

HOME RANGE ORIENTATION OF THE HARVESTER ANT *POGONOMYRMEX BARBATUS* SMITH

HUEI-JUNG WU

Institute of Zoology, Academia Sinica
Nankang, Taipei, Taiwan 11529
Republic of China

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Huei-Jung Wu (1989) Home range orientation of the harvester ant *Pogonomyrmex barbatus* Smith. *Bull. Inst. Zool., Academia Sinica* 28(2): 87-96. Orientation in a barren area by the ants of *Pogonomyrmex barbatus* Smith (Texas variety) was studied by adding or removing distinct visual markers and/or chemical orientation cues on or along the ant roads. Ants were also individually marked and released into the herbage away from the ant roads at various distances away from the nest and their homing paths were monitored. Field orientation tests have revealed that both visual markers and chemical orientation cues are responsible for a precise road orientation. The ant showed high degree of road fidelity and site fidelity. This suggests that the workers of *P. barbatus* usually forage in a certain area where they are familiar with. Although given foragers generally remain associated with specific roads, they can be directed from one to another. The ants showed different degrees of disorientation after they were released into the herbage away from the ant roads. The results of the above studies conformed Holldobler's (1976) observations to the road-maker *Pogonomyrmex* ants in general.

Key words: Orientation, Ant road, Harvester ant.

Pogonomyrmex barbatus Smith (Texas variety of the Mexican *barbatus*) is the second most abundant Western granivorous ant (Hutchins, 1967). The nests of this ant are usually found in hot grassy plains (Cole, 1968). The nest itself is constructed in the ground and, in general, there is an altered cleared courtyard (or disk), 1-3 m in diameter, over the nest and 1-6 smooth roads (or ant trails), 5-15 cm wide, which radiated from the courtyard to a distance of 10-50 m (Fig. 1). The ants mainly collect seeds for food primarily in areas to the sides of their ant roads. McCook (1879) has described the structure of nests, briefly distinguish-

ing six types: the mound, the mound-belt (Fig. 1), the cone, the cone-belt, the gravel, and the flat nests. He suggested that the ant roads are used for communicating with harvesting grounds and facilitate the transport of seeds homeward. In view of the great abundance of this ant and their considerable ecological importance, surprisingly little has been learned to the present time concerning the ecology of its nest surface architecture. For example: why should the ants clear a big, barren courtyard over their nest; and what benefits that the ant might derive from the ant roads.

This paper presents the analysis that ant roads are responsible for a precise

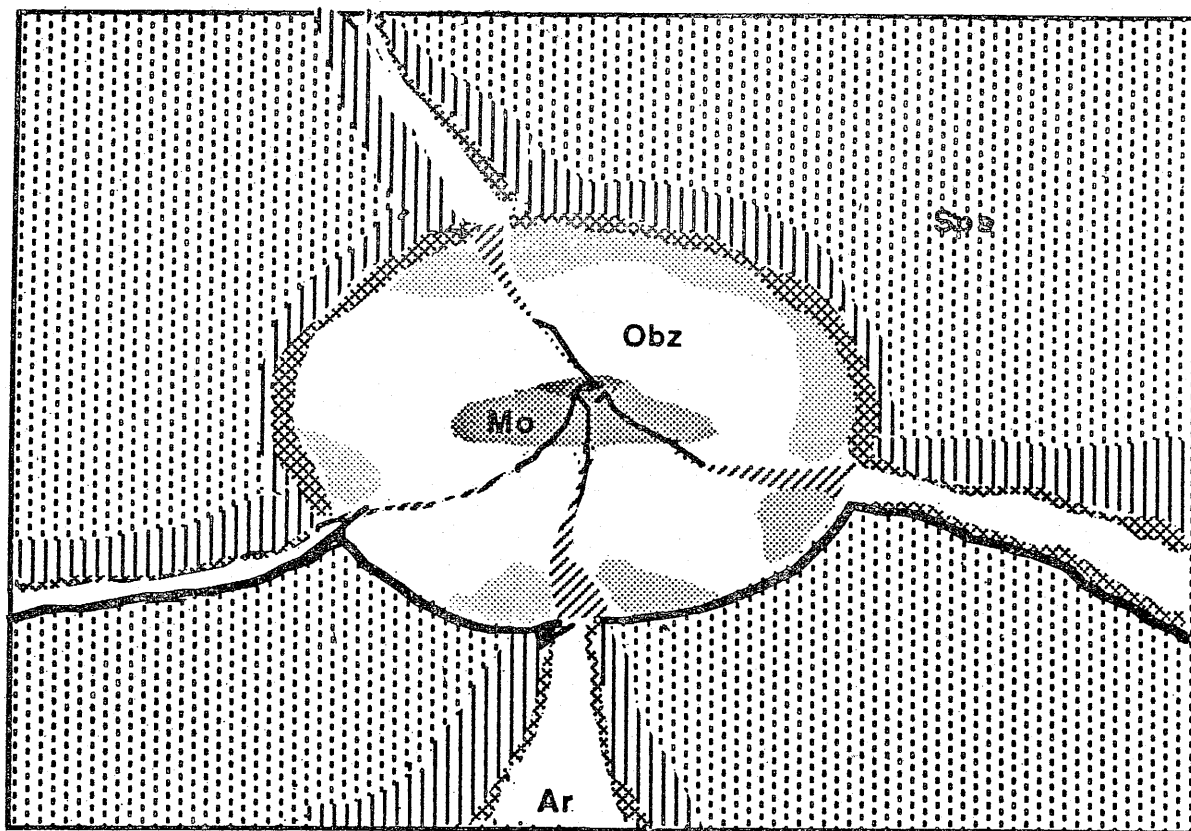


Fig. 1. The surface architecture of a mound-belt nest of *Pogonomyrmex barbatus*. Note the big bare, open-belt zone (Obz) beyond the center elevated mound (Mo). There are 4 ant roads (Ar) which radiate from the courtyard and penetrate into the surrounding vegetation (Sps).

home range orientation to *P. barbatus* during their foraging and homing excursions. Most studies were conducted at Brackenridge Field Laboratory of the University of Texas at Austin, Texas, USA. There is abundance of wild and undisturbed nests in this area.

MATERIALS AND METHODS

Field test

In order to determine whether visual markers and/or chemical cues along the road are responsible for orientation during foraging and homing, an open-gravel nest (N1) established in a level barren patch (Bp) was selected (Fig. 2-I). The only two plants growing on patch Bp were two shrubs (s, 86 cm high, and s',

79 cm high) which were the only two distinct landmarks along the regular route *lss'm* (19 m long) which connected the exit point in the courtyard (1) and the mouth of the road (m) (Fig. 2-I). The ants of nest N1 had been observed to use route *lss'm* since June 15, 1986. Distinct artificial landmarks [i.e., black cardboard flags (30×30 cm) and/or a blue cardboard flag (20×20 cm)] were positioned, removed, and/or repositioned along route *lss'm* and/or the other five designed routes (i.e., by setting flags as described above along each of the designed routes) as shown in Fig. 2, and/or the chemical cues on the route(s) removed (i.e., by covering a layer of sand onto the route) during June 21 to July 17, 1986; the reaction of the ants of nest N1 to the manipulation

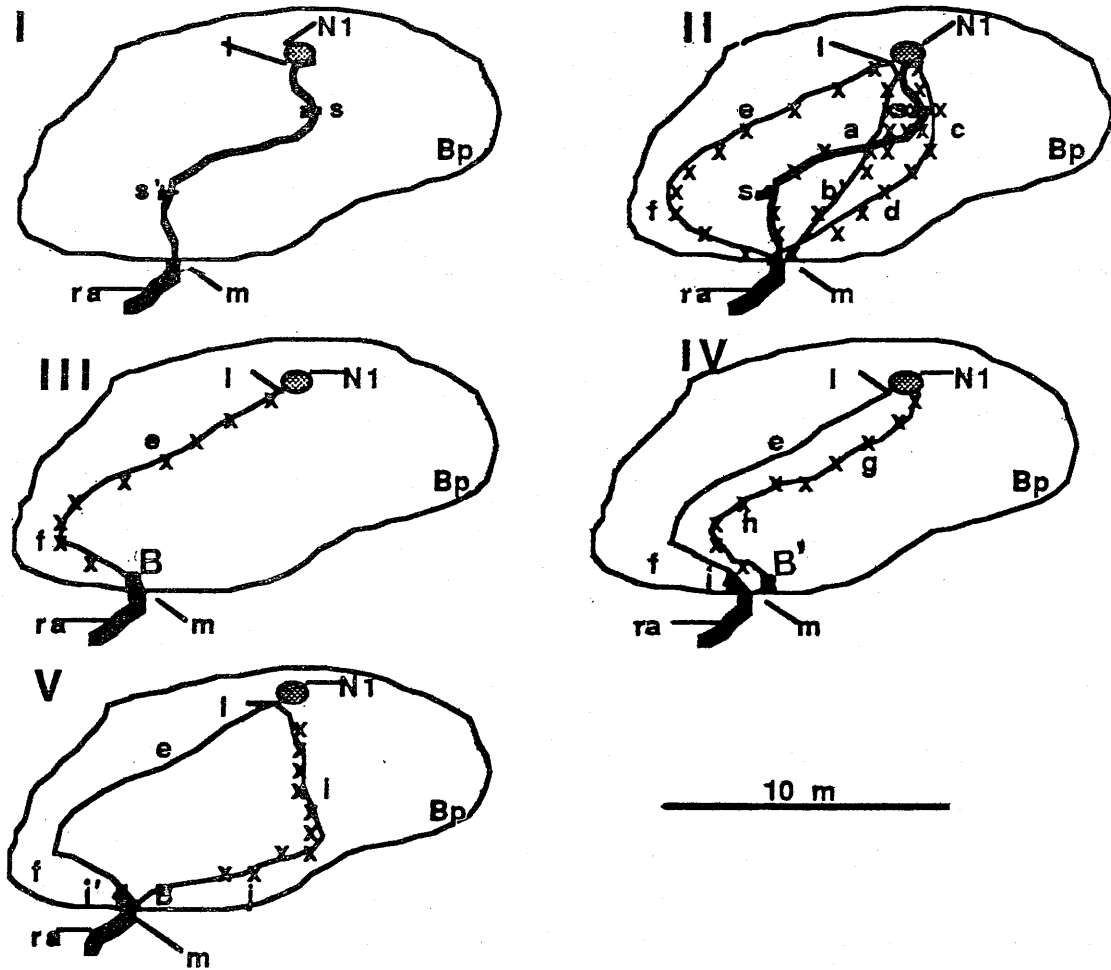


Fig. 2. Orientation tests carried out with *Pogonomyrmex barbatus* (see text for the description). **Bp**, barren space around nest **N1**; **lss'm**, original regular route used by the ants of nest **N1** to connect **l** (leaving point upon the courtyard) and **m** (road mouth of road **ra**); **labm**, **lcdm**, **lefm**, **lghm**, **lijm**, designed routes; **ra**, one of the ant roads of nest **N1**; **s**, **s'**, two shrubs along route **lss'm**; **x**, black cardboard flag; **B**, a blue flag; **im**, **i'm**, section of route **lefm** where was covered with a layer of sand.

and the choice of route were recorded.

Road fidelity and site fidelity

In order to know whether the ants usually forage in a certain area where they are familiar with, 3 experiments were conducted following the methods as described by Holldobler (1976):

Experiment 1: A gravel nest (**N3**) that had 2 busy foraging roads (**re** and **rd**) and a flat nest (**N4**) that had 3 foraging trails (**re**, **rf**, and **rg**) were selected

on July 1986. On each of the 5 roads, 400 foragers were individually marked with a spot on the pronotum or abdomen using a brush pen: ants running on road **rc** were quickly marked white, ants on road **rd** were marked yellow, ants on road **re** were marked blue, ants on road **rf** were marked green, and ants on road **rg** were marked orange. During the next five days each road was searched twice daily, 30 min per road in the morning and 30 min per road in the afternoon, for marked

ants. The marked ants were captured, counted, and released onto the courtyard after each check.

Experiment 2: A gravel nest (N5) that had 3 foraging trunks (rh, ri, and rj) was selected on 23 July 1986. On road rh of this nest 500 foragers were individually marked with a yellow spot and on road rj 500 ants were marked with a blue spot. During the next 3 days all the 3 roads were repeatedly checked and all marked ants recaptured, counted, and released as described above. On the fifth day (July 27) a rich seed source of *Bouteloua barbata* was offered at the terminus of road ri. On July 27 and the following day all the 3 roads were repeatedly checked and all marked ants counted and released in the same way.

Experiment 3: The foraging ground

along a road (rk) of a gravel nest (N6) was subdivided into 3 sectors (Sc1, Sc2, Sc3) by setting slender sticks as border lines between the sectors on 30 July 1986. 300 foragers were individually marked in each of the 3 sectors: ants foraging in Sc1 were marked with a yellow spot, those in Sc2 were marked with a blue spot, and those in Sc3 were marked with a white spot. During the afternoons of the following 3 days the marked ants were recaptured, counted, and released in each of the 3 sectors as described above. On the fifth day (3 August) a rich seed source of *Bouchloe dactyloides* was offered in sector Sc2. On 3 August and the following day all 3 sectors were searched repeatedly and all marked recaptured ants were counted and released in the same way.

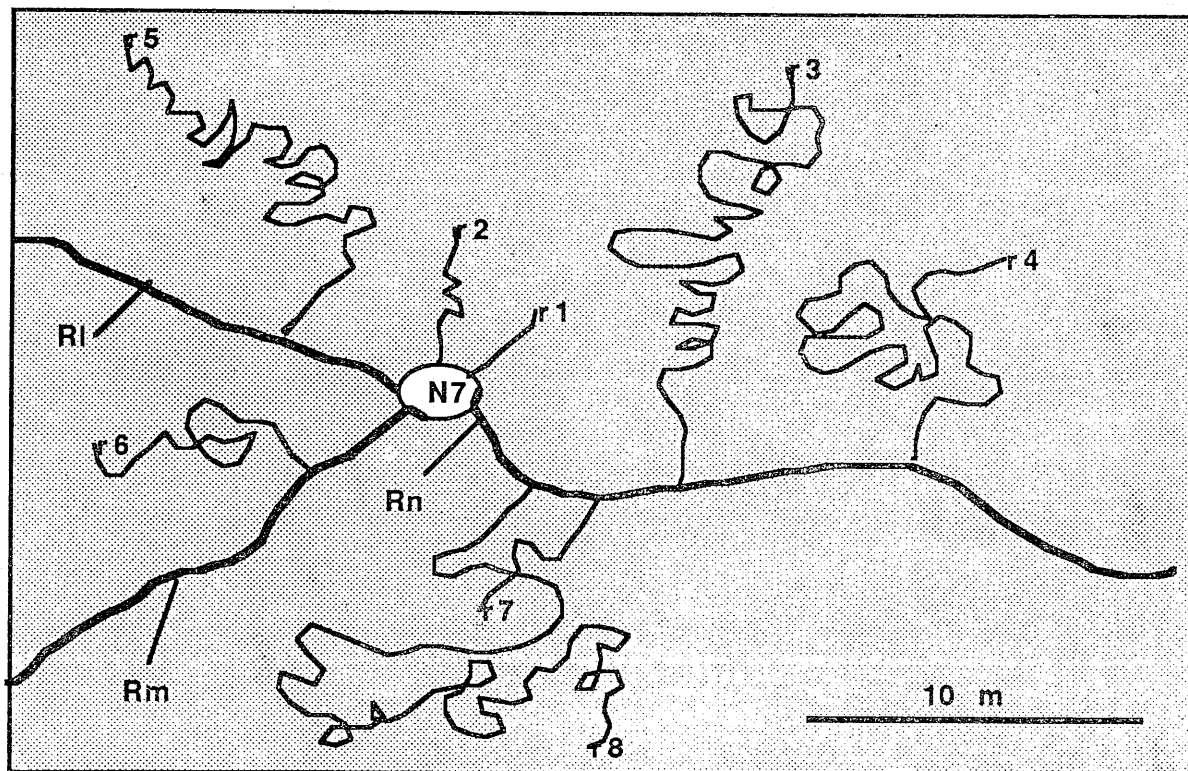


Fig. 3. Orientation test carried out with *Pogonomyrmex barbatus*. 8 marked ants were individually released to the herbage at various distances from nest N7 and the homing path of each ant was traced. Rl, Rm, Rn, 3 foraging trunks of nest N7; r1-r8, the points where 8 ants were released and the homing routes which the ants chose. (see text for the description.)

Orientation in a strange area

Ants were randomly chosen from a nest (N7), individually marked, and released into the surrounding vegetation at various distances, 5-21 m, from the nest as shown in Fig. 3. In each observation the release point (**r**) was marked with a green flag (10×10 cm). The homing path that the released ant traversed from **r** to any point on the circumference of the courtyard of nest N7 was traced by setting a prenumbered slender green stick (50 cm high) at the ant's location in the vegetation once every 1-2 min. The time each ant spent on the homing path was recorded and the homing path was mapped according to the locations of the numbered sticks set in the vegetation. A total of 8 repeated observations were made.

RESULTS AND DISCUSSION

Field orientation cues

Orientation on the routes in a barren area (**Bp** in Fig. 2-I) by the ants of nest N1 was studied by adding or removing distinct visual markers and/or chemical orientation cues on or along the routes. The only two distinct landmarks along the original regular route (**lss'm**) which the ants of nest N1 used for connecting the exit point (**l**) in the courtyard and the mouth of one of the roads (**m** of road **ra**) were two shrubs (**s, s'**) (Fig. 2-I). The ants of nest N1 had been observed to use route **lss'm** since June 15, 1986. On June 21, 10 extra distinct visual markers (i.e., black cardboard flags, 30×30 cm) were positioned along route **lss'm** (marked **x** along route **lss'm** in Fig. 2-II). Another three routes (**labm**, **lcdm**, and **lefm** in Fig. 2-II) were designed to connect points **l** and **m** by setting 10 flags along each of the designed routes on the same day. After these 40 flags were set onto the barren patch (**Bp**) the ants still

followed exactly the old path (**lss'm**) during the next 2 days (22-23 June). One reason for this result could be that there were 2 shrubs along route **lss'm** while there were no shrubs along the 3 designed routes (**labm**, **lcdm**, and **lefm**). However, after the shrubs along route **lss'm** were removed on 24 June, the ants still followed exactly the old route (**lss'm**). In this case we might assume that the ants had been guided either by the distinct visual markers (i.e., the flags) or some other invisible orientation cues. The flags along route **lss'm** were removed on June 25, the ants, again, still followed exactly the old path (**lss'm**). In this case, we may assume that the ants had been guided by the cues other than visual markers, most likely chemical cues. The flags were later repositioned back to route **lss'm** in the evening on June 25.

On the next day (June 26), route **lss'm** was covered with a layer of sand, but the flags along the route were not removed. This manipulation caused a considerable disturbance. After about 5-10 minutes in disorder each ant began to choose its own path by randomly connecting the flags set along routes **lss'm**, **labm**, and **lcdm**. However, no ant chose a route by connecting the flags set along route **lefm**. About 3 hours later one of the designed routes (**labm**, now route **labm**) became a common regular route used by most of the ants for connecting points **l** and **m** (thus the old regular route, **lss'm**, was removed). This result suggests that (1) the ants might have been guided by the familiar distinct visual markers (i.e., the flags) for route orientation, and (2) removed chemical cues might serve as an important role for a precise route orientation. One of the reasons that no ant chose a route by connecting the flags set along designed route **lefm** might be that this designed route was far from the original route (**lss'm**). The other reason might be that

this designed route (**lefm**), unlike the other two designed routes (**labm**, and **lcdm**) which pointed to a rather similar direction as that of the original route (**lss'm**), pointed to a rather dissimilar direction as that of the original route. In this case, we can hypothesize that the ants might be also guided by the so-called "direction cues" (i.e., such as using a time-compensated orientation to the sun's position or to the pattern of the polarized light of the sky, as suggested by Holldobler, 1976). Between 1300 and 1500 h on 27 June, all the flags along routes **lss'm** and **lcdm** were removed and the routes were covered with a layer of sand. After such manipulations route **labm** became the only regular route for all the ants. On the next day (28 June), all the flags along route **labm** were removed and the route was covered with a layer of sand. These manipulations, again, caused a considerable disturbance. The ants were in disorder and each of them began to search for its own route. Hundreds of private routes were used by different ants for the next 2 days although a relatively larger number of ants were seen using designed route **lefm** along which the set flags were not removed. However, on the 4th day (1 July) most of the ants had been directed to designed route **lefm** (new route **lefm**).

On 6 July, in addition to the original 10 black flags along route **lefm**, a blue cardboard flag (20×20 cm) was positioned facing the mouth of road **ra** (**m**) at a point (marked **B** in Fig. 2-III) 10 cm away from **m**. At 1000 h on 10 July, when the ants of nest N1 were busy foraging, all the 10 black flags and the blue flag along route **lefm** were removed and repositioned 25 cm rightward from the route at points marked **x** (black flags) and a point marked **B'** (blue flag) along a newly designed artificial route (**lghm**) as shown in Fig. 2-IV. The ants returning within the next 5 minutes were counted at the mouth of

the road (**m**) and the choice of the homing route monitored. Since the blue flags (**B**) were the most distinct familiar visual markers along route **lefm** upon the mouth of road **ra**, it is apparent that a considerable number of fast-moving ants (74, about 23%) were guided onto designed route **lghm** by this visual marker alone. However, those ants (247, about 77%) that still followed the old route (**lefm**) must have been guided by some other cues. That these are most likely chemical cues can be concluded from the result of the following experiment. A section on route **lefm** (the section marked **im** in Fig. 2-IV), about 1 m long, was covered with a layer of sand. Within the next 5 minutes, 225 (82%) homing ants ran to blue flag (i.e., ran to designed route **lghm**), apparently dependent on the visual marker, whereas only 48 (18%) chose the old route (**lefm**). Since there were still a considerable number of ants (48, about 18%) following the old route after both the distinct visual markers (the flags) and chemical orientation cues were removed, we might assume that there are still other cues used by the ants for a precise orientation. These are most likely direction cues (i.e., such as time-compensated orientation to the sun's position as suggested by Holldobler—1976; note section **im** of route **lefm** was about 20° deviated from section **B'm** of designed route **lghm**). All the flags along route **lghm** were later repositioned back to route **lefm** and the ants were guided back to route **lefm** during the following 6 days. On July 17, all the black flags and the blue flag along route **lefm** were removed and repositioned along another newly designed route (**lijm** in Fig. 2-V) as described above. Designed route **lijm** was about 120° deviated from the original direction as shown in Fig. 2-V. The ants returning within the next 5 minute were counted and the choice of the homing route recorded. 41 (about 16%) out of

257 ants ran to the blue flag, the remaining 216 ants (about 84%) followed the old route (**lefm**). A section of route **lefm** (the section marked **i'm** in Fig. 2-V), about 1 m long, from the mouth of road **ra** was covered with a layer of sand. Within the next 5 minutes, 155 ants (67%) ran to the blue flag whereas only 77 (33%) chose the old route (**lefm**).

Road and site fidelity

Ants were individually marked on the roads of nests N3 and N4 and their degree of road fidelity monitored in July, 1986. Tables 1 and 2 show that most of the recaptured marked ants were found on

the road (**rc**, **rd**, **re**, **rf**, or **rg**) where they had been marked. Only 8 out of 385 recaptured marked ants of nest N3 and 6 out of 505 of that of nest N4 were seen during the next 5 days (after marking) leaving the nest on another road.

The marked ants of nest N5 also showed high degree of road fidelity (Table 3). Only 2 out of 172 recaptured marked ants of nest N5 deviated from the road (**rh** or **rj**) where they had been marked during the 3 days after marking. However, after a rich seed source was provided at terminus of road **ri** of nest N5, a relatively large number of ants deviated from roads **rh** and **rj** to road **ri** (Table 3). The reason for this deviation might be that the number of foragers on road **ri** increased generally, perhaps due to a recruitment effort of original foragers on road **ri**. Holldobler (1976) had similar observations to *Pogonomyrmex* ants in general.

The marked ants of nest N6 showed a high degree of site fidelity (Table 4). Only 21 out of 142 recaptured marked ants of nest N6 deviated from the foraging site (sector **Sc1**, **Sc2**, or **Sc3**) where they had marked during the 3 days after marking. However, after a rich seed source was offered in sector **Sc2**, a relatively large number of ants deviated

Table 1

The distribution of recaptured marked ants on 2 ant roads (**rc** and **rd**) of a *Pogonomyrmex barbatus* nest (N3)

Day	Road rc		Road rd	
	White ^a	Yellow ^b	White ^a	Yellow ^b
Jul 17	26	0	0	30
Jul 18	51	2	2	62
Jul 19	33	1	0	27
Jul 20	29	0	3	42
Jul 21	48	0	0	37
Total	187	3	5	198

a. White: ants which were marked on road **rc**.

b. Yellow: ants which were marked on road **rd**.

Table 2

The distribution of recaptured marked ants on 3 ant roads (**re**, **rf**, **rg**) of a *Pogonomyrmex barbatus* nest (N4)

Day	Road re			Road rf			Road rg		
	Bl ^a	Gr ^b	Or ^c	Bl ^a	Gr ^b	Or ^c	Bl ^a	Gr ^b	Or ^c
Jul 17	24	0	0	0	18	0	0	0	31
Jul 18	47	0	0	0	25	0	0	0	35
Jul 19	45	0	0	0	30	0	0	0	43
Jul 20	37	1	0	0	27	1	0	0	16
Jul 21	56	2	0	2	31	0	0	0	40
Total	209	3	0	2	131	1	0	0	165

a. Bl (blue): ants which were marked on road **re**.

b. Gr (green): ants which were marked on road **rf**.

c. Or (orange): ants which were marked on road **rg**.

Table 3

The distribution of recaptured marked ants on 3 ant roads (rh, ri, rj) of a *Pogonomyrmex barbatus* nest (N5) before and after a rich seed source was offered at the terminus of road ri

Day	Road rh		Road ri		Road rj	
	Yellow ^a	Blue ^b	Yellow ^a	Blue ^b	Yellow ^a	Blue ^b
Before seeds were offered to road ri						
Jul 24	32	1	0	1	0	19
Jul 25	28	0	0	0	0	30
Jul 26	36	0	0	0	0	27
Total	96	1	0	1	0	76
After seeds were offered to road ri						
Jul 27	20	0	13	11	0	22
Jul 28	27	0	9	8	1	28
Total	47	0	22	19	1	50

a. Yellow: ants which were marked on road rh.

b. Blue: ants which were marked on road rj.

from sectors Sc1 and Sc3 to sector Sc2 (Table 4). This deviation might be because that the number of foragers in sector Sc2 increased generally, perhaps due to recruitment effort of original foragers in sector Sc2.

In summary, *P. barbatus* shows a high

degree of road fidelity and site fidelity. The above results conformed Holldobler's (1976) observations to the road-maker *Pogonomyrmex* ants. Although given foragers generally remain associated with given ant roads and foraging areas, they can be directed from one to another.

Table 4

Distribution of recaptured marked ants in three foraging sectors (Sc1, Sc2, Sc3) along sides of road rk of a *Pogonomyrmex barbatus* nest (N6) before and after a rich seed source was offered in sector Sc2

Day	Sector Sc1			Sector Sc2			Sector Sc3		
	Ye ^a	Bl ^b	Wh ^c	Ye ^a	Bl ^b	Wh ^c	Ye ^a	Bl ^b	Wh ^c
Before seeds were offered to sector Sc2									
Jul 31	20	1	1	0	9	1	3	1	23
Aug 1	17	2	1	2	14	1	0	1	16
Aug 2	15	1	3	0	11	1	0	2	17
Total	52	4	5	2	34	3	3	4	56
After seeds were offered to sector Sc2									
Aug 3	5	0	0	18	15	19	0	0	6
Aug 4	9	0	0	8	17	6	1	0	10

a. Ye (yellow): ants which were marked in sector Sc1.

b. Bl (blue): ants which were marked in sector Sc2.

c. Wh (white): ants which were marked in sector Sc3.

Orientation in a strange area

Marked foragers of nest N7 were individually released into herbage away from the ant roads at various distances, from 5-21 m, away from the nest; the homing paths chosen by the ants were traced. All the 8 individually released ants first stood still for a few seconds, then searched around before running off. Most of them continued to keep a straight course nestward for 1-6 m before starting to conduct a zigzag or circular searching (Fig. 3). Throughout the homing path the ants paused very often. Although the ants were released to places, from 5-15 m, away from the roads 6 of the 8 released ants were able to return to the roads within an hour (Table 5) from which they went home to the nest (Fig. 3). The other 2 ants, which were released to places (r1 and r2 in Fig. 3) within 8 m away from the nest, were able to return directly to the nest with a relatively straight path in the vegetation within 14 minutes. Although none of the 8 released ants became lost in the herbage the mean homing speed of these ants,

ranging from 0.28 m/min to 1.02 m/min, was 0.477 m/min (Table 5) which was much slower than when an ant used a road (about 4 m/min, $n=10$).

CONCLUSIONS

Holldobler (1976) has reported that *Pogonomyrmex* ants in general can be stimulated to follow the ant road by the specific trail pheromone along. And this pheromone cue can be eliminated by covering a layer of sand onto the ant road, as it has been previously shown for *P. rugosus* (Holldobler, 1976). Field tests showed that the ants had great difficulty in locating their regular route immediately after the removal of such chemical orientation cue. This result strongly suggested that the trail pheromone on or along the ant road is responsible for a precise road orientation. However field tests have also indicated that visual markers also play an important role in precise orientation along the ant road. The ants, as suggested by Holldobler (1976), might also use a time-compensated orientation to the sun's position or to the pattern of the polarized light of the sky, as it has been previously shown for other species (Jander, 1957). This explains why the ant shows high degree of direction fidelity as shown in the field tests.

P. barbatus showed high degree of road fidelity and site fidelity. This suggests that the workers usually forage in a certain area where they are familiar with. Although given foragers generally remain associated with specific roads, they can be directed from one to another.

As suggested by McCook (1879) that the ant roads are used for communicating with harvesting grounds and facilitate the transport of seeds homeward as can be seen from the orientation of the ants in a strange area (Fig. 3).

Table 5

Orientation tests carried out by 8 *Pogonomyrmex barbatus* ants which were individually released to the herbage at various distances, from 5-21 m, away from the nest (N7)

Ant No.	Releasing point and homing distance from the nest (m)*	Time spent on homing	Mean speed (m/min)
1	R1 (5)	6.9	0.82
2	R2 (8)	13.7	0.73
3	R3 (18)	52.9	0.34
4	R4 (21)	21.0	1.02
5	R5 (19)	63.3	0.30
6	R6 (10)	17.7	0.56
7	R7 (12)	14.2	0.85
8	R8 (16)	42.9	0.28
Total	111	232.6	0.477

* The releasing points are shown in Fig. 3.

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收割蟻 (*Pogonomyrmex barbatus*) 歸巢定方位能力之分析

吳 輝 榮

收割蟻除掉其蟻巢表面上的雜草，清出直徑 1-3 公尺的光禿區，並由此光禿區向外開出 1-6 條平整而達 10-50 公尺長的螞蟻小路。本研究設計各種方法，來分析收割蟻在出外採收種子以及搬種子回巢時是如何定位和定向而不致於在草堆中迷路。研究和觀察指出沿著蟻路上的可見物體以及螞蟻在蟻路上分泌的化學物質是該蟻定位定向的主要依據。此外，有證據顯示該蟻尚能利用陽光的偏光來定向。每隻工蟻通常只沿著固定的某一條蟻路收集種子，更指出工蟻們只在牠們自己熟悉的蟻路上工作。