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Foraging Navigation of Hornets Studied in Natural Habitats and Laboratory Experiments

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ABSTRACT—Foraging flights have been studied in three species of hornets (*Vespa mandarinia*, *V. simillima* and *V. analis*) in the field and the laboratory.

Hornets seem to use multiple navigational cues for visiting a familiar feeding place. They could orient towards the feeding place immediately after they rose in air from the nest without directly viewing the feeder. They could visit the feeding place after dark at a luminosity 8 lux. These data suggest that they can navigate for some distance with few external cues. Hornets also seem to rely on visual cues for their mid-range navigation. They used some structures on their way as navigational landmarks to negotiate. Individual hornets are supposed to have their own landmarks. Olfactory cues seem to be used to find a new feeding place or to recruit other member. In the approach flight hornets seemed to use multiple visual cues such as the visual characteristics of the feeder and the wider scenery around the feeder. Even if the feeder in training was removed during the test, they flew with a smooth course as if they were pin-pointing the missing feeder, but without sitting on the ground. Hornets learnt how to fly to reach the feeder without external cues after passing by the last visual landmark under conditions with extremely poor visual cues.

The present work suggests that hornets retain multiple navigational cues during repeated foraging behavior, and which cues they use seems to depend upon environmental conditions.

Key words: hornet, vespine wasp, learning, visual navigation

INTRODUCTION

The navigational ability of an insect between its nest and a familiar feeding place has for a long time been one of the interesting subjects in research on insect behavior. There have already been many behavioral accounts on navigation in hymenopteran insects, especially in ants and honeybees (e.g., Wehner, 1981). Since honeybees are flying insects, their navigational paths are more difficult to follow than those in ants that move two-dimensionally on the ground (e.g., honeybees: von Frisch, 1967; Dyer, 1996; ants: Wehner, 1981, Wehner *et al*., 1996, Wohlgemuth *et al*., 2002). Navigation of honeybees and other flying hymenopterans has been studied in two distance ranges, short-range navigation (e.g., approach flight to a feeding site or a hive) and long-range navigation. Mechanisms short-range navigation have been well documented because experimenters have been able to analyze flight trajectories by direct observations and by video recordings (e.g., Collett, 1996; Lehrer, 1996; Zeil, 1993a, b). On the other hand, the long-range navigation has been analyzed using two major methods. One was an analysis of the waggle dance performed by foragers, which told experimenters how far and in which direction the bees navigated for forage (von Frisch, 1967). The other was to measure the vanishing bearings of bees to estimate their flight directions (Dyer, 1996). Behavioral observations by these methods have shown that honeybees utilize both celestial and terrestrial cues for navigation (Dyer, 1996 Dyer *et al*., 1993; Wehner *et al*., 1990; Menzel *et al*., 1996). However, navigation of honeybees could not be directly followed due to their small size.

Hornets are also social hymenopterans: foragers seem to take similar navigational strategies to those made by honeybees. Since hornets have a large body size, observers can follow their flight courses visually farther than those of honeybees. Japanese giant hornets are the largest hornets in the world (27–40 mm in body length), and they can be followed as far as 100 m with the naked eyes. Hornets, especially Japanese giant hornets, are therefore one of the most favorable hymenopterans for behavioral experiments by virtue of their large size, but even so there have been few publications on their navigation.

In the present study the basic foraging behavior has been observed in three species of hornets including giant hornets. Unlike many previous works reported for honey-

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bees and other hymenopterans a large number of individuals could not be used in the present study, because hornets forage alone or in a group of only a small number of individuals. Given this limitation, and the present rather poor state of knowledge of hornet foraging behavior, the aim of the present study is to describe main features of foraging behavior in hornets in comparison with that of honeybees than to analyze any individual feature of the behavioral repertoire in detail.

MATERIALS AND METHODS

Hornets and Field Sites for Experiments

Three species of hornets were used in the present study. Their common names in Japanese have been translated literally into English for descriptive convenience only as follows: giant hornets (*Vespa mandarinia* Smith), small hornets (*Vespa analis* Fabricius) and yellow hornets (*Vespa simillima* Smith). Giant hornet workers are 27–40 mm in body length. Small hornets resemble giant hornets in their external appearance but are smaller, their body length ranging between 21 and 27 mm, whereas yellow hornets are 17–24 mm in body length with a lighter body color than the two other species (Matsuura and Yamane, 1990).

The foraging behavior of the hornets was observed under both field and laboratory conditions. Field experiments were carried out in an open place in the country-side (Field 1) and in an experimental field on the University campus (Field 2). In addition the flight paths of a single small hornet were followed between the laboratory building and its nest 70 m away. Laboratory experiments were carried out by attracting small hornets and yellow hornets into an experimental apparatus placed near the window in the laboratory.

Sketch of Field 1

Field 1 was 125 m in an east-west direction. It was narrow in the east end down to 30 m wide, but widened to 100 m at its west end (Fig. 1). The field was surrounded by precipices about 10 m high except for the north west side, where trees, bamboo and bushes grew. A nest of giant hornets was located under the ground near the south precipice in the eastern most region of the field. The nest went to the ground through a tunnel 30 cm long with its opening pointing to the north. Bushes and grass covered the opening. For our observation a narrow path (5 m long and 1 m wide) was prepared from the opening toward the north by mowing grass and bushes. Bamboo, short leafy trees and tall grasses grew on either side of the path, looking like natural hedges. A pole (20 cm in diameter and 4 m high) stood on the path 5 m from the opening of the tunnel. This pole was defined as the datum-pole for purpose of subsequent description. A feeder containing a sugar solution was placed at a distance 90 m west of the datum-pole, where the second pole (a feeder-pole) stood. The line containing the two poles was regarded as the datum line, and a polar coordinate system with its origin at the datum-pole was established with lines at 6° intervals from the datum line. Two arcs 40 m and 70 m from the datum-pole were drawn on the ground, and small landmarks for experimenters were placed at intersections between the arcs and the radial lines. The flight paths of giant hornets were specified by their intersections with the 40 m and 70 m perimeter arcs, and by the directions with which they approached the feeder, which were both recorded in a notebook. Two additional poles stood at distances of 40 m and 70 m from the datum point. In some experiments these additional poles were placed along the datum line, and in other experiments they were placed +6° or –6° from the datum line (Fig. 1).

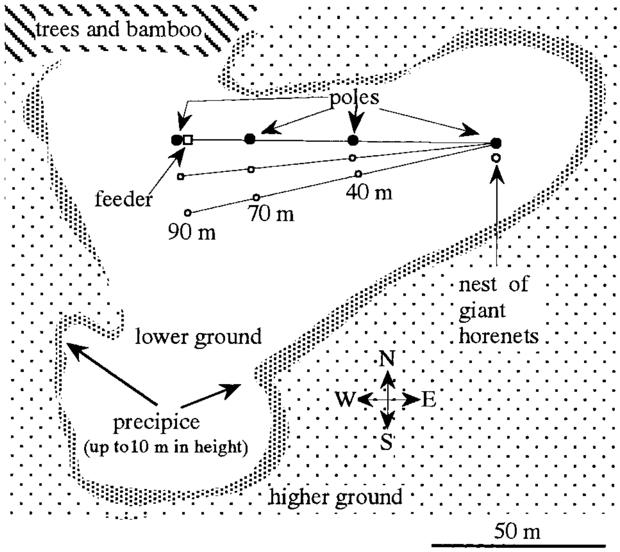

Fig. 1. A bird's eye view of Field 1. The experimental field is bounded by a precipice 3–10 m in height (heavily dotted) from surrounded the higher ground (lightly dotted) except for the western part of the northern boundary, occupied by bamboo and trees. A nest of hornets occurs near the east end of the field, the entrance to which opens towards the north. The feeder is placed 90° west from the nest. A virtual polar coordinate system is applied to the ground, with its origin near the nest. Four poles are stood, near the nest, 40 m and 70 m from the nest and behind the feeder.

Observations on the flight paths of giant hornets in Field1

Giant hornets were attracted to the feeder. In order to let such hornets visit the feeder continually throughout a two-week period of observation, a sugar solution was provided in the feeder all day long. Thus, the hornets could take sugar solution at any time even before and after experiments. To identify each hornet a streamer was attached to the constriction between the thorax and the abdomen. The streamer was 40 mm long and 5 mm wide made from a plastic shopping bag, painted different colors and patterns to enable identification.

Experiment 1

In order to know how and when giant hornets orient to the feeding place their flights immediately after rising in the air were recorded by a video-camera set at a height 4 m above the path at 2 m from the opening of the tunnel. Flight paths were analyzed frame-by-frame, and flight directions were obtained when they were out of the frame.

Experiment 2

In order to see whether individual hornets take a rather fixed path during repeated visits to the feeder the flight paths were recorded for identified hornets, and their inter-individual differences were statistically tested by the Mann-Whitney U-test. Outgoing and homeward flight paths were also recorded for some individuals in order to see whether they took similar routes in the two directions. In order to see whether giant hornets navigated using artificial landmarks such as the feeder-pole or the 40 m- and 70 m- poles as navigational cues, these poles were displaced by 6° in a clockwise or anticlockwise direction with respect to the datum line and their flight paths compared with those before the displacement of the poles.

Experiment 3

In order to see whether the height of the feeder was learned hornets were trained to take a sugar solution from a feeder placed at a height of 45 cm. After training the feeder was removed, and coming hornets flying over the place where the feeder had been were video-taped by two video cameras directed horizontally

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toward the feeding place at heights of 30 cm and 60 cm. Videotapes of the two cameras were simultaneously displayed on a monitor, and the number of individuals below 30 cm, above 60 cm, and between 30 cm and 60 cm in height were counted for every frame. Counted numbers for 4,000 frames (about 2 min) were summed for each height range, and compared among the three ranges. Similar observation was carried out after training to a feeder at a height of 75 cm. The statistical significances in the distribution of hornets among the three height ranges were evaluated by a qui-square test.

Observation of the approach flight to the feeder in Field 2

Field 2 was a square about 500 m^2 in an area hedged by trees. This area is located peripherally in an experimental field of the Biology Department with an area of about 5,000 m^2, and in close vicinity to two campus buildings, as shown in Fig. 2.

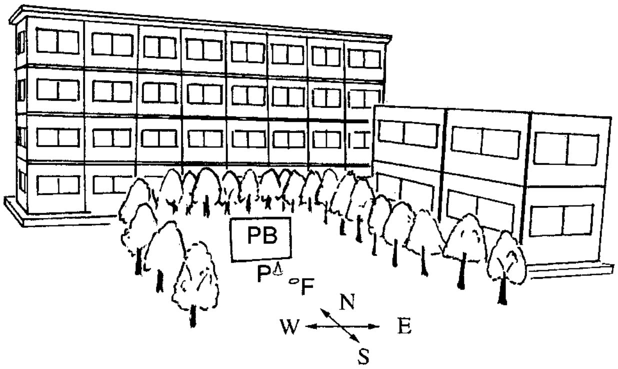

Fig. 2. A sketch of Field 2. Hornets enter the field passing the corner of the two-story building on the east side. In the field a plywood board (3 m×2 m, PB), a pylon (P) and a feeder (F) are placed for Experiment 4 (details in text).

Experiment 4

Approach flights of giant hornets to the feeder were followed while changing the relative positions of some landmarks. A white plywood board (3 m wide and 2 m high) and/or a white pylon (30 cm in basal diameter and 50 cm high) were placed as landmarks. The plywood board was stood 1 m behind the feeder, and the pylon was placed between the feeder and the plywood board during the training period. The feeder was a dish 20 cm in diameter, and was placed in a hollow of the ground so that its top level with the ground. After giant hornets learnt the position of the feeder, the feeder was covered by fallen leaves and grass to camouflage it. Even if the feeder was not directly visible, the hornets learnt to land near the feeder and walk towards it passing among the leaves to take the sugar solution. After training with a given arrangement of the plywood board and/or the pylon these landmarks were displaced laterally for 1 m and the feeder was removed. When the feeder was removed, leaves and soil around it were also replaced by new ones to minimize any possible chemical cues. Approach flights of giant hornets were video-taped by a camera set at a height 5 m above the feeder. The landing places were measured together with their trajectories before and after displacement of the landmark.

Experiment 5

In order to see whether a conspicuous feeder itself can be an effective landmark for attracting hornets, hornets were next trained to take a sugar solution from a prominent feeder, which consisted of a white dish (20 cm in diameter) and an underlying light brown brick (30 cm wide and 14 cm high). The ground was covered by three plastic sheets (3.5×5 m) that were arranged side by side to form a large sheet (10.5×5 m). The feeder was placed at the center of the central sheet in the training. After training the feeder was removed or moved, and their trajectories before and after displacement of the feeder were video-taped by a camera placed at the side of their approach path. In the second experiment, the central blue sheet was replaced by a white one and the feeder removed, and the flight trajectories were compared with those before the replacement.

Observation of the outgoing and homeward flight paths in a small hornet

Experiment 6

Flight paths between a feeder placed on the windowsill on the 4th floor of the building and its nest 70 m away were followed for a single small hornet. The small hornet visited the feeder at an interval less than 15 min for more than 10 days. Many structures on the ground such as flat roof-houses, a wood cabin and a large metal liquid gas container (3 m in diameter and 10 m in length) were all possible visual cues between the feeding place and the nest, as shown in Fig. 3. Flight paths were recorded with reference to these structures.

Observation of approach flights to the feeder in laboratory-equipment

Experiment 7

Small hornets and yellow hornets were attracted to an experimental table (180 cm×90 cm) placed near an open window. The table was surrounded by white curtains 1.5 m high except for an entrance facing the open window. A plastic Pertri dish of 10 cm diameter with a green bottom was placed on the table, and hornets were trained to take sugar solution from the dish. After training the feeder was removed or moved for 1 m. Flight paths were videotaped by a camera set at a height 2 m above the table before and after displacement of the feeder.

Experiment 8

In order to see the approach flights of small hornets and yellow hornets while minimizing visual cues they were attracted into a drum (1.8 m in diameter and 2 m in height) through a window 10 cm in diameter at a height of 50 cm. The inside of the drum was white. The drum was suspended from the ceiling to keep its bottom 1cm above the floor so that hornets could crawl out the drum. A video camera was set 2 m above to record the flight paths of the hornets. Hornets were trained to take sugar solution from a feeder placed on a given position on the floor. After training the feeder was removed, and their flight paths were compared with those during the training.

RESULTS

Behavioral characteristics of hornets under natural habitat conditions

Some characteristic behaviors found in the present study are presented in advance of detailed experimental data.

1) Hornets repeated their forage flights for a wider time range and under worse weather condition than honeybees. Hornets visited the feeder after sunset until the luminosity of the sky decreased to 8 lux. They also visited the forage site under heavy rain and against strong stormy winds.

2) Hornets flew at altitudes less than 6 m when navigating for 90 m in Field 1, whereas they increased their flight altitude to more than 25 m when navigating more than 1 km from Field 2.

3) It is well known that a dozen giant hornets gang up on honeybee hives and exterminate an entire colony within a

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few days (Matsuura and Yamane, 1990). How do hornets recruit other hornets? The following findings suggested the importance of chemical communication. First, when several giant hornets that were caught 30 km away from our the laboratory were kept in a cage in the laboratory with the windows open, hornets from a near-by colony came flying into the laboratory within a few days and hovered outside the cage. Since the visitors could not initially see the cage from a distance, they seem to have been chemically attracted to it. Second, giant hornets usually attacked in a small group either a specific hive or two hives in an apiary where more than thirty hives were situated. This was interpreted to indicate that attacking giant hornets released some chemicals to assemble their comrades.

4) Chemical messages seemed to be critical when experienced hornets visited the familiar forage site. A pair of antennae were cut off to eliminate the olfactory sense in several hornets that had visited the feeder for a few days in Field 2. Forage flight in such hornets was not impaired. The shortest intervals between several successive visits were measured in 10 intact hornets. They ranged in 13–22 min (16.4±3.3 min, means ± sd). In two hornets lacking antennae the values were 17 min and 18 min, similar to those for intact hornets.

5) Partial occlusion of the dorsal part of the compound eye on either side impaired foraging activities of hornets. The dorsal part of the paired compound eyes was masked by paint in five giant hornets previously trained in Field 2, and after the masking was complete they were released at the site. They almost lost their flight activity and crawled around the feeder. Even if they rose in the air, they slowly circled above the field, and then again landed on the ground or sat in the tree. They did not return to the nest, but stayed near the feeder in subsequent days.

6) Hornets coming to the feeder in Field 2 were captured before landing on the feeder, and transferred beyond our laboratory building, which was located about 100 m apart from the feeding place, and deviated by an angle of 45° from a straight line connecting the nest and the feeder. They were released there. Although the released hornets could not directly view the feeding place they returned to it within 1 min.

7) Giant hornets seemed to decide where to fly before leaving the nest. In Field 1 hornets were trained to take sugar solution from a dish placed 90 m away from the nest. Then, another identical dish filled with sugar solution of the same concentration was placed at an entrance to the nest. All hornets could neither enter nor exit the nest without touching the sugar solution by their legs. The behavior of trained hornets when they left the nest was observed for 15 min. None stopped at the unfamiliar feeder to take sugar solution, and they rapidly left for the feeder 90 m away.

Orientation of the initial flight in giant hornets

Experiment 1

Hornets were trained to visit a feeder placed 90m south from the nest in Field 1. Flight orientations of the hornets just after leaving the nest were recorded by a video camera. The hornets changed their flight directions while flying on the path, although they could not directly view the feeding place 90 m away. The hedge of the path blocked their sight lines towards the feeding place (Fig. 1). Flight directions when disappearing from the frame of the camera measured for 40 flights ranged between –38° and 29° (–5.4°±14°;

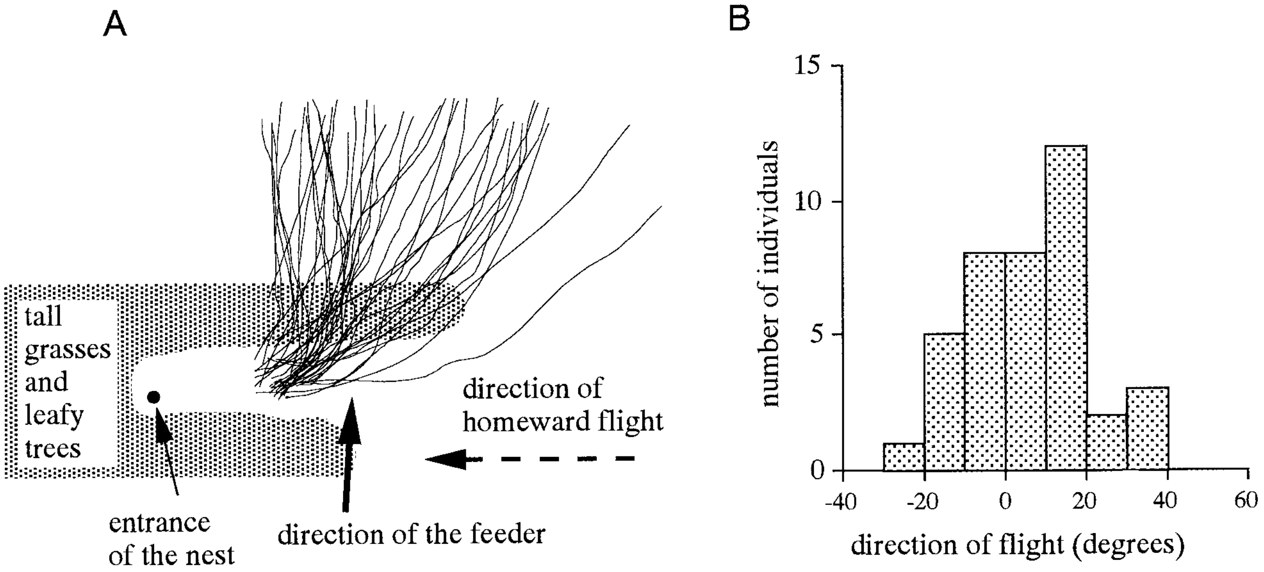

Fig. 3. A: Directions of the initial flight of a total of 40 hornets immediately after rising in the air. Their flights were recorded by a video camera set at a height of 4 m, and the flight path of each hornet was analyzed frame by frame. The sight line of the hornet to the feeder 90 m west was blocked by a hedge of tall grasses and bushes. B: Distribution of the flight directions of the 40 hornets shown in A. Their directions just before they exit the frame are measured. Broken arrow shows a direction of homeward flight.

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mean ± sd) with respect to the direction to the feeding place (Fig. 3).

Outgoing flight paths of hornets

Experiment 2

Outgoing flight paths of giant hornets in Field 1 are drawn on the polar coordinate system in Figs. 4 and 5. Paths collectively drawn without identifying individuals varied from a rather straight to a gently curved trajectory (Figs. 4B, 5B). When hornets pass across the 70 m-arc, their flight paths diverge in a range of about 18 m (Fig. 4B) and 20 m (Fig. 4C), but converge on the feeder when they approach it. Several successive flight paths of three identified hornets included in Figs. 4B and one hornet in Fig. 5B are drawn in Figs. 4C–E and Fig. 5C, respectively. Variations in the flight paths are much smaller in each of the four hornets than those collectively drawn in Figs. 4B and 5B. Moreover, the flight paths differ among the three hornets in Figs. 4C–D. When crossing the 40 m-arc the hornet in Fig. 4C passes north (upper part in Fig. C) of the 40 m-pole, while that in Fig. 4D passes south of it, and that in Fig. 4E passes further south. When crossing the 70 m-arc, hornets in Figs. 4C, 4D and 4E are distributed at –4.6 to 5.7 m, at –15. 4 to 2.6m and –15.2 to –12.6 m, respectively, with respect to the 70 m-pole (north or upper is positive). Their means and variations are 0.1±3.1 m, –7.3±4.3 m and –11.1±4.8 m, respectively, and their distribution differed significantly between C and E as well as between D and E ($P < 0.05$, Mann-Whitney U-test). The hornet that changes flight directions gradually twice as shown in Fig. 5C, also takes similar outgoing paths

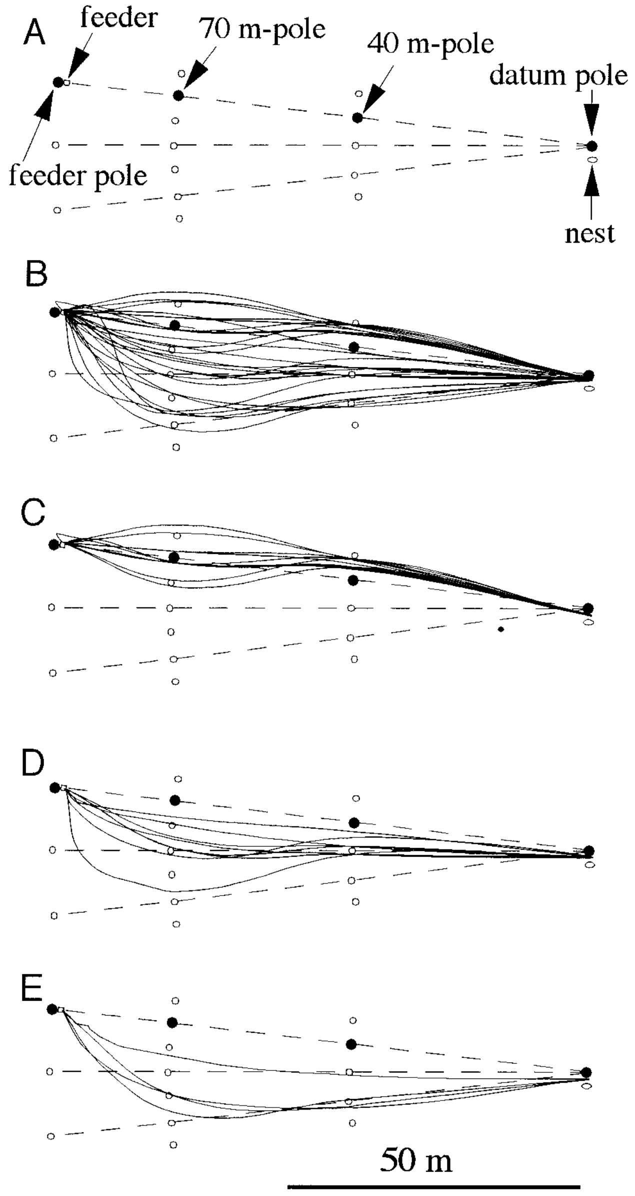

Fig. 4. A: A polar coordinate system for recording the flight paths of hornets. In this arrangement 40-m and 70-m poles are on the datum line which includes the feeder and the datum-poles. B: Collectively drawn flight paths of hornets from the nest to the feeder without identifying individuals. C–E: Flight paths of three individuals included in B are drawn.

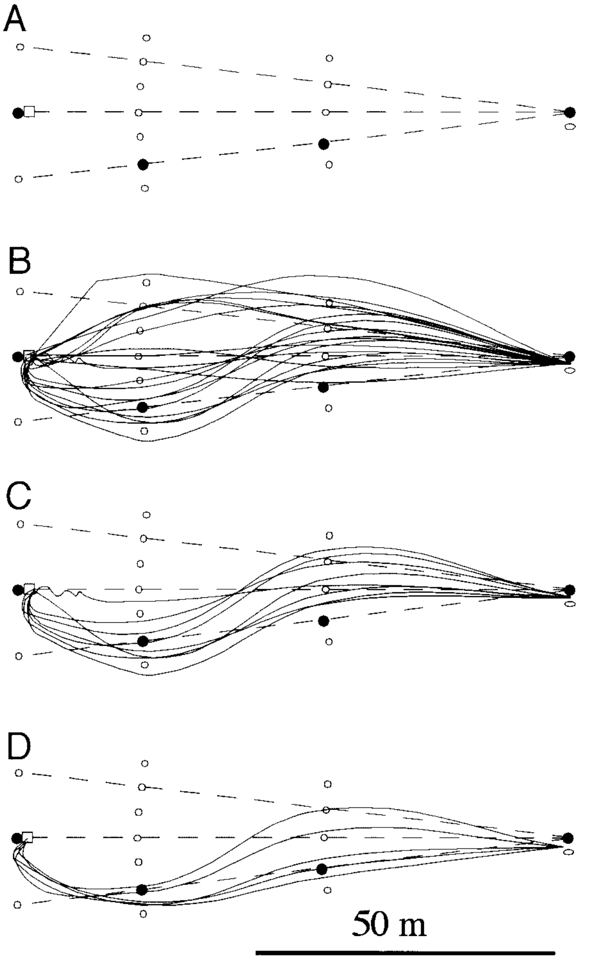

Fig. 5. A: A polar coordinate system for recording of flight paths of hornets. In this arrangement 40-m and 70-m poles are deviated by 6° from the datum line. B: Collectively drawn flight paths of hornets from the nest to the feeder without identifying individuals. C: Flight paths of one individual included in B. D: Flight paths of the same individual drawn in C, but recorded on the next day.

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on the next day, as shown in Fig. 5D.

Comparison between outbound and homeward flight paths

Experiment 2

Do giant hornets return to the nest flying backward along their outgoing path? In Field 1 it took 15–22 sec (18±2.0 sec, means ± sd, n=14) for hornets to fly from the nest to the feeder, whereas it took 18–30 sec (23.3±4.1 sec, n=12) for their homeward flight. As shown in Fig. 3 hornets flew along different routes when leaving and approaching the nest: outgoing hornets turned left as soon as they rose in the air, whereas returning ones directly approach the nest from the north along an extension of the path. Except near the nest, the entire outward and homeward flight paths were similar in some hornets, but differed from each other in other hornets (Fig. 6).

Experiment 4

Different outbound and homeward paths were more clearly shown in observation of a single small hornet around our campus building. Its nest was located 70 m from the laboratory room. The small hornet was trained to take sugar solution from a dish placed on the windowsill of the fourth floor laboratory. There were many obstacles between the laboratory and the nest, and many leafy trees and grasses around the nest, as shown in Fig. 7. When the hornet left the nest, it flew upward in a direction towards the feeder, although its entire flight paths could not be followed. On its homeward navigation it first flew down to take a path along a metallic cylindrical container (10 m in length and 3 m in

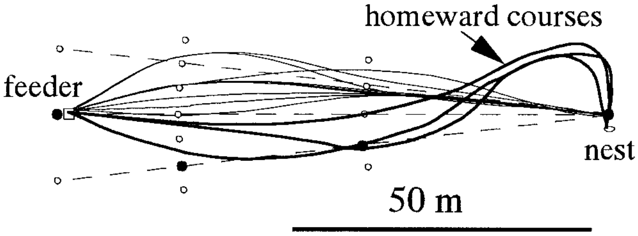

Fig. 6. Outgoing flight paths (thin lines) and return flight paths (thick lines) of a single identified hornet.

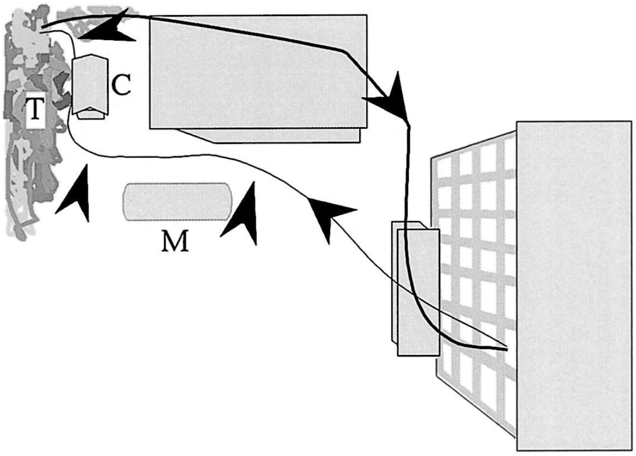

Fig. 7. An outgoing flight path (thick line) and a homeward flight path (thin line) of a single small hornet. The homeward path is stereo-typed: flying along the metallic container (M), turning right on confronting the clump of leafy trees (T), flying a narrow path between the clump and the wood cabin under the eves of the cabin (C), and then turning left to enter space among leafy trees. Three arrowheads on the homeward path indicate points of observation.

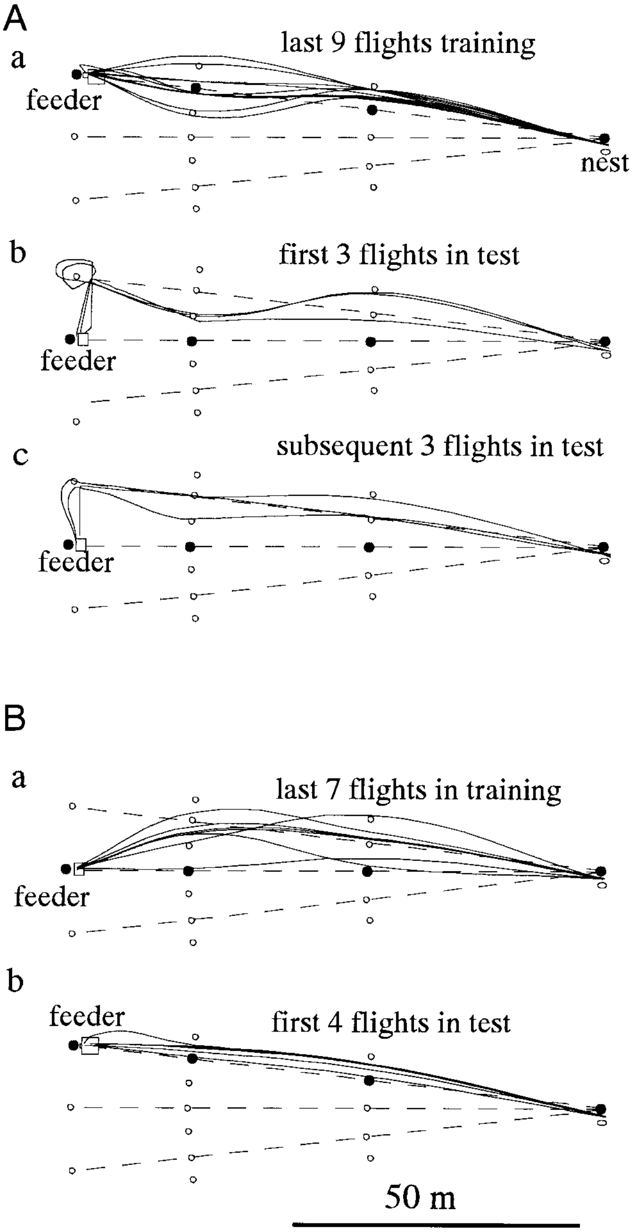

Fig. 8. Effects of displacing the feeder, and the 40-m and 70-m poles on the outgoing flight paths of identified hornets. A: In the training 40-m and 70-m poles are on the datum line (a), and they are displaced anti-clockwise by 6° in test (b, c). Successive flight paths are not affected by the displacement of poles. B: In the training 40-m and 70-m poles are on the datum line (a), and they are displaced clockwise by 6° in test (b). This hornet changed its flight paths in accordance with the displacement of the poles, and smoothly reached the moved feeder.

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diameter, placed 1 m above the ground) at a height of 2–3 m, and faced the hedge of trees. It turned right and flew below the eaves of a small wooden cottage. Passing through the narrow path by the cottage it appeared in open space, and then flew up turning left to penetrate the spaces among some leafy trees. Five return flights were observed for each of three days. The hornet took a similar path in 15 observations.

Possible landmark navigation examined by displacement of artificial landmarks

Experiment 2

The gently curved flight paths between the nest and the feeder shown in Figs. 4 and 5 suggest that the hornets use some visual cues for their navigation. The natural habitat was extremely rich in visual structures: the geometric arrangements of which could not be changed by experimenters. The three poles, 40 m-, 70 m- and the feeder-poles in Field 1 were all movable landmarks, however, although the possibility that the hornets might use them as navigational cues seemed very low. The 40 m- and 70 m-poles were on the datum line or deviated by 6° in a clockwise or anticlockwise direction from the line. Around noon the paths of the last several flights of identified giant hornets were recorded under a given arrangement of the three poles, which had been there since the afternoon of the day before the observation. Then, the three poles were moved through an angle of 6°, and the first several flight paths were recorded, again. Most hornets did not change their flight paths after movement of these artificial landmarks, as shown in Fig. 8A. These hornets came flying along paths similar to those before the movement of the landmarks, and they spent a long time cruising over the position at which the feeder had been placed during the training. They looked as if they were approaching by chance a new feeder and landed around it. They followed similar paths in their several subsequent visits (Fig. 8A). The hornets seemed to navigate using other visual cues than the artificial landmark. In contrast, however, a few hornets did change their path in response to displacing the artificial landmarks, as shown in Fig. 8B.

Approach flight to the feeder observed in Fields 1 and 2

Experiment 3

Arriving hornets have finally to find the feeder around which they should land. For such approaches they should know the altitudes of the feeder. Hornets were trained to take sugar solution from a feeder placed at a height of 45 cm, and in a subsequent test both the feeder and supporting plate were removed. Incoming hornets cruised over the position where the feeder had been placed. The number of individuals in each frame of the video was counted sorting their heights into three ranges; below 30 cm, above 60 cm and between 30 cm and 60 cm. Counts totalled for 4,000 frames showed that hornets trained to take sugar solution at a height of 45 cm cruised more frequently in a range between 30cm and 60 cm than below 30 cm or above 60 cm, even if the feeder was removed (Fig. 9A). Since hornets were not individually identified, the same individual might appear repeatedly. Moreover, hornets cursing near the video camera could be observed in fewer frames than those cursing far from the video camera. Thus, data in Fig. 9A cannot be statistically tested in a strict manner. However, if we regard video-taped hornets collectively, their height distribution was significantly dense in a range between 30 cm and 60 cm at height ($P<0.01$, qui-square test) as compared with two other ranges. Hornets trained to the feeder at a height of 75 cm were distributed frequently in the range 60-

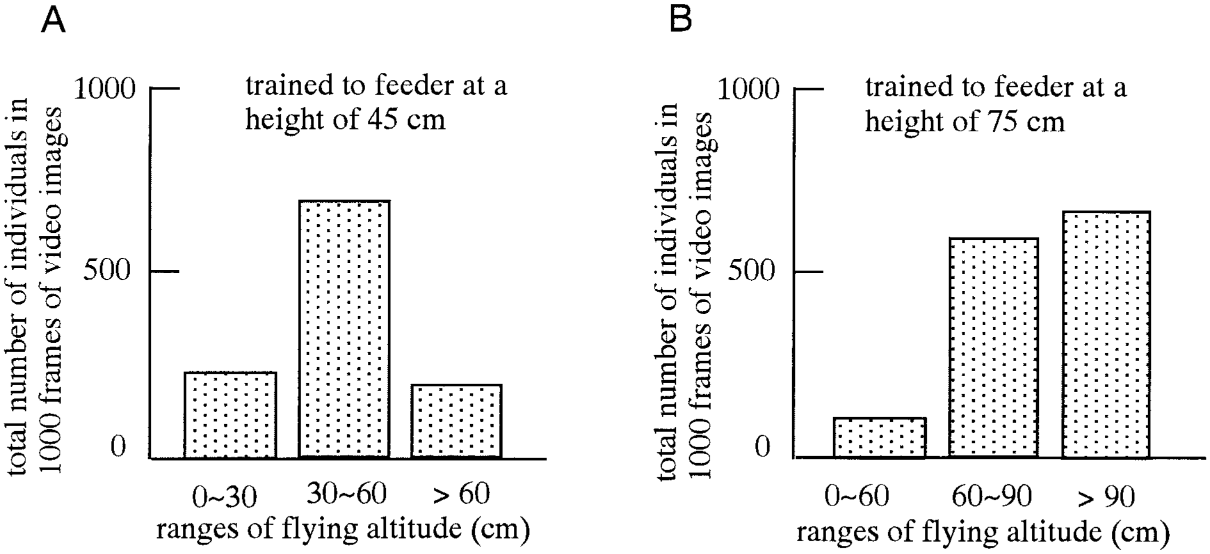

Fig. 9. Learning the height of the feeder. Hornets were trained to take sugar solution in a dish placed either 45 cm (A) or 75 cm (B) in height. In the test the dish was removed. Heights of the search flight of trained hornets are recorded and analyzed by videotape. Counts of cumulative numbers of hornets in 4,000 frames at three different height ranges.

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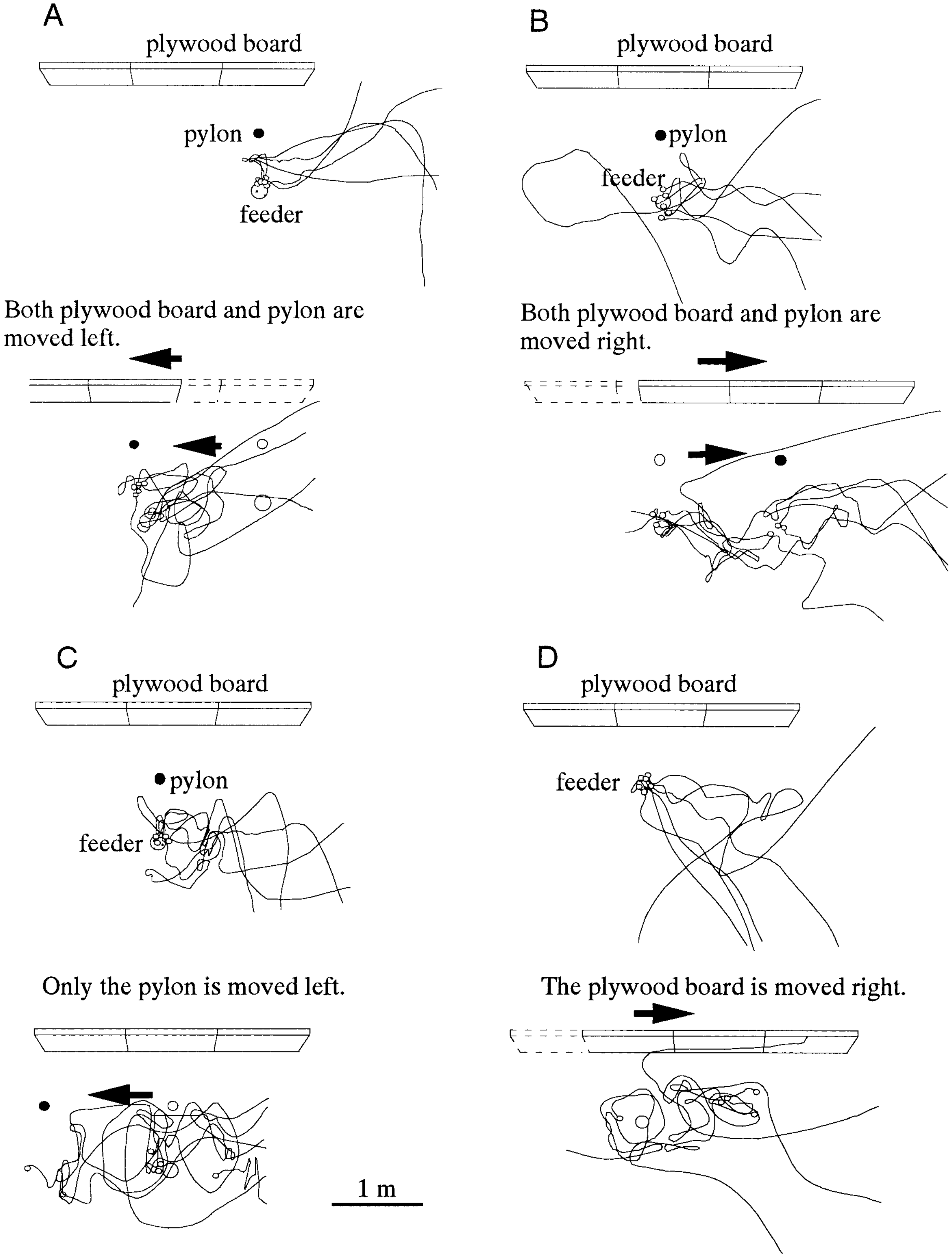

Fig. 10. Hornets are trained to take sugar solution from a feeder placed 1 m in front of a plywood board (3 m in width and 2 m in height). A pylon 50 cm in height is placed between the feeder and a plywood board in A–C (upper in A–C). In bottoms in A and B both plywood board and pylon are moved laterally for 1 m, and subsequent changes in approach flights are traced. In A the feeder faces the edge of the board, whereas it faces the center of the board in the training. In bottom of C only the pylon is moved, but the plywood board is not moved. In D only the plywood board is placed at the training and moved in the test.

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90 cm and in the range above 90 cm, but less in the range below 60 cm (Fig. 9B).

Experiment 4

Giant hornets were trained to take sucrose solution from a feeder placed 1 m in front of a plywood board (3 m in wide and 2 m in height) in Field 2. A white pylon (30 cm in basal diameter and 50 cm high) was placed between the feeder and the plywood board as shown in Fig. 2. Hornets approached the experimental field from the south or south-east (lower or lower left in Fig. 2) passing by or turning near the corner of the building. During training hornets approached the training feeder along rather gentle paths with a few turns near the feeder (Fig. 10). It took 5–7 sec for hornets to land on the ground after first appearing in the frame of the video camera. After training the plywood board and the pylon were laterally displaced by 1 m. Most hornets shifted their landing place according to the displacement of the landmarks (Figs. 10A, 10B). When the feeder was

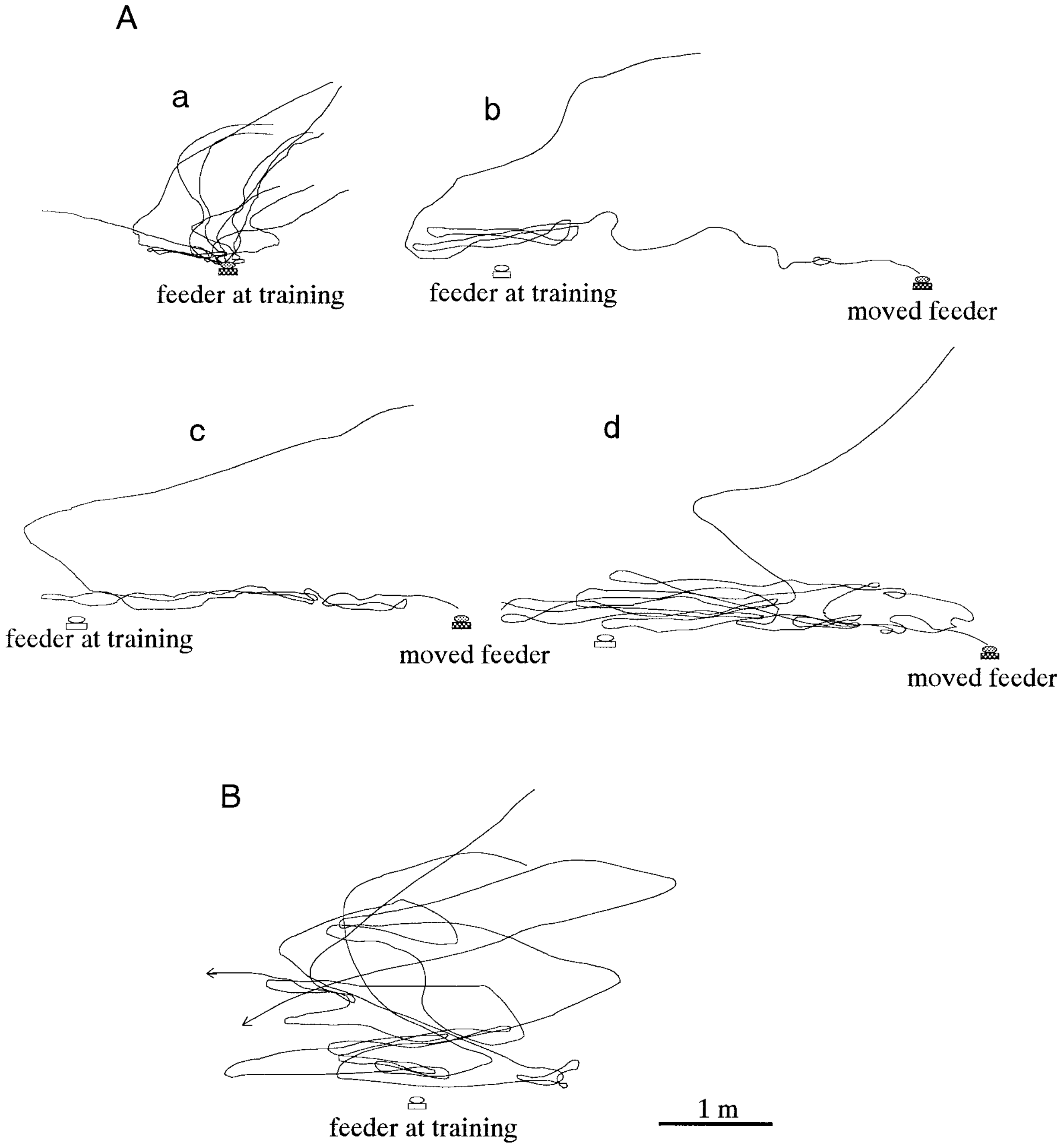

Fig. 11. A: Approach flights of hornets to the feeder placed on the ground viewed from a side of their approach paths (a). Flight trajectories of hornets in test (b–d). The feeder is moved 4 m right in the test. B: Hornets are trained to take a sugar solution from a white dish on a brick. The feeder is placed in a center of the three-part blue plastic sheets (not shown). In the test the feeder is removed and the central part of the three-part blue sheets is replaced by a white sheet.

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placed in the front and center of the plywood board in the training, 12 out of 15 arriving hornets shifted their landing place (Fig. 10A), whereas when the feeder was placed in front of the plywood board in the training, but to one side, 17 out of 18 hornets shifted (Fig. 10B). Hornets appeared in the frame of the video camera for longer times with frequent turns (15–30 sec and 5–15 turns) in the test than in training. When either plywood board alone or the pylon alone was moved laterally for 1 m, the ratio of hornets which shifted their landing place was lower than when both landmarks

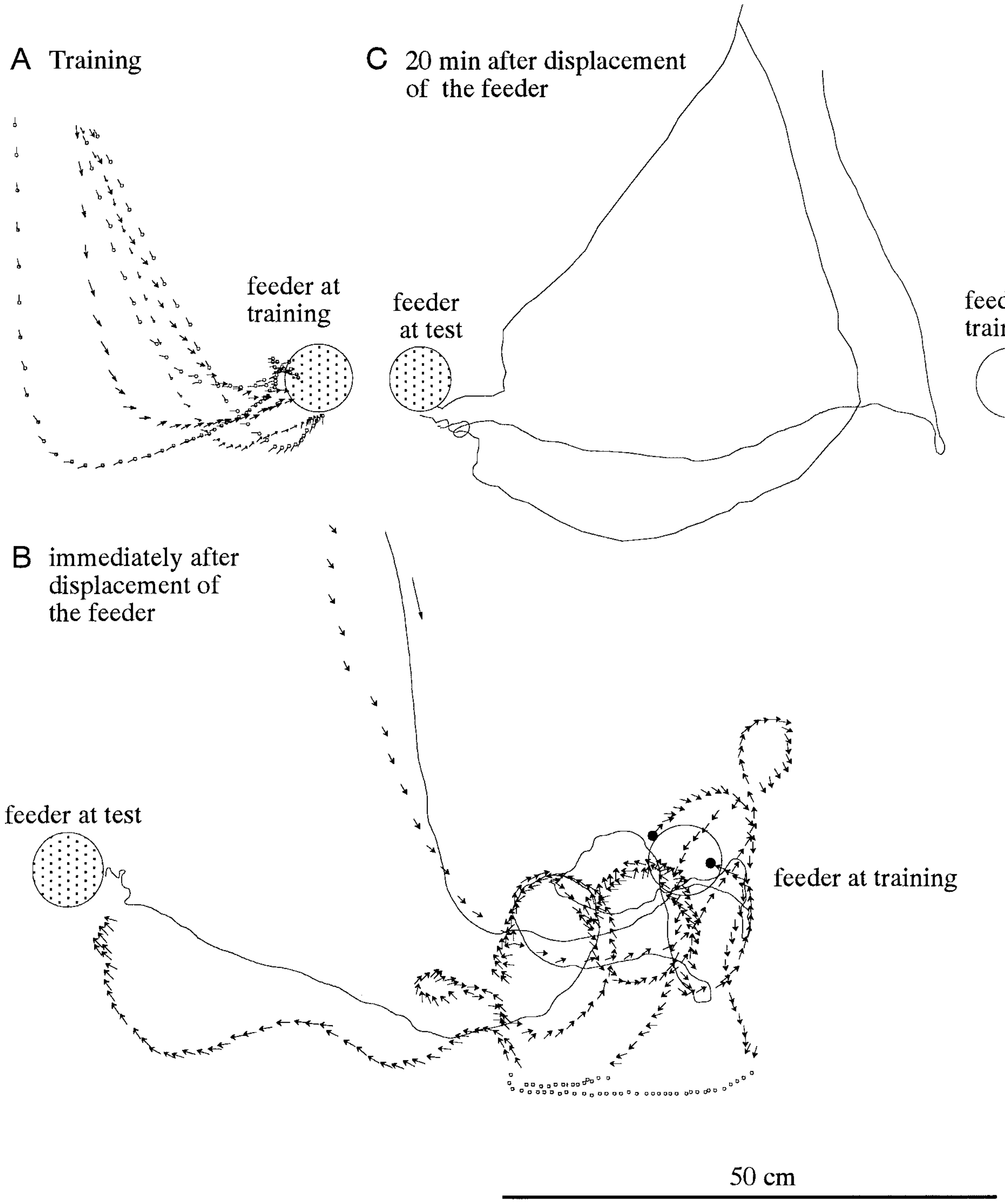

Fig. 12. Approach flights to a feeder in laboratory experiments. Flight trajectories are expressed either solid lines or sequential marks of frame to frame. Each mark shows orientation of the body axis. A: Small hornets and yellow hornets approaching the feeder in training. B: Flight paths of two hornets while the feeder is moved 60 cm left. A hornet expressed by sequential arrows once lands where the feeder was in the training, and again rise in air. The landing and leaving are shown by filled circles. A train of open circles on the left bottom indicate the hornet is out of the frame. C: Approach flights of three hornets to the moved feeder 20 min after displacement.

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were displaced (Figs. 10C, 10D). Four out of 13 hornets shifted their landing place when the plywood board was moved laterally, whereas one of the 13 shifted its landing place when the pylon was moved laterally.

Experiment 5

Hornets were trained to take sugar solution from a feeder placed on the center of a three-part blue plastic sheet (10.5 m in north-south 5 m in east-west) in Field 2. Since hornets approached the feeder from the south or south-east, their flight paths were recorded in a vertical plane in a north-south direction. Hornets approached the feeder with smooth flight paths, and landed around it after 1–2 turns (Fig. 11Aa). It took 5–10 sec for hornets from appearing in the frame of the camera till they landed. When the feeder was moved south for 4 m, the incoming hornets approached the place where the feeder had been during the training, then they cruised with frequent turns (8–20 turns till landing) (Fig. 11Ab–d). They appeared to approach the moved feeder by chance and land around it 20–60 sec after appearing in the camera frame.

Do hornets learn the place where the feeder had been during their training as the center of the blue plastic sheet? In order to examine this possibility, the central sheet of a three-part sheet was replaced with a white sheet and the feeder was removed. In spite of replacing the color of the central sheet hornets spent a long time above the white sheets with frequent turns (Fig. 11B).

Approach flight to the feeder observed in experimental sets

Experiment 7

Small hornets and yellow hornets were trained to take sugar solution from a blue Petri dish (10 cm in diameter) placed on the table (180 cm×90 cm). Hornets approached the feeder smoothly with only a few turns, and landed near the feeder (Fig. 12A). In the test the feeder was removed and an identical new feeder was placed 60 cm apart from the training feeder. This procedure is equivalent to displacing the feeder for 60 cm, but also eliminating chemical cues. Trained hornets approached the position where the training feeder had been placed as previously during their training, and cursing there with more than five turns at low altitude. They cruised more widely over the table (Fig. 12B), and then some found the new feeder and landed there. Some hornets approached the new feeder as if by chance: some landed it, but some returned to the training place, once again. Even if they finally took sugar solution from the new feeder, they usually visited the training place first in their next visit. As shown in Fig. 12C most hornets still flew toward the previous feeding place even in their third visit, though they smoothly and quickly changed their flight towards the new feeder: one hornet in Fig. 12C even flew directly to the new feeder.

Experiment 8

In order to see the approach flight of hornets while further minimizing visual cues, small hornets and yellow hornets were attracted into a drum (1.8 m in diameter and 2 m in height) and trained to take sugar solution from a feeder on a place on the floor. They entered the drum through a narrow circular entrance (10 cm in diameter) and approached directly towards the feeder and landed on the surrounding region (Fig. 13A). In the test the feeder was removed, but trained hornets took similar paths to where the feeder had been originally placed as they did during the training (Fig. 13B).

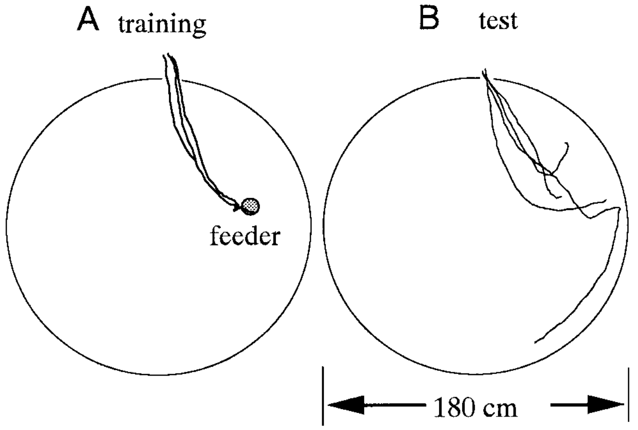

Fig. 13. Flight paths of small hornets and yellow hornets to a feeder placed on the floor in a drum. A: Hornets enter the drum through a small entrance (10 cm in diameter) and approach the feeder with gently curved path. B: In the test the feeder is removed, but hornets approach where the feeder was placed.

DISCUSSION

In the present study the control of flight paths between their nest and the forage site has been studied for three species of hornets. Although each of the three species may possess its own habits, only a behavior that is common to all three was dealt with in the present study. The experimental procedures mainly used in the present study differ from those in previously reported works on honeybees in the following ways. First, the number of hornets coming to a given feeding site was usually too small to evaluate their behavior statistically. In Experiment 6, for example, the behavior of a single hornet was observed. Second, hornets under the present observation were well acquainted with the feeding site because they continued to visit it throughout the period of our experiments. The present work, in spite of its unusual experimental procedures, revealed several behavioral characteristics, some of which have been already well documented in other hymenopterans.

Mid-distance navigation

The present data are discussed first from the perspective of mid-distance navigation and then to the approach flight. The present observations suggest that hornets decide to the site they will visit in advance of leaving their nest, and thus they seem to know in advance their flight paths to the

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forage site. This view is based upon the following observations. First, hornets that had already experienced a familiar forage site disregarded a sugar solution placed at the entrance of the nest. Second, hornets oriented towards the invisible forage site immediately after rising in the air. Third, hornets controlled their flight altitude depending on their flight distance, as if they knew beforehand how far to fly to reach the forage site. It is not known how hornets retain such memories for the flight paths they will adopt, but it may include an efference copy of the motor system.

Even though memory may provide an outline of the flight paths independent of the hornet's external senses, its delicate flight maneuvers must be, undoubtedly, be controlled by other navigational cues, sampled by multiple sensory systems. Olfaction and vision are likely senses for the control of navigation, but olfaction may play a limited role. Since antennal amputation did not impair the ability of shuttle flight in the hornets, it is concluded that olfactory sense is not indispensable for a mid-distance navigation. However, when hornets search a new forage place or are recruited by their comrades, their navigation seems to depend in part on olfaction. Selective attacking of one of many honeybee hives in the farm, and the attraction of hornets to decoy individuals placed in the laboratory room both support such a role for olfaction.

The existence of visually-guided navigation has been widely accepted in insects. The roles of visual cues such as skylight polarization (e.g., von Frisch, 1967, Wehner, 1981, 1989), visual landmarks (e.g., Cartwright and Collett, 1979, 1983) and optic flow (e.g., Esch and Burns, 1996; Srinivasan *et. al.*, 1996) have all been reported in honeybees. Outbound flights in Field 1 in the present study suggest a role for landmark navigation in hornets, too. The orientations of hornets immediately after rising in the air from their nest were distributed in an angle of 24°. If we extend their initial orientations towards the feeder, they would be distributed over a distance of 30 m at the 70-m arc. Their actual distributions were within 12 m wide on the arc, however. This means that the hornets compensate for their paths in mid-course, on their way to the feeder. The closer they approached the feeder, the more they correct the paths: they finally approached the feeder with a smooth path. There were many possible natural landmarks in the field such as the terrain and vegetation. It was difficult to specify which landmark the hornets utilize for navigational cues. As shown in Figs. 4 and 5 individual hornets seem to take similar paths during their repeated visits, but the paths differ among individuals. These data suggest that an individual hornet uses some specific structures in the field as its own landmarks, and such landmarks differ from individual to individual. The mid-course compensation of flight paths twice during the 90-m navigation shown in Fig. 5C suggests that the hornet control its path referring sequentially to more than two landmarks. Otherwise, the memory for such sequential landmarks seems to be retained for more than 1 day as shown in Fig. 5D.

The displacement of feeder-pole and 30m- and 70-m poles after training also supports the existence of landmark navigation. A few hornets changed their flight path in accordance to the displacement of the three poles, and reached the new feeder with smooth paths (Fig. 8B). Those few hornets seem to have regarded the poles as visual landmarks.

Landmark navigation is more clearly shown in homeward navigation of a small hornet shown in Fig. 7. The shortest path from the feeder at the fourth floor to its nest was a straight line passing above the metallic container in Fig. 7. However, the hornet navigated along the complicated path as shown in Fig. 7. This complicated stereo-typed path cannot be explained without visual cues. The metallic container, the hedge of trees, and the end of the path below the eaves may all be landmarks, which give an indication for a subsequent action, such as a turn. This learning behavior may be equivalent to sequence learning as reported in experimental research on honeybees (Collett *et al.*, 1993).

Multiple navigational cues

In the present study a particular idea for navigational tactics that can be deduced from a given observation is not always supported by other observations. One conflict is introduced concerning behavior in daytime and after dark. Both giant hornets and small hornets continued to visit the feeder after sunset until the luminosity of the sky dropped to 8 lux. It is doubtful whether hornets can navigate relying on visual cues alone after sunset. Although olfactory cues for long-distance navigation can be excluded as mentioned above, it may be effective after sunset. Moreover, hornets may retain during their repeated visits some memories that are independent of external cues, and these may assist navigation under poor visual conditions.

Even though our observations after dark do not seem to favor visually-guided navigation, as mentioned above landmark navigation is most likely in daytime. Furthermore, other observations also suggest a role for additional visual cues as follows. First, immediate returns to the feeding site of hornets that were captured near the feeding site and released about 100 m away suggest that they may orient the feeding place even if they view it from outside their routine forage paths. Since an ability to retain a cognitive mental map has not been supported in honeybees (Dyer, 1996; Dyer *et al.*, 1993, Wehner *et al.*, 1990), such representation of the external world is unlikely in hornets, either. Since the feeding place in Field 2 was located in a close vicinity of the two-story building at the periphery of the 10,000 m^2 open grass field, such a terrain viewed at a high altitude may itself be a landmark for hornets. Second, straight paths to the feeder against a strong head wind in the storm are suggestive of visual navigation. Since a flight time under such weather condition was longer by a factor of 1.5 times that under mild weather, navigation depending on internal memories such as efference copy or path integration seems to be less likely. Third, skylight polarization could not be controlled in the present field experiments. However, the fact that

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masking of the dorsal part of compound eyes resulted in circular cruising and failure to make the homeward flight suggests some role for skylight polarization in mid-range navigation, because it is known in many insects that the dorsal rim of the compound eyes is concerned with polarized-light detection (e.g., Wehner, 1989). Thus, the present data suggest that hornets appear to retain multiple navigational cues during repeated flights to a familiar place, and which cue they use depends upon the environmental conditions.

Approach flight

As compared with mid-range navigation short-range navigation such as the approach to a goal has been well documented in honeybees and wasps. How these hymenopterans utilize near-by landmarks has been analyzed in details (e.g., Collett *et al.*, 1993; Lehrer, 1996; Zeil, 1993a, b). Similar mechanisms have also been confirmed in the present study as follows.

Approaching hornets took smooth paths to land around the feeder under both field and laboratory experiments. Even when the feeder was moved or removed, hornets also approached smoothly the place where the feeder had initially been placed, but then spent a long time cruising to search the missing feeder (Figs. 10–12). These observations clearly show two different approach maneuvers. On the one hand, the adoption of a gently curved smooth approach to the feeding place, even if the trained feeder is no longer there, suggests that hornets approach the feeder referring to the surrounding view until they come very close to it. The predominant influence of the surrounding scenery is also supported by the fact that even if they approach the moved feeder during the cruise, they did not always sit on the feeder, but often fly back over the previous feeding place in both field and laboratory experiments. On the other hand, the long time spent cursing over the trained site suggests that it takes careful image matching between the hornet's visual memories of the feeder's features and those seen in its current view to make final landing. Since visual images around the feeder are changed depending on flight altitudes, hornets must keep their flight altitude rather constant. Experiment 3 showed that hornets learnt the height of the feeder: they cruised at the level of the feeder they learnt during their training, or above it, even when the feeder was removed (Fig. 9).

Since there were many distinct structures around the feeder in the fields, it is impossible to imagine how and what kind of images the hornets learnt in reference to the feeder. The feeder-pole (4 m in height and 20 cm in diameter) in Field 1 might be a poor landmark, because most hornets were not attracted by the pole when it was moved (Fig. 8A). A plywood board placed in Field 2 might be an effective landmark, because its displacement resulted in shifting the landing point for most hornets. Its edges seemed to be more effective, since hornets trained to the feeder close to the edge of the plywood board shifted their landing places more quickly than those trained in front of the featureless central part of the board (Figs. 10A, 10B). The vertical edge of the white plywood board gave a high contrast against the dark background. Colors or color edges on the ground seemed to be less effective, because coursing over a missing feeder was not affected by changing the color of a sheet on the ground (Fig. 11B). Displacement of the pylon only was less effective for shifting the landing point than that of both the pylon and plywood board, suggesting that a large landmark may be more effective than a small one. Since it took a longer time for those hornets to landing on the ground after displacement of the landmarks, they also apparently used other visual cues. Disagreement between the topographical arrangement of artificial landmarks and other fixed scenery between the training and the test choice may have resulted in the longer search flight (Fig. 10).

Similar flight maneuvers during the approach to the feeder was also confirmed in laboratory experiments, though the scale of the flight path was small. Although the surrounding visual cues were reduced in experiments on the table surrounded by a curtain, cursing for long time over the missing feeder as shown in Fig. 12B suggested there might still remain some visual cues such as the corners of the table, to which the hornet responded. Smooth approaches to the feeding site in both training and test experiments shown in Fig. 12 suggest that the entrance seems to be regarded as a final visual landmark to fly past. The hornets seemed to learn how far and in which direction to fly from the entrance to reach the feeder. Such approaches without external cues were more clearly shown in Experiment 8 (Fig. 13). There were few visual cues except for the feeder itself and the circular entrance in the drum. Nevertheless, hornets flew smoothly to the place in the test where the feeder had been placed in the training.

Hornets that took a sugar solution once from the moved feeder flew toward the trained place in their subsequent visits as shown in Figs. 8A and 12C, and then directed to the new feeder. They may learn a sequential path from the training position to the new feeder.

Further problems

In the present study both the stereo-typed properties and the plastic nature of forage navigation have been dealt with for three species of hornets. Visually guided approach by hornets to the feeder seems to adopt the same tactics as that in other hymenopterans. Thus, honeybees may be more rewarding hymenopterans to examine foraging behavior near the feeding site than hornets, because the number of inviduals for observation allows statistical comparisons more readily, but is smaller in hornets. On the other, hornets may be better suited to examine mid-range navigation, because their flight paths can be followed for a long distance. The present work revealed the influence of extremely stereo-typed navigation and path control by near-by landmarks en route to the feeding site. However, more analytical and elaborate analysis is required to understand mechanism of mid-range navigation.

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