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The Directional Homing Behaviour of the Subsocial Shield Bug, *Parastrachia japonensis* (Heteroptera: Cydnidae), under Different Photic Conditions

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ABSTRACT—The female subsocial shield bug, *Parastrachia japonensis*, provisions its nymphs by foraging on the ground in the forest during the Japanese rainy season, and the bug uses homing navigation to drag a drupe back to its burrow by the shortest route during the day. To study whether or not this bug performs this provisioning behaviour under different photic conditions, we observed the homing behaviour and homing direction of bugs in the field around the clock and/or under various weather conditions. The bugs foraged the whole day during the busiest provisioning period, and the number of walking bugs was not affected by the different weather conditions. Such navigational behaviour, regardless of the time of the day and the weather conditions, is rare in insect navigation. To test whether the bug uses visual cues, we covered the compound eyes and ocelli with opaque or clear paint just before homing began. During the day and at night, and in all weather conditions, the homing direction of blind bugs, but not those with clear-painted eyes was disoriented, indicating that this species uses visual cues dominantly under all photic conditions.

Key words: Heteroptera, homing, navigation, orientation, visual cue

INTRODUCTION

Homing is one of the most fascinating phenomena of spatial behaviour in the animal kingdom. Even micro-brain navigators exhibit amazing powers of homeward orientations. The most intensively studied micro-brain navigators are social insects, such as ants, bees and wasps. They construct their own colony, then forage continually from the site of the colony to retrieve food from widely scattered sources. During foraging, away from their own colony, and homing, these insects cannot detect their goals directly and instead rely on several environmental cues. Navigational systems using environmental cues for long-distance navigation can be classified roughly into three different groups, based on trail pheromones, landmarks and path integration. Many species of ants usually deposits a chemical substance, the trail pheromone, which is used both for locating a food source and for homing (Hölldobler and Wilson, 1990). Landmarks can provide insects with geo-stable information: Ants and bees are able to store landmark scenes in memory as visual snapshots (Collett, 1996). Path integration has come to be known as “dead reckoning”: On leaving the colony, an insect updates an accumulator that keeps a running tally of its current direction and distance from the starting point so that it can always take a direct path back to its colony (Collett and Collett, 2000). These studies using insects have revealed substance of remarkable navigational systems, however, little is known about the performance of these systems in different environments.

Recently, Hironaka *et al*. (2001) found that adult females of the subsocial shield bug *Parastrachia japonensis* (Heteroptera: Cydnidae) perform long-distance navigation. In early June, each female makes an individual shallow bur-

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row under leaf litter and lays an egg mass. After the first nymphs hatch, the female leaves her burrow in search of drupes, from the tree *Schepfia jasminodora* to feed to the nymphs (Tsukamoto and Tojo, 1992). Because its burrow is often at some distance from the host tree (up to 15 m away; Filippi-Tsukamoto *et al*., 1995; Filippi *et al*., 2001), the female cannot directly detect its burrow entrance when visiting the host tree. This female bug has consequently acquired a remarkable navigational behaviour. When the bug leaves her burrow, she follows a tortuous foraging path until she encounters a drupe. Once a ripe drupe has been selected, the female inserts her proboscis into the drupe and drags it back to the burrow.

During the various stages of nymphal development, an adult female *P. japonensis* must collect many drupes to provide food for her growing nymphs. It continues, alone, for about ten days to raise its nymphs in the rainy season, during which the environmental cues in woodland might be easily changed. What cues does the bug use in such changeable conditions? Observations were performed to investigate whether the bug collects food during the whole day and/or under any weather conditions, and how she navigates under those conditions. The field observations on the provisioning behaviour were carried out with regard to the homing direction through the entire provisioning season.

MATERIALS AND METHODS

The study was carried out from mid-June to mid-July, from 1998 to 2000 at Hinokuma-yama, a small hill in Saga Prefecture, Japan (lat. 33°C16' N, long. 130°16' E). The site is secondary forest with a variety of small to large deciduous and perennial trees. A study area 15×15 m was selected, on gently sloping ground, and transected with yellow twine in a grid with a 1 m mesh. For night observations, a piece of paper covered with luminous paint (Toho Sangyo Co. Ltd.) was placed on each intersection. A small flag was placed at the edge of each subject burrow, and the females' wings were marked with a synthetic resin (Holt Products Ltd.) in order to check each burrow and animal after the observation of provisioning behaviour.

All observations were conducted in the field. We observed the provisioning behaviour of each bug from a distance of about 2 m. The provisioning path consists of two different paths: the first is the foraging path during the search for a drupe; and the second is the homing path while dragging the drupe back to the burrow. When a female finds a drupe on a foraging journey, she immediately drags it back to her burrow soon after she penetrates it with her proboscis. Since she appeared to show the same homing behaviour as in the natural condition when we gave her a drupe directly in front of her while foraging, we routinely placed a ripe drupe on her foraging route to elicit the homing behaviour. Bugs that forage more than two meters from their burrow were used for this homing test, and the homing direction was measured at one minute after the bug began its homeward journey.

A marker was inserted in the ground at the place where the ripe drupe was deposited, and white twine was fixed between the marker twig and the small flag beside the burrow. As the bug began to drag the drupe, a 50 cm ruler was placed on the ground along the longitudinal body axis of the bug. The homing direction was measured as the angle between the direction of the ruler and the fixed white twine. The photic conditions and time of the day were also recorded.

At night, a triangular piece of paper covered with luminous paint was attached to the scutellum of the bug to enhance observations. While determining the homing direction, a far-red flashlight (>640 nm) was used briefly for only one or two seconds.

Eye-masking test

Bugs foraging more than two meters from their burrow were also used for the eye-masking test. Both the compound eyes and ocelli of each bug were painted with silver paste (Nilaco Corp. Tokyo), and the bug was then released at the point of capture, with a ripe drupe. At one minute after the bug started to walk, its homing direction was measured. As a control experiment, the head of the bug was painted with transparent enamel.

Statistics

Statistical analysis of distributions of homing direction was performed according to the methods of Batschelet (1981). For each distribution, the mean resultant vector was calculated and the *V* test was applied to determine whether the observed directions have a tendency to cluster around the home direction. The zero direction is the direction of the burrow.

RESULTS AND DISCUSSIONS

During the provisioning period of the subsocial shield bug, *P. japonensis*, many drupes of the source tree, *Schepfia jasminodora*, are scattered over the ground, which is covered with fallen leaves. Several groups of drupes were observed in the food source area, groupings which might be caused by terrain and/or the weather conditions. The study area covered this food source area.

After the nymphs hatch, almost every day each female bug was observed to search tortuously around the source area, until it encountered a ripe drupe. As soon as it obtained a drupe, the bug took the shortest route back to its burrow over terrain. The duration of provisioning behaviour increased with each progressive stage of the development of the nymphs. When the nymphs are young, foraging and homing behaviour was observed only during the day. When the bug was providing for nymphs around the 3rd stage, similar provisioning behaviour was observed at night, too.

Fig. 1a shows a single observation day on the dates from 18th to 19th June 1998 at the busiest provisioning period in this season. The number of walking bugs, foraging and homing bugs, observed in the study area was counted every two hr. After dusk, the number of bugs increased, and showed a small peak at midnight. From minimum near dawn, the number of walking bugs gradually increased again and showed the highest value around 14:00 to 16:00. This clearly shows that the bugs forage during the whole day in the busiest provisioning period. This round-the-clock provisioning behaviour of *P. japonensis* may be a result of the relatively limited food resource (Filippi *et al*., 2001).

The provisioning period of this bug corresponds with the Japanese rainy season. To investigate whether or not the weather conditions affect their provisioning behaviour, the number of walking bugs was counted in the same study area every day at noon. The first walking adult females were

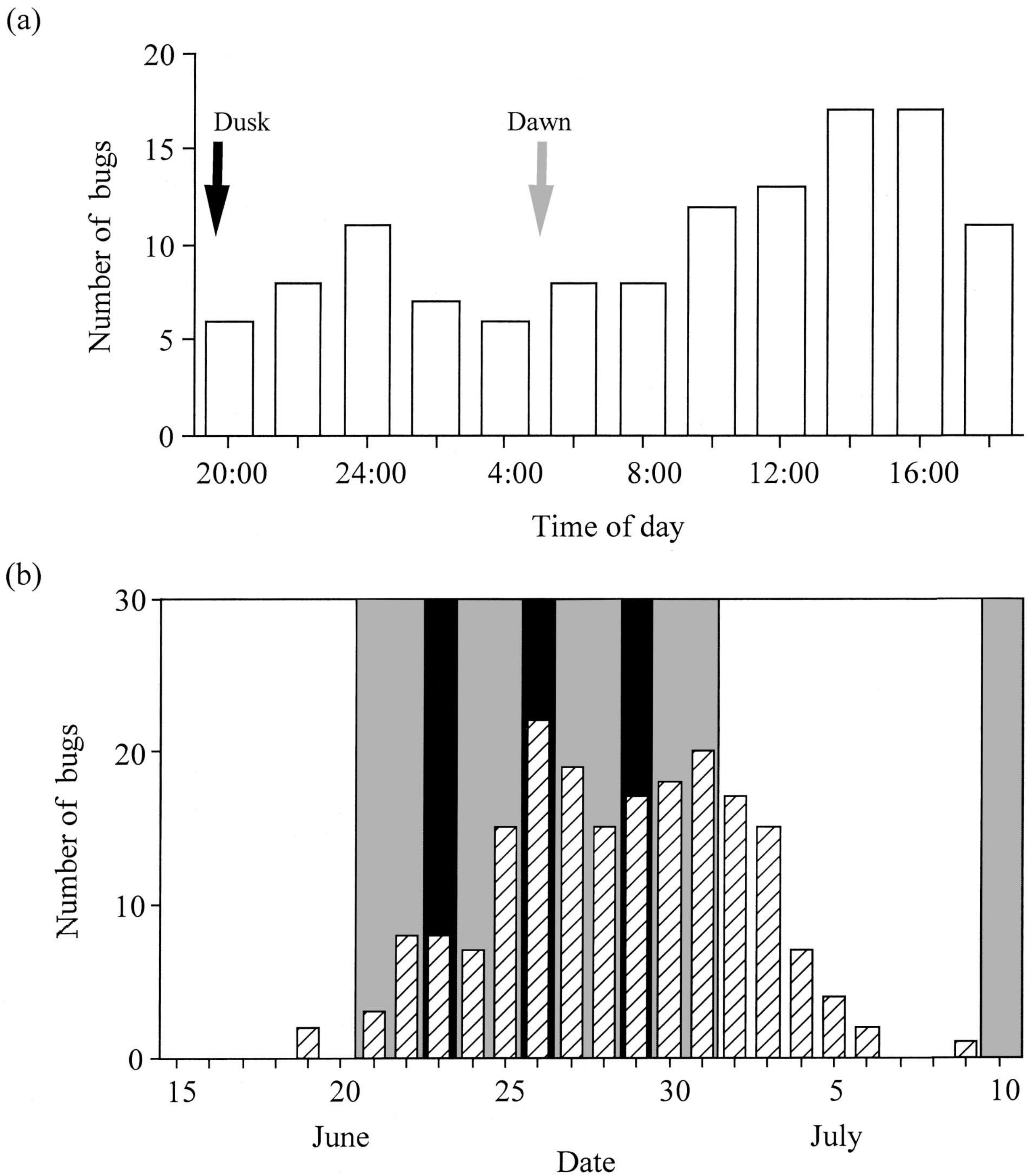

Fig. 1. (a) Changes in the number of walking bugs during a single 24hr period. (b) The number of walking bugs at noon under several different weather conditions. White, grey and black areas indicate fine, overcast and rainy conditons, respectively. Hatched columns indicate the number of walking bugs.

observed on 19th June, 2000 and the number of walking bugs increased during the week at the end of June. There was no obvious pattern of the number of walking bugs and the weather conditions, which included fine, overcast and rainy days (Fig. 1b). As shown in Fig. 1a, many bugs were observed walking during the night when the busiest provisioning period started. These observations indicate that provisioning behaviour is not affected by photic conditions.

P. japonensis shows long-distance navigation during the day: when a bug leaves its burrow, it follows a tortuous seeking route until it encounters a drupe, and it always takes the shortest route back to its burrow when a drupe has been obtained (Hironaka *et al.*, 2001). To investigate whether the different photic conditions affect the shortest route homing behaviour, the observation was performed under several environmental conditions. Their homing pathways always showed the shortest routes, never tracing the path taken during foraging, under all conditions. The homing direction results were grouped according to environmental conditions and displayed on circular charts (Fig. 2). In all conditions, each homing direction was clustered around the direction of the burrow. The linear component of each vector shows a high value, from 0.885 to 0.975. The probabilities using the *V* test show that each homing direction is significantly clustered toward the burrow (P<0.0001), showing clearly that the adult female bug can orient directly toward its burrow under any weather and photic conditions.

The most intensively studied insect navigators walking on the ground are ants. Worker ants use one or more navigational systems during foraging and homing (Wehner,

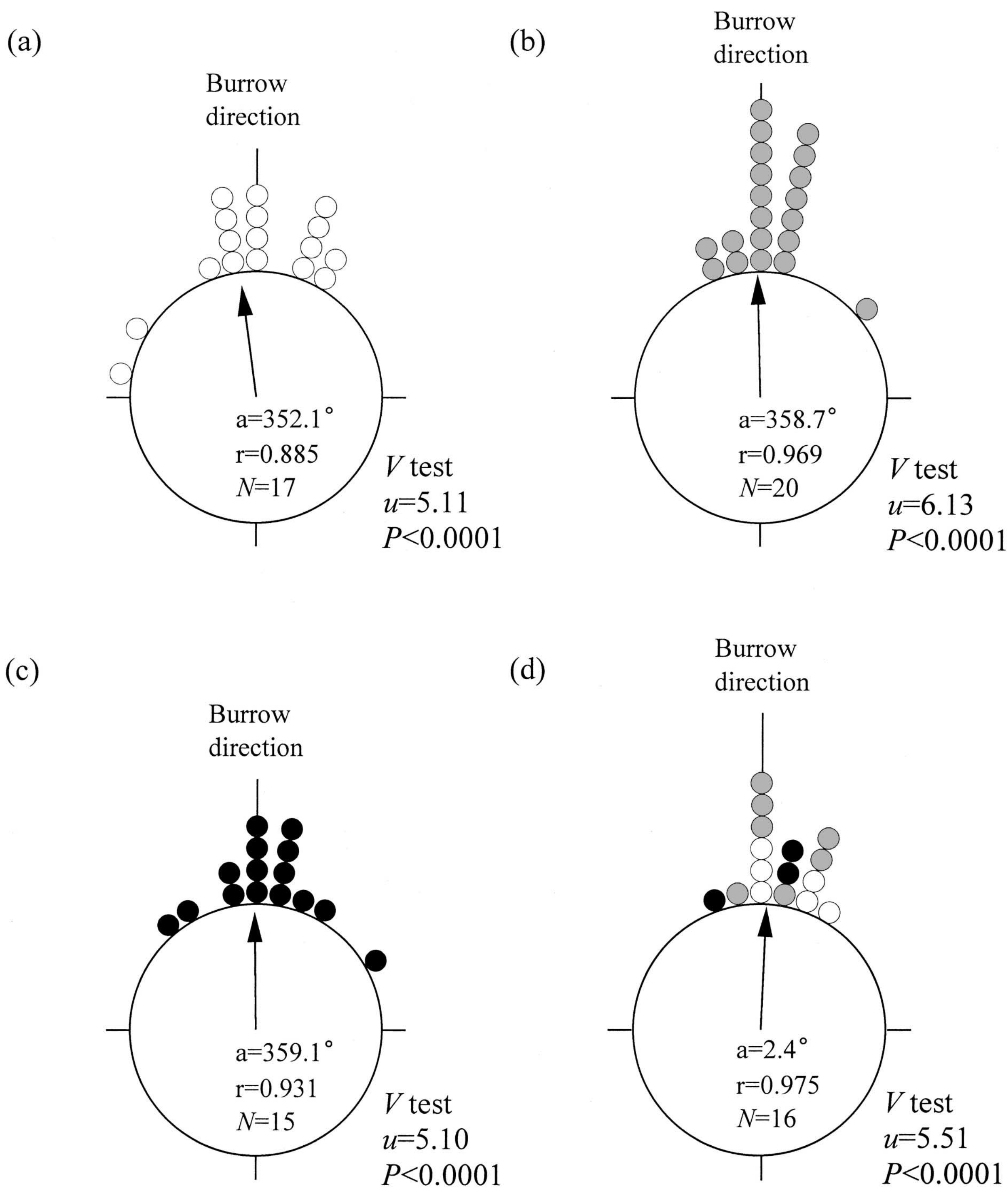

Fig. 2. Circular charts of the distribution of homing direction. (a) Fine day (white circles). (b) Overcast day (grey circles). (c) Rainy day (black circles). (d) Night, including several weather conditions. Arrows indicate direction of mean resultant vectors. a, mean direction of resultant vector; r, radius of circle corresponding to a vector length of 1; *N*, sample size; *u, V* test statistic; *P*, probability level of *V* test.

1981), based on trail pheromone, landmarks and path integration. The various navigational systems are usually not in operation simultaneously: their sequence is dependent on a hierarchy of importance of the orientation cues available dependent on the different environmental conditions (Hölldobler, 1971, 1976; Aron *et al.*, 1988). For instance, visual cues such as sun and polarized skylight (Wehner, 1984) may be effective cues in bright environment, whereas the trail pheromone (Hölldobler and Wilson, 1990) may be a powerful cue in a dark environment. Red wood ants, *Formica nigricans*, forage using landmarks and chemical cues, both during the day and at night. When a discrepancy was experimentally induced in the directional information provided by the landmarks and chemical cues, landmarks were preferred during the daytime, chemical cues at night (Beugnon and Fourcassie, 1988). In the present study, *P.*

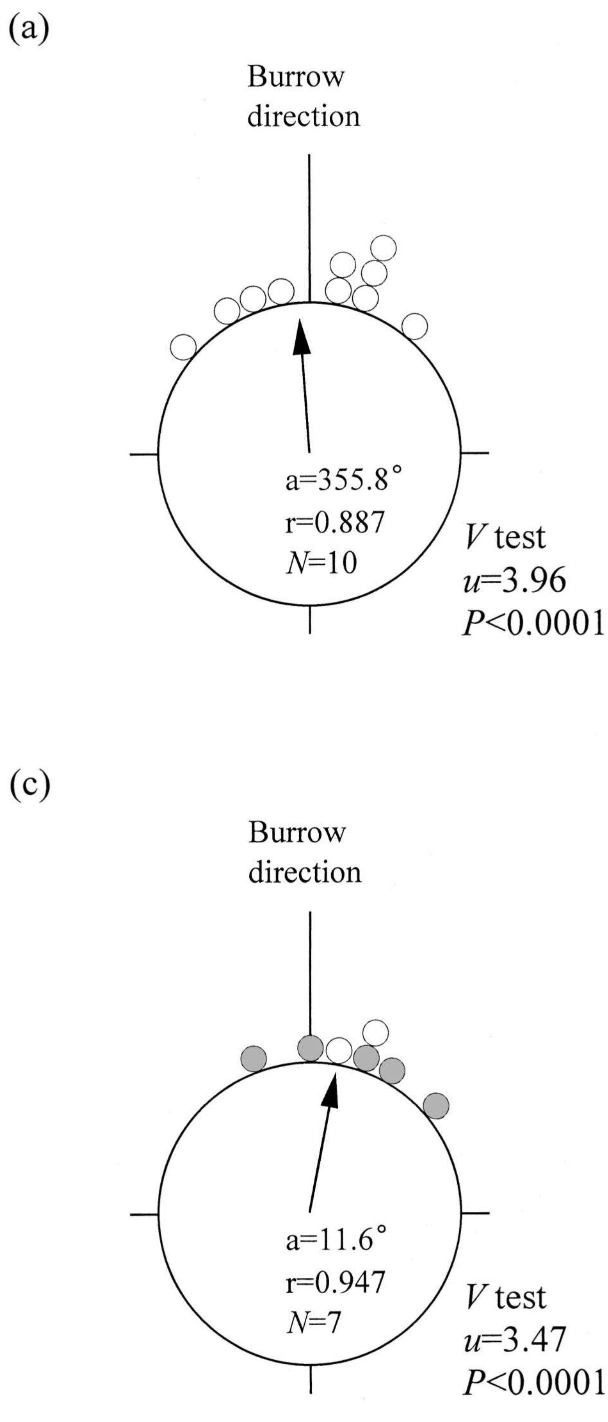

Fig. 3. Distribution of homing direction for bugs with the compound eyes and ocelli painted with clear enamel (a, c), and with silver paste (b, d). Both during the day (a, b) and at night (c, d), the blind bugs (b, d) could not orient to their burrow (for further explanation, see legend of Fig. 2).

japonensis did not trace back along its foraging path during homing, suggesting that it does not rely on a trail pheromone for its long-distance navigation, under different environmental conditions. What kind of indirect cue is reliable in the long-distance navigation of *P. japonensis*? To test whether the bug uses visual cues, the compound eyes and ocelli were painted with silver paste just before homing. Control bugs painted with clear enamel could orient to their individual burrows same as the unpainted bugs both daytime (Fig. 3a) and night (Fig. 3c). However, the blind bugs were disoriented to their burrow direction during daytime (Fig. 3b) and night (Fig. 3d).

It is therefore clear that visual cues are important for long-distance navigation under several photic conditions even at night in this species, although it is still unclear whether this bug changes visually guided navigational systems depending on each photic condition. However, it is very interesting to find an insect that uses visual cues predominantly under all photic conditions. The kind of visual information the bug using in the navigation, under such wide photic conditions, is currently being investigated.

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