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SHORT COMMUNICATION

Canopy compass in nocturnal homing of the subsocial shield bug, *Parastrachia japonensis* (Heteroptera: Parastrachiidae)

Mantaro Hironaka · Koichi Inadomi ·
Shintaro Nomakuchi · Lisa Filippi · Takahiko Hariyama

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Abstract In contrast to an open environment where a specific celestial cue is predominantly used, visual contrast of canopies against the sky through the gap, known as canopy cues, is known to play a major role for visually guided insect navigators in woodland habitats. In this paper, we investigated whether a subsocial shield bug, *Parastrachia japonensis*, could gauge direction using canopy cues on a moonless night. The results show that they could perform the round trip foraging behaviour even in an experimental arena with only an artificial round gap opened in the ceiling of the arena and adjust their homing direction for a new azimuth when the gap was rotated. Thus, *P. japonensis* can use slightly brighter canopy cues as a compass reference but not complex landmarks during nocturnal homing behaviour.

Keywords Canopy orientation · Navigation ·
Nocturnal foraging · Subsocial shield bug ·
Parastrachia japonensis

M. Hironaka (✉) · T. Hariyama
Department of Biology, Faculty of Medicine,
Hamamatsu University School of Medicine,
Handayama 1-20-1,
Hamamatsu, Shizuoka 431-3192, Japan
e-mail: kd0334@hama-med.ac.jp

K. Inadomi · S. Nomakuchi
Department of Applied Biological Sciences,
Faculty of Agriculture, Saga University,
Honjo 1,
Saga 840-8502, Japan

L. Filippi
Department of Biology, Hofstra University,
Hempstead, NY 11549, USA

Introduction

Insect navigators, such as ants inhabiting a woodland, quickly find their way back to their nests. In this type of dense habitat, the view of the sky is mostly blocked by the leaves of the forest canopy. Therefore, celestial cues, such as direct sun and moon cues, can probably not be used for orientation. On the other hand, visual contrast between the sky through the gap and the canopies (canopy cues) might provide navigators with stable clues; thus, upward and/or overhead canopy cues allow various forest-dwelling ants to orient during their provisioning trips (Hölldobler 1980; Oliveira and Hölldobler 1989; Baader 1996; Ehmer 1999).

Females of the subsocial shield bug, *Parastrachia japonensis* (Heteroptera: Parastrachiidae) forage on the floor of a heavily wooded forest and provide food to nymphs in their burrows (Tsukamoto and Tojo 1992; Filippi et al. 2001). The provisioning females tortuously leave their burrows to find drupes around the host tree site by walking and, upon finding a drupe, home directly back to the burrow using path integration (Hironaka et al. 2007a, b). These provisioning behaviours are observed during the day and night under several weather conditions in early summer (Hironaka et al. 2003). Nocturnal provisioning could be observed only five nights during the field season; a displacement test and an eye-painted test revealed that the bugs use path integration based on visually guided orientation (Hironaka et al. 2003, 2007b).

Because the foraging area of *P. japonensis* is covered with a dense canopy, direct celestial cues are likely to be unreliable, especially at night. In this study, we investigated whether *P. japonensis* females use visual cues from the canopy in nocturnal homing behaviour.

Materials and methods

For the experiments, we collected seventy *P. japonensis* females guarding their egg masses from the field site, Hinokuma-yama, a small, forested hill in Saga Prefecture, Japan (33°20′N, 130°21′E), in June 2006. The collection site is a secondary forest with a variety of small and medium-sized deciduous and evergreen bushes and trees. Several tall deciduous and evergreen trees provide a dense and complex canopy pattern. Each egg-guarding female was reared in a clear plastic cup (diameter 8 cm; height 4 cm) lined with substrate (soil and leaf litter) at 22°C in an incubator. The cup was covered with a plastic lid to prevent escape. After nymphs hatched, we continued to rear them together with their mother and ripe drupes of the host tree, *Schoepfia jasminodora*, until they reached the third stadium. We turned the lights on at 5:00 and off at 19:00 (14:10, light/dark), a light regime that corresponded with dawn and dusk in the natural condition of the reproductive season.

We conducted experiments from late June to early July in an experimental arena (3×3 m and 2 m high, see Fig. 1), which was set on the ground on the campus of Saga University. The floor was covered with soil and divided by a 50-cm grid of yellow lines that allowed us to record each bug's path on a reduced scale. The walls and ceiling were covered with dark blue plastic boards. We cut a hole (diameter 90 cm) at one side of the ceiling to simulate a canopy gap in the natural habitat (Fig. 1). We chose a dark place to set the experimental arena without artificial lighting; therefore, the experimental animals in the arena could only see the night sky through the gap. Cloudy nights were chosen as the weather conditions in all experiments because the bugs could not see the moon and stars in the sky. The light intensities in the arena were measured using a radiometer (LM-331, As One, Osaka, Japan). At ground level, the highest illumination was 0.05 lux just below the gap and did not exceed 0.01 lux at any other point in the arena. These light intensities were nearly equal to those on a cloudy night at the open site, just under the canopy on the forest floor that the experimental population originally inhabited. Temperature during all experiments was 24±2°C.

We set a 50-cm^2 feeding site at the centre of the arena containing ten ripe drupes on the floor. The burrow-containing lidded cups with reared bugs were divided into four positional groups, a, b, c and d (Fig. 1), each position being one meter from the centre of the arena. At the time of experimentation, a cup was set at each of the positions, but only one female was allowed to provision at a time.

The experiments were conducted at night from 22:00 to 3:00. To facilitate nocturnal observations, a camcorder with a 'Night Shot Infrared System' (HDR-HC3, Sony, Tokyo, Japan) was handheld by an experimenter who followed the subjects. The experimenter stood at the corner of the arena and frequently changed position. Each female's hemielytron was marked with a synthetic resin (Musashi Holt Products, Tokyo, Japan) for individual discrimination. In all experimental trials, we used bugs that had not yet experienced leaving the burrow to forage and used each individual only once.

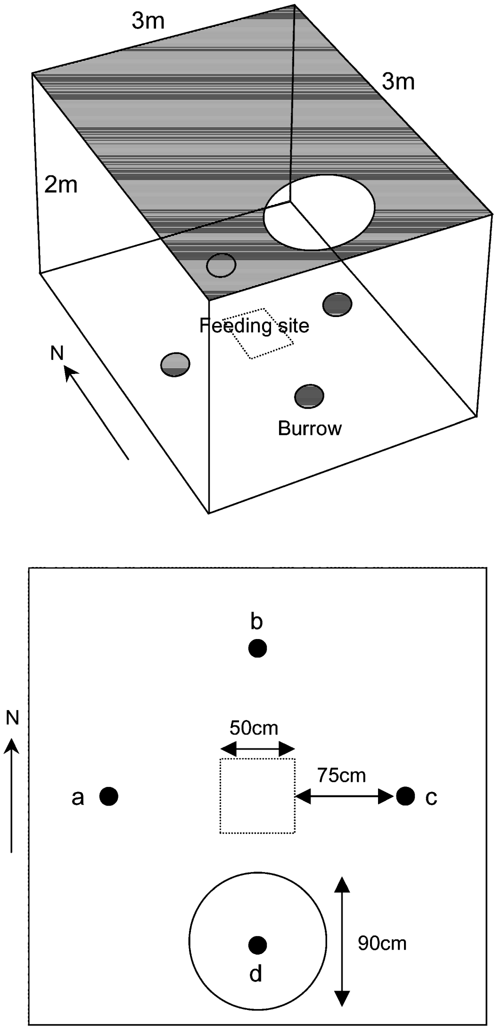

Fig. 1 Schematic representation of the experimental arena. The walls and ceiling were made of dark blue plastic board. A round hole (diameter 90 cm) simulating a canopy gap was opened in the ceiling; initially, it was positioned south from the centre of the arena. A square feeding site (one side, 50 cm) containing several drupes was located in the centre of the arena. The experimental burrows were set on the floor 1 m from the centre of the feeding site and grouped into four positions (*a*, *b*, *c* and *d*)

As a control experiment, we first observed whether bugs could orient towards their own burrows on homing in this experimental arena. When the lid of a cup set at one of the four positions was removed, the female spontaneously started the provisioning trip for its young, showing the wandering path of movement. After the female reached the feeding site, we placed a metal marker at the point where it found a drupe and scratched a circle of 50 cm in diameter with a compass set at the marker. When the bug started homing and crossed the perimeter of the circle, we measured the angle between the line from the burrow to the marker and the line from the marker to the crossing point on the circle. If the bug did not reach the feeding site within 15 min or took a wide detour from the direct outbound course, we ceased the trial and omitted it from the data. These criteria were used for all observations.

Next, we observed whether bugs homed back based on the position of the canopy gap. When a female reached the feeding site and found a drupe, we immediately rotated the plastic board of the ceiling by 180° and observed the bug's homing behaviour. To see whether they correctly oriented towards the burrow, we measured the angle using the same method described above.

Statistical analysis of the distributions of walking directions was performed according to the methods reported by Batschelet (1981). For the distribution, the mean resultant vector was calculated, and a V test was applied to determine whether the distribution differed from randomness.

Results

The bugs in three groups, with their burrows set at the left (a group), right (c group) and opposite (b group) side of the feeding site from the gap in the experimental arena, foraged tortuously until they encountered a ripe drupe, then walked directly back to their burrows, dragging the drupe. In these three groups, no behavioural differences were observed in the provisioning excursions. The homing directions of these bugs were significantly clustered towards their own burrows (Fig. 2a; V test: $u=4.578$, $N=12$, $P<0.0001$). On the other hand, the homing directions of the bugs with their burrows set under the gap (d group) were scattered. As soon as a bug started to home, it showed wandering behaviour mainly around the feeding site; therefore, the homing directions were statistically indistinguishable from random (Fig. 2b; V test: $u=0.533$, $N=8$, $P>0.10$).

Under the experimental condition, the canopy gap was rotated to the opposite side of the homing course while the bugs in groups a–c were checking the drupe at the feeding site. When the bugs started to home, they chose the opposite direction and moved away from the burrow, maintaining their initial angle to the gap. After walking almost the same homing distances, the bugs showed the typical burrow-searching behaviour (Fig. 2c). The homing directions of these experimental bugs were significantly clustered towards the opposite direction of the burrow (Fig. 2d; V test: $u=4.146$, $N=12$, $P<0.0001$).

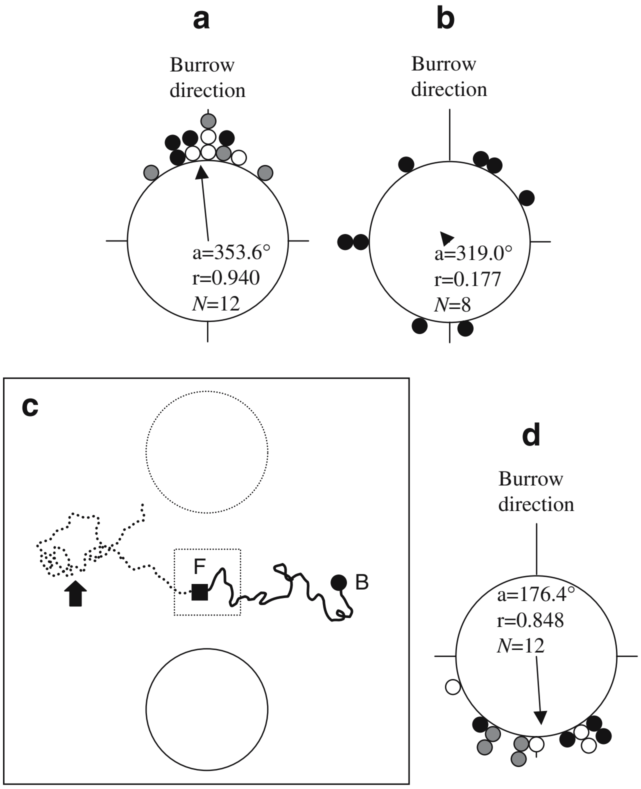

Fig. 2 **a** Distribution of homing directions of control bugs whose burrows were set away from the gap. *Small circles* on the circular graphs indicate orientation angle of each bug. We established the direction from the burrow to the feeder as being 180° and that from the feeder to the original burrow as 360° and apply these criteria to all four burrow positions. The *white*, *grey* and *black circles* indicate the position of the burrows set at the left (a group), right (c group) and opposite (b group) side of the feeding site from the gap in the experimental arena in Fig. 1, respectively. *Arrows* indicate mean vectors. *a* Mean angle of orientation, *r* length of the mean resultant vector, *N* number of animals tested. **b** Distribution of homing directions of bugs in group d, whose burrows were under the gap. **c** A typical homing path of a bug after gap rotation. An experimental female in group c was exposed to a positional change of 180° from the *solid-line circle* to the *dashed circle*. The *solid line* indicates the foraging trajectory, and the *dashed line* indicates the homing trajectory. It turned 180° and took a direct route towards the fictive burrow. *B* (*black circle*) Burrow, *F* (*black square*) point where the bug discovered the drupe. *Arrow* indicates the position of the fictive burrow. **d** Distribution of homing directions in bugs in three groups, with their burrows set away from the gap when the gap was rotated. The *white*, *grey* and *black circles* indicate the position of the burrows in a, b and c, respectively

Discussion

Homing *P. japonensis* perform their diurnal and nocturnal provisioning behaviour using visually based path integration from the feeding site to the vicinity of their burrow (Hironaka et al. 2003; Hironaka et al. 2007a, b); however, the details of the visual cue itself remained controversial. We showed here that the nocturnal homing bug followed the rotation of the artificial canopy gap on a cloudy night.

This suggests that visual cues from the canopy are indeed the predominant directional cues for homing bugs, at least for nocturnal provisioning trips.

How do the bugs use the canopy cues? Homing bugs in groups a–c could orient well and headed towards the menotactical direction instead of the original home direction when the gap was rotated (Fig. 2c and d). This experiment strongly suggests that *P. japonensis* can use the canopy gap as a light compass reference. For angle measurement in the light compass, insects refer only to the azimuth of the light source and not to its elevation (Wehner 1984), therefore, the light compass is useless when the light source is placed in the zenith, or its zenithal angle is indistinguishable from 0° (Lindauer 1957; Duelli and Wehner 1973). We observed the homing behaviour in a spatial configuration such that the gap was directly in the zenith (group d). The path of these bugs contained numerous twists and turns, and they clearly lost the homing direction even in the control condition (Fig. 2b). This finding also supports the hypothesis that *P. japonensis* can use a canopy gap as a compass reference.

We assume that the canopy gap is unstable as a compass reference because it is not at infinity and is subject to the phenomenon of motion parallax. Considering the navigational scale of *P. japonensis*, however, with the direct distance between the burrow and the foraging site generally being no more than about 5 m (Filippi-Tsukamoto et al. 1995), the motion parallax may have only a slight influence on their orientation. The highest tree heights in the foraging area of our experimental population were about 10–12 m. By selecting a canopy gap that is far from the burrow and not directly overhead in their complex canopy hemisphere, the bugs may obtain suitable angle information from the canopy gap.

The navigational strategy whereby diurnal ants use canopy cues for orientation is known as canopy orientation (Hölldobler 1980). Oliveira and Hölldobler (1989) demonstrated that the complex canopy pattern of radial stripes above the Neotropical ant, *Odontomachus bauri*, provides a major visual orientation cue. It is unclear whether *P. japonensis* use a single canopy gap in the daytime and the complex canopy pattern; further investigations are needed to clarify these points.

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