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ASTRONAVIGATION IN INSECTS

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INTRODUCTION

The study of insect astronavigation began in 1911 when Santschi (139) showed that some species of myrmicine ants used the sun as a reference point in navigating home from their foraging grounds (18, 72, 142). But it was not until the discovery of the time-compensated sun compass orientation in bees (170), and concomitantly in birds (89), that this line of research gathered momentum almost forty years later. The demonstration that bees used the pattern of polarized light in the daytime sky (169), and that nocturnal arthropods such as amphipod crustaceans relied on the moon as a navigational aid (120), paved the way for an upsurge of experimental work in a variety of species. These studies were summarized to some extent in the early sixties (4, 12, 69, 94, 95, 105, 119, 124, 132, 134, 155, 171) but then reached an impasse. In more recent reviews on animal navigation, insects are barely represented (53, 54) or not represented at all (123, 147, 156), and emphasis is largely placed on sensory mechanisms rather than navigational strategies (179, 186).

Curiously enough, what contributed to the early decline of interest in insect astronavigation was the common belief that the principal questions had already been settled. Many ideas outlined in the early work on insect navigation seem to have become widely accepted and have even advanced to the rank of established textbook statements (e.g. 26, 149). To cite just a few: (*a*) The insect is informed exactly about the azimuthal position of the sun at any time of the day; (*b*) it is able to infer the correct position of the sun from any particular point of the pattern of polarized light in the sky; (*c*) it performs true vector navigation (by using a skylight compass and a means of measuring distance). As it now appears, such statements may not be true in the strict sense mentioned above.

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Instead, the insect almost always seems to rely on approximate rather than exact solutions to the underlying navigational problems. A number of experiments are described below that make this point with particular force.

Current interest in insect navigation derives mainly from two sources: neurobiology and behavioral ecology. Even though the former aspect should be kept in mind throughout this chapter, no attempt is made to discuss recent neurophysiological work in any detail (183, 186). The main focus is on navigational strategies, as derived from behavioral approaches, and on the adaptive significance of these strategies. In the last few years, experimental techniques for eliciting and recording behavioral responses of freely moving insects have been refined to such an extent that more specific questions can be raised.

At present, no up-to-date reviews on insect astronavigation are available. Furthermore, because the primary literature tends to be a bibliographic jungle of short reports and conference contributions, the coverage can by no means be encyclopedic. What I intend to do is to organize some particulars into comprehensible patterns, so that broader questions can be asked.

USE OF SKYLIGHT CUES IN ORIENTATION

Skylight cues—the sun, the pattern of polarized light, the moon, and the stars—are effectively at infinity and thus not subject to the phenomenon of motion parallax. Therefore, they can readily be used as a means for defining directions. Insects seem to be specially predisposed to use skylight cues for one kind of orientation or another, because their large-field compound eyes often view the entire celestial hemisphere (154, 183).

Selecting and Maintaining Direction

VISUAL STABILIZATION OF COURSE Even if an animal does not select a course by celestial cues, it can use retinal images of the sky to maintain its course. This is because the retinal image of any celestial cue does not change as long as the animal moves along a straight line but does change when the animal rotates, say, about its dorsoventral body axis. Thus, any image displacement caused by some involuntary disturbance that results in rotation can be corrected by compensatory body movements. In order to get aligned in its former direction, the animal must rotate until it has reestablished its former retinal image. In functional terms, such a control system is reminiscent of the optomotor system (59), which stabilizes steering courses by exploiting the visual flow-field of landmark panoramas that appear at finite distances.

It is well known that insects can exploit the overall illumination field for stabilizing course against roll or pitch by using their compound eyes (57, 109, 127, 157, 159) and ocelli (153, 157), but little work has been done to test the hypothesis that they use similar cues to stabilize against yaw, i.e. to maintain a straight course. When tethered flying fruit flies, *Drosophila*, are illuminated from above with linearly polarized light, they fly straight; but when the polarizers are removed and the flies are exposed to diffuse overhead illumination, they engage in tortuous flight maneuvers (197).

SKYLIGHT COMPASS If the insect is able to associate particular retinal images of the sky with corresponding directions in space, it can use the sky as a compass. Consider an insect performing a full turn, i.e. rotating through all points of the compass. Then, the image of any skylight cue sweeps across the insect's retina. For example, the retinal displacement of the symmetry line of all skylight patterns (the solar and antisolar meridian) is directly proportional to the amount of angular turn. However, as the skylight pattern moves during the course of the day, an earthbound reference system is required to set the compass (see section on time compensation).

Talitrid amphipods (25, 124), crabs (65, 66), spiders (122), and many other marine or fresh water invertebrates face the problem of finding and remaining in a narrow strip of suitable habitat at the water's edge. In accomplishing this task, they rely, among other strategies (55, 66), on skylight compasses. As the home range of any shore-living species is a line rather than a point in space, the courses to be steered run simply at right angles to this line, either landward or seaward, irrespective of the animal's current position. This behavior has been termed *y*-axis orientation (48).

Central place foragers (116), such as social insects, must return repeatedly to the same point in two-dimensional space. In this case, a skylight compass is used in the context of a dead reckoning (path integration) strategy. The animal must record all rotatory and translatory components of the outbound path and compute the mean vector leading back to the start.[1] Some arthropods [spiders (58, 111, 112), crabs (66, 172), isopods (62, 97)] have been shown to perform path integration by referring exclusively to nonvisual (e.g. idiothetic) stimuli. But when bees and ants forage over distances of several hundreds or thousands of meters, they use a skylight compass for determining directions. It is this kind of astronavigation that is discussed in this chapter.

Establishing Geographical Position

In human astronavigation, skylight cues are used not merely as a compass to define directions, but, more importantly, as a means to establish position (67). Armed with both some basic knowledge about celestial geometry and the tables

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[1] Recently, 20 vespid wasps, *Polistes*, have been displaced passively over a distance of 1 km and then released within an arena (160, 161). Even though the arena shielded the wind and obscured all visual landmarks, the wasps headed towards home. How they determined their home direction is not easy to explain. As reported, the wasps could see the sky (and landmarks passing by?) when displaced in closed Plexiglass tubes, so that they might have obtained some information about the direction of their displacement. Wasps transported in the dark have not been tested. Further experiments of this or a similar kind are certainly needed.

of the Nautical Almanac, one can solve the problem of finding geographical position by using a sextant, a chronometer, and a chart. Employing such a strategy frees one from the need to collect and store information continuously en route. All one needs for determining one's location relative to home is astronomical information collected on site.

In the study of bird navigation and homing, navigation by celestial cues alone (often referred to as "true" astronavigation) has been proposed off and on (100, 126, 143) but has subsequently been refuted by convincing experimental evidence (79, 195). In insects, the distances traveled during foraging and homing are not large enough to render true astronavigation possible. Even in migratory insects, which sometimes move over thousands of kilometers, establishing a fix by purely astronomical means can be ruled out for a number of reasons (see also section on insect migration). In all cases in which animals—birds and insects alike—have been displaced from home so that they had to navigate back by exploiting information collected on site rather than en route, they relied on earthbound cues: familiar landmark maps or far-ranging grid maps consisting of some still elusive system of coordinates, e.g. fields of geophysical gradients (61, 178). Present evidence indicates that insects employ only the former strategy. It is fascinating to speculate on the "mental map" that a bee or ant is obviously able to form of its foraging area and to ask to what extent celestial and non-celestial systems of navigation are used simultaneously or successively in establishing and reading this map (187). For example, do insects use the points of the compass as a reference system in defining directions of landmarks relative to home?

DAYTIME COMPASS

Compass Cues Used in Navigation

In the daytime sky, the celestial hemisphere displays a set of conspicuous visual cues: the direct (unpolarized) light from the sun and the scattered (polarized) light from the sky. The latter forms a well-defined pattern characterized by the spatial distribution of angle of polarization, degree of polarization, radiant intensity, and the way in which all these parameters vary with the wavelength of light.

Three-dimensional representations of the patterns of skylight polarization are given in (185). Here, only three aspects of skylight patterns are mentioned. First, light is scattered much more effectively in the short than in the long wavelength range of the spectrum. Hence, light from the sky contains relatively more short wavelength components than direct light from the sun. Second, light is maximally polarized at an angular distance of 90° from the sun. Third, angles of polarization (*e*-vector directions) are oriented in such a way that they form concentric circles around the sun.

These geometrical predictions, derived from the theory of primary (Rayleigh) scattering of light, are only partially true for the real sky where multiple scattering, absorption, and other factors related to atmospheric disturbances like haze, fog, or clouds (103) markedly distort the ideal patterns of scattered light. Under such conditions, radiance and degree of polarization are highly variable and hence unpredictable, and the pattern of *e*-vector directions is the most reliable criterion (15). Nevertheless, the way radiant intensity varies with the wavelength of light across large areas of the sky might provide some useful cues for orientation.

That insects and many other arthropods can use both direct sunlight and scattered skylight as compass cues has been amply documented, mostly more than 20 years ago [bees (94, 95, 134, 171); ants (19, 73, 174–176); beetles (52); crustaceans (2, 27, 124, 148); spiders (118, 121, 122)]. Our present understanding of the insect's skylight compass has grown mainly out of more recent experiments in which dancing bees (14, 38, 41, 137, 138, 165, 166, 173, 184, 189) or freely walking ants (33–35, 91, 180, 183, 188) were exposed to well defined celestial stimuli (Figure 1).

DIRECT SUNLIGHT How does an insect identify the sun? In the unobscured clear sky, this seems to be an easy task, because then the sun is unambiguously defined as the brightest point. However, when the sky is partially covered by clouds or obscured by a canopy of vegetation, this simple criterion might no longer suffice. As mentioned above, points in the sky close to the sun possess not only maximum intensity, but also zero percent polarization and a low relative content of ultraviolet radiation. Bees indeed take advantage of both optical characteristics when deciding whether a bright patch is the sun or sky. When they perform their waggle runs on a horizontal comb, they interpret an artificial source of unpolarized monochromatic light as the sun when $\lambda > 410$ nm, but as part of the sky (with its azimuth opposite to the sun: "anti-sun") when $\lambda < 410$ nm (40). In *Cataglyphis* ants the sun is identified correctly when it is viewed through spectral cut-off filters that allow for stimulation of the green receptors only (35). In an elegant set of experiments, Gould & Brines (14) have displayed to the bees artificial light sources in which degree of polarization, content of ultraviolet radiation, and angular subtense of the source were varied systematically. Irrespective of its degree of polarization, the light source was taken for the sun as long as its ultraviolet content was less than 0.2 and its diameter less than 20°.

In the natural sky, the sun does not appear as an isolated point in an otherwise dark surround but as part of a radiance distribution in which all optical parameters characterizing the sun decrease gradually the farther one moves away from the sun. To what extent is the insect's skylight compass influenced by the sun embedded in the proper radiance field? Strongly diurnal desert ants,

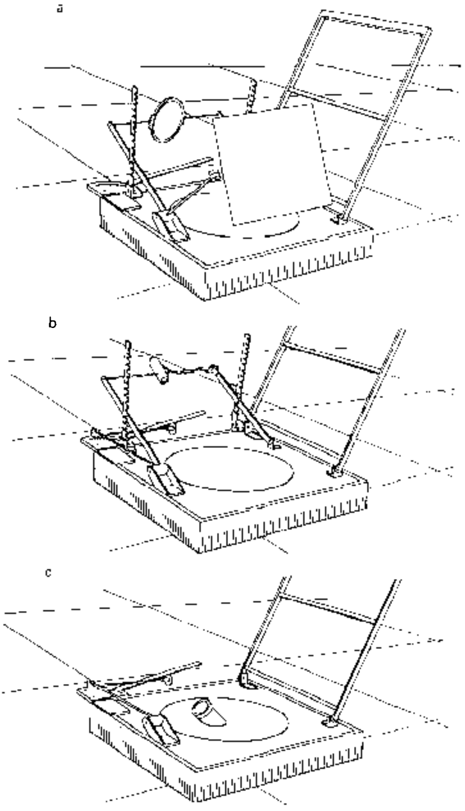

Figure 1. Device for modifying skylight vision in freely walking desert ants, *Cataglyphis bicolor*. A frame equipped with different optical gadgets is mounted on wheels and moved along with the homing ant in the direction in which the ant is walking. The frame excludes any view of the skyline or other terrestrial markers, and shields the wind. A grid of white lines (mesh width 1 m) is painted on the hard, desert ground (test area) to facilitate the recordings of the ant's homing path. Prior to the experiment the ant has completed its foraging run over a minimum distance of 15 m and has then been displaced to unknown territory (test area). In (*a*) the sun is screened off and mirrored from the opposite side. The large horizontal aperture (diameter 134°) is equipped with spectral cut-off filters ($\lambda > 510$ nm) or depolarizers that make it impossible for the ant to perceive polarized skylight. (*b*) At night, an artifical light source emitting long-wavelength radiation is used as a substitute for the sun. The diurnal ants, trained at daytime and tested at night, take this point-like source for the sun. In (*c*) a polarizer (Polaroid HNP-B) is fitted into the opening of a red Plexiglass tube (diameter 27°). By adjusting both the azimuthal position of the tube and the orientation of the *e*-vector within the tube, any *e*-vector orientation can be displayed to the ant at any azimuthal distance from the ant's home direction. The sun is screened off (not shown here) and the remainder of the sky is depolarized by filters fitted into the large horizontal aperture. The latter setup allows one to determine at what position in the sky the ant expects any particular *e*-vector to occur. By this means, the ant's celestial map can be derived. For further experimental details see (183).

Cataglyphis, take the moon for the sun when tested at night (91, 183, 188). In this case, however, a phototactic component directed towards the moon, or an artificial light source presented instead, is superimposed on the ant's compass course. A similar phototactic component is found when ants are tested under the daytime sky but with the sun and the sky seen through an orange cut-off filter ($\lambda > 510$ nm), which completely distorts the radiance distribution of the natural sky (91, 183). In both cases, systematic navigational errors occur which are due to a phototactic response towards the moon or towards the sun displayed within a spectrally uniform sky. If home is at an azimuthal distance α to the right (or left) of the moon or the sun, the course actually steered by the ant is $\alpha \pm \Delta\alpha$ with $\Delta\alpha$ depending on α and several other parameters.

If the contrast between a light source and the dark surroundings is very high, many insects including bees exhibit positive phototactic respones towards that light (167). These responses can be triggered by monochromatic lights of any particular wavelength (77), while only long-wavelength sources are taken for the sun (38, 40).

Another question not yet tackled is how steep the intensity gradient around a point-like source must be to enable the bees to compute the center of gravity and to interpret this center as the sun. Fish can derive the azimuthal position of the sun from the underwater light distribution [p.236 (63)], and homing pigeons use the sun compass even when wearing frosted contact lenses (146). Among arthropods, the solifugid arachnid *Galeodibus* (96) and the collembolid *Podura* (168) have been reported to orient by means of the centers of gravity of smooth light intensity gradients.

So far we have dealt with the problem of how the sun is identified. Once identified, how is it used as part of the celestial compass? It is generally agreed that insects, like birds (79, 195), refer only to the azimuth of the sun while navigating [p.136 (171)] and not to its elevation. This is, of course, to be expected, because it is only the azimuth of the sun, i.e. the horizontal component of its celestial position, that provides compass information. *Cataglyphis* ants maintain their compass course even when the elevation of the sun is changed by ± 40° (35, 91, 183). In addition, when released several hours after having established a compass course, the ants do not refer to the elevation of the sun in determining time of day (91).

While the elevation of the sun is not part of the insect's compass, it is important in other behavioral contexts. The phototaxis effect exhibited by the sun when displayed within a spectrally uniform radiance field (see above) depends strongly on the elevation of the sun (91). In the laboratory, wood ants, *Formica,* have been successfully trained to discriminate between different elevations of an artificial light source [(84); for birds see (191)].

SCATTERED SKYLIGHT Shortly after having discovered the sun compass (139), Santschi demonstrated that ants were able to use not only the sun but also small patches of blue skylight to determine their home directions (140). Even though he lived in a rather remote place in North Africa, with no optical equipment at hand, he did not dodge the task of speculating about what skylight parameters the ants might have used. He thought of gradients of some light phenomenon not visible to man (142), but the conclusion that these were gradients of skylight polarization (*e*-vector patterns) had to await von Frisch's (169) later discovery in bees [for ants see (19, 73, 174–176)].

These pioneering studies stirred up extensive research and theorizing about how insects perceive polarized light [(11, 85, 107, 164, 165, 181); for summaries see (179, 185)] and how they derive compass information from the polarized skylight patterns (14, 50, 51, 87, 137, 138, 180, 184, 186). As both questions are certainly intertwined, solving one will provide the key for solving the other. In this account, we are concerned mainly with the latter.

Bees are able to use their *e*-vector compass even if they have access to nothing but a small patch of blue sky, less than 5° in visual angle (14, 40, 41, 137, 138). By displaying to them such small parts of the *e*-vector pattern, and recording the waggle dances performed on a horizontal comb, one can infer where they expect a given *e*-vector to occur in the sky. According to recent results, they seem to use a generalized rather than an accurate model (or map) of the *e*-vector pattern in the sky. Let us briefly highlight a few features of this map. First, the bee's map is restricted to the more highly polarized half of the sky, i.e. the half lying opposite to the sun (14, 137, 138, 184). Second, the bee's map does not change with the elevation of the sun as the actual *e*-vector pattern does. The bees seem to employ an invariable strategy in correlating *e*-vector orientations with azimuth positions (137, 138, 184). This hypothesis has been tested and confirmed under a variety of experimental conditions: by displaying to the bees one (137, 138) or two spots (137, 189) of artificially polarized ultraviolet light and small (138) or large parts (185) of the natural sky. Third and finally, the bee's map can be derived theoretically from the actual *e*-vector patterns in the sky by referring exclusively to the maximally polarized *e*-vectors (137).

The recent studies also confirm [p.397 (171)] that bees and ants ignore the degree of polarization. This comes as no surprise, because the degree of polarization is extremely susceptible to atmospheric disturbances (15) and hence does not provide reliable cues.

It might not have escaped the reader that throughout the preceding discussion the term "map" has been used in a figurative rather than literal sense of the word. The use of this term is not to conjure up any explanation of what the map could mean in neurophysiological terms. Little is known about how *e*-vector information is processed within the insect's visual system (179, 186); thus the formulation of any specific model might appear premature.

Nevertheless, one is tempted to speculate about where the "map" resides within the insect's visual system. As a first hypothesis, let us assume that the insect comes programmed with a peripheral map. Imagine that an array of polarization-detecting units (polarization detectors) constitutes the map. Each detector antagonistically compares the output of a pair of orthogonally arranged (crossed) analyzers (183) and is thus invariant against changes in light intensity. Provided that the spatial array of polarization detectors meets certain geometrical conditions, the insect could efficiently apply some kind of scanning strategy by rotating about its dorsoventral body axis and thus sweeping its array of polarization detectors across the *e*-vector pattern in the sky. From the resulting response pattern it then might be able to deduce how it is oriented with respect, say, to the antisolar meridian. In this case, it is not necessary for the insect to extract and process *e*-vector directions, i.e. to know unambiguously what *e*-vector occurs at any one point in the sky.

As a second hypothesis, let us conceive of a more central map laid down somewhere within the insect's visual neuropiles. In selecting a given compass course the insect could rotate about its dorsoventral body axis until it achieved a match between its current neural image of the *e*-vector pattern in the sky and its celestial map set for the given point of the compass. More specifically, the insect could determine *e*-vector directions in the sky, by applying one of several possible strategies (11, 85, 181), and could then compare this neural image of the sky with its celestial map. According to both hypotheses, the observed navigational "errors" are due to the assumption that the insect uses an invariable map of the celestial *e*-vector pattern, even though the actual *e*-vector pattern changes as the sun moves across the sky.

The two strategies outlined above are just two possibilities at both ends of a wide range of other ways to solve the problem, but this article does not pursue the question of how the map is actually implemented in the hardware of the insect's visual system.

In both bees (173) and ants (35), ultraviolet receptors are necessary for detecting polarized light. They are also sufficient when monochromatic beams of polarized light are used, but this does not imply that they are the only receptors involved whenever the insect must read compass information from the real (colored) sky. It has already been mentioned (see section on direct sunlight) that spectral cues are used to discriminate between sun and sky, and it has also been reported (164–166) that bees can derive compass information from unpolarized color patterns.

Why do ultraviolet receptors play such a special role in skylight navigation? There is no easy way of answering this question. As scattered skylight is rich in ultraviolet, but reflected light from the ground is not [with the remarkable exception of light reflected from water surfaces (20)], any visual system whose spectral range extends into the ultraviolet is advantageous in discriminating between sky and ground (182, 183), e.g. in detecting the sky when taking off the ground [(82); p.230 (102); (106)], or in any kind of course control in which skylight is involved. It might also be advantageous in exploiting spectral gradients across the sky. Furthermore, the scattering of sunlight beneath the clouds generates patterns of polarization that continue the pattern in the blue parts of the sky (155), and, as recently emphasized (15), these patterns are strongest in the ultraviolet.

Now that we have discussed the significance of direct sunlight and scattered skylight in insect orientation, we may wonder whether one cue takes precedence over the other. In mirror experiments, in which the position of the sun was artificially shifted with respect to the natural pattern of polarized light, it has often been claimed that sunlight outweighs skylight, or vice versa (35, 68, 73, 125, 139), or that a compromise direction is steered [p. 406 (171)]. However, in all these experiments the stimulus conditions have not been varied carefully enough to allow for worthwhile generalizations.

Time Compensation

During the course of the day, sun and *e*-vector pattern move across the sky. The movement of the sun along its arc is uniform (15°/h), and so is the rotation of the whole *e*-vector pattern about the north (or south) pole of the sky, but any reference point of the celestial compass—be it the solar or the antisolar meridian—moves along the horizon with nonuniform speed. The rate of movement is low at dawn and dusk, but high at noon. The relation between the azimuth of the sun and the time of day, the well-known sun-azimuth/time curve, varies with latitude and time of year. It has long been known that the insect compensates for the movement of the reference point of its celestial compass by reading time from an internal clock (73, 104, 132, 170). But how accurately this compensation is done has remained elusive.

First and foremost, foraging bees in which the internal clock has been time-shifted (10) or which have been trained at one longitude, then tested at another (133), do not orient in their true home direction. Hence, at least in these situations, they do not determine true north either by referring to earthbound stimuli, e.g. the earth's magnetic field which they are able to perceive (30, 99), or by observing the rotation of the celestial sphere (13). Second, what can be deduced from these and other investigations (10, 39, 114, 133) is that the bees do not simply use the average rate of movement (15°/h) of the sun's azimuth.

Nevertheless, all studies mentioned above are not detailed enough to decide whether the bees are informed exactly about the local sun-azimuth/time curve. Desert ants are certainly not. They underestimate the highest rates of movement of the sun's azimuth and overestimate the lower ones (91, 188). This is in accord with the hypothesis that the ants acquire their knowledge of the sun's azimuth movement by interpolation between successive memorized positions of the solar meridian along the horizon skyline. The data are at variance with the hypothesis recently proposed for bees (60) that the insect just extrapolates from the most recently observed rate of movement. Further support for the interpolation hypothesis comes from experiments in which bees and ants cannot experience the sun's azimuth because the sun is either below the horizon (91) or at the zenith (39, 114). However, when confronted with a sun substitute (moon or artificial light), or when dancing on a vertical screen where "upright" means "towards the sun," ants and bees, respectively, are not disoriented. They behave as if they infer the sun's azimuth by dividing azimuthal distances between known positions of the sun by time.

Any earthbound frame of reference could be used to set the celestial compass. The earth's magnetic field and visual landmarks are plausible candidates. For insects, all evidence at hand favors the latter possibility [for birds see (196)]. Under a totally overcast sky, dancing bees can convey compass information by relating the position of the sun to the local landmark panorama (37). Furthermore, when time-shifted they can read local time from the azimuthal position of the sun relative to the landmarks along the horizon (10).

NIGHT-TIME COMPASS

Because of the optics of their eyes, insects equipped with apposition compound eyes cannot see the stars [(86); p.272 (136)], nor are they likely to resolve the phases of the moon even though both capacities have sometimes been claimed (9, 22, 69, 141).[2] The larger optical apertures provided by superposition compound eyes (21, 86) might allow for the detection of the brightest stars, but the evidence that moths use such cues in navigation (8, 152) is very slim. The moon is bright enough to be detected as a point-like source even by apposition compound eyes. Moonlight is sunlight reflected from the lunar surface; it has nearly the same spectral composition as sunlight, but with a shift somewhat toward the red [p.365 (88)]. If diurnal ants are confronted with the moon at night, they mistake it for the sun (91, 183).

The obstacles encountered in using the moon as a compass are much more formidable than using the sun as a compass. First, the moon is visible for only a part of the night and, on successive nights, for different parts of the night. Second, the moon-azimuth/time curve changes much more drastically from night to night than the sun-azimuth/time curve does from day to day. Third, a lunar compass requires a timing mechanism (moon clock) that operates independently of the circadian (sun) clock. Such lunar rhythms certainly exist (45,

[2] If a light bar 0.5° long and 0.125° wide is viewed by a hexagonal array of receptors in which sets of 4 receptors are wired up as 2 antagonistic pairs of receptor, mutually perpendicular orientations of the bar cause a change in the output signal of about 10%. The assumptions underlying this computation (angular distance between receptors 1°, width of receptive field 1°) are rather unrealistic for a crepuscular insect, but a fine compound eye may be just on the verge of being able to discriminate between a full moon and a half moon.

113, 117, 151), but how they are used in navigation is not known. Furthermore, dawn and dusk cannot be used as signals for synchronizing a moon clock. What could provide such signals are factors correlated with the tides or with the maximum elevation of the moon. As an alternative to the cyclic moon clock, it has been proposed that amphipods use a single-cycle night clock set by moonrise and operating at the rate of the circadian clock (43). Fourth and finally, if landmarks provide the frame of reference necessary to set the celestial compass, this reference system can be used less readily and precisely at night than during the day.

In insects, lunar orientation has been reported only occasionally (73, 92, 139), but substantial work has been done in talitrid amphipods and tylid isopods, which are active at exposed shores during nighttime. As first claimed in 1953 (120), and carefully reexamined almost twenty years later (44), these beachhoppers are supposed to use the moon as a compass just as they use the sun as a compass. Evidence for this conjecture has been derived from experiments in which the position of the moon has been artificially shifted by mirrors. The results, however, are controversial and not unambiguously in favor of a time-compensated moon compass orientation (44, 119). More crucial experiments involving time shifts or longitudinal displacements have not been done. All that can be said with certainty is that nocturnal beachhoppers use the moon, in one way or another, as a reference point in selecting and maintaining their seaward courses. One should bear in mind, however, that these amphipods have a number of alternative strategies at their disposal depending on skyline cues (25, 64, 194), the earth's magnetic field (3), the slope of the beach (24, 46, 62), and the direction of the prevailing winds (120). Such cues have not always been controlled carefully enough in experiments testing the moon compass hypothesis. Furthermore, it is only by appreciating the functional interrelationships between all these strategies that both the significance and the mechanism of lunar orientation can be understood.

INSECT MIGRATION

In many insects, especially odonates, orthopterans, and lepidopterans, persistent one-directional movements occur more or less regularly at particular times of the year (23, 75, 144, 192). One of the most spectacular of these phenomena is the migration of the monarch butterfly, *Danaus plexippus*. As revealed by numerous recaptures of alar-tagged migrating specimens, monarchs from the eastern United States and Canada descend in the fall upon localized overwintering sites in the mountains of Central Mexico (17, 162). While migrating they move rather persistently southwest, more or less in accordance with the orthodrome direction (145), towards their wintering grounds. Upon arrival, some have been recorded 3000 km from their points of release, and have travelled up to 130 km per day (162, 163). There is not much information available on the return spring flight, which is less obvious. Breeding near the overwintering areas has been observed (16), but there is no doubt that the majority of butterflies that return to repopulate eastern North America in the spring are those same individuals that flew southward in the fall (L. P. Brower, personal communication). The individual butterflies flying south next fall are descended (by several generations) from their ancestors that migrated north during the previous spring.

Virtually no experimental work has been done on the sensory cues and the navigational strategies involved in butterfly migration. The observation that butterflies, while migrating, orient at a constant angle with respect to the sun [(5–7, 78); but see p.703 (75)], is not sufficient proof for supporting the view that the selection of the migratory direction is governed by a skylight compass.

It has often been assumed that migratory insects exhibit an innate sense of direction independent of local environmental conditions (192) and that they use celestial—or magnetic (8)[3]—cues for holding to one compass direction for hours and days. To use a celestial compass for long-range migration implies that the insect is continually able to recalibrate its daily sun-azimuth/time function (because of changes in latitude) and to reset its internal clock (because of changes in longitude). To accomplish both tasks the insect needs time, at least several days (10, 73, 93, 131, 132). Furthermore, as migratory insects are not walking on solid ground but are flying within a medium that is moving by itself, a given direction once selected by any compass system cannot be maintained without optomotor feedback from the ground. It is well known that many flying insects adjust their ground velocity by optomotor control (28, 29, 80, 83, 90, 115), but to what extent such control is used in maintaining directions has not yet been studied.

Questions of this kind will open a fascinating field of research. For example, no one has yet tested—either in the monarch or in any other migratory butterfly (e.g. *Pieris, Vanessa, Aglais*)—whether migratory directions can be changed in caged animals by time-shifting the butterfly's internal clock. Nor is it known whether scattered skylight can be used for orientation. Such experiments should have high priority in future research on insect migration.

Even if questions of this kind cannot be answered at present, celestial cues are certainly not the only, and perhaps not even the most important, navigational aids used by migratory insects. Prevailing weather systems characterized by certain wind directions play a dominant role in insect migration. This is to be expected, because insects fly at air velocities that rarely exceed 5 m/sec (190). Indeed, airplane tracking and radar studies show that many large-scale movements of locusts, moths, and butterflies are approximately downwind (32, 129,

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[3] The monarch butterfly must be added to the growing list of species (101) known to possess magnetic (superparamagnetic) material in its body (76).

130, 135, 144). As far as the migration of the monarch is concerned, prevailing wind patterns, up to 500-m in altitude, facilitate southwestward movement in the fall and northward or northeastward movement in the spring (78). In southern Australia, the spring passage of a succession of eastward moving anticyclones and depressions is important for the navigation of several insect species (32, 47, 70). It must be mentioned, however, that it is still a matter of debate to what extent synoptic-scale wind systems in the upper air determine the direction of migration in butterflies (78, 177), as they do in migrant aphids (31, 74, 158) and locusts (80, 128, 129). It is often emphasized that butterflies travel within the "boundary layer" (158) in directions that do not coincide with wind direction [(42, 145, 178); but see p. 267 (80); (81), and the following remarks]. Further work is needed to clarify this crucial point.

Even if many species, once aloft, drift more or less passively on the wind, as is certainly the case in aphids and locusts, this is not to say that they are completely at the mercy of winds. They actively embark on air currents as their transporting vehicle. Hence, they travel on such air currents adaptively rather than accidentally or inadvertently. This requires a number of behavioral adaptations for exploiting local and seasonal wind patterns. First, the insect must launch itself into the air at the right time. Monarchs, for example, appear to be highly tuned to exploit lift by soaring in thermals, but they restrict this kind of behavior to days when there is a wind in the appropriate direction (55, 56). Then, having penetrated the boundary layer, they keep themselves airborne by persistent wing-flapping. Furthermore, even when flying downwind the insect must select its flight direction actively, at least in all cases in which its ground velocity vector exceeds the wind velocity vector, and such cases have been reported for many migratory species (144). Among other directional cues, visual contact with the ground is required to accomplish this task. Thus, several systems of orientation must be involved and must be functionally interrelated.

If insects travel on air currents, they always take the risk of being caught in unfavorable air flow. Monarch butterflies captured in England in September represent a small fraction of the southward moving North American populations, caught perchance by the prevailing westerly winds blowing across the Atlantic [p.65 (23)]. Similar "anomalous" long-range displacements correlated with corresponding patterns of air flow have been reported for other species and for other geographical regions as well (36, 49, 71, 98, 108, 150). The point to be made here is that even such anomalous displacements are a constituent, though misdirected, part of migration. The species involved are migratory species, and the time of the year at which such displacements occur is the migratory season of the species. Hence, in migratory insects—just as in many small migratory birds (1, 193)—natural selection has acted strongly upon the ability to depart under favorable conditions, i.e. to forcast favorable winds by other meteorological factors.

CONCLUSIONS

By now the reader is well aware that insects are not astronomers in the strict human sense of the word. In retrospect, this is not astounding. Many aspects of astronavigation involve rather abstract knowledge of celestial geometry that the insect might not have had the chance to acquire during its evolutionary history. The insect's navigational strategies have evolved in the context of local life-history patterns rather than of solving global astronomical problems.

First, true astronavigation as defined above—establishing a fix by purely astronomical means—is beyond the insect's capacities and those of the pigeon, and has not been demonstrated in any animal species. It would require not only the sensory capacity to detect and localize the relevant celestial cues, and an extremely precise chronometer always synchronized with local time at home, but also a set of rules by which the daily, seasonal, and geographical variations of skylight patterns could be handled and used. With respect to both space and time, insects are bound to more local problems.

Second, even when using a celestial compass insects have not arrived at exact astronomical solutions. To illustrate this point two examples are mentioned. (*a*) By performing spherical trigonometry in the sky one can compute the position of the sun at any time of the day by knowing time, geographical latitude, and the declination of the sun. (*b*) If the sun is obscured by clouds, but small patches of polarized skylights are visible, the position of the sun can be inferred from tracing great circles at right angles to e-vector directions. Such or similar models have been proposed in trying to define the conditions that the animal's system of navigation should meet (87, 110). At present, however, the overwhelming weight of experimental evidence, discussed above, indicates that insects do not employ such models of the sky but resort to what the human navigator would call shortcut solutions. In applying such shortcuts, they seem to use skymarks merely as some kind of local, albeit moving landmarks.

When confronted with certain stimulus conditions, bees and ants deviate slightly, in some cases even considerably, from their homing or foraging courses (14, 137, 138, 185). It is from analyses of such navigational "errors" that the aforementioned shortcut solutions, or rules of thumb, have been derived. Under natural conditions, navigational errors are kept down by the simultaneous use of a number of backup systems drawing upon landmarks, wind directions, olfactory cues etc. These complementary strategies do not merely increase the redundancy within the insect's overall system of navigation but are functionally interrelated in a way we are just beginning to understand. There is an urgent need for more detailed experimental and descriptive data on how the insect orients under natural conditions, with the whole repertoire of navigational strategies at its disposal. As paradoxical as it may appear, future progress in unravelling the insect's strategies of astronavigation will largely depend on how well the functional interrelationship between celestial and non-celestial systems of navigation is appreciated.

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