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Round-the-clock Homing Behavior of a Subsocial Shield Bug, *Parastrachia japonensis* (Heteroptera: Parastrachiidae), Using Path Integration

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Females of the subsocial shield bug, *Parastrachia japonensis* (Parastrachiidae), are central-place foragers, collecting drupes for their young from nearby host trees by walking along the forest floor both during the day and at night. Because burrows are often some distance from the drupe-shedding tree, the bugs must repeatedly leave their burrows, search for drupes, and return to the burrows. After a bug leaves its burrow, it searches arduously until it encounters a drupe. When a drupe is obtained, the bug always takes the shortest route back to its burrow. It has been clarified that this bug utilizes path integration during diurnal provisioning excursions. In this paper, we examined nocturnal behavior and some parameters of the path integration utilized by *P. japonensis*. There were no observable differences between day and night in the patterns of foraging and direct-homing behavior. When the bug was displaced to another position during the day or night, it always walked straight toward the fictive burrow, the site where the burrow should be if it had been displaced along with the bug, and then displayed searching behavior in the vicinity of the fictive burrow. The distance of the straight run corresponded accurately with a straight line between the burrow and the place where the bug obtained the drupe. These results indicate that *P. japonensis* orients toward the burrow using path integration both during diurnal and nocturnal provisioning behavior.

Key words: homing, navigation, path integration, nocturnal foraging behavior, subsocial shield bug

INTRODUCTION

Insects have evolved navigational strategies with various navigational systems to achieve spatial orientation. One of the most advanced strategies is found in central-place foragers such as foraging ants. For instance, in the *Cataglyphis* ants, path integration is the predominant system used in long-distance foraging excursions (Müller and Wehner, 1988). Path integration is a navigational system that relies on indirect cues: on leaving a starting point, such as a nest, an animal updates an accumulator that keeps a running tally of its current direction and distance so that it can always take a direct path back to its starting point (Collett and Collett, 2000). *Cataglyphis* additionally relies on visual landmark-based route memories (Wehner, 1992; Wehner *et al*., 1996). The ants usually follow multi-segment paths by memorizing a series of landmark views, each associated with a local vector (Collett *et al*., 1998; Bisch-Knaden and Wehner, 2001).

Although central-place foraging is a well-studied navigational task, almost all studies have been concentrated on eusocial hymenopteran species (Wehner, 1984; Collett, 1996). In order to advance our understanding of insect navigation, it is necessary to study the mechanisms used in other taxonomic groups.

Several species of subsocial heteropterans forage on the ground and provide food for their young, such as ants do (*Sehirus cinctus*, Sites and McPherson, 1982; *Parastrachia japonensis*, Tsukamoto and Tojo, 1992; *Adomerus triguttulus*, Nakahira, 1994). One such species is *Parastrachia japonensis* (Heteroptera: Parastrachiidae, recently removed from Cydnidae and elevated to family status; Sweet and Schaefer, 2002), a univoltine monophagous shield bug of about 18 mm in length (Tachikawa and Schaefer, 1985). In early June, a female makes an individual shallow burrow under the leaf litter and lays a spherical egg mass. After the nymphs hatch, the female repeatedly leaves her burrow to find drupes from the single host tree, *Schoepfia jasminodora* (Olacaceae: Rosidae: Santales) (Tsukamoto and Tojo, 1992). Once a female has selected a ripe drupe by assessing its odor, taste, and consistency (Nomakuchi *et al*., 1998), it inserts the proboscis into the drupe and drags it back to the burrow. The female must travel far from the burrow to search for drupes because the burrow is usually located > 5

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m, and up to 15 m, from the foraging area (Filippi-Tsukamoto *et al*., 1995; Filippi *et al*., 2001).

In a previous paper (Hironaka *et al*., 2007), we showed that *P. japonensis* uses path integration during daytime, and that it hierarchically uses path integration and chemical cues to complete its provisioning excursion. However, we found that this progressive provisioning behavior occurs regardless of the time of day (Hironaka *et al*., 2003). In the present paper, we report the results of quantitative field observations and experiments on the provisioning behavior of *P. japonensis* that were conducted to investigate some parameters of path integration during day and night, and discuss aspects of the navigation strategy utilized by this heteropteran species, comparing it with that used by ants.

MATERIALS AND METHODS

The study was carried out from mid-June to mid-July, from 1998 to 2000, at Hinokuma-yama, a small, forested hill in Saga Prefecture, Japan (lat. 33°16' N, long. 130°16' E). The experimental site is a secondary forest with a variety of small to large evergreen, deciduous, and perennial shrubs and trees. The environs of the site are mostly agricultural. A study area (15×15 m) was selected on a gently sloping area and transected with twine into a grid with a 1m mesh. A camcorder with a 'night-shot infrared system' (Sony Corp., Tokyo, Japan) was hand-held by an experimenter who followed the subjects for the nocturnal observations. Sixty-four burrows with nesting females were found in the study area in 1998, 40 in 1999, and 56 in 2000. A small flag was placed at the edge of each subject burrow, and females' wings were marked with a synthetic resin (Musashi Holt Products Ltd., Tokyo, Japan) in order to distinguish individual animals and burrows. Diurnal and nocturnal observations and experiments were conducted in the field from 10:00 to 17:00 and from 22:00 to 03:00, respectively.

Paths and orientation directions during foraging and homing trips

We mapped the experimental site at a scale of 1:100 and plotted the provisioning paths of the bugs on this map. The provisioning path consists of two different main paths: the first is the foraging path, taken when the bug searches for a drupe, and the second is the homing path, used when it drags the drupe back to the burrow.

In order to investigate the 'foraging direction', we measured the direction of departure from the burrow at a distance of 50 cm. The burrow was first covered with a clear plastic cup (height 10 cm, diameter 7 cm) for several days, until the female started the provisioning behavior. We checked inside the plastic cup daily to determine whether or not the bug was roaming about, an indication that it was attempting to provision. The insect's initial foraging trip was then recorded, and the general direction was measured. To facilitate the angle measurements, a small flag was placed at the actual point where the bug crossed a circle (50 cm radius) that had been scratched on the ground with compasses, and a piece of twine was drawn between the flag and the burrow. We measured the angle between the twine and the direction to the nearest drupe-producing tree by means of a protractor. If the bug encountered a drupe on this first trip, its 'homing direction', the direction of departure from the point at which the drupe was discovered, at a distance of 50 cm from that point, was measured (initial homing direction). It was common for the bug to repeatedly return to the burrow empty-handed before actually acquiring a drupe. Since it often took several days to encounter a suitable drupe, we checked the burrow several times a day to ascertain whether or not the bug had brought any drupes into its burrow. If the bug had at least one drupe in its burrow, we determined it had successfully started provisioning (experienced bug). The foraging and homing directions of the experienced bugs were also measured as described above.

These angle-measurement procedures yielded results with a precision of 1°, but the data in the figures are presented in 10-degree sectors.

Displacement test

The displacement test was carried out in the homing phase. A foraging bug that had walked more than 2 m from the burrow was gently urged onto a plastic board. A twig was used as a marker to identify where the female on the board had been captured (capture point), and a line of twine was extended to connect the twig and the flag at the burrow. The bug on the board was gently placed on the ground on the opposite side of its burrow, 1 m away, and released (Fig. 1). For the control experiment, a bug was gently urged onto the board, but was replaced at the same point where it had been captured. After being placed on the ground, both control and displaced bugs were immediately given a ripe drupe, after which they initiated homing behavior. We mapped the homing path for 10 minutes and the homing direction of departure from the displaced point at a distance of 50 cm.

The displaced and control bugs showed direct homing behavior, then performed a sharp turn and showed typical searching behavior. To determine whether the displaced bug could estimate distance, we measured the distance between the site of release and the place where the bug showed the sharp turn, and considered this distance as the 'homing distance'. An index of the accuracy of distance estimation was calculated as the homing distance divided by the actual distance from the point of capture to the burrow.

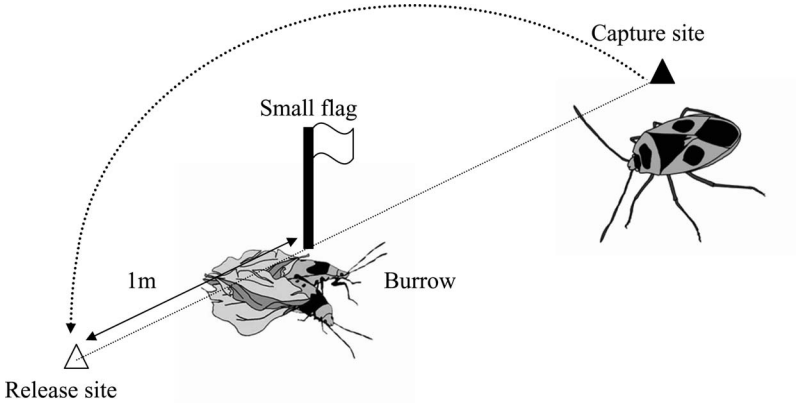


Fig. 1. Schematic drawing of the displacement test. A foraging bug was gently placed on a board and displaced from the point of capture (▲) to the point of release (△) on the opposite side of the burrow (small flag). The displaced bug was given a drupe from the host tree at the point of release, which was 1 m away from the burrow. It then started to travel with the drupe.

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Statistics

Statistical analysis of the distributions of walking directions was performed according to the methods reported by Batschelet (1981). For each distribution, the mean resultant vector was calculated and a *V* test was applied to determine whether the distribution differed from randomness. A Mann-Whitney *U* test was used to test for significance between the mean accuracy of the distance estimation of the control bugs and that of the displaced bugs.

RESULTS

General observations of provisioning behavior during the day and night

Four host trees, *Schoepfia jasminodora*, stood in a cluster in our study area. During the provisioning period of *Parastrachia japonensis*, many drupes from the host trees were scattered over the ground in the crown area (the area of ground directly under the crowns of the four host trees). Many burrows were observed along the periphery of the crown area. Bugs observed in the study area predominantly used these host trees, which we considered for practical purposes to be the equivalent of one big drupe-producing tree. When nymphs were as young as 1st or 2nd instars, provisioning behavior was observed only during the day; however, after the 3rd instar, provisioning behavior was also observed at night.

Foraging, the homing path, and orientation directions

A female first started to search for a drupe after the nymphs hatched. The bug usually failed to find a drupe on its initial trip; sometimes it took a few days to encounter a ripe drupe. Fig. 2A shows a typical round-trip provisioning excursion of an experienced bug. After the first successful trip, the experienced bug left the entrance of its burrow daily to search actively around the host-tree area. When it finally found a suitable drupe, it started to return directly along a

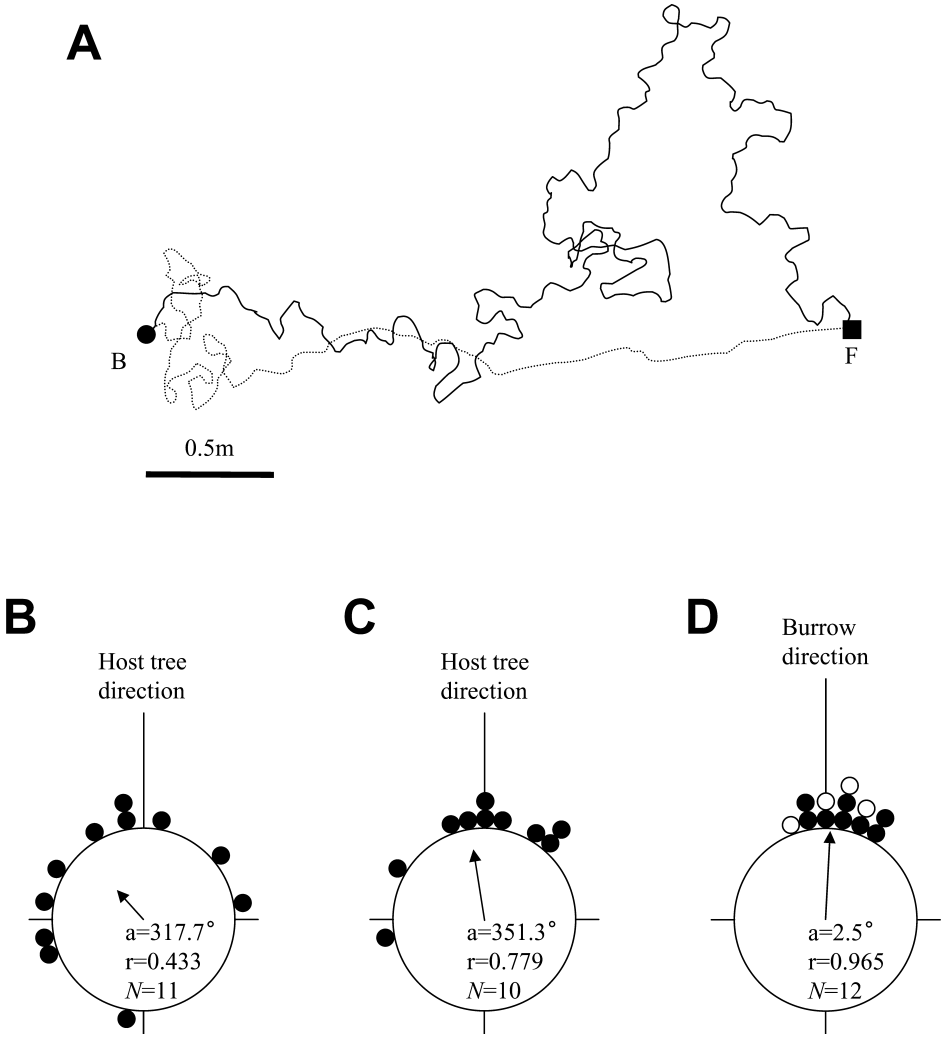


Fig. 2. A diurnal provisioning path and the distribution of foraging and homing directions. **(A)** A typical example of a diurnal provisioning excursion of *P. japonensis* under natural conditions. The solid and dotted lines indicate the foraging and homing paths, respectively. The experienced female searched actively until it encountered a drupe. After accepting a provided drupe, it took a direct route back to the burrow over coarse terrain. B (●), burrow; F (■), location where the bug discovered the drupe. **(B)** Initial foraging directions; **(C)** foraging directions of experienced bugs; **(D)** homing directions of initial and experienced bugs. Orientation angle for each bug is shown as a small circle. The open circles in (D) indicate the initial homing bugs. Arrow indicates mean vector. a, mean angle of orientation; r, length of the mean resultant vector; n, number of animals tested.

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straight path, dragging the ripe drupe to its burrow. When the bug reached the vicinity of its burrow, it stopped the straight run, made a quick turn, and then started searching behavior.

The foraging directions of individuals were measured using initial and experienced bugs. At the initial foraging, the orientation directions from the burrow were randomly distributed (Fig. 2B; *V* test: u=1.502, N=11, P>0.05); in many cases, the female returned to the burrow after failing to find a host drupe. Only a portion of the initial bugs discovered a drupe on their first trip out; these bugs showed a straight run even at the initial homing. After females first successfully acquired a drupe, subsequent foraging directions showed a marked tendency toward the place where they had last encountered a drupe. The foraging directions of experienced bugs were significantly clustered toward the host tree (Fig. 2C; *V* test: u=3.443, N=10, P<0.0001).

Both initial and experienced bugs always took the shortest route back to their burrows. The homing directions of all bugs were significantly clustered around the direction toward the burrow (Fig. 2D; *V* test: u=4.722, N=12, P<0.0001).

At night, provisioning behavior and paths taken were indistinguishable from those during the day (Fig. 3A). Foraging directions measured during nocturnal provisioning showed that most bugs headed for the nearest host tree: the foraging directions were significantly clustered around the direction of the target tree (Fig. 3B; *V* test: u=4.100, N=10, P<0.0001). The homing directions were significantly clustered around the direction to the burrow (Fig. 3C; *V* test: u=5.401, N=16, P<0.0001).

Displacement test

Bugs walked in a convoluted path on the foraging trip, but always took the shortest route for the homing trip. These results strongly suggest that this direct homing run is based on path integration. To confirm whether the female uses

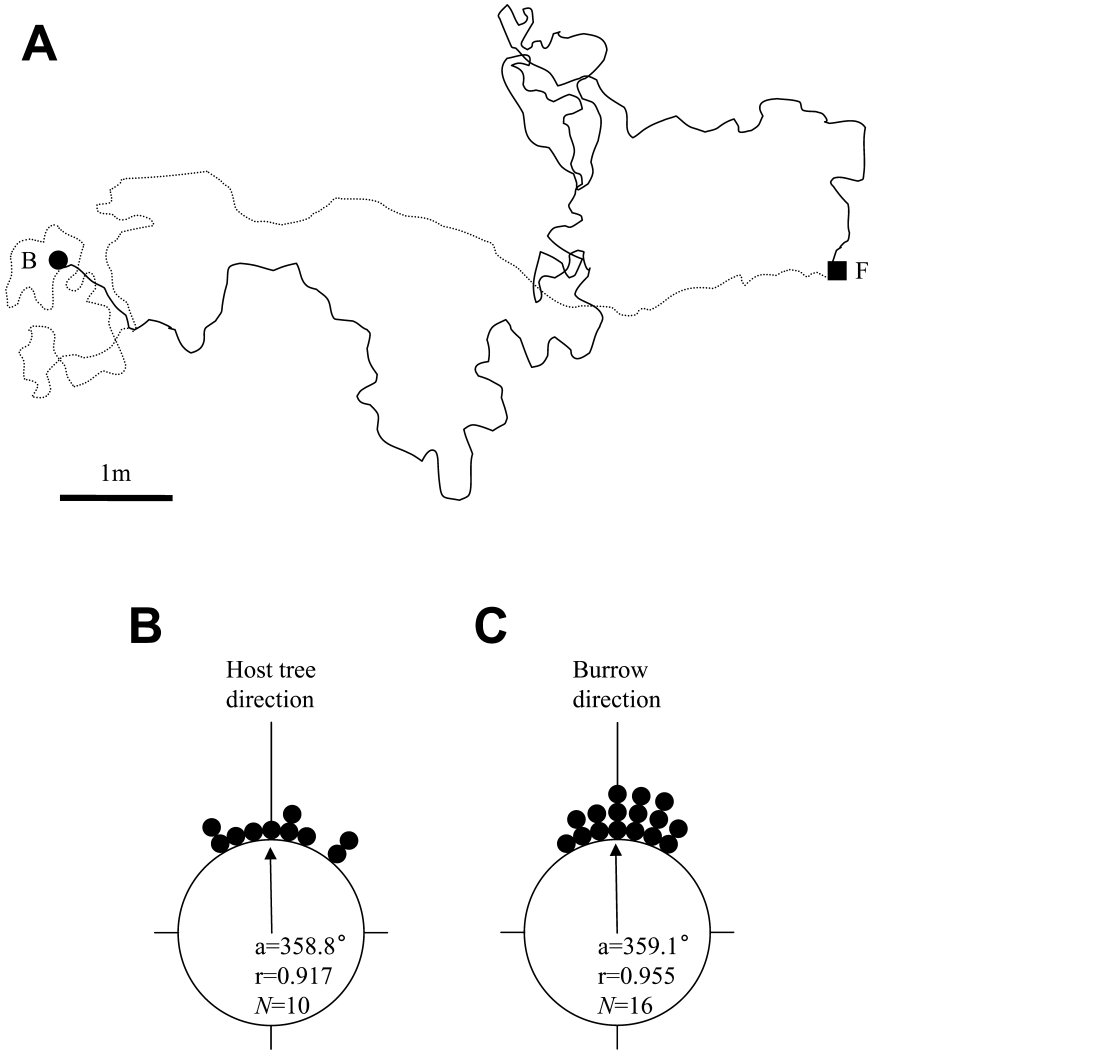


Fig. 3. A nocturnal provisioning path and the distribution of foraging and homing directions. **(A)** A typical example of the nocturnal provisioning excursion of *P. japonensis* under natural conditions. Continuous and dotted lines indicate foraging and homing paths, respectively. B (●), burrow; F (■), location where the bug discovered the drupe. **(B)** Nocturnal foraging directions. **(C)** Nocturnal homing directions. The orientation angle for each bug is shown as a small circle. Arrow indicates mean vector. a, mean angle of orientation; r, length of the mean resultant vector; n, number of animals tested.

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path integration in the provisioning excursion, a displacement test was carried out. There were no differences in homing behavior between control bugs in the displacement test and bugs under natural conditions during day and night. The experimental bug was gently captured and displaced to a site on the opposite side of its burrow (Fig. 1). During the daytime, the bug did not head for the true burrow, but headed in the direction of the fictive burrow, that is, where the burrow should have been if it had been displaced along with the bug. When a female had walked almost the same distance as that between the site of capture and her true burrow, she showed the quick turn and then typical searching behavior (Fig. 4A). The homing directions were significantly clustered around the direction toward the fictive burrow (Fig. 4B, *V* test: u=4.379, N=10, P<0.0001).

The displacement test was also performed at night. The homing behavior of bugs displaced at night was indistinguishable from that observed during the day (Fig. 5A). The homing directions were significantly clustered around the direction of the fictive burrow (Fig. 5B; *V* test: u=4.315, N=10, P<0.0001).

Because both displaced and control bugs walked nearly the same distance from the point of release, which was essentially the same distance as that between the point of capture and the burrow, and both initiated searching behavior during the day and night, we calculated an index of the accuracy of distance estimation. A mean index close to 1 indicates the bug has a very high accuracy of distance estimation. The distances between the points of capture and the burrows ranged from 2.0 to 7.1m. There was no significant

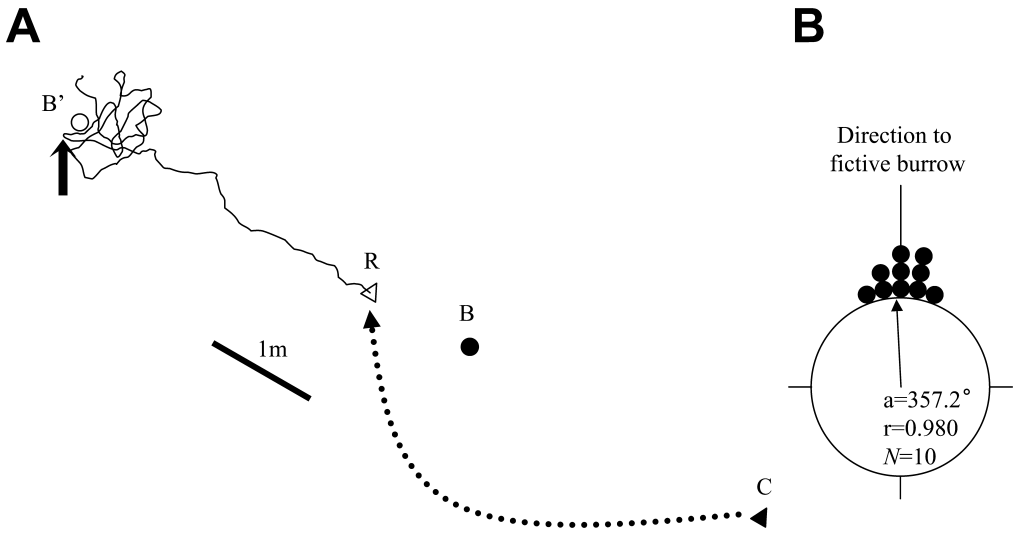


Fig. 4. Homing path and distribution of homing directions in a diurnal displacement test. **(A)** An example of the homing path for 10 minutes. B (●), burrow; C (▲), point of capture; R (△), point of release; B' (○), location of fictive burrow (approximately 180° from true burrow site). The bug was displaced from C to R (curved arrow). The arrow indicates the point where the bug initiated searching behavior. **(B)** Distribution of homing directions of the displaced bugs (for explanation, see legend for Fig. 2).

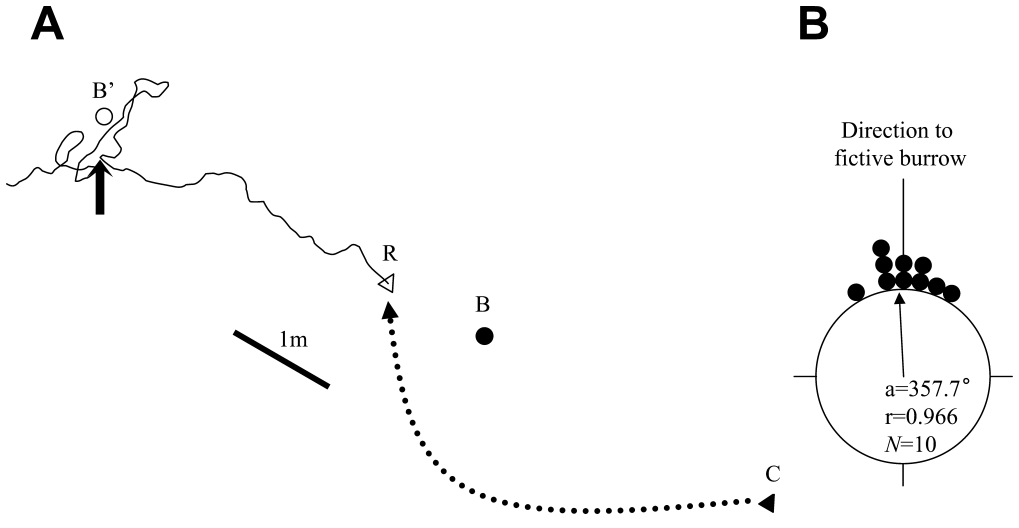


Fig. 5. Homing path and distribution of homing directions in a nocturnal displacement test. **(A)** An example of the nocturnal homing path for 10 minutes. **(B)** Distribution of nocturnal homing directions of the displaced bugs (for explanation, see legends for Figs. 2 and 4).

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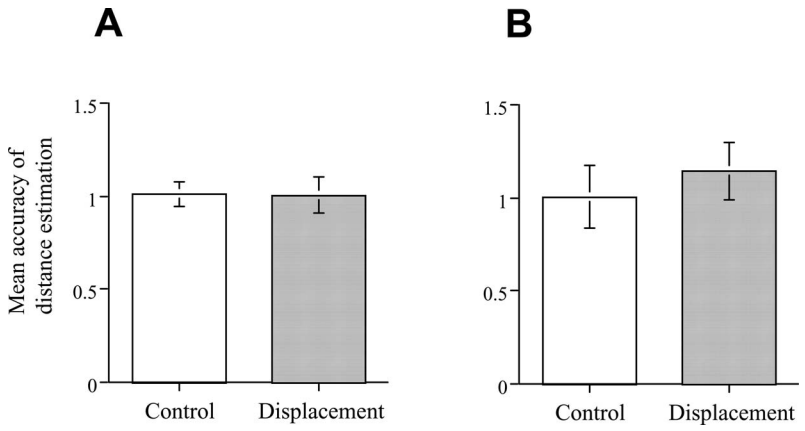


Fig. 6. Accuracy of distance estimations of homing bugs **(A)** during the day and **(B)** at night. An index of the accuracy of distance estimation is shown as the homing distance divided by the actual distance from the point of capture to the burrow (see Methods). Mean values with SD (vertical bars) are represented in the histogram.

difference in the mean indices of control and displaced bugs during the day (approximately 1.01 for both; Fig. 6A; Mann-Whitney *U* test=63.5, *N1*=*N2*, *P*=0.6209). At night, the index of accuracy of distance estimation for the displaced bug was about 1.14, only marginally significantly different from the control (approximately 1.00 for control bugs; Fig. 6B; Mann-Whitney *U* test=14, *N1*=*N2* *P*=0.0587). The distance estimations of the displaced bugs were accurate during both day and night.

DISCUSSION

It has been proposed that systems used in long-distance navigation are of three types: the route-following system, the route-integration (path integration) system, and the geocentric system (Wehner and Wehner, 1990; Wehner *et al*., 1996). These navigational systems for foraging and homing have been widely investigated in ants. Many species of ants usually rely on the route-following system using a pheromone trail to orient (Hölldobler and Wilson, 1990). The forager deposits a chemical substance as a trail during the foraging trip and traces the trail back home. In the present study, we observed that *P. japonensis* never traced back along its foraging path during homing, suggesting that it does not rely on a pheromone trail. In the geocentric system, also known as the landmark system, ants determine their current position in relation to acquired geocentric information, such as memorized landmarks (Collett, 1992). Accordingly, if an animal utilizing landmarks is displaced in a familiar place, it can compensate by redirecting toward the homeward course and correctly orient toward the goal (Fukushi, 2001). However, *P. japonensis* could not orient toward its burrow, even when it was displaced in a familiar place.

Path integration has been discovered in a wide variety of animals; ants and honeybees are the best examples among insects. Experimentally displaced homing ants using path integration orient to a fictive place where the nest should be if it had been displaced along with the ants, because they continually update a 'home vector', which at any point indicates the homing direction and the distance to the goal (Wehner and Srinivasan, 1981). In the present study, displaced bugs chose a course parallel to their predisplacement course (Figs. 4, 5) and walked for a distance equivalent to the predisplacement distance (Fig. 6). These field observations and displacement tests provide clear evidence that *P. japonensis* females use path integration as a navigational system to return to their burrows during both day and night.

Path integration requires a compass by which the insect can measure the angular components of its movement; what compass is the bug actually using? It is known that insects are able to use the sun (Santschi, 1911; Hölldobler, 1971), polarized skylight (Duelli and Wehner, 1973; Wehner, 1984), or magnetism (Lindauer and Martin, 1968) in the daytime, and the moon (Jander, 1957; Klotz and Reid, 1993) or polarized moonlight (Dacke *et al*., 2003) at night, as compass references. Both in the day and at night, when the compound eyes are screened with silver paste, the bugs can not orient to their burrows (Hironaka *et al*., 2003). If bugs always rely on celestial compass cues, it is reasonable to assume that there should be differences between day and night in terms of accuracy, because celestial cues by night are probably considerably more difficult to use than by day from the forest floor. In daytime displacement trials, the bugs' estimation of both direction and distance was almost perfect, but even in displacement trials at night, their rate of error remained relatively low. It is thus reasonable to assume that the forest canopy is used as a compass cue. Even at night, the forest canopy was visible as a dark silhouette on a grayish sky in our experimental area.

The navigational strategy of path integration used by *P. japonensis* is very interesting from two aspects of insect navigation. The first is round-the-clock utilization of path integration based on visual cues. Previously, we reported that *P. japonensis* individuals forage throughout the day and night, determining the homing direction visually (Hironaka *et al*., 2003), and this study revealed that they performed provisioning excursions using path integration 24 hours a day. The second interesting aspect of the navigational strategy of *P. japonensis* is the environment where it navigates while provisioning. Navigational systems of insects are dependent on the insects' individual habitats, because each environmental structure limits the utilizable cues. For instance, in *Cataglyphis* ants, which inhabit largely feature-

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less areas, path integration generally supersedes landmark cues in competition experiments (Wehner *et al*., 1996). In such an unobstructed environment, long-distance cues such as celestial cues would probably be more useful than terrestrial landmarks. In contrast, in a closed and crowded environment, insects cannot easily detect long-distance cues because of structural impediments. Many species of ants that inhabit woodlands use landmarks as their navigational system rather than path integration. In particular, use of the canopy pattern as landmarks is well known (Hölldobler, 1980; Baader, 1996; Ehmer, 1999; Fukushi, 2001). Despite living in a closed environment, *P. japonensis* use path integration, rather than landmarks.

This unique navigation might have evolved in response to ecological factors, such as environmental structures, food distribution, or sparse availability of the food supply, that might require mechanisms that support round-the-clock provisioning to sustain nymphs, or it might reflect phylogenetic differences. Analysis of the navigation system of *P. japonensis* could provide us with an interesting model that will facilitate our understanding of the types of biological factors that are important for the evolution of navigational systems in insects.

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