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EFFECTS OF HORIZON LANDMARKS ON HOMING SUCCESS IN  
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**Abstract.**—A hypothesis is proposed and field data presented indicating that in long-distance navigation, honey bee foragers use horizon landmarks to determine the direction of their home site. Metal tags were recaptured from marked foragers released at various distances and directions from their nests located in mountainous or flat terrain. The proportion of tagged foragers returning to their nests decreased as distances of the release points from the natal colony increased. However, the fraction of returns versus distance differed according to site horizon features. Twice as many foragers returned to their home nests located in mountainous terrain as compared to returns in flat terrain. Maximum distances from which honey bee foragers found their nests were about 5 km in flat terrain with no skyline features and about 9 km in a mountainous region. The data support the hypothesis that orientation cues relied on by foragers for distance navigation include deformations in the landscape horizon when available. A searching flight pattern is used when no such key physiographic features are conspicuous in the region.

In eusocial organisms adequate colony nutrition depends on how well foragers locate food resources, collect food at resource sites, and transport the food back to the home colony. Greater effectiveness can increase the rate of food accumulation in the colony, which heightens reproductive success and survival of the colony. The first two tasks, finding and collecting food, have been the subjects of intensive study for several decades.

Successful food exploitation requires effective orientation. Foraging insects and other animals rely on multiple environmental cues in orientation (reviewed in Able 1991). Pheromone trails are used by leaf-cutter ants (Wilson 1984; reviewed by Hölldobler and Wilson 1990). The ants can locate known food sources and return to their colony. Other ant species apparently follow a pheromone trail to locate an identified food source but use visual cues and navigational learning for homing (Jaffe and Villegas 1985). Olfactory mechanisms are important even in flying animals, including bees when near their home sites (von Frisch 1950; Judd and Borden 1989; Murlis et al. 1992; Wcislo 1992). At greater distances individuals must use other cues as they return to their home sites. Studies of homing after procurement of food by social bees and wasps indicate that learning

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the nest position relative to visual landmarks is achieved during orientation flights (reviewed by Gary 1992; Zeil 1993*a*, 1993*b*).

Seminal work by von Frisch and his coworkers resulted in an understanding of information transfer in honey bees related to distance, direction, and quality of a food source (von Frisch 1948, 1950, 1967; Lindauer 1961). The honey bee dance language was described, along with the importance of environmental cues in orientation. Bees react to a combination of chemical pheromones and floral odors, visual patterns, the position of the sun, polarized light, colors, and magnetic anomalies. Attempts to clarify details of bee orientation to food sources in the field, including the use of landmarks, have been continued by many researchers (see, e.g., Cartwright and Collett 1982; Dyer and Gould 1983; Hsu and Li 1994).

Most published work on orientation in the field by eusocial insects deals with foragers' abilities to locate food sources. Findings indicate that foraging bees depend on their outgoing flight for the information they later incorporate in their dance (von Frisch 1948). However, little work has been done on homing, especially from distances greater than a few hundred meters. In short, controlled feeding flights, Kastberger (1992) found that honey bees behave differently on the flight out to a feeding patch than on the homing flight and that visual cues seem essential for both. It is well-known that once foragers learn the locations of feeding sites, they follow a "bee line" to and from the site and their home colony (Edgell 1949; Beutler 1954). This behavior requires learning and orienting to local landmarks.

After studies attempting to explain orientation and homing, Gould (1986, 1990) suggested that individual foragers form cognitive mental maps and follow compass directions according to the maps rather than landscape cues. This idea helped explain the movement of foragers in the field between their familiar home nest site and a forage patch where they may know local landmarks. It was attractive because it did not require foragers to learn the landscape between the nest and food patch, but only the compass direction. Other reports convincingly refuted this contention by showing that foragers navigate by the sun and local landmarks near nests (Cartwright and Collett 1982; Cheng et al. 1987; Menzel et al. 1990; Wehner and Menzel 1990; Wehner et al. 1990; Dyer 1991; Collett and Baron 1994). No mental map is needed to explain bee flight behavior in familiar landscapes, but route landmarks do not explain homing from unfamiliar territories.

There are inconsistent reports on orientation cues used at long distances from home colonies and average or maximum flight ranges of honey bees in natural, agricultural, or urban ecosystems. In alfalfa field monocultures in the Pacific Northwest, Levin (1959, 1961) found that young honey bees foraged on the first day only about 250–300 m from their nests. The distances increased somewhat as they aged. In 10 other agricultural monocultures, bees were generally found to forage within 300 m of their hives and ventured farther only when more attractive fields were located farther away (Robinson 1966; Gary 1977). If nectar and pollen are abundant, foragers venture only 1 km or less and use local landmarks to return home (Visscher 1982). Interpreting distances from rates of waggle dances of returned honey bee foragers observed in glass-sided bee hives shows

that most foraging takes place within 600–800 m from the nest. Foraging distances of 2 km are common, sometimes extending to 5 km (Visscher and Seeley 1982). Under extreme experimental conditions of food or water deprivation, marked foragers have reportedly been recovered 13 km from their nests (Eckert 1933). When foraging conditions are rich and plentiful in the nest vicinity, foragers will not likely venture to distant floral patches. Visscher and Seeley (1982) stated that their greater values for foraging distances in a natural setting may represent more natural values for honey bee foraging than those found in the often homogeneous planar crop environments reported by other workers.

To study the ranges of successful homing of honey bees and the cues they may exploit in nature, we modified a magnetic mark-recapture tagging system (Gary 1971). We report here results of field tests in which tagged bees were released at unfamiliar sites located as far as 10 km from their home nests. We wished to ascertain whether homing and orientation in honey bees foraging under natural conditions are influenced by large physiographic deformations in the horizon. Patterns of successful returns could indicate that honey bees memorize and use large horizon features in homing orientation.

#### METHODS

##### *Homing in Mountainous and Flat Regions: Sonoran Desert, Arizona*

Study colonies of Italian honey bees (*Apis mellifera ligustica*), headed by naturally mated queens housed in standard Langstroth equipment, were located at two sites (one colony at each site) in Arizona within the Sonoran Desert biotic province near Tucson. During the course of our studies over two seasons, the colonies consisted of 30,000–50,000 workers, of which about 20%–35% were estimated to be of foraging age. One colony was kept at the Carl Hayden Bee Research Center, some 5 km northeast of downtown Tucson (hereafter referred to as the “Arizona Flat Site”), while the other was located 30 km west of Tucson on the grounds of the Sonoran Arthropod Studies Institute (SASI) at the Arthropod Discovery Center on the west-facing bajada of the Tucson Mountains (hereafter referred to as the “Mountain Site”).

The Arizona sites are quite different; the Flat Site had access to numerous small cultivated and artificially irrigated floral patches and located on flat terrain, with mountains only visible in the distance; the Mountain Site provided only wild flowers in the natural Sonoran Desert west of the Tucson Mountains (study colony at an altitude of 900 m, partway up the base of the mountain range, which peaks at 1,500 m).

In Arizona nearly all test days were ideal for flight, with shaded air temperatures ranging from a low of about 20°C in the morning to a high of about 35°C in midday. Shaded air temperatures were recorded at 5-min intervals throughout the study period and stored on a Campbell Scientific data logger that was later downloaded to a desktop microcomputer. Average wind vectors were determined during the hours of flight activity (1000–1900 hours) using circular statistics (Zar 1984) and Excel on a Macintosh microcomputer. Good flight activity was indi-

cated by the large numbers of out-flying and returning foragers. Ten days after the study was concluded, one of the study colonies swarmed, which indicated rapid growth during the study.

#### *Homing in Flat Terrain: Western New York State*

In New York state, the study colony was kept on the campus apiary of the State University of New York at Brockport, about 35 km west of Rochester in a farmland/forest area ("New York Flat Site"). The New York Flat Site was rather similar to the Arizona Flat Site but gave access to mixed hardwood forest second growth and cultivated agricultural land, including fruit tree orchards in flat terrain. In New York, cool and overcast days prevailed, with early morning lows of 15°C and midday highs of 20°–25°C. On several study days, rain occurred after releases had been made. The activity at the entrance of the study hive indicated considerable foraging, however, even in the cool weather conditions.

All colonies at all sites were given minimal management routinely during the year but received no disruptive colony inspections at any time during the present studies. Each hive enclosed a volume of 60 L with  $21 \cdot 10^3 \text{ cm}^2$  of comb area.

#### *Tagging and Recapturing Foragers*

Exiting foragers were captured by fixing a large hardware cloth cone ( $45 \times 35 \times 60 \text{ cm}$ , 8 mesh) near and in front of the hive entrance until approximately 30–50 out-flying bees had accumulated inside the cone. After about 1 min, the cone containing bees was removed and placed on the ground nearby and wrapped in black cloth, with light entering only a small opening to which the bees were attracted and from which they escaped. Escaping foragers were collected in an insect net and taken to a nearby building for tagging.

As we did not want to influence the physiology and behavior of the test foragers, we did not use any anesthetic, nor did we cool the bees for tag attachment. For marking, groups of 20–40 foragers were individually held for 30–45 s in a 2.5-cm diameter plastic cylinder with a nylon mesh cover. A foam-ended plunger gently nudged each bee with its dorsal side against the nylon mesh, so it could be held motionless during tag application. A small drop of about 1–2  $\mu\text{L}$  of Elmer's white glue was applied to the dorsal side of the second thoracic segment. Individual ferrous metal circular tags (2.3-mm diameter) were affixed to the glue and held there for 5–15 s with gentle pressure from a pair of fine forceps. Tags were made from shim steel stock using a Jackson press modified for the correct diameter. The tags were painted solid colors and/or with one or several dots applied with Pilot paint pens. The bare metal tags were 0.25-mm thick and weighed (on a Mettler H15 analytical balance)  $9.8 \pm 0.99$  (SD) mg ( $n = 30$ ) and only  $10.5 \pm 1.02$  (SD) mg ( $n = 30$ ) when recovered, even with their attached dried glue, painted color codes, and body hair. Other details of magnetic tagging and release/recapture were very similar to those described in the original article by Gary (1971).

Metal-tagged bees were then dropped through the neck of a plastic funnel into a covered 2-L glass flask containing crumpled tissues (Kimwipes) for a foothold and kept at 25°C for about 20 min until they were transported to the release

sites in an automobile at preselected distances (i.e., 0.1–10 km) from the source colonies. Although preselected, the daily order of release sites was determined randomly to reduce variation due to time of day, weather, and other unknown factors. Each release from initial capture to subsequent release at any particular site on any day took about 30–45 min. All bees released at any release point carried tags of the same color code (e.g., a solid red tag with two white dots at 0.3 km on the first day; a green tag at 0.6 km on the same day, and a green tag with a red dot for 0.6 km distance on day 2, etc.). To avoid confusion from released bees that might return even after an overnight stay in the field, no color code was used more than once. The same set of release sites was used on at least three different days, and all data for each site were pooled. Locations of release sites and beeline distances from home nests were determined using Trimble Navigation System coordinates from Global Positioning System (GPS) satellite data (fig. 1). From this colony (*I* in the figure), 977 outbound honey bee foragers were captured, marked, and released. The farthest release point from which there were successful returns (*I5*) is 9.2 km from the home nest.

Foragers were tagged and released between 0800 and 1430 hours Mountain Standard Time on 12 d from 18 March to 3 April 1991 in Arizona. In New York, outbound foragers were studied from 0800 to 1430 hours Eastern Standard Time from 2 June to 19 July 1992. Foragers were not fed any sugar water or honey after capture or while in transit, since they naturally held some contents in their honey stomachs as out-flying foragers, and they had access to floral resources when released in the field. In order to determine energy available to the foragers, samples of 6–10 outbound foragers were taken at each marking time and placed on ice in sealed vials and later analyzed for honey stomach sugar contents. The contents of the honey stomach were forced out of the mouth parts by careful squeezing of the abdomen of the bee and captured in a 10- $\mu$ L glass micropipette. The constant bore pipette allowed easy determination of volume, and sugar concentration was found using a temperature-compensated optical refractometer (American Optical model 10432) modified for small volumes (Southwick et al. 1981).

### *Recapturing Released Foragers*

Successful homing of metal-tagged foragers was monitored at all sites by magnetic traps at hive entrances. Hive entrances were each fitted with a centrally placed row of four 1-oz horseshoe magnets. Wooden and screen devices to cause most outgoing bees to segregate from the largely inbound foragers returning under the magnets were nailed to the hive fronts.

The metal tags represent a nominal payload of about one-half a corbicular pollen pack. Tested on Italian honey bees at Davis, California (Gary 1971), they had a >90% probability of recapture by hive magnets over the course of 1–2 h following bee tagging in agricultural fields. Once the returned tagged bees pulled free of the magnet's grip, the tags remained on the magnets indefinitely until removed by the experimenter. We collected tags intermittently (about every hour) on experimental days, with the final collection at sundown on the tagging date. A total of about 3,300 workers was tagged and released—2,200 from both Sonoran



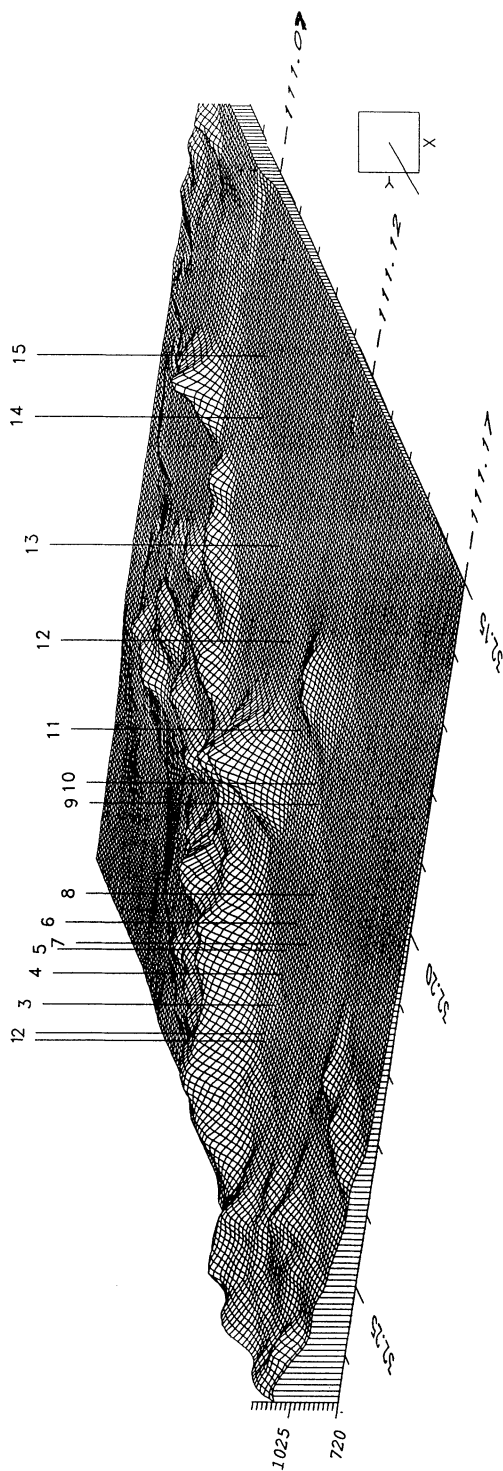


FIG. 1.—The study area for honey bee homing experiments at the base of the Tucson Mountains (Pima County, Arizona). The three-dimensional contour plot is rendered from a GPS using satellite data. Vertical postings give the locations for one home colony (*number 1*) and release points (*numbers 2–15*). Degrees W longitude and N latitude are indicated along the *X*- and *Y*-axes, respectively. Altitudes in meters are shown on the *Z*-axis.

Desert sites during the 9 d of the study in 1991 and about 1,100 workers from the New York site during the 5 d of the study in 1992.

We noted that the metal tags were unlikely to fall off flying bees en route to their hives from release points. Even if a tagged forager managed to slip into the hive without its tag being removed and the tag fell off or was later removed by hive mates in the colony, tags were removed from the colony by "house" bees and promptly caught by the magnets. Similarly, a returning bee whose tag was not pulled off by the magnets was almost always removed on a subsequent colony exit or entrance later that day. In a test for the effect of time of day on successful returns, 177 foragers were tagged and released at hourly intervals from 1.6 km between 0855 and 1645 hours. Of all those released before 1430 hours,  $93.4\% \pm 5.8\%$  returned successfully. Successful returns decreased to  $<70\%$  after 1500 hours. Therefore, in our studies we released no bees later than 1430 hours, to avoid having any late arrivals encounter difficulty because of orientation during twilight hours. To check for drifting and hive fidelity, when foragers were tagged and released from one hive, magnets were placed on other adjacent hives. The returning foragers did not make any mistakes by returning to the wrong hive; they always returned to their natal hive. There was no difference in successful returns of marked foragers released at the same distance (3.9 km) from sites in four compass directions from their home colony (Arizona Flat Site at approximately  $90^\circ$ ,  $180^\circ$ ,  $270^\circ$ ,  $360^\circ$ ), so we did not attempt to repeat the extensive releases in other directions.

Only bees that had firmly attached tags and flew out of the holding jars or flew after dropping to the ground were scored as successful releases. About 96% of the tagged workers were successfully released from the 41 sites at the three study locations.

## RESULTS

### *Distance of Release and Successful Returned Foragers*

The relationships of returning bees to the distances of release sites are shown in figure 2. Most bees released within a few hundred meters of their home nests returned successfully. As the distances to the release sites increased, the fraction of successful returns decreased. Beyond a certain limit (e.g.,  $>5.6$  km at the New York Flat Site; see fig. 2A), no released bees returned. Although decreasing numbers of returning foragers from increasing distances are expected, the shapes of the curves from all sites would be expected to be similar if local landmarks, routes, and/or nest odors were being used in orientation and homing. However, on best-fit regressions, the New York Flat (fig. 2A) and Arizona Flat (fig. 2B) Sites showed curvilinear (log-linear) relationships of percentage returning foragers to distance of release, while the Mountain Site had a closer linear result (fig. 2C).

In flat terrain, bees successfully returned from a maximum distance of only about one-half that from which bees returned at the Mountain Site. The range of the returning flight for the Arizona Flat Site colony (5.3 km) was similar to that found in New York (5.6 km) but much less than that of the Mountain Site (9.2 km). In all cases, there was at least one release point at a greater distance than the outermost point from which released foragers successfully returned. We are



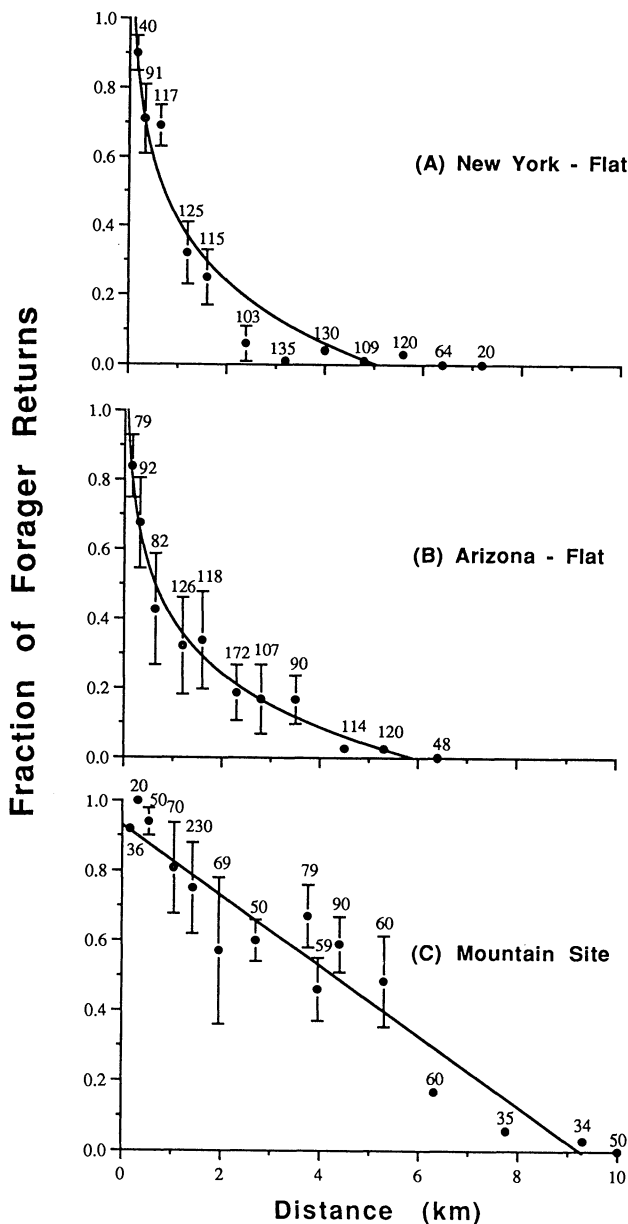


FIG. 2.—A, The relationship of the fraction of recaptured honey bee foragers ( $y$ ) to distance ( $x$ ) of release sites from their home colony in flat terrain in western upstate New York (New York Flat Site). The expected maximum distance of return was 5.1 km; however, foragers returned successfully from release sites at 5.6 km from the home nest. The numbers on the plots are successful releases of tagged bees. Vertical stopped bars indicate the standard error of the means of fraction of returns of groups of 20–30 bees each (where no stopped bar is shown, the SE is within the plot symbol). B, The relationship of returned foragers to the distance from their home colony in flat terrain in southern Arizona (Arizona Flat Site). The expected maximum distance of return was 5.9 km; however, foragers did not return from release sites farther than 5.3 km from their home nest. C, A linear relationship of returned foragers to the distance from their home colony at the base of the 1,500-m Tucson Mountains (Mountain Site). The expected maximum distance for successful return was 9.3 km, nearly equal to the actual maximum distance of 9.2 km, and no bees returned from release sites at a greater distance.

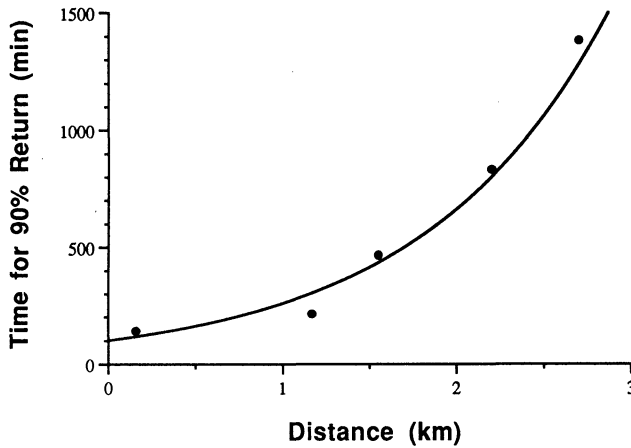


FIG. 3.—The elapsed time from the moment of release of tagged worker honey bees and the return to their home colonies from five release sites in flat terrain without horizon features (Arizona Flat Site). Each data point indicates the time taken for 90% of the released bees to return from specific release sites at the distances indicated.

quite sure, therefore, that we have not missed any more distant points of release from which they might have returned. In order to check for effects of heteroskedasticity, because means have a bias in estimates of the curves, we applied the Breusch-Pagan correction (Judge et al. 1988). The standard errors were changed only slightly, insignificantly revising the covariance matrix.

The return curves for both sites in flat terrain are nearly identical; for New York (fig. 2A),  $y = 0.419 - 0.595 \cdot \log(x)$ ,  $r^2 = 0.938$ ,  $n = 1,167$  marked and released, 272 recaptured; and for Arizona (fig. 2B):  $y = 0.398 - 0.517 \cdot \log(x)$ ,  $r^2 = 0.981$ ,  $n = 1,148$  marked and released, 327 recaptured. The Mountain Site (fig. 2C) showed a better linear relationship with distance ( $y = 0.930 - 0.100x$ ,  $r^2 = 0.928$ ,  $n = 992$  marked and released, 597 recaptured; expressed as log-linear, the results were  $y = 0.737 - 0.546 \cdot \log(x)$ ,  $r^2 = 0.780$ , and the maximum theoretical distance for successful homing would be extended to 22.4 km).

#### *Distance of Release and Trip Time of Returned Foragers*

The amount of time taken to return to the natal nest by the released foragers varied according to a number of natural factors. Return times for foragers released at the Arizona Flat Site are indicated in figure 3. Marked foragers released in close proximity to their home colonies were often back before the experimenters could return from the release sites in New York and Arizona, no matter at what time of day their release occurred. As the distance to the release sites increased, the time to return increased geometrically, with successful returns from the greatest distances requiring several hours or even overnight stays. The best-fit regression of time on distance,  $y = 101.45 \cdot 10^{(0.408x)}$  ( $r^2 = 0.952$ ;  $n = 128$ ), indicates that at 540 min (9 h), no more bees can return in the same day (probably because of darkness).

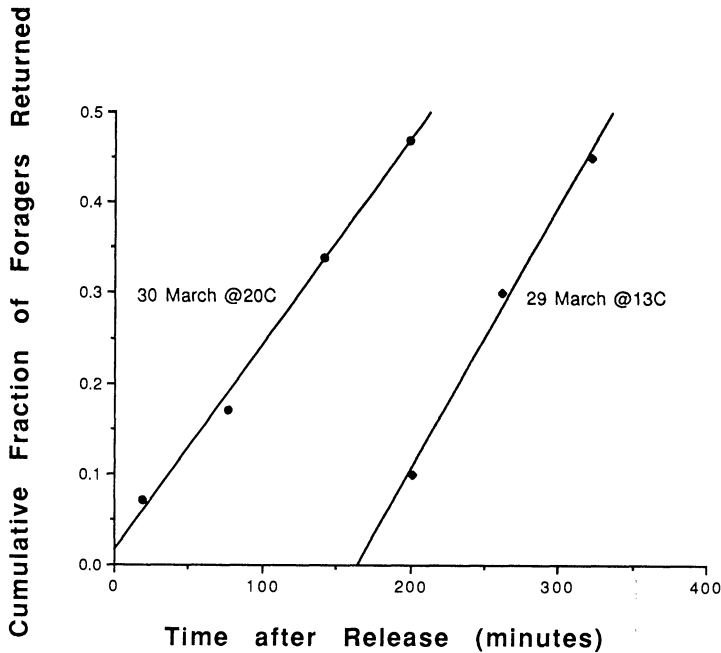


FIG. 4.—The times to return for tagged and recaptured honey bee foragers released on two days with different average air temperatures at the Mountain Site. There is about a 2-h displacement of returns on the cooler day (13°C vs. 20°C at midday).

Figure 4 shows the return times of released foragers on two different days with markedly different air temperatures. The second day had midday temperatures about 7°C cooler than the first day, and return times were nearly 2 h longer. The record time during all of these studies was the return of a forager released at 5.6 km after spending 5 d in the field in New York. The time period during which that forager was in the field included 2 d of cool (15°C), overcast, and rainy weather.

#### *Distance of Successful Returns and Food Supply*

In most cases there were ample food supplies in the form of floral nectar resources in the vicinity of the release sites, so there should not have been a difficulty of released foragers having insufficient sugar supply from their hemolymph or honey stomach to make the return flight. Foragers leaving the hive carry in their honey stomachs small amounts of honey for possible use during their foraging bout. We found that the time of day made little difference in the amount carried. Of the total 168 bees sampled on their way out of the hive, honey stomach contents averaged  $2.6 \pm 0.27$  mL containing 1.4 mg sugar. This amount of sugar is sufficient for a bee to fly to a flower patch about 1,700 m from the nest without any need to stop and refuel on flower nectar (calculated from flight energy requirements given in Nachtigall et al. 1989). By that calculation, bees

flying to greater distances would have to stop and feed at flowers before being able to complete the return flight home.

#### DISCUSSION

##### *General Implications of Successful Homing Behavior*

The distribution of natural honey bee nests is determined primarily by the availability of both nest sites and food resources (Roubik 1989). Food resource exploitation and the distribution of foragers in the field are dependent on environmental factors (such as air temperature, wind, and sunshine) and foraging characteristics of the colonies. These include numbers and rates of foragers leaving and returning to the nest, effectiveness of their pollen gathering and nectar imbibing, and distances traveled or foraging areas utilized. Where bees are found in the field is also dependent on their ability to orient to natural features allowing them to be able to find their way home again. Honey bee nests are distributed rather closely together in the tropical habitats, where they are known to occupy virtually any available cavity (Boreham and Roubik 1987; Ratnieks et al. 1991). Honey bees occupying north temperate deciduous forests are limited in ability to switch cavities, and their nest density is thus less, being only about 0.5 nest per km<sup>2</sup> (upstate New York). Honey bees are clustered in rocky canyons in the Arizona desert at about 2.9 nests per km<sup>2</sup>—with wide spaces in between canyons (Taber 1979; Ratnieks et al. 1991). The area foraged by these desert colonies is likely to be considerably less than 75 km<sup>2</sup> (for a foraging range of 5 km).

For a colony to exploit floral resources, individual foragers must become familiar with landmarks near the resource, the nest, and the direction between the two. This does not imply that foragers recognize landmarks between the foraging patch and the nest. In the simplest model, they need only fly in the “correct” nest direction. Once close to their nest, recognition of local landmarks and/or odors would allow “homing in.” The use of local landmarks in nest location behavior by wasps and bees has been known for at least 60 yr (see, e.g., Tinbergen 1932; Baerends 1941; Robinson and Dyer 1993).

For honey bees there seems to be a different behavior for distance navigation and local orientation near the nest site (Lindauer 1961; Collett and Baron 1994). In our study, the release sites close (<1 km) to the home sites were likely to be within a recognized foraging territory; foragers then would simply need local landmarks to make their way home. From greater distances the released individuals would be less apt to recognize their surrounding; this results from the geometric increase in area with which each bee would have to become familiar as the distance increased. In our study, the bees were probably unfamiliar with the most distant release sites from which they successfully returned. The forager’s choice of flight direction toward home, then, was probably not a case of simple landmark recognition. But, how do foraging honey bees determine their way home from *terra incognita*?

Once a forager locates a good food source, it will be able to fly directly to and from that flower patch using local landmarks and the sun for orientation. Such

direct flight, however, depends on the bee learning the route, so how can it find its way home if it has never been at the flower patch before, as was the case for all of our distant release sites? It seems highly unlikely that the released foragers in our study had ever before been at the specific release sites, especially those at greater distances from the hive. To suggest that they might be familiar with even the most distant release sites from which they successfully returned implies (in the case of Arizona Mountain Site at 9.2 km) that they are familiar with the landscape encompassed in an area exceeding 260 km<sup>2</sup>. Clearly this does not seem feasible. The forager's choice of flight direction to go home is probably not, then, a case of recognizing landmarks. Orientation to the solar position is also unlikely since the bees were transported in covered containers and would not know which direction was the way home.

One concept proposed for insect flight orientation is the odor-search hypothesis advanced by Wenner and his coworkers (Friesen 1973; Wenner et al. 1992; reviewed in Murlis et al. 1992). It is well known that most terrestrial social insects use chemical odors, especially in indicating routes to and from food sources and the home nest. In the odor-search hypothesis for bees, newly recruited honey bee workers rely principally on odor cues as they search for food sources exploited by hive mates. By noting the times it takes for foragers to fly directly to and from the food patch, it is easily seen that recruits seem to take far too long a time for a straight-line flight. In our tests, workers released in unfamiliar distant sites took exceptionally long times to make their way back to the home colony. Return times for release distances of 4.5 km and greater from the home hive were usually in excess of several hours and quite often in excess of a day (with the longest recorded time between release and return of 5 d after release from 5.6 km at the New York Flat Site). We had a number of releases that did not return for 2 or 3 d. Yet a direct flight, even from 5.6 km, would not take over 15 min (at a flight speed of 20 km/h). Even allowing for time to feed and collect pollen or nectar, the time interval should not extend over 30 min or so. In fact, in the study in New York, of all our data from 1.5 and 2.4 km, fully 44% of the released foragers that returned successfully required more than 3 h, and 6% returned after 4 d spent in the field. By looking at the numbers of released marked foragers that actually returned to their nests, we believe that familiarity with the landscape again seems less and less likely as the release points became more distant from the home nest and fewer and fewer bees returned.

Wenner et al. (1992) point out that new recruits make numerous exploratory flights before they finally locate feeding stations indicated by the dance of successful foragers. Released foragers in our study made similar exploratory flights in a number of directions from the release points. It is likely that only if they encountered recognizable landmarks or odors could they make their way home. The odor-search hypothesis also involves recruited bees leaving the colony and flying in ever-expanding spirals until they perceive odor molecules from the floral resource similar to those present on the body of the returned forager back in the hive. When they encounter the odor, they begin a zigzag pattern of flight, moving toward the increasing concentration of odor molecules just as leaf-cutter ants stay on a forager trail (Wilson 1984). Should the bees stray from the odor plume,

they immediately reverse their direction to get back into the plume. In this way they can zero in on the food source.

Possibly the released foragers in our study fly outward from distant release points in ever-expanding spirals (or some random walk form of flight pattern) until they perceive recognizable landmarks or odors coming from their nest. Although spiral flight behavior was observed in some released foragers at distant sites in our field tests, wind vectors during most days were nearly perpendicular to home directions; thus, odor search homing behavior was improbable. In the early tests on wasps released in unfamiliar territory, disorientation behavior was also reported (Baerends 1942). The wasps "wandered in irregular loops" (Baerends 1942, p. 189), often never finding their nest sites. Recently, *Cercercis* wasps have been documented to fly in ever-increasing arcs in the vicinity of their nest when performing orientation flight on departure (Zeil 1993a). On return, these wasps fly again along these same arcs as they approach and finally reach the nest entrance. The notion is that they are not using odors but visual motion parallax that must be repeated in successful homing.

#### *Do Honey Bee Foragers Use Horizon Landmarks?*

Examining the pattern of successful returns at the Mountain Site in Arizona (fig. 2C) reveals another possibility. West of the Tucson Mountains, the horizon provided a visual skyline that was large enough to be virtually unchanged even when observed from the greatest release distances. That mountain range is a distinctive landscape feature available for directional information that is missing in flat terrain. The discerning horizon feature of the mountain range removes one dimension with which the forager has to contend as compared to the case found on flat terrain (as at the Arizona Flat and New York Flat Sites), where no such recognizable landscape feature was available to determine direction. Using this evidence, at the Mountain Site, bees released from greater than 1 km likely flew in the general direction of the Tucson Mountains; when they encountered known landscape features (or odors) close to the nest, they could readily find their natal colony.

The fraction of returning foragers at the mountain site showed a linear relationship with increasing distance (fig. 2C). In flat terrain a lack of topographic directional aid is reflected in the log-linear shape of the curve for the percentage of recaptured foragers versus distance (fig. 2A, B). That foragers released at distances greater than 2 km in flat terrain flew in a search pattern and not in some known direction is also supported by the long times taken to return (fig. 3).

Both of these facts indicate indirectly that the bees can orient to the mountain range horizon and determine at least the general home direction. The horizon is used by ants in visual topographic orientation (Klotz and Reid 1992). Red wood ants associate the location of their nest with the position of the highest trees on the skyline (Fourcassie 1991). Thus, it is likely that horizon features may be used by other hymenopteran species as well. The three ocelli, present on the head between the compound eyes of many insects, have been shown to function as horizon detectors involved in the stabilization of flight, important in homing orien-



tation (Fent and Wehner 1985). Since honey bees can visually discriminate objects based on their angular size (Horridge et al. 1992), it is likely that they orient to large irregularities in the horizon as they fly home. Olfactory nest recognition is prevalent among bees, but it may be valuable only very close to the nest. Visual learning is expected to be the primary reason for orientation flights in the vicinity near the home nest (von Frisch 1967; Zeil 1993*b*). Cheng et al. (1987) showed that in their final search for the nest, honey bees weigh near landmarks more heavily than distant ones.

Finally, examining all the data on releases and returns of tagged foragers in our studies shows that a sharp skyline allowed for twice as many successful returns as compared to flat terrain without such a silhouette. At the site with a mountain skyline, a total of 63.4% of all foragers released actually returned (excluding sites beyond the most distant site of successful returns). For flat terrain without the horizon feature, in Arizona 29.7% returned, and in New York only 25.1% returned. The New York returns may be particularly low because of the added effects of low temperature and rainy weather.

#### *Significance of Foraging and Successful Homing Range*

Average and maximum flight ranges of bees (Apinae) in natural ecosystems are unknown (Knaffl 1953; Beutler 1954; Roubik and Aluja 1983). Yet these are crucial to an understanding of the foraging behavior and ecology of these insects as they gather floral resources and, additionally, to studies of plant community reproductive dynamics. Honey bees are one of the most highly polylectic, or generalized, of any eusocial bee, taking pollen or nectar from almost all families of sporophytes. The tens of thousands of daily foraging bouts flown by thousands of worker bees from a single colony can be likened to a superorganismic "amoeba," with pseudopodia of winged foragers exploiting near and distant rich floral patches (Moritz and Southwick 1992). The distances reached by these forager pseudopodia are likely to be farther than previously thought and greatly influenced by conspicuous landmarks. Thus, there is an impact of foraging bees on the biota that is greater than anticipated. The importance of honey bees in the pollination of agricultural crops alone is estimated to be a multibillion-dollar annual asset in the United States (Southwick and Southwick 1992).

Ecologically important parameters such as colony foraging area, genetic neighborhood sizes of angiosperms pollinated by honey bees, and the distribution and distances between managed and feral colonies in any area are all functions of worker bees' orientation and behavior in the field, ability to find their nest or home, and their flight ranges (Lee 1961; Lindauer 1961). Similarly, "gametic shadows" of virgin drone and queen honey bees are a function of colony spacing, orientation, and average flight distances by drones to and from areas where mating takes place (Ruttner 1988). Our results show that ranges of successful homing in honey bees foraging in natural ecosystems are strongly influenced by physiographic features. We conclude that prominent landmarks can extend the range of successful homing in honey bees in a single nest from about 5 km to about 9 km, tripling the area of probable foraging.

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