among the five sets of colonies subjected to the same treatment (each set consisting of one colony and its neighbors), the analysis was a split-plot ANOVA in which the effect of colonies was split into those of sets and colonies within sets. The effect of day (days 0, 5, 10 and 15) was divided, using a linear contrast, into its linear and non-linear components. The overall error term was the colony × day interaction. An examination of the residuals indicated that the data met the assumptions of the ANOVA.

Figure 1 A illustrates the trails during the period of enclosure in one of the five sets of colonies mapped. The enclosure, about

1 m in diameter, is shown as a circle immediately surrounding the nest entrance. A colony's foraging range was arbitrarily defined by drawing a polygon formed by connecting the furthest point reached by each of the colony's foraging trails on the day before the enclosure was set up (Fig. 1A). For each day that trails were mapped during the period of enclosure, and on days 16 and 20 (days 1 and 5 after colonies were released), I counted the number of neighboring colonies whose trails entered the foraging range of the enclosed colony.

3. Interactions of neighbors of varying age: enclosure experiment. This enclosure experiment, made in 1990, involved 18 pairs of neighboring colonies. Colonies were of three age classes: (1) young colonies ('Y') in which workers active outside the nest first appeared in 1990, probably founded in 1989 and thus 1 year old. (2) Intermediate 3 to 4-year-old colonies ('I') that first appeared in 1987 or 1988, and were active every year since. (3) Old colonies 5 or more years old ('O'), that first appeared in 1986 or earlier, and were active every year since. There were six treatments, in which either an Old or Intermediate colony was enclosed, and the other colony was its nearest neighbor. (Young colonies were not enclosed because preliminary work suggested the disturbance might cause them to stop foraging for several weeks, precluding part of the required observations). Pair types will be designated by the first letters of the age classes involved, with the enclosed colony first, e.g. 'O–Y' refers to an enclosed Old colony with a Young neighbor. The treatments were: O–O, O–I, O–Y, and I–O, I–I, I–Y. There were three replicate pairs for each of the six pair types, a total of 18 pairs of colonies.

The experiment was begun on 20 July with three pair types (9 pairs; O–O, O–I, I–I) simultaneously; and then begun 3 days later for the remaining 9 pairs (I–Y, O–Y, I–O). Foraging trails were mapped 4 and 1 days before enclosure, to serve as a control with which to compare the effects of enclosure. Trails were then mapped on the first day of enclosure (day 1), 5, 10, and 16. Enclosures were removed on day 16 after maps were made, and trails were also mapped on days 22 and 27.

Maps of foraging trails were used to derive three measures of foraging behavior (see *Measures of foraging behavior*, above): extent to which one colony's trails were directed toward the other (index of encroachment); proportion of one colony's trails directed toward the other (proportion encroachment), and total length of foraging trails. These measures were made for both colonies of each pair, the undisturbed neighbor and the colony that was enclosed. The data were divided into three time periods: Before (days -4 and -1 before enclosure), During (days 1, 5, 10 and 16 during enclosure) and After (days 22 and 27 after enclosure). To evaluate the effects of enclosure, I compared During and Before. To evaluate the effect of releasing the enclosed colony, I compared After and During. To evaluate the overall effect of enclosure, I compared After and Before. For each colony, and each of the three measures of foraging behavior, I found the mean for each time period, and then the difference between that colony's means for two time periods (i.e., During − Before, After − During, and After − Before). Differences between the means for two time periods were used in a 2-way ANOVA; examination of residuals showed the assumptions of ANOVA were met. The ANOVA tested for (1) overall mean effect, i.e. a difference between the two time periods significantly different from zero; (2) an effect of the age of the enclosed colony (O or I); (3) an effect of the age of the neighbor colony (O, I, or Y); and the interaction between the ages of enclosed colonies and of neighbors. A separate ANOVA was performed for each comparison of time periods (3), neighbors and enclosed colonies, and each measure of foraging behavior (3). The data used in each ANOVA were the 18 differences between the foraging behavior means for two time periods (O and I enclosed colonies, each paired with O, I and Y; 3 replicates of each pair type). "Overall mean differences" as used below refers to the means of the 18 differences.

Distances between the nest entrances of the 2 colonies of a pair ranged from 4.6 m to 20 m, and the data were also analyzed as above using measures of encroachment converted into a proportion of the distance between the two colonies. The results were identical, with respect to the occurrence of statistical significance, to those using the original measures of encroachment, so results converted to proportions of distances between nests were not considered further.

Relation of colony age and size: nest excavations

To determine how quickly numbers of workers increase from one year to the next in younger colonies, six colonies of known age were excavated in July and August 1991: two each of age 2, 3 and 4 years. Colony age was determined as above, from censuses made each year since 1985. During excavations, all ants and brood were captured, to be counted later in the laboratory. Excavations were begun early in the morning before ants left the nest, so very few ants escaped capture. Each excavation required about 7 h of digging by three or four people; the calichi layer, of the consistency of concrete, was up to 1 m deep.

A separate series of excavations was made to examine whether exterior activity reflects total colony size. Four colonies were excavated in 1990. Ages of the four colonies were estimated to be 2–3 years, by comparison with colonies of known age, using methods outlined in Gordon (1987). To compare mound size and total colony size, before excavation I measured the area of a hypothetical rectangle surrounding the nest mound, using the longest diameter, across the main nest entrance, of mound covered with pebbles, and the diameter perpendicular to it. To compare exterior activity and total nest size, two further measures were made: (1) hourly counts (four per colony on one day) of numbers of workers engaged in any of four activities within 1.3 m of the nest entrance. The activities were foraging, patrolling, nest maintenance and midden work; activities were defined and numbers counted as in Gordon (1986, 1987, 1989a). (2) foraging rate on all trails, the total from 3 counts, an hour apart, from each trail of numbers of foragers crossing an imaginary circle around the nest entrance, of radius 1 m from the edge of the nest mound, in 20 sec. Measures of exterior activity were made on all colonies on the same day (15 July 1990) because there is considerable day-to-day variation in the activity of a colony (Gordon 1991). Excavations were made over the next 4 weeks (16 July–13 August 1990).

Results

1. Actively foraging neighbors (more than 5 years old)

Neighbors of enclosed colonies encroached further than neighbors of active, non-enclosed colonies. Over 16–18 days in 1988, colonies with longer foraging trails, and more foragers, approached colonies with shorter, less populated foraging trails at a rate of about 0.25 m per day (using the index of encroachment described above). These colonies might be expected to encroach heavily on their apparently weaker neighbors. But the difference in encroachment from day 0 (before enclosure) to day 15 (of enclosure) in 1989 was greater for the neighbors of enclosed colonies ($\bar{x} = 12.1 \pm$ st.dev. 2.9 m, $n = 13$, range 7.8–41.2), than for the neighbors of active colonies in 1988 ($\bar{x} = 4.4 \pm 2.1$ m, $n = 7$, range -3.1 to 15.7). The mean for neighbors of enclosed colonies in 1989 was significantly greater (one-tailed t-test, df 18, $t = 1.77$, $P < 0.05$).

2. Interactions of old neighbors: enclosure experiments

Over the 15 days that old colonies were enclosed in 1989, their neighbors advanced toward them at a rate of $0.85 \pm$

0.15 m per day (average over the 13 neighbor colonies using the index of encroachment described above). There were significant differences in encroachment among all neighbors of all enclosed colonies (df 12,36; SS 25427 (in ft); F 5.8, $P<0.001$), but there were no significant differences among the five sets (each consisting of 1 enclosed colony and 2 or 3 neighbors) (df 4,8; SS 6892; F 0.74, n.s.). There was significant day-to-day variation (effect of day, df 3,36; SS 12991; F 11.3; $P<0.001$). The change in encroachment from day 0 to day 15 was entirely accounted for by the linear component (df 1,36; SS 12420; F 34.2; $P<0.001$), while the non-linear component was not significant (df 2,36; SS 571; F 0.8; n.s.).

Neighbors entered the foraging ranges of enclosed colonies. In all five sets, at least one neighboring colony entered the foraging range of the enclosed one within 10 days of enclosure (Fig. 2).

After the enclosed colonies were released, neighboring colonies retreated immediately (compare Figs. 1A and 1B). The day enclosed colonies were released (day 16), neighbors abandoned the pre-enclosure foraging ranges of all but one of the 5 enclosed colonies (Fig. 2). Fighting between an enclosed colony and a neighbor occurred on the day after release in two of the five sets of colonies. In both these cases, the site of fighting was the boundary of the enclosed colony's original foraging range (one case shown in Fig. 1B). Within 5 days after release, all neighbors had retreated from the foraging ranges of all enclosed colonies (Fig. 2).

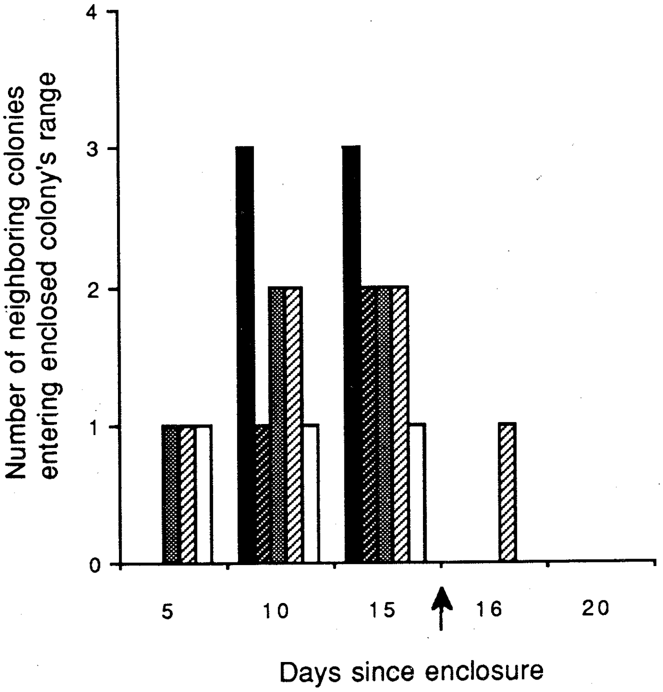

Fig. 2. Encroachment by neighbors of enclosed colonies. The number of neighboring colonies entering the foraging range of an enclosed one (foraging range defined as in Fig. 1A; see text for details). Each *bar* represents the neighbors of one enclosed colony. Each enclosed colony had 2–3 neighbors. Enclosed colonies were released on day 16 (*arrow*)

3, Interactions of neighbors of varying age: enclosure experiment

When colonies were enclosed, neighbors of all ages redirected their foraging to fill the spaces that became available. The mean gain in encroachment by neighbors of all ages during the 16 days of enclosure, relative to the period before it, was 5.9 m (Fig. 3A). Encroachment by neighbors during the period of enclosure was significantly greater than before it (effect of overall mean difference, df 1,12; SS 6693.2; F 13.6; $P<0.01$). During enclosure, relative to the period before it, the mean gain in total length of foraging trails by neighbors of enclosed colonies was 6.1 m, and this difference was significant (effect of overall mean difference, df 1,12; SS 7156.1; F 7.55; $P<0.05$). During the period of enclosure, the proportion of foraging by neighbors that was directed toward the enclosed colony increased by 9%, which is significant (overall mean difference, df 1,12; SS 0.132; F 5.5; $P<0.05$). Thus gains in the total length of neighbors' foraging trails were due mainly to increasing length of those trails directed toward the enclosed colonies (Fig. 3A).

When enclosed colonies were released, their neighbors of all ages foraged shorter distances than they had during the period of enclosure (Fig. 3B). The enclosed colonies, in turn, extended those trails that led toward the nests of their trespassing neighbors. After enclosure, encroachment by neighbors and the total length of their foraging trails both decreased significantly (effect of overall mean difference for encroachment, df 1,12; SS 30143.3; F 60.24; $P<0.001$; total foraging, df 1,12; SS 7296.3; F 10.7; $P<0.01$). Thus when encounters with the enclosed colonies were resumed, all the neighbor's trails shortened, including those that were directed toward the enclosed colonies (Fig. 3B).

For the enclosed colonies after they were released, there were no significant differences in encroachment toward neighbors or in total length of foraging trails [enclosed colonies (not shown in Fig. 3), overall mean differences, After – Before, n.s.]. But in response to the challenge from their neighbors, whose trails toward them had lengthened during enclosure, enclosed colonies when released increased the proportion of trails directed toward their neighbors (increase of 4%, After – Before; effect of overall mean difference, df 1,12; SS 0.03; F 5.0; $P<0.05$). Though the neighbors decreased the length of all their trails when enclosed colonies were released, they did not diminish the proportion of trails headed toward the released colonies (Fig. 3B; mean difference in proportion encroachment by neighbors, After – During, –0.02; effect of overall difference n.s.), and the increase by the enclosed colonies (4%) in proportion encroachment after release was not as great as their neighbors' had been during enclosure (Fig. 3A; gain in proportion encroachment, During – Before, 9%).

For neighbors of all ages, encroachment was greater after enclosure than before it (Fig. 3C). This resulted from a change in the direction, not length of trails; proportion encroachment increased significantly, but total length of foraging trails did not (Fig. 3C). Comparing

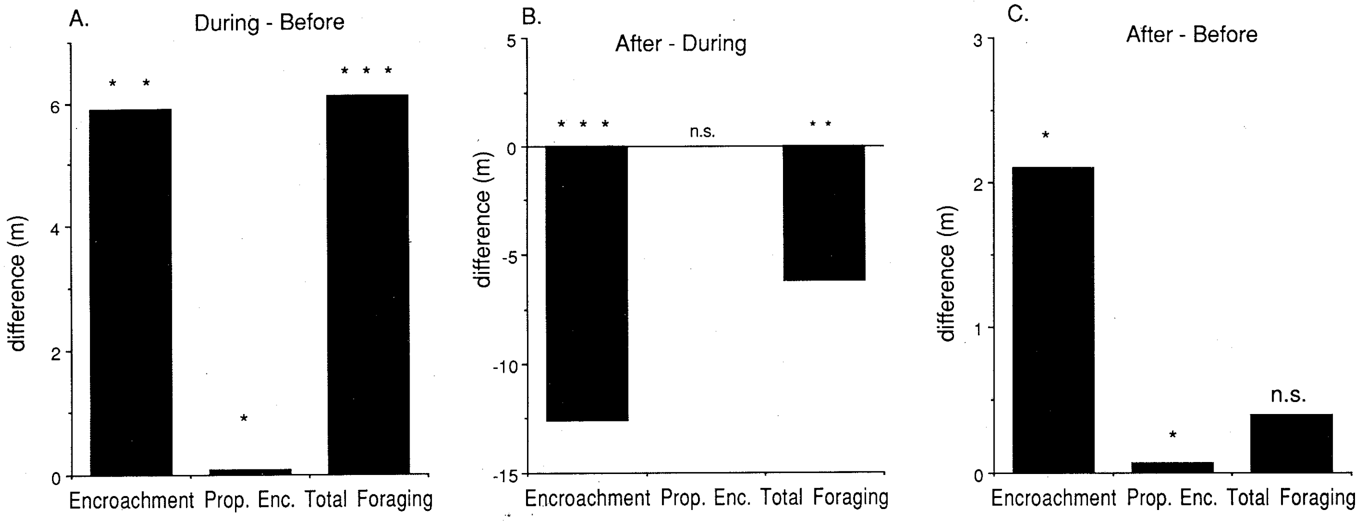

Fig. 3A–C. Results of enclosure experiments with colonies of different age: **A** During – Before; **B** After – During; **C** After – Before. Shown are differences between means of 3 measures of foraging behavior: encroachment, a measure of extent to which one colony foraged toward another; proportion encroachment, a measure of the proportion of trails directed at the other; and total length of all foraging trails. Differences, shown for neighbor colonies only, are between means for the indicated time periods. Note that proportion encroachment varies from 0 to 1; other measures are scaled in meters. * $P<0.05$; ** $P<0.01$; *** $P<0.001$ in an ANOVA; details in text

Table 1. Results of enclosure experiment with colonies of varying age (study 3)

		Neighbors *During – Before*			Neighbors *After – During*			Neighbors *After – Before*			Enclosed *After – Before*		
	Age of enclosed colonies	O	I	Y	O	I	Y	O	I	Y	O	I	Y
Encroachment													
	O	10.7	4.8	1.8	−16.6	−10.2	−16.6	5.4	2.6	−5.2	−0.7	3.1	−0.8
	I	4.8	11.5	1.9	−13.7	−10.8	7.7	−0.3	10.4	−0.2	7.9	−1.9	−1.5
Proportion encroachment													
	O	0.15	0.03	0.09	−0.02	0.04	− 0.12	0.13	0.07	−0.03	−0.01	0.06	0.01
	I	0.09	0.07	0.08	−0.03	0.01	0.02	0.05	0.07	0.09	0.07	0.07	0.09
Total length of foraging trails													
	O	9.6	6.1	6.2	−11.9	−7.6	−7.6	−2.3	−1.5	−1.4	0.3	−3.9	−2.8
	I	3.3	12.5	1.9	−5.6	2.1	−6.6	−2.4	14.6	−4.7	8.8	−3.0	−8.1

Shown are mean differences of two time periods in encroachment, proportion encroachment (the proportion of trails directed toward the neighbor), and total length of all foraging trails, by neighbor and enclosed colony age. 'O' represents older colonies (more than 5 years old), 'I' intermediate-aged colonies (3–4 years old), 'Y' young colonies (1 year old). Mean differences are in meters, except for proportions which have no units. Means are adjusted cell means from ANOVAs

behavior before and after the period of enclosure, the neighbors of enclosed colonies made significant gains in encroachment (2.1 m; effect of overall mean difference, *df* 1,12; SS 847.4; *F* 7.63, $P<0.05$).

Response by neighbors to enclosure depended on colony age. There was a significant effect of neighbor age (encroachment, After – Before, *df* 2,12; SS 2704.5; *F* 12.12; $P<0.001$). Intermediate-aged, 3 to 4-year-old colonies gained most when their neighbors were prevented from foraging. Gains in encroachment were highest in 3 to 4-year-old colonies (After – Before, Table 1). The mean gains (After – Before) in encroachment by neighbors of each age were: old 2.6 m, intermediate 6.5 m, young −2.7 m. Thus while on average neighbors of all ages increased in encroachment during the period of enclosure by 5.9 m, only colonies 3–4 years old retained this gain (6.5 m) after the period of enclosure.

In undisturbed colonies, the distance a colony forages increases as it grows older. Using total length of foraging trails as a measure of foraging distance, Fig. 4 shows the mean foraging distances of neighbor colonies in 1990 (not enclosed colonies) before and after the period of

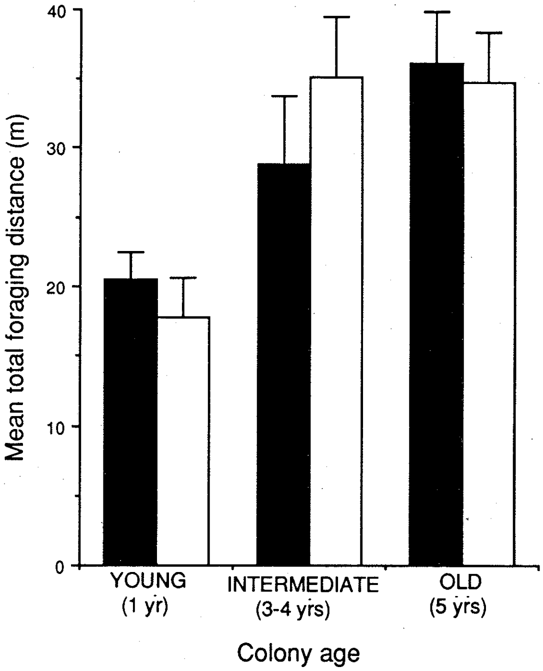

Fig. 4. Foraging distances by colony age. The mean total foraging distances, the summed lengths of all of a colony's foraging trails on a given day, for young, intermediate, and old colonies. Results are from neighbors of enclosed colonies; $n = 6$ for each bar. *Solid bars,* days −4 and −1 before enclosure experiments; *open bars,* days 5 and 10 after enclosed colonies were released

enclosure. Trails ranged from 1 to 20 m in length; a colony had one to eight distinct trails on a given day. Before experiments began, old colonies covered larger foraging distances than 3 to 4-year-old ones, while foraging distances of young, 1-year-old colonies were smallest. The exclusion experiments altered this distribution. On days 5–10 after enclosed colonies were released, the 3 to 4-year-old colonies used trails similar in length to those of the old colonies.

In comparing encroachment by neighbors before and after enclosure, there was a significant interaction of age of the enclosed colony and age of the neighbor (encroachment, After − Before, *df* 2.12; SS 1586.0; *F* 7.14; $P < 0.01$). Of the neighbors of enclosed old colonies, old colonies made the largest gains, while of neighbors of enclosed 3 to 4-year-olds, 3 to 4-year-olds made the largest gains. The same pattern also occurs, though it is not statistically significant, in the mean differences comparing neighbors' behavior during and before encroachment, for both encroachment and total foraging (Table 1). In the I − I pairs, the length of the neighbor's foraging trails actually increased after the enclosed colony was released; this was the only pair type in which this occurred (see total foraging, After − During, After − Before, Table 1).

For the enclosed colonies, I compared encroachment, proportion encroachment, and total length of foraging trails after and before enclosure, and mean overall differences were 1.3, 0.04 and 1.5, respectively. The increase in proportion encroachment was significant (overall mean difference, After − Before, *df* 1,12, SS 0.027, *F* 5.0, $P < 0.05$). There were no other significant overall differences or significant effects of neighbor age, enclosed colony age, or the interaction of the two.

Relation of colony age and size: nest excavations

A rapid increase in colony size occurs when a colony is 3 or 4 years of age. Fig. 5 shows colony size, in numbers of workers (including callows) as a function of age. Also shown are the results of excavation of four colonies of unknown age, estimated on the basis of nest size to be 2–3 years old. Counts from all excavations are shown in Table 2. The majority of brood and callows (recently eclosed, lightly pigmented adult workers) were found near the queen, at the bottom of the nest, at a depth of 1.5–2 m. Ants may have moved to the bottom of the nest in the course of excavation; we found many empty chambers and chambers containing only seeds. Queens were found in all eight colonies except for one, the smaller of the two 4-year-old colonies. The data shown may underestimate colony size for this colony. Excavations were made after mating flights had occurred, and no winged reproductives were found in any colonies.

Exterior activity was measured in the four colonies of unknown age (estimated to be 2–3 years old) the day before excavations began. The four colonies are listed in Table 2 in order of increasing numbers of workers. Nest mound area reflected most accurately the differ-

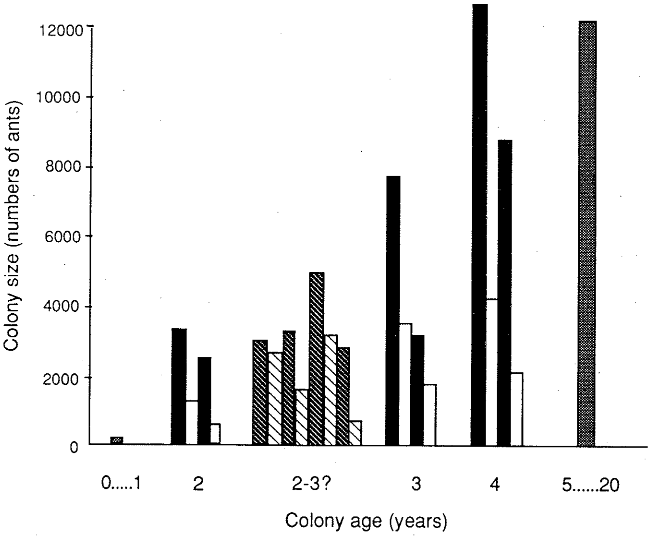

Fig. 5. Colony size and colony age. Results of excavations of 8 nests. Each *solid, filled bar* shows the number of workers and callows in a colony of known age. The *empty bar* to the *right* of each filled bar shows the number of larvae and pupae in the same colony. *Hatched bars* show results for colonies in which the age was not known, but was estimated to be 2–3 years; each *dark hatched bar* shows the number of workers and callows in one colony, and the *light hatched bar* to its *right* shows the number of pupae and larvae in the same colony. *Stippled bars* at ages 0 and 5 indicate that a colony begins with one ant, the founding queen, and reaches a stable size of about 12,000 workers when it is about 5 years old

Table 2. Colony size, age, and exterior activity

Colony age (years)	W	C	P	L	Nest size	Foraging rate	Total active
2	1671	711	291	209			
2	2153	1088	822	372			
3	2008	840	901	740			
3	6619	1223	1867	1705			
4	7207	1495	858	1262			
4	10723	2275	2130	2102			
2–3?	1881	1300	783	812	10.9	75.7	69
2–3?	1906	1800	918	696	40.9	30	49
2–3?	2034	590	269	267	13.7	26.3	58
2–3?	4696	339	1383	1339	98.3	50.7	155

Shown are results from excavations of 6 colonies of known age, and 4 colonies estimated to be 2–3 years old: number of workers 'W', callows 'C', pupae 'P' and larvae 'L'. For the latter 4 colonies, measures of exterior activity made before excavation are also shown: nest size (cm^2); foraging rate (mean total numbers of foragers leaving the nest mound in 20 s); and mean total numbers of ants active outside the nest, within 1.4 m of the nest entrance, engaged in 4 tasks

ences among colonies in numbers of workers, indicating the colonies with the smallest and largest numbers of workers. Callows rarely work outside the nest (pers. obs.), so numbers of callows would not be expected to affect measures of exterior activity.

Discussion

Neighboring colonies of *P. barbatus* actively adjust the partitioning of foraging areas. Two aspects of this behavior are common to colonies of all ages. First, they adjust the direction and length of their foraging trails in response to the foraging behavior of their neighbors. When a space becomes available, they redirect their foraging to fill it. When interaction resumes, they retract their trails. This process of mutual adjustment explains why neighboring harvester ant colonies often use trails directed away from those of their neighbors (Hölldobler 1976; Kugler 1984; Ryti and Case 1986).

A second feature of foraging behavior, common to colonies of all ages, is that frequent interaction with neighbors is required to maintain foraging ranges. If a colony fails to encounter its neighbor, the neighbor will enter its foraging range. In the first experiment, over the 15 days that old colonies were enclosed, their neighbors of similar age advanced toward them at an essentially linear rate of 0.85 ± 0.15 m per day. This rate is a measure of how fast a large colony, more than 5 years old, explores and enters a newly available foraging area. In all five groups of old colonies, at least one neighboring colony entered the previous foraging range of the enclosed one within 10 days (Fig. 2). This suggests that workers from neighboring colonies must interact at least every 10 days in order to prevent overlap of foraging ranges. Further work is needed to investigate how different forms of interaction, such as direct encounters between workers or scent-marking of the ground, may each contribute to partitioning of foraging areas.

The extent of a resident's advantage depends on the age of neighboring colonies. Older neighbors of enclosed colonies retreated immediately when the enclosed colonies were released (compare Figs. 1A and 1B), usually within 5 days after release (Fig. 2). But when pairs of colonies that differed in age were compared, 3 to 4-year-old neighbors persisted in using trails toward newly released colonies. In general, however, neighbors of all ages tended to retreat when the enclosed colony resumed foraging. While in some species an occupant immediately acquires an advantage in a territorial contest (Alexander 1961; Davies 1978), it appears that for a *P. barbatus* colony, familiarity with or proximity to its own foraging range generally outweighs any advantage that accrues to an intruder in 15 days.

The age of the enclosed colony appeared to have little effect on the behavior of its neighbor. This casts doubt on the existence of one kind of historical influence on the interactions of neighboring colonies. If a colony's foraging behavior were influenced by an appraisal of its neighbor's foraging strength, based on information gathered in the past (Rohwer 1982; Parker and Rubinstein 1981), then neighbors might react differently to the absence of a larger, older neighbor than to the absence of a smaller though expanding one. Although neighbors responded differently to old and intermediate-aged enclosed colonies after they were released, i.e., when encounters were resumed, there were no such effects during enclosure.

The extent to which a neighbor will trespass in the absence of encounters, and the extent to which the newly gained territory is held when encounters are resumed, both depend on colony age. Colonies of intermediate age (3–4 years old) are most likely to retain newly gained foraging ranges. Thus colony size does not in itself determine the outcome of contests: smaller, 3 to 4-year-old colonies made significant gains relative to larger ones at least 5 years old. For example, intermediate, 3 to

4-year-old neighbors made greater gains than 5-year-old neighbors against enclosed colonies (6.5 m mean gain for intermediate-aged neighbors vs. 2.6 m mean gain for old neighbors, comparing encroachment before and after enclosure; see Table 1). In contrast to previous results with other species (Adams 1990; Hölldobler 1981), in *P. barbatus* contests are not necessarily decided in favor of the colony with the largest number of workers. Resource holding potential in older colonies could be limited by the number of workers available to defend larger foraging areas, but this seems unlikely. Older colonies' trails are only slightly longer than those of 3 to 4-year-old colonies (Fig. 4), and it takes about 100–300 ants to occupy 1 m of foraging trail (Gordon 1991). But a 5-year-old colony may be larger than a 3 to 4-year-old by thousands of ants (Fig. 5).

These results suggest that resource holding potential does not determine the outcome of territorial conflict in harvester ants. Instead, it appears that for colonies of different ages, the benefits to be gained from conflict with a neighbor may differ in value. This is consistent with previous results, showing that smaller 3–4-year-old colonies persist longer than larger colonies, 5 years or older, in conflicts with neighbors over food, and younger colonies require less food to engage in conflict than do older ones (Gordon 1991).

One source of age differences in the value a colony places on a foraging area may be colony growth. The rate of brood production may be limited by numbers of workers available to feed and care for immature ants (e.g. Brian 1973; Porter and Tschinkel 1985). Much of the energy assimilated by adult ants in *Pogonomyrmex* colonies is spent by workers engaging in activities related to brood care [about 60% in *P. rugosus*; about 30% goes directly to feed larvae (MacKay 1985)]. A colony's demand for food may depend on the number of immature ants to be raised, relative to the numbers of adult workers available to care for brood, collect and process food, and feed it to larvae (Schneirla 1971; Topoff and Mirenda 1980). Though a colony 5 years or older is larger than a 3 to 4-year-old one, a 3 to 4-year-old colony is increasing more rapidly in numbers of workers. As individual *P. barbatus* workers live only a year (Gordon and Hölldobler 1988), a colony must replace all its workers each year merely to maintain the same size from one year to the next. The proportion of immatures to workers, from one year to the next, would be higher in a quickly-growing colony.

The results of nest excavations, presented here, provide the first insight into the relation of age and size in harvester ant colonies living in natural conditions. Colonies of the same age vary in size and in the proportion of immature to adult workers (Fig. 5). Variation in foraging success, queen productivity, and microclimactic differences among nests may all contribute to differences in colony size. Despite the variation, it is clear that much growth occurs in the 3rd and 4th years.

Many ant species show a similar pattern of colony growth: the number of workers produced increases rapidly and then levels off (Hölldobler and Wilson 1990). Does the rapid growth of 3 to 4-year-old colonies continue? A regression of colony size on age, using the numbers of workers found here in six colonies of known age, gives the following equation for a linear growth rate, where y represents colony size and x colony age: $y=4019x\text{-}5722$ ($r^2=0.72$, $P<0.03$). If colonies continued to grow linearly, the average 5-year-old colony would contain 14,374 workers; the average 10-year-old colony would contain 34,470 workers, and the average 15-year-old colony would contain 54,566. MacKay (1981) performed extensive excavations of large colonies of unknown age, in several *Pogonomyrmex* species. The largest *P. barbatus* colonies found contain about 12,000 workers (Wildermuth and Davis 1931; MacKay 1981); MacKay's results were similar for *P. rugosus*, which is the species most closely related to *P. barbatus* (Taber 1990). It appears that in *P. barbatus*, a colony does not increase linearly in worker numbers throughout its life. At what age does growth slow down? Measures of nest size and counts of total numbers active outside the nest in various activities appear to reflect differences in colony size (Table 2). Such measures show little variation among colonies 5 years or older (Gordon 1987). This indicates that in *P. barbatus* colony growth levels off at about 5 years of age.

Foraging area may be more valuable for 3 to 4-year-old colonies that are growing quickly, than for larger, older ones of stable size, because from one year to the next the younger colonies have a higher proportion of brood to adults. However, colonies of stable size (5 years or more) may produce a greater proportion of alate reproductives than younger colonies, and these costs may be important. Here excavations were made soon after the annual mating flight, and no reproductives or reproductive larvae were found. Colonies known to be 3–4 years old occasionally produce reproductives (pers. obs.); large, presumably older colonies have been observed to produce large numbers of reproductives (Hölldobler 1976). MacKay's (1985) physiological studies show that much more energy is devoted to the production of workers than of reproductives in several *Pogonomyrmex* species. Further work is needed to investigate how a colony's territorial behavior depends on the relation between the number of workers and alates being produced, and the numbers of workers available to feed and care for them.

A second source of colony-age differences in territorial behavior may be the prospective value of a foraging area for a young colony. The diet of *P. barbatus* consists mostly of seeds, which are stored inside the nest for many months (MacKay 1981). A colony's food intake may be limited by the size of the area within which it searches for and retrieves seeds. Recent studies indicate that the total size of a colony's foraging area may contribute more to its value than the quality of particular, local resources inside it (Gordon, in prep.). It appears that most mortality in *P. barbatus* occurs at the founding stage; once a colony reaches the age of 2 years, there is little change in mortality rates (Gordon 1991). This means that interactions between neighbors are likely to go on for many years. Foraging areas of 3 to 4-year-old colonies were smaller than those of old colonies before experiments began (Fig. 4). A young colony may be fighting to acquire a larger foraging area to be retained in the future. Similar pressures determine the territorial behavior of juvenile lizards (Stamps and Eason 1989) and male, red-winged blackbirds (Beletsky and Orians 1989).

It would be interesting to examine how colony growth affects interactions of neighboring colonies in other ant species. Excavation results indicate that caution is needed in using measures of activity outside the nest as measures of colony size. Counts of active foragers are probably inaccurate, because such numbers vary greatly from day to day in a single colony (Gordon 1991), while the production of new workers takes about 6 weeks (MacKay 1981). Large differences in colony size, such as the difference between colony 3 and the others (Table 2), may be reflected in any measure of exterior activity. But to assess smaller differences, a combination of measures may be needed, such as nest size and total numbers active in various tasks outside the nest.

Two theoretical approaches may be relevant to the present results. First, optimal foraging theory predicts foraging distances, and the relation of foraging distance and forager selectivity, in central-place foragers such as harvester ants (Schoener 1977; Taylor 1977). In several studies of seed-eating ants, such predictions have not been upheld (Holder Bailey and Polis 1987; Rissing and Pollock 1984; Davidson 1978; Taylor 1978). These studies have considered the foraging behavior of a colony in isolation, some using experimental designs that specifically exclude interactions of neighboring colonies (e.g. Holder Bailey and Polis 1987, Taylor 1978). The present study does not directly test optimal foraging theory, but does show that interactions among neighboring colonies strongly influence foraging distances.

Second, interactions between colonies of different ages may be considered an example of an asymmetric contest (Schoener 1983; Parker and Rubinstein 1981; Hammerstein 1981). To apply such models to encounters between neighboring *P. barbatus* colonies, it would be necessary to assess the costs involved in conflict, the costs of not foraging in a particular direction, and the benefits associated with a gain of foraging area, and to distinguish a strategy of escalation from a less costly one (Maynard Smith 1974). Hammerstein (1981) describes a territorial contest between intruders and owners of equal size in which the optimal strategy for the intruders is escalation while for the owners a less aggressive strategy, "display", is optimal. This theoretical result is reminiscent of a puzzling empirical one presented here, expressed by the significant interaction of neighbor and enclosed colony age in the extent of encroachment by neighbors. Intruders (neighbors) were most effective, or escalated most, against owners (enclosed colonies) of approximately equal size (same age): old neighbors encroached most on old enclosed colonies, and intermediate-age neighbors encroached most on intermediate-aged enclosed colonies (Table 1).

Since colony growth influences foraging behavior, the age structure of a population will determine spatial patterns of resource use. Because the distribution of young colonies changes very quickly, due to colony emergence, death, and relocation (Gordon 1992), very young colonies may pose little threat to their older neighbors. Once a colony is 2 years old, it faces several years of expansion and conflict with its neighbors. After about 5 years, it enters into a mature phase for the duration of its active life. During this phase, it avoids conflict with neighbors of the same age. But if workers of old neighboring colonies do not interact for about 10 days, one colony will probably enter the foraging area of another. Spatial patterns of foraging behavior are maintained by continual adjustment, mediated by the interaction of neighboring colonies.

Acknowledgements. I am very grateful to my field assistants, S. DePue, D. Ferrier and G. Tarling in 1989, M. Bateson, E. Lewis and B. Raymond in 1990, and M. Brown, A. Dalrymple and M. Weiser in 1991. I thank the staff at the Southwestern Research Station where this study was conducted, and N. Hall for the use of his land as a study site. Success in nest excavations was due to the amazing skill, patient instruction and strenuous labor generously provided by S. Cover; many thanks also to D. Wagner and L. Henneman. I thank M. Bulmer, F. Marriot, and M. Pagel for statistical advice, and J. Altmann, C. Boggs, B. Crespi, J.R. Gregg, B. Hölldobler, J. Stamps and anonymous reviewers for comments on the manuscript. I am pleased to acknowledge financial support from the National Geographic Society in 1989 and 1990, and a Research Travel Grant from the British Ecological Society in 1990.

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