



## ARTICLES

# Hierarchical use of chemical marking and path integration in the homing trip of a subsocial shield bug

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The female shield bug *Parastrachia japonensis* provisions its young by dragging fruit to its burrow. Field observations showed that the bug took a winding path when searching for a suitable fruit, but took the shortest route when homing to the burrow. Displaced homing bugs always walked straight towards the fictive burrow, suggesting that they use path integration to orient. After a homing bug neared the entrance of its burrow, it stopped and started beating the surface of fallen leaves with its antennae. To determine whether these bugs use navigational cues other than those used for path integration, when in the vicinity of the burrow, we blocked their sensory organs and presented them with their own burrows in a laboratory experiment. Although nearly all bugs whose eyes had been blocked found their burrows, the antennae-blocked bugs did not. Homing bugs encountering various experimentally manipulated burrows, such as those containing their own nymphs with an alien burrow's substrate or their own burrow's substrate with alien nymphs, entered burrows only if they were made of the original substrate. When we presented bugs with their own burrows along the homing route, they entered their burrows at every homing point, even at the earliest stage of the homing process. These results suggest that the chemical cues marked around a female's burrow can suppress the use of path integration, and that *P. japonensis* uses cues hierarchically to accomplish precise homing.

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Long-distance navigators face the problem of heading towards a point-like goal, which they cannot detect directly along the homing path. To cope with this problem, navigators choose a navigational system according to the distance to the goal (Dyer 1998). Among insects, navigation by the solitary forager ant, *Cataglyphis*, has been extensively investigated. *Cataglyphis* ants forage individually, making long excursions that extend as far as 200 m (Wehner 1987). They use two complementary

navigational systems to reach the nest. The first is path integration (Wehner & Srinivasan 1981; Müller & Wehner 1988; Collett et al. 1999; Wehner et al. 2002): while searching for food, the ant keeps a running total of its distance and direction from the nest so that it always has a vector pointing home. However, this mechanism is not perfect, and it is supplemented by the ants' second system that of piloting by familiar landmarks (Wehner & Rüber 1979; Collett et al. 1992; Collett 1996). Once the home vector has brought an ant close to its nest, the entrance is pinpointed by means of visual landmarks. The ant is drawn to its goal by a process of image matching: it moves so as to maximize the fit between the present retinal image and its memory of the landmarks as seen from the nest entrance.

Like ants, the female of the subsocial shield bug *Parastrachia japonensis* (Heteroptera: Parastrachiidae, recently

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removed from the Cydnidae and elevated to family status; Sweet & Schaefer 2002) forages on the forest floor and provides food to its nymphs. In mid-June, after the nymphs hatch, the female leaves its burrow to find drupes, fallen fruits with a hard stone-like endosperm, from the single host tree, *Schoepfia jasminodora* (Olacaceae: Rosidae: Santales) (Tachikawa & Schaefer 1985; Tsukamoto & Tojo 1992). The burrow is usually more than 5 m from the foraging area (Filippi-Tsukamoto et al. 1995; Filippi et al. 2001). After the bug leaves its burrow, it searches arduously until it encounters a drupe (foraging). When a drupe is obtained, the bug always takes the shortest route back to its burrow (homing; Hironaka et al. 2003a, b). This direct homing behaviour suggests that the bug uses path integration, but this has not been confirmed.

After the straight run towards its burrow, the bug reaches the vicinity of its burrow and starts to wander, as if searching for the burrow entrance (Hironaka et al. 2003a). The burrow is made under leaf litter on the forest floor, and its small entrance opens through the fallen leaves. Because there is no obvious and distinct structure, such as the mound that ants build, at the entrance (Tachikawa & Schaefer 1985; Tsukamoto & Tojo 1992), it seems unlikely that the bug could orient by using visual landmarks. Nevertheless, it must somehow find the entrance of its own burrow, which is visually featureless, in the last stage of homing. Does the bug merely wander until it encounters the entrance during searching behaviour, or does it use another navigational cue? We investigated whether *P. japonensis* females use path integration and how they search for their burrows during the last stage of the homing process.

## METHODS

### Field Observations

We carried out field observations of homing behaviour from mid-June to mid-July 1998 at Hinokuma-yama, a small, forested hill in Saga Prefecture, Japan (33°16'N, 130°16'E). The site is a secondary forest with a variety of small to large evergreen, deciduous and perennial shrubs and trees. A study area (15 × 15 m) was selected, on a gently sloping area, and transected with twine into a grid with a 1-m mesh. We found 64 burrows with nesting females in the study area in 1998. A small flag was placed at the edge of each burrow, and the females' wings were marked with a synthetic resin (Musashi Holt Products Ltd., Tokyo, Japan) to distinguish each bug and burrow. We mapped the experimental site at a scale of 1:100 and plotted the provisioning paths of the bugs on this map. Observations were conducted in the field from 1000 to 1700 hours.

We also observed the homing behaviour of 10 displaced bugs. A foraging bug that had walked more than 2 m from its burrow was gently urged on to a plastic board. We used a twig as a marker to identify where the female on the board had been captured (capture point), and we connected the flag at the burrow and the twig with twine. The bug on the board was gently placed on the opposite side of, and 1 m away from, its burrow and released. We immediately gave the bug a ripe drupe, after which it

initiated homing behaviour. We mapped the homing path for 10 min after the bug started to walk.

### Laboratory Experiments

For the laboratory experiments, we collected *P. japonensis* in reproductive diapause phase from our experimental field site, during March 2000 and 2002. We terminated the reproductive diapause of these bugs by maintaining them for 5 months at 5°C in total darkness, followed by 1 week at 15°C and 4 weeks at 25°C on a 16:8 h light:dark regime, in clear plastic cages (20 × 12 cm and 12 cm high); only water in moistened cotton pads was provided. After the bugs showed increased movement and increased excretion, we concluded that they were active and allowed them to mate in a meshed cage (40 × 25 cm and 30 cm high) at 25°C in a 16:8 h light:dark regime. We placed mated females in clear plastic cages (20 × 12 cm and 12 cm high) and supplied them with drupes from the host tree, *S. jasminodora*. Gravid females (those with a clearly swollen abdomen) were transferred to individual lidded, clear plastic cups (diameter 8 cm; height 4 cm) lined with substrate (soil and fallen leaves), where they each deposited an egg mass that they guarded.

We conducted experiments during the daytime in a temperature-controlled room (8 × 3 m and 2.5 m high) maintained at 20 ± 2°C under natural light conditions. The floor was covered with soil and fallen leaves, simulating the environment of the natural forest floor. A large square window (1.8 × 1.8 m) with clear plate glass, through which the experimental bugs could see natural light, was situated in the middle of one of the 3-m walls. The remaining three walls and the ceiling were covered with a blackout curtain. There was no artificial light source in the room. After a female's eggs hatched, it started to provision its young: the female left the experimental plastic burrow to forage, and returned to the burrow with a drupe provided by an observer (described below). The plastic cup containing the female and her burrow had been previously set into the artificial 'forest substrate' on the floor of the experimental room, and the lid was removed to allow foraging at the start of each trial. Before the experiments, we mapped the homing paths of each female for the undisturbed and displaced conditions in the experimental room. All individuals showed the typical direct homing behaviour to both the actual and fictive burrows.

We carried out the following three experiments using females with third-instar nymphs. For each experiment, we observed whether the homing female could successfully enter its burrow. In all experiments, differences between each experimental condition were analysed with Fisher's exact probability test. After the study, nymphs were reared to adults and released in the wild.

### Experiment 1: Sensory Blocking

To identify which sensory organ a bug uses for homing navigation in the vicinity of its burrow, we blocked the eyes and/or antennae during the wandering phase of homing. The experimental burrow containing the female and nymphs was set on the floor in the experimental

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