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20. We thank M. James and W. Anderson for helpful discussion, I. Weissman and H. Gershenfeld for sharing material (including the λgt10) and results prior to publication, and D. Oare for preparing the manuscript. Supported by the Medical Research Council of Canada, the National Cancer Institute of Canada, and the Alberta Heritage Foundation for Medical Research provided salary support.

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The Locale Map of Honey Bees: Do Insects Have Cognitive Maps?

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Whereas higher vertebrates are able to construct a mental "map" of their home area and so use their knowledge of the spatial relations between landmarks to navigate along novel routes, invertebrates have been thought able to use landmarks in their navigation only as a familiar, route-specific series. Experiments with honey bees show that these insects have and use landmark maps thus invalidating this presumed invertebrate-vertebrate dichotomy.

ALTHOUGH HONEY BEES USE CELESTIAL cues in their navigation to unfamiliar food sources (*1*), they frequently begin to rely on prominent landmarks, at least on the outward journey, as the route becomes familiar (*2, 3*). Wehner (*4*) has proposed that the landmark memory of invertebrates is stored as a series of route-specific photographs; hence, bees and other insects could use landmarks only in serial order and along familiar routes. This model stands in sharp contrast to the way higher vertebrates are thought to use landmarks as part of a map; in this system, the relative location of familiar landmarks is understood—presumably stored in the brain as a map—so that novel routes based on new combinations of landmarks may be used, freeing the animal from dependence on route-specific combinations.

To put this presumed vertebrate-invertebrate dichotomy into concrete terms, consider the area around an animal's home (Fig. 1). If the hive is its home and site A is a food source, an insect would be presumed to know site A in terms of a set of landmarks regularly encountered there; if displaced to site B, the insect would, at best, recognize site B as part of some other route leading from home to another food source, and perhaps be able to follow that route back home. A higher vertebrate familiar with the same area, on the other hand, would be able to use the landmarks visible at site B to determine the direction of site A, and set off directly toward it even though it had never traveled from site B to site A before; the vertebrate, it is supposed, has integrated its landmark knowledge into a map.

Two observations suggest that the map alternative might be available to bees. First, older foragers captured while leaving the hive, transported in darkness to a location hundreds of meters away and out of sight of the hive, fed a highly concentrated sugar solution, and released can fly directly home (*5, 6*); that young foragers cannot suggests that some familiarity with the locale may be important. This result is not conclusive since the foragers might have recognized the release site as part of their route-specific memory.

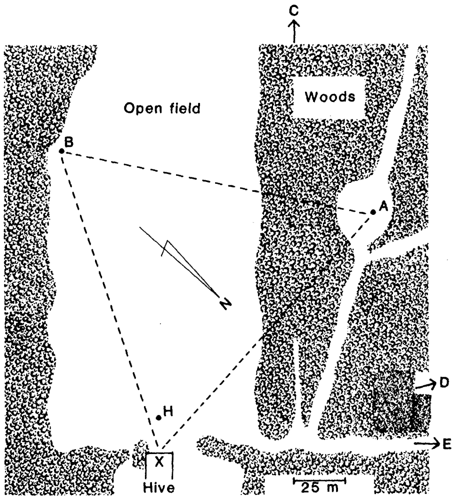

Fig. 1. Bees from a hive (bottom center) were trained to either site A, site B (both 160 m from the hive), or (off the top of the map) site C (350 m from the hive); on subsequent days these foragers and others were captured and transported to a different site and released—site B for those trained to A, site A for those trained to B, and site D (350 m from the hive) or site E (4425 m from the hive) for those trained to site C. As a control, some trained foragers were released at site H as well. Arrow N marks north.

The second suggestion comes from experiments in which forager dances were manipulated to indicate a location either in the middle of a lake or on the far shore (*7, 8*). Recruitment was effective only to the latter, more plausible site, suggesting that the dance coordinates enabled recruits to make some sort of judgment about the suitability of the advertised site before leaving the hive; recruits make economic judgments about the distance versus the quality of the food being advertised before leaving (*9*). But the lake results could be explained on the basis of environmental factors (*8*). The purpose of the experiments reported here was to determine whether bees are limited to route-specific navigation or, instead, have a true locale map available to them.

Individually marked honey bees (*Apis mellifera ligustica*) were first trained to site A 160 m west of the hive (Fig. 1) along a path through the woods at Stony Ford, the Princeton University field station in Princeton, New Jersey. On the basis of the training procedure and the observed departure bearings from both the hive and the food source, foragers flew either directly to and from the hive to reach the feeding station or along a two-legged route that included the last portion of the training route (the path). All bees visiting the station were either marked or captured.

On subsequent days, foragers regularly visiting site A were captured at the hive entrance in a 600-ml beaker placed in their takeoff path. Each trapped forager was then carried in the dark across an open field to site B, 160 m south-southwest of the hive, and released. Two foragers were sometimes captured and transported together, but bees

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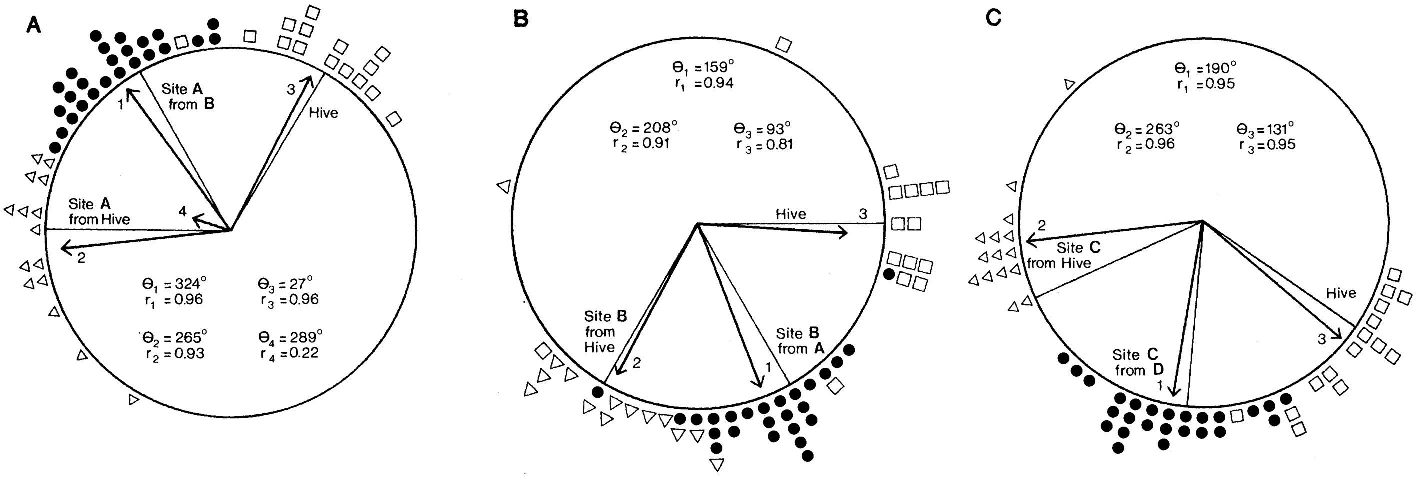

Fig. 2. Bees were trained to one site—site A in (A), site B in (B), and site C in (C)—and then transported and released at another site the same distance from the hive but in a different direction; bearings of bees as they vanished are indicated by the circles at the periphery of these circular distributions. The relative bearing of the feeding station is labeled "Site A from B" in (A), "Site B from A" in (B), and "Site C from D" in (C). The mean vector—a measure of the average direction and degree of clustering—is shown, and the values for mean direction θ_1 and vector length r_1 listed (*12*). The triangles represent the vanishing bearings for trained foragers released at site H; the corresponding predicted bearing (site from hive), mean vector, and associated values are also presented. The squares represent the vanishing bearings of incoming foragers transported to the release site. The predicted bearing (hive), mean vector, and associated values are shown. All three mean vectors in all three distributions are significant (z test, $P < 0.001$). The shorter mean vector in (A) represents unmarked foragers captured as they left the hive and transported to the release site. There is no predicted bearing for these bees.

were always released individually. The released foragers typically circled and flew off; bearings of bees as they vanished were recorded (circles at the periphery of the circular distribution in Fig. 2A). The displaced foragers could not see the feeding station or even the terrain beyond the northwest side of the field during circling: the mean altitude at which circling ended was 9.2 m (*10*); the ground slopes upward on the northwest side of the field, so that the treetop horizon ranges from 24 to 28 m above site B, and so at least 15 m above the circling foragers, thereby cutting off all view beyond the northwest side of the field.

If the foragers were disoriented, either as a result of the capture and release technique or because they could not accommodate the sudden change of landmarks, they would be expected to fly off in random directions. If they failed to recognize that they had been displaced, they might be expected to continue on their normal outward bearing from the hive (210°). If they had only route-specific landmark memory and were familiar with a route leading to food out past site B, they might be expected to be able to fly directly back to the hive (30°) and there pick up the route to their intended destination, site A. If they have true maps, they would be expected to fly directly off toward site A (330°), which is precisely what they did (Fig. 2A) (*11*). An inspection of flight times, which largely matched those of direct flights from the hive, indicates that most of these bees must have flown directly to the feeding station: 25.2 ± 5.5 seconds (mean ± SD, $n = 15$) from the hive to site A, versus 28.9 ± 9.4 seconds ($n = 25$) from site B to site A; given the flight speed of bees and allowing for initial circling time, a dogleg from site B to the hive and then to site A would take about 45 seconds. Ten different foragers were tested in this part of the experiment (*12*). The mean bearing for the first release of the ten bees tested was 325° ± 14° (the map prediction is 330°) with a length of radius $r = 0.97$ (*13*); for all 25 releases combined the values were 324° ± 16° and $r = 0.96$. None of the displaced foragers departed toward the hive; all arrived at site A.

As controls, the bees were also displaced and released in three additional ways. (i) The second and (if it happened) fourth times a marked forager was caught for release, it was transported halfway to site B and then back to site H, 15 m in front of the hive, and released. These bees, having experienced the same capture and handling time, would be expected to fly directly to site A, which they did (Fig. 2A, triangles). (ii) Unmarked incoming foragers were caught, transported to site B, and released. They would be expected to depart directly toward the hive, which they did (Fig. 2A, squares). (iii) Unmarked foragers were caught leaving the hive, transported to site B, and released. These bees would be expected to depart for their intended destinations in various directions; indeed, their departure bearings were widely scattered (Fig. 2A) (for simplicity, only the mean vector is shown).

To control for any possible asymmetries between sites B and A, a new hive was established and individually marked foragers were trained to site B; displacements were to site A. Again, ten experienced foragers displaced en route to a location well away from any plausible flight path to the food source they were visiting were nevertheless able to orient quickly and fly directly there; the mean bearing for the first release of each bee was 157° ± 11° (150° was predicted by the map hypothesis) with a length of $r = 0.98$; the combined values for all 25 releases were 159° ± 20° and $r = 0.94$ (Fig. 2B).

To determine whether bees can use map information farther from the hive, individually marked foragers were trained from the hive to a heavily wooded location (site C) 350 m west-southwest of the hive, and ten of these bees were then displaced as before to a small clearing (site D) 350 m west-northwest of the hive; again, the hive and the two sites formed an equilateral triangle. The results of this experiment (Fig. 2C) also support the map hypothesis.

As a final check, ten foragers visiting site C were transported and released at site E, an open field 4425 m northwest of the hive—a distance outside the normal foraging range of honey bees (*14*). Foragers depending on familiar landmarks would not be expected to orient accurately at this distance, and indeed the vanishing bearings of the ten transported bees were highly scattered: mean vector at 113° ± 73° (140° to site C) with an $r = 0.30$, which is not significant ($P > 0.1$). None of these bees returned to the feeding station or the hive (*15*). Different results were obtained when ten foragers visiting site C were transported halfway to site E and then returned and released at site H; these bees were well oriented: mean vector, 257° ± 14° (245° to site C) with $r = 0.97$.

The route-specific hypothesis of navigation, which these results seem to rule out as the sole landmark-based navigational system in honey bees, is in some respects analogous to the original formulations of learning theory, in which animals were supposed to be incapable of learning outside the context of performing the specific behavior that was being conditioned (*16*). Tolman (*17*), however, demonstrated the reality of learning out of context, or latent learning, in rodents: animals allowed to observe or explore in the absence of a food reward, for example, were later able to use information gathered during these episodes in performing tasks rewarded with food. He called this instrumental learning without performance of the relevant response a "cognitive map." Later work, particularly by Olton and his colleagues (*18*), indicates that at least higher vertebrates can plan behavior to make use of novel and efficient routes on the basis of maplike cognitive representations. The results of my experiments suggest that this ability, which is often considered a basic form of thinking (*16*), is not limited to vertebrates.

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10. Altitude was measured with a rangefinder for the first departure of each of the ten trained foragers displaced to site B; SD, ±2.3 m; observer-to-bee distance averaged 12.9 m.
11. One possible concern is that the trained foragers might be in the habit of visting the training and release site as part of a single route. This was not possible during training since only one site ever had food during the tenure of a given hive; moreover, foragers could be observed arriving directly from the hive direction, feeding to repletion, and then departing directly for the hive. The possibility is unlikely at other times as well: bees are flower and patch constant [T. D. Seeley, *Honeybee Ecology* (Princeton Univ. Press, Princeton, NJ, 1985)]. Moreover, care was taken to ensure that the natural flora in the open field site was different from that of the woodland path site; indeed, the latter had no flowers at all. Nor, given the extent of the woods to the northeast, could site A plausibly be imagined to be on a route to a hypothetical second patch, even if bees were in the habit of visiting multiple scattered patches on single trips? Sites C and D lacked flowers of any sort.
12. The unlikely possibility that bees are capable of nonvisual route–based navigation during displacement [J. L. Gould, *Am. Sci.* **68**, 256 (1980)] is ruled out by displacement experiments performed in the absence of prominent landmarks [2; F. Otto, *Z. Vergl. Physiol.* **42**, 303 (1960); J. L. Gould, thesis, Rockefeller University (1975)], in which bees departed as though they had not been displaced, and in the absence of familiar landmarks (*7*), in which bees were disoriented.
13. Statistics after E. Batschelet in *Animal Orientation and Navigation*, S. R. Galler *et al.*, Eds. (NASA, Washington, DC, 1972), pp. 61–92. The tip of each mean vector lies at the "center of mass" of the vanishing bearings; a length of $r = 1.0$ corresponds to perfect clustering, and so the degree to which $r < 1$ is a measure of the scatter about the mean. (The value of r is normally used in place of SD in circular distributions, since SD can be approximated by taking the inverse cosine of r. There is no standard way of calculating the uncertainty in r). The z test compares the actual distribution to the predicted bearing. Since the first releases are consistent with the map hypothesis rather than the route-specific hypothesis, combining those data with the subsequent releases is justified.
14. P. K. Visscher and T. D. Seeley [*Ecology* **63**, 1790 (1982)] showed, from measurements of dances in natural colonies, that most foraging takes place within about 2500 m of the hive, with a mean of 1700 m. Trips beyond 4000 m are extremely rare.
15. The maximum flight range of bees can be inferred from experiments in which bees were trained as far as possible; H. Knaffl and M. Lindauer [cited in K. von Frisch, *The Dance Language and Orientation of Bees* (Harvard Univ. Press, Cambridge, MA, 1967)] trained bees to fly as far as 12,000 m. Although unlikely, it is possible that the foragers took longer than normal to get their bearings so that they were out of sight when they became oriented, and their failure to return was a consequence of not having enough "fuel." To control for this possibility, 25 foragers were captured leaving the hive, transported in the dark to site E, fed honey ($n = 10$) or 2*M* sucrose solution ($n = 15$) to repletion, marked, and released; none of these bees returned.
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19. I thank K. Monahan for technical help. Supported by NSF grant BNS 85-06797.

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Memory Constraints and Flower Choice in *Pieris rapae*

ALCINDA C. LEWIS

Darwin hypothesized that flower constancy in insects that feed on nectar results from the need to learn how to extract nectar from a flower of a given species. In laboratory tests, *Pieris rapae*, the cabbage butterfly, showed flower constancy by continuing to visit flower species with which it had experience. The time required by individuals to find the source of nectar in flowers decreased with successive attempts, the performance following a learning curve. Learning to extract nectar from a second species interfered with the ability to extract nectar from the first. Insects that switch species thus experience a cost in time to learn. These results support recent suggestions on the importance of learning in animal foraging.

IN 1876, DARWIN (*1*, P. 419) MADE THE following suggestions about the well-known flower species constancy of certain insects:

> That insects should visit the flowers of the same species for as long as they can, is of great significance to the plant, as it favors cross-fertilization of distinct individuals of the same species; but no one will suppose that insects act in this manner for the good of the plant. The cause probably lies in insects being thus enabled to work quicker; they have just learned how to stand in the best position on the flower, and how far and in what direction to insert their proboscides.

As pointed out by Waser (*2*), this hypothesis implies that a limited memory capacity can be one cause of floral constancy: were the insect able to recall nectar extraction methods of more than one species, there would be less need for constancy (*3*). Despite recent emphasis on the potential role of learning in animal foraging (*4*), this hypothesis has received little empirical attention. I present here results for *Pieris rapae*, the cabbage butterfly, that support Darwin's hypothesis: (i) the insect displayed flower constancy, (ii) the insect learned how to extract nectar from flowers, (iii) learning a second species interfered with recall of the first, and (iv) experience with a flower species influenced choice between species.

Recent field observations suggest that some butterfly species, including *P. rapae*, exhibit the constancy reported for certain bee species (*5*). This possibility was tested with Bateman's procedure (*6*) in which the insect is given a binary choice with equal quantitites of both species. The identities of the first and second species used are recorded; constant insects will feed from the same species on both visits irrespective of their initial preference. Both preference and constancy influenced choice in *P. rapae*: most butterflies initially fed from *Vicia cracca* in test 1 and from *Lotus corniculatus* in test 2 (Table 1). Thus, initial preference depended on the identities of the test species, but in both tests, butterflies continued to feed from the species they initially fed from, demonstrating constancy.

To determine if butterflies exhibit the kind of learning hypothesized by Darwin as an explanation for constancy, caged, individually marked butterflies were given flowers and their behavior was observed. When butterflies first land on a flower, they search the sepals and corolla with their probos-

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