

Navigation in context: grand theories and basic mechanisms

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Among the movements of animals across the surface of our planet, the wide-ranging migratory journeys of birds and the smaller-scale foraging excursions of social (hymenopteran) insects provide some of the most intriguing examples of biological systems of navigation. Many sensory cues have been found to be involved in accomplishing these tasks, but how this sensory information is integrated into the animal's overall system of navigation has remained elusive. Several over-arching concepts such as sun- or star-based systems of astronavigation, E-vector-based spherical geometry, map-and-compass and bi-coordinate position-fixing schemes have been developed to account for the animals' performances. Although these metaphors have some heuristic value, they are potentially distracting and might obscure some of the most important computational strategies used by the brain. Moreover, these top-down approaches are especially inappropriate in trying to understand the evolutionary design of an animal's navigational system. Instead, we must go back to basics, use modern recording technology to unravel the detailed spatial and temporal structures of migratory routes and foraging trajectories, study the animal's sensory and computational abilities by combining behavioural and neurophysiological approaches, then work bottom-up, as evolution did, by trying to integrate the individual navigational methods. Rather than being part of a general-purpose navigational toolkit, the various guiding mechanisms have most certainly arisen from an opportunistic grafting of particular special-purpose modules on to pre-existing sensory-motor control systems.

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The surface of our planet is populated by a wide variety of mobile animal species, rendering the thin layer of biosphere a fascinating theatre of locomotor activities of all sorts. In fact, it is precisely this mobility that determines the lifestyle of many species – small and large, far-ranging or confined to mere pixels of terrestrial space.

Two introductory examples – one of a large-scale, and the other of a small-scale foraging and homing excursion – might suffice to give a flavour of the argument. At the Crozet Islands in the southern Indian Ocean, Wandering Albatrosses *Diomedea exulans* leave their nesting sites to set out on foraging flights which take them over distances of hundreds or even thousands of kilometres. Finally, however, they return to their home island, a tiny speck within the vast expanse of water, with seemingly unerring precision (Jouventin and Weimerskirch 1990, Weimerskirch et al. 1993). If one looks at these flight trajectories from quite some

distance (as one can now so readily do by way of satellite-based radiotelemetry), one observes a sequence of rather straight vector courses; but close-up views through the eye of a tracking-radar beam show that the foraging albatrosses engage in a variety of flight manoeuvres including frequent turns, pull-ups and descents, which continue for periods of seconds and minutes, and which must be integrated by the birds into the consistent overall orientation vectors recorded by satellite telemetry (Fig. 1A).

Let us now turn to the other side of the globe, switch from the marine to the terrestrial world, and shift our gaze from the sky close to the surface of the earth. We shall then discover long-legged desert ants, *Cataglyphis fortis*, roaming about the widespread areas of flat desert terrain. I shall not easily forget the day when I recorded the foraging path of one of these ants within a vast salt pan of the Saharan desert at a time of the day when the air temperature rose to 53°C. Meanwhile, the record

obtained in this way has become one of the hundreds of examples we have collected since then. In general, the ants would leave their central place, a tiny hole leading to their underground colonies, separately and travel for distances of several hundred metres to capture their

prey. They then return directly along a straight path to the starting point of their foraging excursion (Fig. 1B; Wehner 1987).

Although the two types of animal navigator – the soaring-and-gliding seabird and the dashing-and-darting desert ant – differ in body size and foraging range by several orders of magnitude, in theoretical terms they must accomplish somewhat similar navigational tasks: they must return to the starting point of a far-ranging journey, which has taken them well beyond the range within which they could detect the goal directly. Furthermore, if *Diomedea* and *Cataglyphis* are prevented from reaching their feeding grounds actively by their own locomotor activities, by displacing them experimentally for thousands of kilometres in the case of *Diomedea* (Kenyon and Rice 1958, Fisher 1971) or tens of metres in the case of *Cataglyphis* (Wehner et al. 1996), they still would return to their nesting sites much faster than random search movements would lead one to assume.

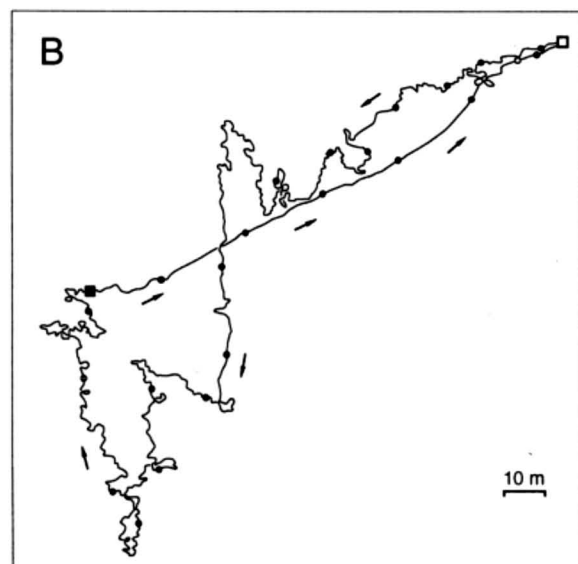
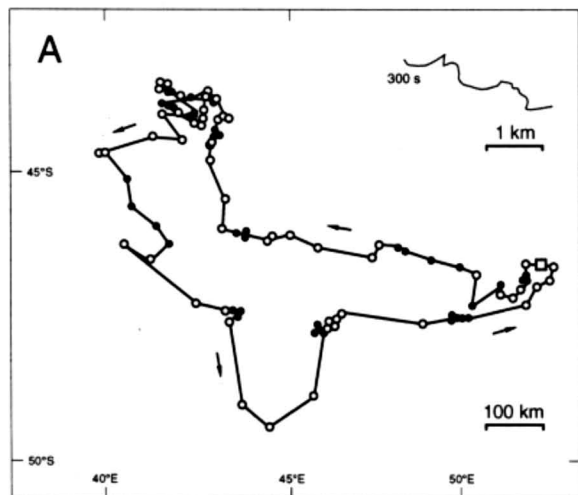


Fig. 1. Round-trip foraging excursions of insects and birds. (A.) Wandering Albatross *Diomedea exulans*. The male bird tracked here by satellite-based radiotelemetry returned to its breeding site, Crozet Islands (open square), 2400 km off the coast of Antarctica, after it had completed a 4372-km foraging flight. Open and filled circles indicate daytime and nighttime locations, respectively. The inset depicts a 300-s flight path of a Grey-headed Albatross *Diomedea chrysostoma* recorded by radar tracking. Based on Weimerskirch et al. (1993) and Alerstam et al. (1993). (B.) Desert ant *Cataglyphis fortis*. The 592-m and 18.8-min foraging run and the adjacent 140-m and 6.5-min return run were recorded in a North African salt pan, the Chott el Djerid (southern Tunisia). Time marks (black dots) are given every 60 s. Nesting and prey-capture sites are indicated by open and filled squares, respectively. Based on Wehner and Wehner (1990).

Outlining grand theories

In this light, it comes as no surprise that many theoreticians, especially those belonging to the cybernetics and control-theory camps, have tried to construct the computational schemes, or algorithms, required to solve the underlying navigational problems from first principles. As birds are the most prominent and best-known migrants, it is with them that such grand theories have been developed first. At the end of the 19th century Viguier (1882), and more than one hundred years later Gould (1985), assumed that birds were able to determine their global position by detecting features of the earth's magnetic field, such as field intensity and inclination, for reading a bi-coordinate magnetic map based on these features. In the present account, however, I would like to make my point by referring mainly to visual navigation – not least because vision provides an animal with the highest degree of spatial resolution and, hence, the greatest accuracy of navigation.

For any long-distance traveller, the sky and its celestial bodies are useful sources of information, but how do animals actually make use of this information? These have been burning questions since the mid-twentieth century when sun navigation became a main focus of interest (Matthews 1953, Pennycuik 1960). In particular, the sun-arc hypothesis implied that birds could determine their position relative to home by comparing the actual movement of the sun along its arc with the remembered one at home (Fig. 2A). In making such comparisons, one must measure and compute how the sun's arc – for example, its point of culmination – and the local time differ between home and where one happens to be at that moment; in short, one must

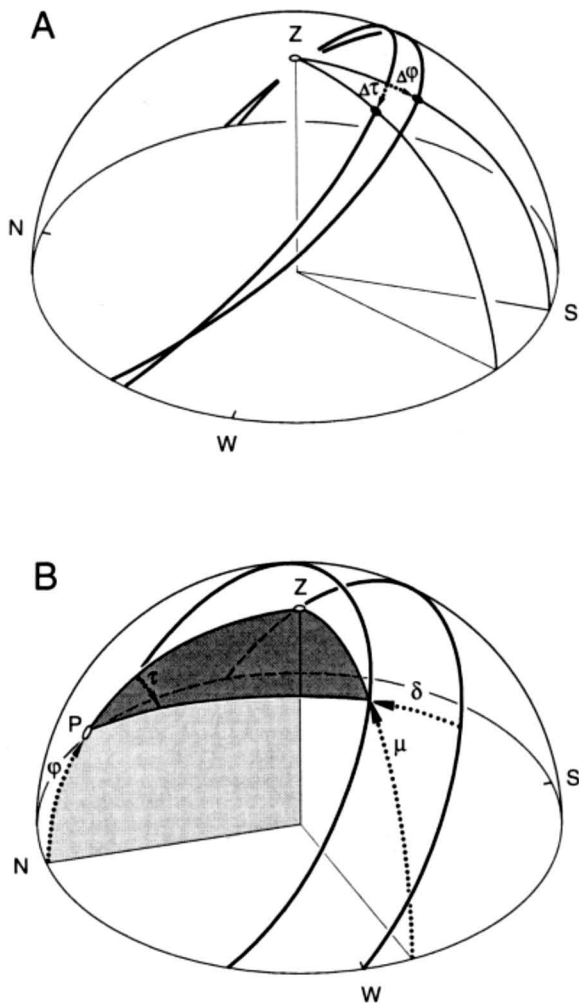


Fig. 2. Astronavigation as a means of taking positional (geographical) fixes. (A.) Sun-arc navigation. The figure shows the position of the sun (filled circle) for Paris at local noon, when the sun culminates in the south, and simultaneously for Rome. In order to be able to fix its geographical position, a diurnal migrant could determine Δt (the local time difference between, say, home and the migrant's present abode) and $\Delta\phi$ (the angular difference between the points of culmination of the sun's arc at the two locations). (B.) Stellar navigation. In a way analogous to sun-arc navigation, a nocturnal migrant could determine its distance and direction of displacement by comparing the elevation and azimuthal position of a selected star with the remembered position of the star at home, or some other goal, and by using an extremely accurate and stable internal clock. A human navigator would use the elevation (μ) of a particular star, its declination (δ) taken from an astronomical almanac, and the hour angle (τ). P marks the north pole of the sky (elevation ϕ). The dark area depicts the so-called astronomical triangle. — In figures A and B the observer is in the centre of the celestial hemisphere. Z marks the zenith. S, W, N indicate the cardinal points of the compass.

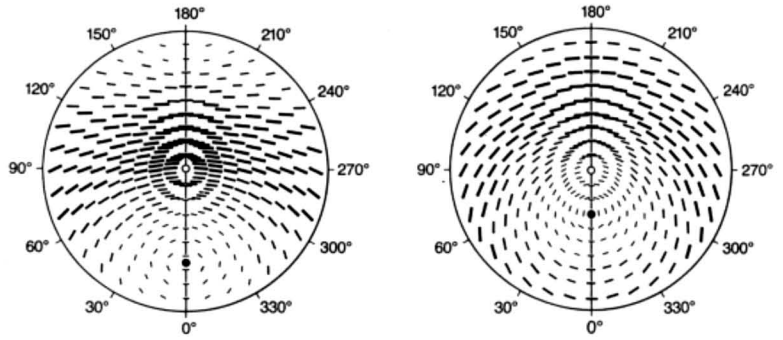
determine $\Delta\phi$ and Δt , respectively. Hence, for the navigator the essential requirements are memory, good eyesight, and an accurate sense of time. Nevertheless, even if an animal fulfilled these criteria — for instance,

if it were able to measure the sun's movement within periods of a few seconds or minutes (see, for example, Soodak and Simpson 1988 and Nalbach 1989), and if it could do so while flying when it needs to compensate for self-induced image flow — it would still have to be equipped with sufficient astronomical knowledge in order to make proper use of all these sensory data. Be this as it may, all experimental evidence clearly shows that birds are not astronomers in the sense that they can use the sun for taking positional fixes anywhere on the surface of our globe (Kramer 1957, Gwinner 1971, Keeton 1974).

Nor can birds use the stars for fixing their position at night. If they were able to do so (as assumed by Sauer and Sauer 1960), that is to perform "true" astronavigation (Hill et al. 1958), they would have had to organize the sensory data obtained from the sky within quite some sophisticated conceptual framework (Fig. 2B). Not only would they have to know that, within the common horizon system of coordinates, the positions of the stars (azimuth and elevation) change during the course of the night; but they would also have to conceive of a celestial system of coordinates, in which the positions of the stars were fixed, and defined in terms of ascension (or hour angle) and declination, and which rotated about an imaginary axis passing through the south pole and the north pole of the sky. Metaphorically speaking, they would have to solve the problem of finding geographical position by using a sextant to measure the elevation of any particular star, a chronometer to determine the hour angle, and an astronomical almanac to read off the declination of the star. No species of bird, or other animal, has been found to perform these conceptual tasks, or to have the necessary general-purpose astronomical knowledge about the stars' daily and seasonal movements across the sky.

Insects are not even able to see the stars; the light-collecting powers of their facet lenses are too small to catch enough quanta from even the brightest stars (Rodieck 1973, Kirschfeld 1974). On the other hand, insect navigators can detect a conspicuous pattern in the daytime sky — the pattern of polarized light, or E-vector pattern (Fig. 3) — and use it for navigation. Invisible to man, this pattern provides them with a powerful wide-field skylight compass that is coupled to the movement of the sun. Again, however, the task the navigator must accomplish is not an easy one. Substantial knowledge about straylight optics and spherical geometry is required to solve the compass problem in all-inclusive terms. For instance, during the course of the day the E-vector pattern changes with the elevation of the sun. While changing it rotates about the zenith of the sky and does so with non-uniform speed (the latter depending on both time of year and geographical latitude). Furthermore, the entire skylight pattern is not necessary for steering proper compass courses. Small parts of it — in the extreme, single E-vectors — suffice to

Fig. 3. Two-dimensional representations of the celestial E-vector pattern (the pattern of polarized light) depicted for two different elevations of the sun (filled circle): 25° in left figure, 60° in right figure. The orientation and size of each black bar mark the angle and degree (percentage) of polarization, respectively. The open circle indicates the zenith. The solar meridian (the line from the zenith down to the horizon) and the anti-solar meridian represent the symmetry plane of the celestial E-vector pattern. From Wehner (1994a).



do the job. If one stops and thinks about these complications, the task of solving them becomes dauntingly complex.

Resorting to grand solutions (Fig. 4), the navigator could determine, at any particular time, the orientation of at least two E-vectors in the sky by taking multiple sets of optical measurements, and then perform some geometrical constructions across the celestial hemisphere (Kirschfeld et al. 1975); or it could single out that particular E-vector in the sky that changed its orientation continually by exactly 15° per hour. It is this E-vector that marks the position of the north pole of the daytime sky (Brines 1980). All the experiments we have run on this topic for almost a decade have clearly shown that even the most highly advanced of all insect navigators – ants and bees – do not come genetically programmed with the astronomical knowledge outlined above. Nor do they acquire this knowledge during their lifetimes (Rossel and Wehner 1984, 1986, Fent 1986; for a review see Wehner 1994a, b).

In summary, in using celestial cues for navigation, neither birds nor insects have adopted a heliocentric or a general geocentric view of the skylight world surrounding them. They do not have any idea in their minds that the earth is a globe, nor do they draw upon spherical geometry to perform the proper constructions and computations in the daytime or nighttime sky. Rather than embarking on such rational detours, as humans do, they solve their navigational problems in more immediate ways. How then do they proceed?

Searching for basic mechanisms

Hymenopteran insects

Let us now continue with the insect case and inquire how – paradigmatically – *Cataglyphis*, the desert ant, steers its courses by deriving compass information from the patterns of polarized light in the sky. An intricate experiment has revealed an idiosyncratic property of this compass. If the ants are presented with individual E-vectors, or particular combinations of E-vectors, rather

than with the entire skylight pattern, and if this is done only episodically during either the outbound or inbound runs, the ants deviate by consistent error angles from their correct homeward courses. These error angles and the systematics behind them can be used to reconstruct the ant's internal representation of the daytime sky. This results in a stereotyped template – a generalized map of the sky, so to speak – that is used by the animal invariably under all possible skylight conditions (Fig. 5).

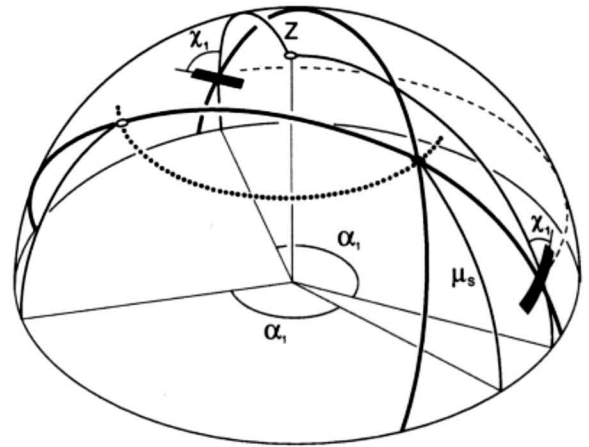


Fig. 4. Three-dimensional constructions required to infer the position of the sun – and hence the azimuthal position of the solar meridian – from at least two patches of polarized light in the sky. The black bars indicate the orientation of the E-vectors (χ) at two points in the sky. The following directives would yield an all-inclusive solution of the problem: First, determine the E-vector orientation at two points in the sky (a task not discussed here); then construct the great circles (heavy black arcs) running at right angles through the E-vectors; finally determine the position of the sun (filled circle) as the point of intersection of the two great circles. With one E-vector alone, the position of the sun cannot be determined unambiguously. If the elevation of the sun (μ_s) were known at a particular time of day, two intersection points of the great circle inclined orthogonally to χ_1 and the parallel of altitude defined by μ_s could be determined. These intersection points define the correct position of the sun (filled circle), as well as a fictive position (open circle), which is separated by the azimuthal difference α_1 from the correct one. The insect's E-vector compass does not operate this way, but is based on a set of simpler rules (see text and Fig. 5). Modified from Wehner (1981).

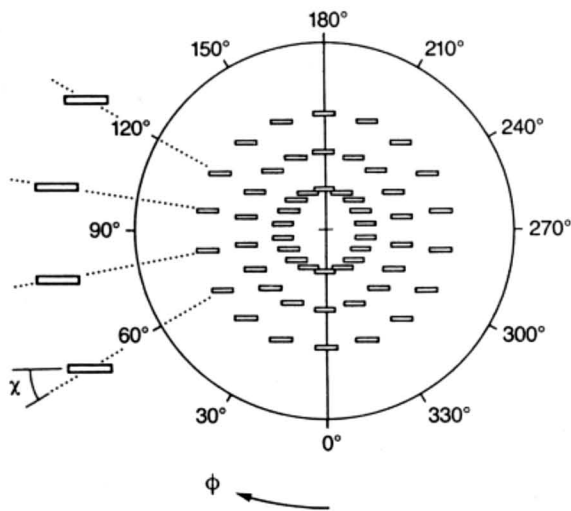


Fig. 5. The ant's internal representation of the celestial E-vector patterns as derived from behavioural experiments. For comparison with the external E-vector patterns see Fig. 3. The open bars indicate where in the sky the insect assumes any particular E-vector to occur. This "template" is used invariably for all elevations of the sun. χ and ϕ indicate the orientation of the E-vector (relative to the corresponding celestial meridian, see Fig. 4) and its azimuthal position (relative to the solar meridian), respectively. For details see Wehner (1994a).

Before asking what this template metaphor means in terms of the ant's neural hardware, we should try to understand how the insect could navigate correctly by using a map that is not a correct copy of the outside world. First, we assume that the animal works according to some kind of template-matching scheme. Then, under the full cloudless sky, the best possible match between template and outside world is achieved when the animal is adjusted with the symmetry plane of the E-vector pattern, the solar and/or anti-solar meridian. Seen in this way, searching for the best match is equivalent to setting the zero-point of the compass. However, due to the fine-grain discrepancies between the animal's internal template and the daytime E-vector pattern, the zero-point no longer coincides with, say, the solar meridian whenever individual E-vectors or particular combinations of E-vectors are displayed. Of course, for the navigator this is disadvantageous only if the skylight conditions vary during the course of the experiment, or the ant's natural round-trip excursion. It goes without saying that, if the external conditions remained the same – that is, if human investigators did not interfere or if the large-scale clouding did not vary substantially in the natural sky – the animals would always have adjusted their compass in the same way. Consequently, systematic errors should not occur. Experiments show that this is actually the case (for data and further references see Wehner 1991, 1997). What follows is that evolution has provided the insect navigator with only some general characteristics rather than

the detailed spatial structure of the daytime skylight patterns, but this basic information is sufficient, if the animal restricts its navigational exercises to short periods of time, so that the same patches of unobscured sky are available during the entire field trip. Given the ant's short foraging times (tens of minutes rather than hours), this condition is usually met.

In summary, the insect's compass mechanism accomplishes a particular, time-constrained task. This accords with what one discovers by taking a closer look into the cockpit of the *Cataglyphis* navigator. There we find dedicated neural machinery comprising only a limited number of polarization analyzers (photoreceptors) and large-field polarization-sensitive interneurons, which sample the outputs of particular receptor populations. Even though in the present account the neural hardware is not at stake (for a review see Wehner 1994a, b), there is one important conclusion to be drawn from this detour into brain research. The system is not able to determine the orientation of individual E-vectors *per se*. It merely provides the animal with information about the points of the compass, that is, the direction in which it currently moves – and this is all that matters.

The celestial compass discussed so far is only part of a more complex system of navigation, which includes the insect's way of integrating the angles steered and the distances covered (Ronacher and Wehner 1995, Srinivasan et al. 1996) by employing a special dead-reckoning algorithm (Müller and Wehner 1988, Hartmann and Wehner 1995). Furthermore, due to the daily rotation of the skylight pattern, the zero-point of the compass must be calibrated, or "time-compensated", that is, correlated with an earthbound system of reference (Wehner and Müller 1993, Dyer and Dickinson 1994). I shall skip any discussion of how *Cataglyphis* accomplishes these additional tasks (see references given above), but hasten to mention that in all these cases the insect again resorts to what a human navigator would call approximate rather than complete solutions. These imperfections, however, are only in the eyes of the beholder. They disappear immediately, if the questions are posed within the spatial and temporal contexts of the ant's foraging behaviour.

Although these shortcut adaptations are well designed to meet the animal's demands, and to prevent the various subsystems from introducing systematic errors, random noise will greatly interfere with any system of path-integration. Even in the grand-design case, egocentric systems of navigation – such as path integration (dead-reckoning) – are prone to cumulative errors. Back-up systems are needed to compensate for such errors, in order to correct the animal's representation of its position from time to time by taking a positional fix. One important back-up system, or emergency plan, adopted by insect navigators exploits the use of landmark information. *Cataglyphis*, for example, is able to memorize the configuration of landmarks

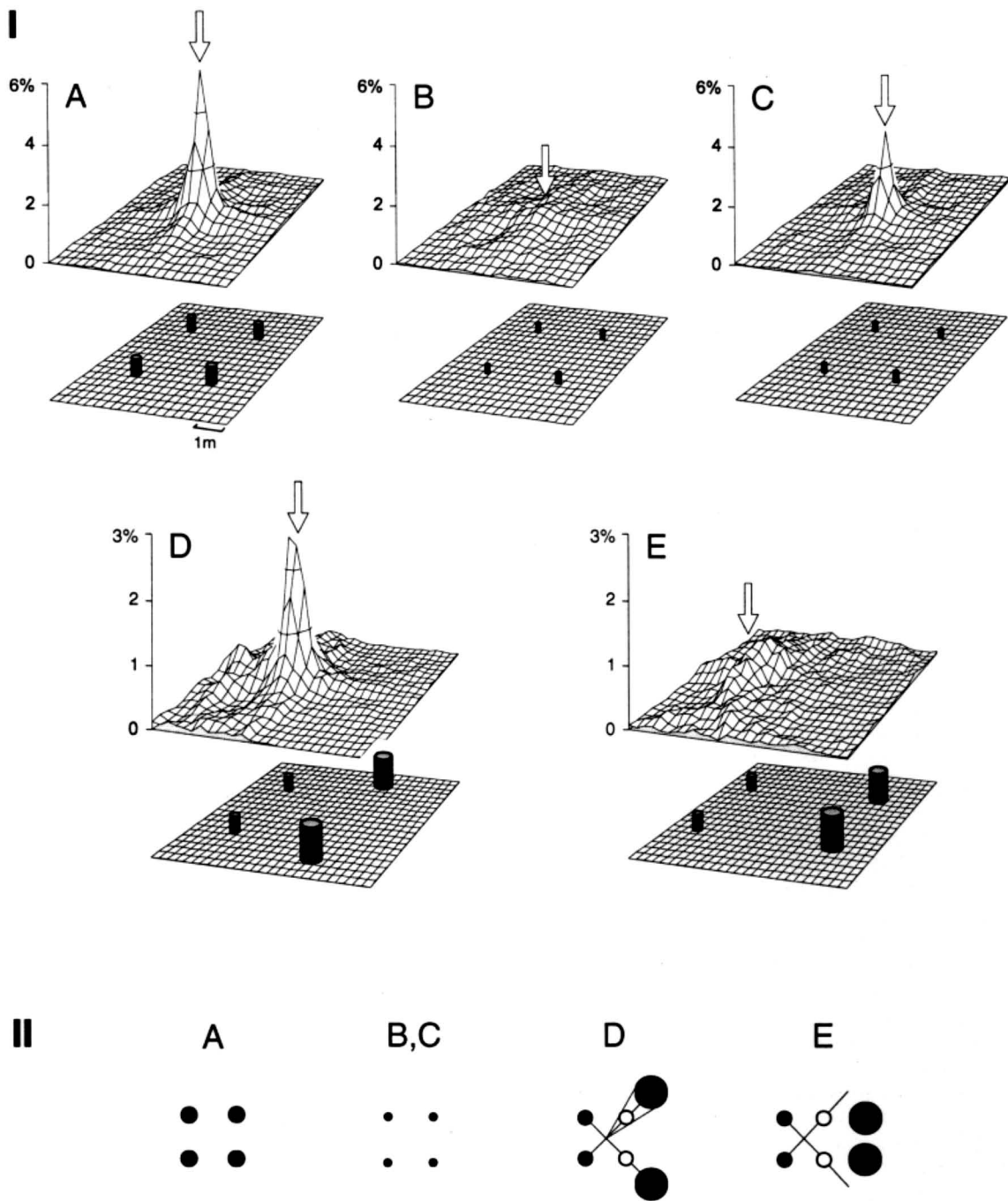


Fig. 6. Terrestrial navigation in desert ants, *Cataglyphis fortis*. (I.) Search density profiles of ants presented with the 4-cylinder square-array landmark configurations shown in the lower parts of the figures. (A.) Training array. The fictive goal (nest entrance) is positioned in the centre of the landmark array. (B.) Test with landmarks decreased to half the training size. (C.) The positions and sizes of the landmarks are the same as in B, but the ants are not only tested but also trained within the same small-landmark array. (D.) Two of the landmarks are increased to double size and positioned at double distance, but separated by the same azimuthal distance (90°) as in the training situation (see A). (E.) Same as in figure D, but with the two large landmarks separated by a smaller azimuthal distance (35°) than during training. In all figures, the open arrow points at that position within the square array, at which a snapshot-matching model yields the best possible fit between the current retinal image and the stored snapshot. (II.) Top views of landmark arrays used in experiments A–E described above. Based on Åkesson and Wehner (1997).

around a goal, be this the nesting or the feeding site, and later moves so as to match the current retinal image with the memorized "snapshot" (for a review see Wehner 1992). Experiments in which special contact lenses have been fitted to the ant's compound eyes show that the stored images – the neural snapshots – are retinotopically fixed within the visual system. They do not rotate within the animal's head (Wehner and Müller 1985, Wehner et al. 1996). Furthermore, they are only retrieved from memory if the animal, while continually using its path-integration system, has already come close to its goal. If an artificial landmark configuration, usually positioned around the nesting site, is experimentally displaced, say, half-way between the ant's nesting and current feeding site, it is completely ignored by the homing animal. Only after the homebound vector has been almost "reeled off", so to speak, is the snapshot-matching system switched on. This is an important prerequisite for the latter system to be useful at all. Otherwise, when moving about in its natural habitat, *Cataglyphis* would easily get distracted by similar landmark configurations experienced *en route* homeward.

Although *Cataglyphis* makes effective use of landmark information, this does not mean that the insect navigator assembles some kind of mental topographic map of its nest-site surroundings. The latter has been claimed (Gould 1986) but could not be confirmed (Wehner and Menzel 1990, Wehner et al. 1990, Dyer 1991, 1996). For instance, in employing their snapshot-matching mechanisms, ants and bees confound distances and sizes of objects. Landmarks placed at double (n-fold) distance and increased to double (n-fold) size give rise to the same retinal image and are taken by the animal for the original marks (even though, under certain conditions, insects are able to gain and use information about the third dimension; Srinivasan 1993, Wehner 1994b). What is crucially important are the angular sizes and azimuthal positions of the landmarks. If they are changed only slightly, the accuracy of pin-pointing the goal decreases dramatically (see Figs 6B and 6E, respectively).

Whenever available, landmark information is used not only at the nesting and feedings sites, but also along routes frequently travelled through a cluttered environment (Wehner et al. 1996). How, then, does *Cataglyphis* overcome the problem that patterns learnt at one place are not recognized somewhere else? Contextual cues – such as more distant landmarks or the portion of the vector course already completed – help to activate the appropriate memory store at the right time and place (for bees see Collett et al. 1997). In summary, the insect forager gathers quite different types of information and interprets them with remarkable acumen. As schematized in Fig. 7, there are various systems of navigation that *Cataglyphis* has at its disposal at any one time of its round-trip excursion. Let us assume that

a forager has learnt to return from its feeding site to its central place along the route FN depicted in Fig. 7A. If later displaced from the feeding site F to open territory that is devoid of any landmarks, and if released there at R, the ant follows a straight vector course (egocentric vector V_{ego} in Fig. 7B), even though within its own foraging area it has never been able to do so. Note that the egocentric vector V_{ego} has a geocentric component in so far as it is anchored to the starting point of the round-trip excursion. This anchor, however, breaks free as soon as the animal is displaced during its journey. If, in a second type of experiment, the ants released at R have been taken from N rather than F, that is, if they have already completed their homeward run ("zero-vector ants"), they do not display V_{ego} again, but switch to a systematic search programme (not shown in Fig. 7, but see Wehner and Srinivasan 1981, Müller and Wehner 1994). If the zero-vector ants are displaced together with the (artificial) landmark configuration, they use this landmark-based route information and follow the

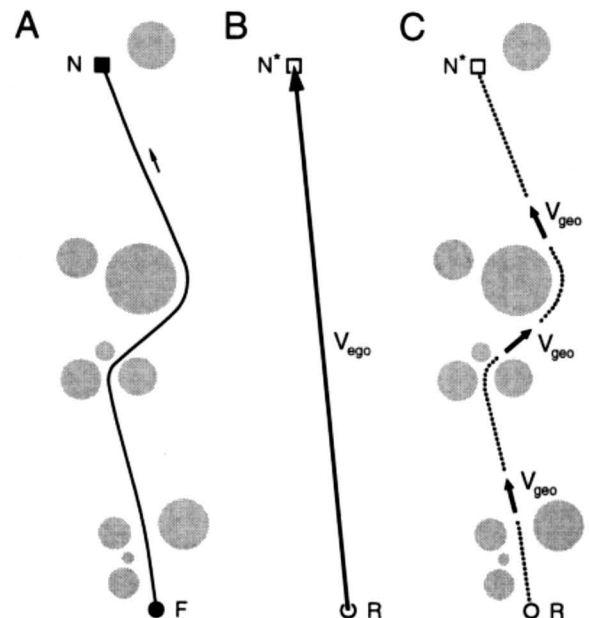


Fig. 7. Navigation mechanisms in desert ants, *Cataglyphis*. (A.) A particular (individually marked) ant has learnt to negotiate its way from a frequently visited feeding site (F) to its nesting site (N). The route taken by the ant through a cluttered environment – a low-shrub desert or an array of artificial landmarks – is marked by the solid line. (B.) Egocentric vector course (V_{ego}) travelled by the ant when displaced from F to open (landmark-free) territory, and released there at R. N^* indicates the fictive position of the nesting site. For data see Wehner and Srinivasan (1981). (C.) The route (dotted line) selected by a "zero-vector ant", that is, an ant that has already returned from F to N, and is then displaced, together with the (artificial) landmark array, to novel territory. For data see Wehner et al. (1996). To accomplish this task, the ant relies on sequential landmark memories and geocentric (site-based) local vectors (V_{geo}) that are linked to particular landmark configurations. For data see Bisch and Wehner (1998).

course originally taken in the training area (LR in Fig. 7C). During foraging they might have learnt a series of snapshots and might later try to match their current retinal images to the sequentially-retrieved snapshot images. Circumstantial evidence for this kind of interpretation derives from experiments, in which the axis of the landmark array has been rotated by 90° without preventing the ants from following LR, even though they do this less efficiently than in the former case in which the landmark array was oriented as during train-

ing. The sequential matching-to-memory process is facilitated by the ant's ability to associate particular landmark configurations with the appropriate local vectors. These site-specific, geocentric vectors (V_{geo} in Fig. 7C) are a further means to keep the animals on their familiar landmark routes (Bisch and Wehner 1998).

Lepidopteran insects

At this juncture, let us leave for a while the *Cataglyphis* case and switch from small-scale insect foraging to large-scale insect migration. One of the most spectacular examples of such migratory movements is provided by the North American monarch butterfly *Danaus plexippus*. From late August to early September, millions of monarchs leave their breeding sites in the eastern United States and Canada to migrate up to 3600 km to their overwintering sites in the high-altitude forests of central Mexico (Fig. 8A). As numerous recaptures of alar-tagged individuals show (Urquhart and Urquhart 1978, Brower 1995), some of them may travel, on average, 130 km per day (mean value: 50 km per day during a period of about 75 days). The return migration is much less conspicuous. At about the spring equinox the overwintered adults embark on a rapid northbound mass exodus. Some individuals migrate at least as far north as Maryland and Kansas, and a few even reach the northern United States, which they left more than six months ago, but the majority stops after having reached the Gulf Coast states (mainly Texas and Louisiana), lays eggs on the resurgent milkweed plants, and dies. The return migration is completed by two or more short-lived breeding generations, which slowly spread northwards and eastwards. Hence, the individual butterflies flying southwards next autumn are descended by several generations from their ancestors that have left the Mexican overwintering sites during the previous spring.

The sensory cues used by the butterflies as navigational aids are largely unknown. As monarchs are

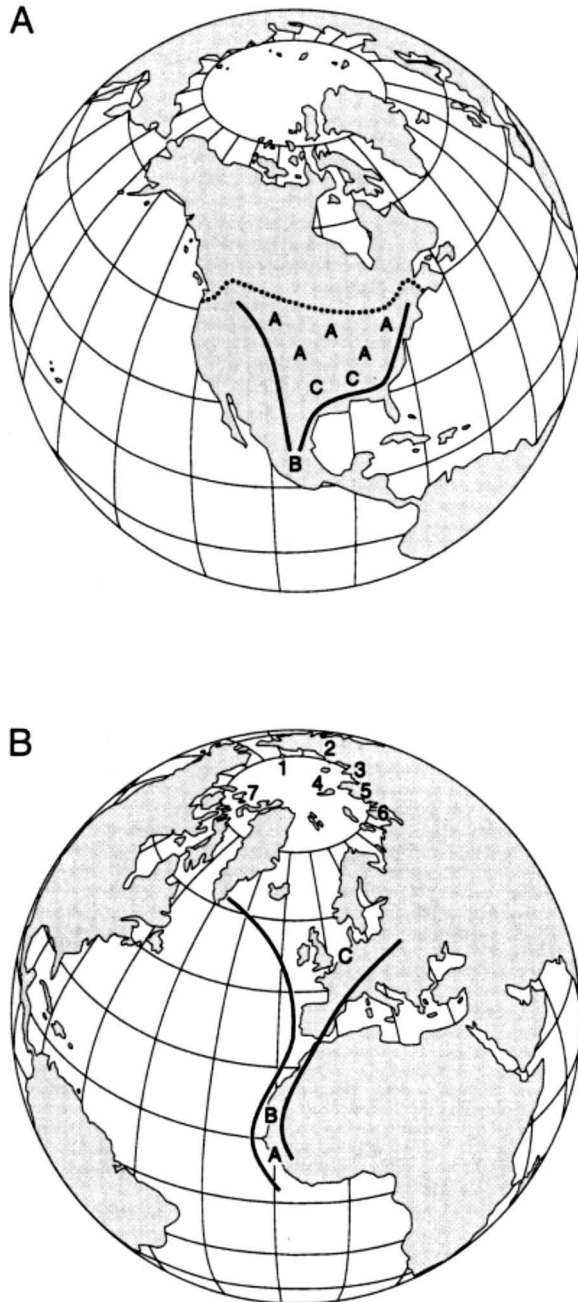


Fig. 8.

Fig. 8. Long-range migration in insects and birds. (A.) Autumn and spring migration of the eastern population of the North American monarch butterfly *Danaus plexippus*. The letters A indicate the breeding range; letter B marks the highly localized overwintering site in the mountains of the Mexican Neovolcanic Belt; the area indicated by the letters C constitutes the summer breeding range of the monarchs that overwintered in Mexico and subsequently produced the first new spring generation in the area of the Gulf Coast states. This generation migrates northeastwards across the midwestern states to southern Canada. The dotted line depicts the northern limit of the butterflies' *Asclepias* (milkweed) food plants. Based on Brower (1995). (B.) Spring migration of Siberian waders. The letters A and B indicate the West African wintering sites (Guinea-Bissau and Banc d'Arguin, respectively); letter C marks the staging (stopover) site (Dutch Wadden Sea). The breeding areas of the migrants are numbered as follows: 1, Wrangel Island; 2, Indigirka River; 3, Lena River; 4, New Siberian Islands; 5, Taymyr Peninsula; 6, Yamal; 7, Ellesmere Island. Based on Wymenga et al. (1990).

diurnal migrants (at dusk they glide down into trees where they form temporary overnight clusters), claims that they exploit sun-compass information are not surprising (Kanz 1977), and recent work provides some clock-shift evidence for such proposals (Perez et al. 1997). Further evidence comes from an elaborate experimental study of neotropical pierid butterflies, *Aphrissa statica* and *Phoebis argante*, migrating across the isthmus of Panama (Oliveira et al. in press). Individuals submitted to a 4-h advance clock-shift and then released in the open exhibited vanishing bearings that deviated significantly from those of control butterflies. The direction of this deviation was consistent with the use of a sun-compass mechanism, but the magnitude was less than the predicted value by some 25 to 30%. The latter difference could be largely attributed to the direction and speed of the prevailing winds. However, monarchs (Gibo 1986, Schmidt-Koenig 1993) and other diurnally migrating species (Walker and Litell 1994) fly on overcast days as well – and continue to do so under clear-sky conditions when the sun is in the zenith (Larsen 1991). Magnetite particles have been found in adult monarchs (MacFadden and Jones 1985, Jungreis 1987), and the higher-than-normal magnetic field intensities recorded near the centre of the overwintering area have led some authors to assume that the butterflies may be attracted to these areas by sensing the strong fields (Monasterio et al. 1984). But there is no experimental evidence to confirm that the monarchs actually use any parameters of the earth's magnetic field for navigation. Furthermore, based on observations of butterflies moving close to the ground, it has long been assumed that the migration directions are independent of the directions of the prevailing winds (Walker and Riordan 1981). It has even been argued that the butterflies follow the orthodrome (shortest-distance) rather than loxodrome (constant-angle) route (Schmidt-Koenig 1979), even though both routes along the North American flyway are very similar.

Clearly, the general grand-theory approaches described above are ill-conceived. It is crystal-clear that migrating butterflies cannot accomplish their navigational tasks without exploiting large-scale synoptic weather systems. For example, in flapping flight lepidopteran insects rarely exceed air velocities of a few metres per second (Weis-Fogh 1976), but migrating monarchs have been observed to achieve ground speeds exceeding that value by more than one order of magnitude (Gibo and Pallett 1979). During autumn migration the butterflies select flight altitudes of up to 1250 m above ground (Gibo 1981), where they take advantage of strong northeasterly tailwinds (Dennis 1993). If the wind is from the south, they aggregate in staging areas and enter nectar-searching periods (Gibo and Pallett 1979, Schmidt-Koenig 1985). The near-pristine condi-

tion of the butterflies after reaching central Mexico (Brower 1985) is further evidence that winds are important in assisting monarchs on their autumn migration. Soaring and exploiting tailwinds are the most conspicuous features observed in the migration of these spectacular butterflies. In fact, it is the synoptic system of large-scale weather patterns prevailing above North America that favours southwestward movements in the autumn and northward or northeastward movements in the spring (Kanz 1977), thereby making the 3000-km journey of a 0.5-g butterfly possible at all. It seems reasonable to conclude, then, that the overall migration pattern of monarch butterflies would not have evolved in the absence of these weather systems.

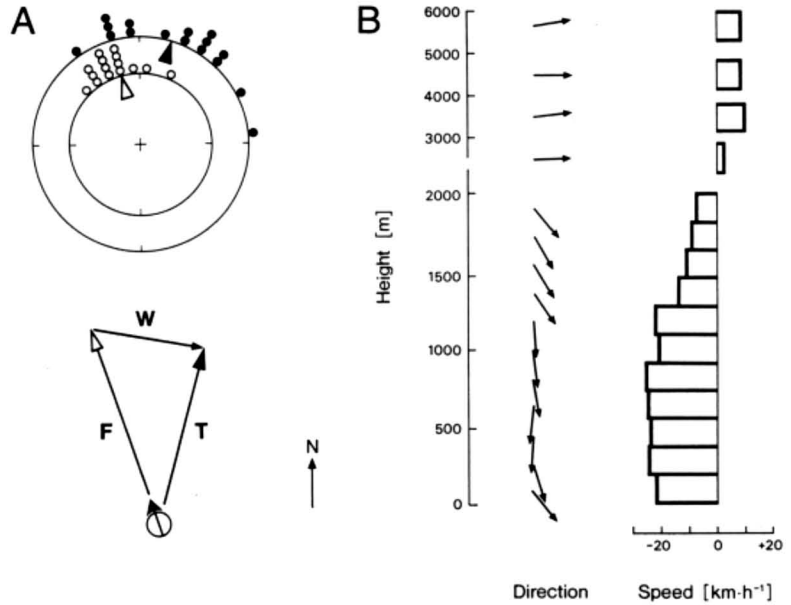
This does not mean, however, that the butterflies are completely at the mercy of winds. They must actively embark on air currents by launching themselves into the air at the right time, and must exploit lift by soaring in thermals, but should do so only when there is wind in the appropriate direction. They must also select the right flight vectors and control the track vectors by visual contact with the ground. Furthermore, there is clear evidence that they adjust their headings so as to compensate for wind drift, at least partly and occasionally (Srygley et al. 1996). Consequently, by following a set of particular rules, they travel on air currents adaptively rather than inadvertently. Unfortunately, the means whereby these criteria are met have not yet been elucidated. When will the time come that progress in technology will finally enable us to track individual butterflies while they are *en route* and displaying their full migratory repertoire? Do recent improvements in tracking airborne insects (Osborne et al. 1997) by radar techniques (Riley and Reynolds 1979) provide some hope?

Birds

This dream has already come true in birds. From short-distance tracking radar registrations to long-distance satellite-based radiotelemetry, a variety of methods is available to record flight routes of migrating birds at different geographical scales (Alerstam 1996). For instance, in White Storks *Ciconia ciconia*, the migratory routes of individual birds have been satellite-tracked during the entire 16000-km round trip from eastern Germany to Tanzania and back (Berthold et al. 1997). Neither the storks nor the Brent Geese *Branta bernicla*, which have been tracked by satellite telemetry from their spring stopover sites in Iceland across the Greenland icecap towards their breeding range in arctic Canada, travel along the direct, shortest-distance route to their destination (Gudmundsson et al. 1995).

The geese depart from Iceland by selecting a mean northwesterly course of 250°, veer towards west-south-

Fig. 9. Flight characteristics of waders leaving their West African wintering sites (site B in Fig. 8B) during spring migration. (A.) Departure tracks and headings. Upper figure: Heading (open symbols) and tracking angles (filled symbols) of Dunlins *Calidris alpina* are depicted on the inner and outer circles, respectively. Mean angles are indicated by arrowheads. Lower figure: Schematic representation of the migrant's air speed and heading direction (flight vector, F), wind speed and wind direction (wind vector, W), and ground speed and track direction (ground or track vector, T). N marks north. (B.) Average wind directions (left) and wind speeds (right) encountered by waders while ascending from the West African coast to altitudes of up to 6 km. North as in (A). Based on Piersma et al. (1990).



west when reaching the pack-ice zone off the steep coast of eastern Greenland, stop there for 2–7 days, and then continue across the icecap of southern Greenland by maintaining about the same navigational course they had selected in Iceland (Gudmundsson et al. 1995). Obviously, they do not travel continually along either an orthodrome or a loxodrome route, but display a set of rules that cry out for analysis. These rules might include a number of navigational sub-routines such as selecting and maintaining constant compass courses over open sea, relying on topographical guidance at the Greenland stopover site, recalibrating the sun compass by resetting the bird's internal clock and, possibly, using position-control systems. The migratory programme adopted and used by the Brent Geese has most probably evolved as an economically optimal adaptation to the large-scale topographical features characterizing the birds' North Atlantic flyway.

An even more telling example of how bioenergetic constraints might have shaped travel programmes of long-distance migrants is provided by Siberian waders using the East Atlantic flyway during their spring migration. It is along this route portrayed in Fig. 8B that multitudes of Knots *Calidris canutus* and plovers, Dunlins *C. alpina* and sandpipers, Whimbrels *Numenius phaeopus* and godwits, Turnstones *Arenaria interpres* and Redshanks *Tringa totemos* travel from their West African wintering sites, the coastal mudflats of Mauritania, Guinea-Bissau and Sierra Leone, to their arctic breeding areas. During their journey they effectively exploit synoptic seasonal weather patterns – a behaviour that is reminiscent of, but much more elaborate than, the migratory strategies of monarch butterflies discussed above. Careful studies by Dutch researchers

(e.g. Ens et al. 1990, Piersma 1994) have shown that upon departure and *en route* the birds must make a number of deliberate decisions. They must decide when to depart, at what altitude to fly, how to adjust their air speed and what heading to keep relative to the wind. For example, they must leave the West African coast at altitudes greater than 3 km, because it is only there that favourable tailwinds keep the flight costs within reasonable ranges, thereby enabling the birds to complete the 4300-km non-stop flight to their next staging area, the Dutch Wadden Sea. Furthermore, in order to accomplish this task, they must adjust their flight vectors (their headings and air speeds) relative to the prevailing wind vector in such a way that the resulting track vectors follow more or less the shortest-distance (great circle) route. If, instead, they headed directly for their destination, that is, if their flight angles and track angles coincided, they would be wind drifted at remarkably high speeds directly eastwards into the Sahara desert. A comparison between Fig. 8B and Fig. 9 will make the point convincingly.

Given the existing sizes of transmitters and batteries, satellite-tracking recording techniques are restricted to birds with body masses exceeding 1 kg. Consequently, we do not yet know what the actual flight routes of individual waders look like, nor do we have any idea about which compass systems – either celestial or magnetic, or both – and what other navigational aids are involved in setting and maintaining the proper flight and track angles. Finally, are the birds innately informed about what directions to steer and what distances to cover?

The latter question can be answered, at least partially, for European warblers travelling from their

Palaearctic breeding areas to various parts of Africa. The warblers – especially the best studied case, the Blackcaps *Sylvia atricapilla* – exhibit a fairly sharp “migratory divide”, with the western German and the eastern Austrian birds flying south-westwards and south-eastwards, respectively (for a theoretical treatment of such behavioural differentiation see Lundberg and Alerstam 1986). Studies of inexperienced, hand-raised birds tested in orientation cages at the time of day and year when they would normally migrate clearly show that the first-year migrants possess and use an innate vector programme (Helbig et al. 1989, Helbig 1991a). In cross-breeding experiments the first-generation offspring of mixed pairs of south-westward and south-eastward migrants choose migration directions that are intermediate between those of their parents (Helbig 1991b). The vector programme may even contain information about two vector routes displayed in succession, as is the case with the eastern Blackcap population. When tested in orientation cages, hand-raised Austrian birds orient south-eastwards in October and south-southwestwards in November, with a clockwise shift of about 60° occurring within a 10-day period (Helbig et al. 1989). This accords with the natural two-leg migration route which leads the birds first across Anatolia to the Near East and then southwards to East Africa. These experimental findings – together with some earlier displacement experiments performed with White Storks (Schüz 1951) and Common Starlings *Sturnus vulgaris* (Perdeck 1958, 1967) – clearly show that at least some migratory birds are endowed with endogenous vector programmes.

In evolutionary terms, these programmes seem to be rather flexible with respect to both migratory distance and direction. Within the last three to four decades, which have been characterized by progressively milder winter seasons, a fraction of the southwest-migrating Blackcap population has shifted its vector course towards the west and northwest and established new winter quarters in Britain (Berthold and Schlenker 1991). This microevolutionary process, based on geographically-restricted frequency shifts within the range of pre-existing genetic variation of migratory directions (Helbig 1994, Helbig et al. 1994), has led to a suite of ecological advantages; for example, vector courses that are shorter by as much as 1500 km than the usual south-westward route. A similarly rapid microevolutionary change has occurred in monarch butterflies after they were introduced to Australia, together with their milkweed food plants, at the end of the last century. In contrast to their North American ancestors, the Australian monarchs have reversed the timing and direction of their migratory behaviour by 6 months and 180°, respectively (James 1993).

Regardless of which cues migratory birds use in running their vector programmes, there is one decisive point I would like to make in this context. The birds

seem to follow a detailed set of instructions adopted to the particular needs of their migratory endeavours rather than computing a global navigational course upon departure. The navigational techniques used in following these instructions include a wealth of orientation mechanisms and behavioural strategies, such as using celestial and magnetic compasses, odometers of one kind or another, internal clocks, time compensators, course stabilizers, altimeters, feature detectors or photoperiodicity recorders; all integrated in completely unknown ways. We do not even know yet whether the migratory birds, when running their vector programmes, take positional fixes; nor do we know what the earthbound systems of reference are, within which such fixes could be represented. Moreover, how is this allocentric information correlated with the egocentric vector programmes, which it might even supersede? For example, do the first-year birds after arrival at their overwintering sites (i) determine their geographical position in one way or another, and then use map information to compute their spring return route, or (ii) do they resort to some kind of large-scale path-integration scheme, or (iii) do their endogenous travel plans contain the proper return-flight vectors as well? These are especially intriguing questions in those species of birds that exhibit pronounced annual loop migrations. The Willow Warblers *Phylloscopus trochilus* (Hedenström and Pettersson 1987) and the Nearctic Knots *Calidris canutus islandica* (Davidson et al. 1986) provide clear-cut examples. The Knots travel from their breeding grounds in high arctic Canada and Greenland via Iceland to their winter quarters in Britain and the Wadden Sea. During spring migration they set off for a staging area in northern Norway. Upon departure they deviate by 75° eastwards from the final leg of their autumn migration route. In all these cases, the birds cannot just retrace their former paths. How, then, do they accomplish this task?

Some evidence for the third possibility mentioned above can be drawn from orientation-cage experiments, in which hand-raised warblers were tested during both the spring and the autumn season (*Sylvia borin*: Gwinner and Wiltshko 1978, 1980; *Sylvia atricapilla*: Helbig 1989). During both migratory periods the same hand-raised birds exhibited inherited migratory preferences. In autumn, they oriented towards SW, and later after a migratory shift towards S or SSE, but in spring they headed towards N. If hand-raised buntings, *Passerina cyanea*, were tested in autumn under physiological spring migratory conditions, they selected, in their orientation cages, northerly hopping directions (Emlen 1969). In these cases, the inexperienced birds, although they had never travelled to their wintering sites, still exhibited the proper return flight directions. But what about the albatrosses mentioned in the Introduction (Fig. 1A)? What navigational strategies do they employ when they perform their wide-ranging (up to 15000-km

and 4-week long) round-trip foraging excursions across the southern oceans? Do they integrate their paths, as the desert ants do on a much smaller geographical scale (Fig. 1B), or do they assemble and use bi-coordinate maps? If such maps were based on features of the earth's magnetic field, such as overall field intensity, intensity of the horizontal or vertical components, inclination or declination, there is no particular pair of features that could provide a useful quasi-rectangular grid over the entire circum-Antarctic foraging range of, for example, the Wandering Albatross (Åkesson and Alerstam 1998).

In spite of the impressive body of literature that studies of animal migration and homing have produced in the last decades, we seem only to have touched the surface of the navigational systems at work. In bird migration, the importance of visual, magnetic, infra-sonic and olfactory cues has been discussed, and in some cases elucidated to some degree, but we are far from being able to knit the available loose threads into a coherent fabric. How should we proceed? Should we, for example, raise, displace, and release more pigeons under even more varied experimental paradigms? I doubt it. While initially stimulating, these elaborate exercises seem to have exhausted their potential. The flexible use of multiple cues has led to much confusion in the interpretation of pigeon-homing experiments (Able 1996, Walcott 1996). Moreover, the main message from an abundance of papers on migratory passerines tested in orientation cages is an often bewildering plasticity and flexibility within and among different systems of orientation. For instance, compasses based on magnetic and visual (stellar and sunset) cues interact in intricate ways, are calibrated against each other, replace each other, and do so differently during successive stages of development (Wiltschko and Wiltschko 1995, Able and Able 1996, Wiltschko et al. 1998). How can we unravel the Gordian knot of complexity and the multiplicity of these interconnecting components?

Conclusions

In trying to answer this question, let me start with a few caveats. Any search for unitary mechanisms will turn out to be a futile exercise. As outlined in the beginning, the design and use of grand schemes of navigation depend on abstract concepts and deductions from first principles, such as spherical geometry or trigonometry, which the avian navigator had neither the need nor the opportunity of acquiring during its evolutionary and individual history. Nothing reflects better the rise and fall of early research in animal navigation than the notion that birds might be true astronavigators. Instead, the birds' awe-inspiring navigational perfor-

mances result from an intricate interlocking of a great number of special-purpose sub-routines tailored to the particular environmental conditions that the bird will encounter *en route* – and it is on these sub-routines that future research must focus first and foremost.

As in many fields of behavioural biology, there are two ways to proceed: top-down and bottom-up. The former approach has still much to offer, and the latter has hardly been tried. Technical advances in satellite-based tracking techniques will provide a quantum advance in the top-down analysis of navigational processes. They will enable us to vary our field of view from the global to the more local aspects of migration, and help to elucidate what is actually taking place during a bird's migratory journey. If the flight-path records obtained this way are correlated with the environmental (topographical, meteorological and magnetic) cues prevailing along the routes actually taken by the birds, one might be able to develop more refined hypotheses about the underlying navigational processes. For example, if a bird crossed different time zones (circles of longitude) non-stop, that is, without immediately recalibrating its internal clock, and if it maintained a constant-angle sun-compass course, it would travel almost precisely along a great-circle route (Alerstam and Pettersson 1991). This rule of thumb could be used effectively by birds migrating in polar regions where the sun remains above the horizon for the 24 hours of the polar summer day. Do long-distance migrants actually meet these conditions of slow time compensation that would allow them to adopt this kind of shortcut strategy? Only complete long-term recordings of their flight trajectories can provide an answer. Similarly, detailed information about the migrants' behaviour upon departure, the spatial and temporal characteristics of this event, and the environmental conditions under which it occurs, are needed to understand the decisions at which a migratory bird must arrive before it can embark on a cross-continental journey (see the painstaking work done by Theunis Piersma and his collaborators, e.g. Ens et al. 1990).

Regardless of how essential such close-up "observational" studies will be, the usual answers obtained in this way about mechanisms and processes rely more on advocacy than on direct evidence. They must be supplemented with laboratory-based top-down analyses. A most promising approach recently entertained in this context deals with the ontogeny of orientation mechanisms in hand-raised birds studied *in situ* under conditions in which the relevant orientation cues are controlled and manipulated experimentally. One result of such studies is that nocturnal passerine migrants come programmed with innate representations of their migratory directions, relative to both the earth's magnetic field and the axis of stellar rotation (Wiltschko and Wiltschko 1995, Able and Able 1995). Also, the

latter compass takes precedence and calibrates the former one at least during the early stages of development (Wiltchko et al. 1998). Another result has emphasized the overriding influence that visual cues of the sunset sky exert on the birds' directional choices made upon departure (Moore 1978, Able 1993).

Even though these top-down analyses provide sufficient evidence that various compass systems are used by the birds, either simultaneously or successively, the ways these systems operate remain obscure at present. It is in this context that bottom-up approaches must come to the fore. What are the potentialities and constraints inherent in an animal's navigational performances, and how does the animal's nervous system and physiological machinery – its cockpit and its engine – accomplish these tasks?

In recent years an exciting and promising fresh approach has been taken to the engine-related questions (see most contributions to this volume); but in understanding the migrant's cockpit, new ground has not been broken yet. One obvious reason is that brain research has hardly supported the behavioural analyses of bird migration. Because navigational subroutines – the neural modules involved in navigation – have not been designed evolutionarily from scratch, but have evolved from some pre-existing neural circuitry, we need to inquire more about neural processing in the avian brain; even if at first sight the processes under investigation might not seem to bear directly on certain aspects of navigation.

Let me give an example. The staggered neural layers within the superior colliculus of the mammalian mid-brain provide a basis for combining information about angular displacements of the eye with head-centred position vectors, thereby allowing the animal to map visual and auditory stimuli within a common gaze-centred system of reference (Sparks and Groh 1995). Such coordinate transformations might underlie what Gallistel (1990), in an elegant hypothesis, calls the construction of geocentric maps: the combination of egocentric vectors (specifying the location of landmarks within a body-centred system of coordinates) and geocentric vectors (specifying the animal's position within an earth-centred system of coordinates). Extending O'Keefe and Nadel's (1978) earlier and more informal idea that in mammals the putative cognitive map might reside in the hippocampus, McNaughton et al. (1996) suggest that particular "place cells" and "head-direction cells" of the hippocampus form the neural basis of path-integration. It is also the avian hippocampus, a wedge of neural tissue in the dorso-medial telencephalon (hyperstriatum and accessory areas), that seems to play an important role in spatial orientation. Birds such as food-storers or brood-parasites, which have to meet high demands on spatial orientation and memory skills, exhibit specializations of the hippocampus that are not found in closely related but non-storing and non-parasitic species

(Sherry et al. 1992). Such interspecific differences in neural architectures provide some clues as to the lines along which evolution has worked – but clear-cut evidence is still hard to come by.

Such evolutionary lines might be uncovered more readily in the insect's system of visual navigation, in which various neural subsystems are segregated already at the outermost (retinal) level of sensory processing. The compass systems relying on E-vector gradients (p. 373) and spectral gradients (Wehner 1997) in the sky receive their inputs from two specialized areas in the dorsal parts of the ant's compound eyes. In contrast, the ventral retina and its underlying neuropiles are not capable of handling skylight information. Instead, they are able to record self-induced image flow, and to use perceived image speed for computing distances travelled (Ronacher and Wehner 1995). Finally, it is in the upper part of the visual system bordering on the visual equator that landmark snapshots are taken, and retinotopically arranged spatial memories are formed (Antonsen and Wehner 1995). This modular organization, which holds true also for other visual performances such as the recognition of prey or mate, suggests that various navigational sub-routines discussed for hymenopteran insects have most probably arisen from evolutionary modulations of pre-existing sensory-motor control systems involved in, say, course stabilization or target fixation (Wehner 1994a, Collett 1996, Wehner et al. 1996).

In conclusion, top-down as well as bottom-up approaches lend credence to the notion that systems of navigation consist of numbers of sub-routines each tailored to particular needs and environmental conditions. Often, the methods adopted by the navigator are based on simplifying assumptions that are valid only in particular geographical areas or apply only under certain spatial and temporal conditions, but the navigator's evolutionary design guarantees that these conditions are usually met. Thus, for the time being, the kind of information that is most urgently needed to further our understanding of animal navigation may be obtained more readily from fine-grain local analyses than from global views. Recently such conceptual and experimental programmes in bird navigation have successfully been encouraged and run by Thomas Alerstam and his collaborators (e.g. Alerstam 1996).

Let me close by referring again to human navigation, in which local special-purpose sub routines are used as well. One of the most striking examples is that of the Pacific navigators. Starting about 4000 years ago, several waves of people moved overseas from the Asian mainland into the Pacific and caused what later became known as the Austronesian expansion (Irwin 1992, Bellwood et al. 1995). Among them were the greatest seafarers among Neolithic peoples, the Polynesians, who eventually populated the most remote islands of the Pacific. The kind of non-instrumental navigation

they adopted and used over millennia is still practised in the Central Caroline Islands of Micronesia, where it has recently become the focus of intensive research (Finney 1976, Lewis 1977, Aveni 1981). According to these studies, the traditional Pacific navigators steer by the sun and the stars, even today, but unlike Western navigators, they do not take positional fixes by performing the kind of measurements and computations outlined in Fig. 2A and B. Instead, they employ a dead-reckoning strategy, within which they use the stars as a special kind of sidereal compass (Fig. 10).

This compass consists of the rising and setting positions of the 16 brightest stars in the tropical sky. As these positions do not change over the course of the year, they can reliably be used as the points of a sidereal compass. Furthermore, at the equator the stars rise straight up from the horizon and hence maintain their azimuthal positions at whatever elevation they appear during the course of the night. As a particular star rises (or sets), it will be replaced by another star rising (or setting) at about the same azimuthal position. All the stars that are characterized by about the same rising (or setting) positions form a "star track". These star tracks, rather than individual stars, define the positions of the Polynesian star compass. In higher latitudes any particular star follows an arc that is inclined relative to the horizontal, and its continually changing azimuthal position does not provide reliable compass information. Hence, the sidereal compass is a useful means of navigation only in circum-equatorial areas – exactly where the Polynesians have developed their particular system of navigation.

Using the stars as a compass rather than as a means of performing true astronavigation has another important implication. Compass readings do not provide map

information, but are used by the Polynesians in the context of an egocentric dead-reckoning system. Bound to their self-centred system of coordinates, the Pacific navigators seem to be unable to grasp the concept of a chart. They memorize a list of steering directions (and approximate distances), which connect particular pairs of islands. In the 1770s, when James Cook and Joseph Banks made their famous voyages in the Pacific, they naturally assembled and used nautical maps; but Tupaia, a Polynesian navigator they had taken on board the *Endeavour*, could navigate without such charts (Lewis 1972). "Whatever technique he used", James Cook noted, "he was never at loss to point to Tahiti, his home island, at whatever place we came". In spite of his formidable navigational skills, Tupaia could not make sense of any map that was shown to him. Apparently, the spatial representations he had formed in his mind were completely different from Cook's map-based view of the world. They relied – as we now know – on an egocentric system of reference.

The peculiarities of a surprisingly successful local system of human navigation, as described above for the Polynesian islanders, should caution against any complacent attribution of global, all-encompassing models of computation awarded to animal navigators such as insects and birds. Understanding the minute operational details of an adaptation often casts light on the underlying selection pressures, and vice versa. We can hardly overstate the importance of getting this message across. Animal navigation must therefore be studied within its evolutionary context, with due regard for the historical conditions and evolutionary contingencies that have shaped the survival of organisms over long periods of time.

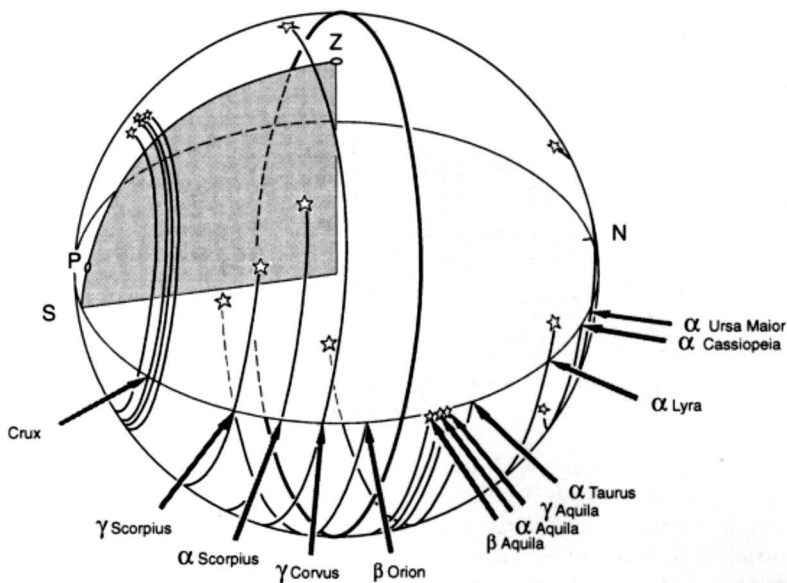


Fig. 10. Sidereal compass used by the Puluwat navigators of the Central Caroline Islands (Micronesia). Twelve out of the in total 16 star paths are shown. The rising positions (marked by black arrows) and setting positions of the brightest stars belonging to particular star paths form the points of the compass. P marks the south pole of the celestial hemisphere; Z is the zenith. Designed on the basis of Goodenough's (1953) data.

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