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Maps in Mind – How Animals Get Home?

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The ability of animals to find their way, without the benefit of mechanical or electronic aids to navigation, has fascinated humans for centuries. Relying on innate knowledge, coupled with the extraction of navigational data from the natural features of the universe, animals continually confound humans with their skills in locomotion. The magnetic compass, sun compass, strip maps, snapshots, target maps, temperature charts and star charts are known to feature in the overall animal navigation kit. Each species selects the most appropriate 'map/chart' and navigation kit for its environment.

KEY WORDS

1. Animal Navigation. 2. Dead Reckoning.

1. INTRODUCTION. In this age of automation, satellite navigation systems and advanced communication systems, with the ability to determine and maintain

position to sub-metric accuracy, it is salutary to reflect on the remarkable ability of animals to navigate without help from mechanical or electronic devices. How animals do this has engaged world-renowned experimental biologists in life long challenges. Now aided by the technological developments so warmly embraced by human navigators, the biologists continue to discover how animals find their way to the nest, the burrow or to a good foraging area.

To an air navigator, an all-encompassing definition of navigation is 'the art or science of carrying out the movement of a craft, a person or another living creature from one place to another on, above, or below the surface of the Earth'. It therefore embraces two terms used by biologists: 'homing' meaning an animal returning to its nest or burrow etc., and 'path integration' meaning dead reckoning.

Does an animal have access to any aids to navigation? We know with certainty that an animal does not have access to a satellite position location system such as the Global Positioning System. Nor does an animal have access to a Flight Management System that carries out automatic dead reckoning and acts as a multi-sensor data fusion system. An animal does not even have access to an old-fashioned astro compass to check direction or a periscopic sextant to check position. But an animal does have access to the natural features of the universe.

2. NATURAL FEATURES OF THE UNIVERSE.

2.1. *Visual observation of the Earth*. The type of feature that is likely to appeal to a migrating animal is a line feature such as a coastline or a major river, both of which were used by air navigators as position lines in the days before automated systems. A bird looking vertically down at the surface itself should be able to determine drift over the ground. And the depression angle of a point on the ground plus height, or the subtended angle of a feature, will give the distance from the point or feature.

2.2. *Visual observation of the Stars and Planets*. The position of the Sun in the sky can provide direction. At 12 o'clock local time the Sun is due south of an observer located at a latitude north of the Tropic of Cancer; the converse is true for the southern hemisphere and the Tropic of Capricorn. At the vernal equinox and also at the autumnal equinox, which are good dates for bird migration, the Sun rises exactly due east and sets exactly due west everywhere in the world. Should there be cloud present, polarized light will reveal the direction of the Sun. The actual pattern of constellations in the sky provides direction and prolonged observation of the sky at night results in circles of light, the origins of which indicate the direction of the earth's axis of rotation.

2.3. *Magnetism*. The horizontal magnetic force gives direction relative to magnetic north. There is a second feature of the Earth's magnetic field, termed field line inclination. Magnetic field lines intersect the Earth's surface at a specific angle ranging from 0° at the geomagnetic equator to 90° at the geomagnetic poles. Animals able to detect these magnetic field lines would have an approximation to latitude.

2.4. *Gravity*. Gravity determines which way is up and thus offers a navigational reference line for angles in the vertical plane.

2.5. *Atmospheric pressure*. Relative and differential atmospheric pressure each assists the navigational problem, including the determination of speed, height, cross wind component and wind velocity.

2.6. *Inertia*. The earth is a spinning gyroscope. An animal able to detect this rotation, plus the direction of gravity, would have the essential elements of an inertial navigation system.

2.7. *Olfaction*. The sense of smell enables us to tell when we pass a brewery or a sewage works – though if blindfolded it is difficult to say which brewery and which sewage works. However, if the smell associated with the nest or burrow is very distinct and familiar, olfaction could play a part in the homing process.

2.8. *Infrasound*. Oceanic waves generate low frequency noise, which is radiated from steep-sided topographical features at long range. It has been suggested by a geological researcher that pigeons may have a stored acoustic map that could be used for navigation.

3. ANIMAL SENSORY PROCESSING. The ability of animals to exploit the natural features of the universe to locate 'home' and foraging areas, to make use of cognitive maps and landmarks, to determine dead reckoning position and to carry out long-range migration will now be illustrated by reference to specific animal species. As dead reckoning is at the heart of any integrated navigation system, it is appropriate that a desert ant, noted for its prowess in dead reckoning, should be the first animal to be considered. This will be followed by bees, pied flycatcher, monarch butterfly, plaice, salmon, aquatic warbler, Clark's nutcrackers, turtles, petrels and pigeons.

3.1. *Desert ants* (*Cataglyphis bombycina*). Desert ants roam far and wide from their nest over undulating desert to forage for food amongst low scrub bushes. The navigational techniques used in their foraging have been subject to rigorous controlled experiments at a special desert ant test site located at Muharès (34°58′N 10°50′E) near Sfax in S.E. Tunisia. The desert ant performs dead reckoning using a simple computer, the start position always being the location of the ant nest. Inputs to this computer are distance taken from a device analogous to an accumulator or odometer, and heading from a sun-compass on sunny days and from a polarized light compass on cloudy days. That ants used a sun-compass for direction was first discovered by Professor Karl von Frisch in 1967. Verification tests have been conducted to determine the ability of a desert ant to perform true dead reckoning procedures. The first test was designed to check whether a desert ant could measure the true horizontal distance when walking in undulating terrain. This involved the construction of an array of uphill-and-downhill channels (Figure 1(a)), within which desert ants were trained to walk for certain specific distances. When later tested within a flat, horizontal channel, the ants covered a distance equivalent to the true horizontal ground distance of the up-and-down trackway, leading to the conclusion that desert ants can sense the angle of slope, as well as distance and orientation.

The second test was a displacement test. As early as 1904, Professor Henri Pièron was able to confirm the ability of ants to perform path integration (Figure 1(b)). First, he displaced a foraging ant at Point A and released it at Point B. The ant immediately started to walk parallel to its outbound track and maintained this track until it intercepted a familiar track at Point C. It then returned to the nest. The test was repeated with the ant returning home on unfamiliar ground. The ant continued to its calculated dead reckoning position of the nest and then started searching at the point where the original dead reckoning track would have reached the nest.

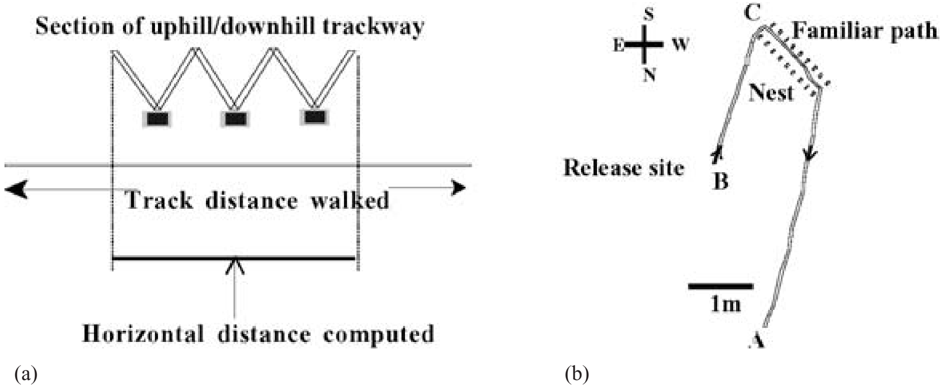

Figure 1. (a) Measurement of distance. (b) Displacement test.

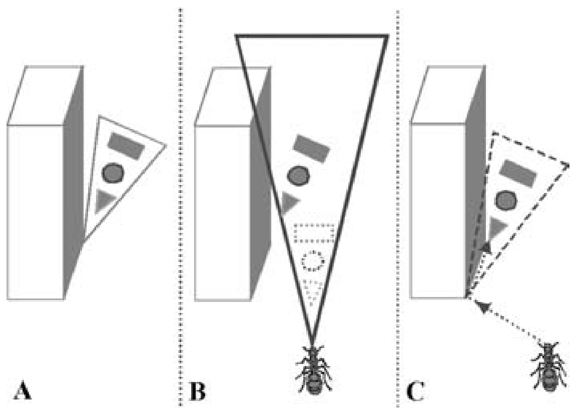

Figure 2. Map-matching (view-based) navigation technique.

Ants, like bees and wasps, use visual landmarks for defining the position of their nests and the location of foraging areas. Stored in a memory bank and accessed by the forward lenses of the compound eyes, ants manoeuvre to achieve a match between the observed image and the stored image. Figure 2 illustrates the technique of map-matching (view-based navigation). The stored image is shown in Section A. In Section B the ant recalls its stored image – dotted images – and sees the actual images in solid lines. To achieve a map-match (Section C), the ant moves closer to and along the wall as shown by the dashed line. Experienced ants, i.e. ants that had made the route a number of times, learned how to cut corners and so speed-up the matching process.

3.2. *Honey bees* (*Apis mellifera*). 'Scout' workers in a bee colony seek out sources of food, namely pollen and nectar. Once they have located a good supply of food, they return to the hive. Soon after their return, 'forager' workers may be seen leaving the hive and flying directly to the food. As the scout workers have been known to stay in the hive for several hours, they must have communicated to the foragers sufficient information for them to find the food on their own. It turns out that the scouts convey to the foragers information about the odour of the food, some of which is attached to their legs, its direction from the hive and its distance from the hive.

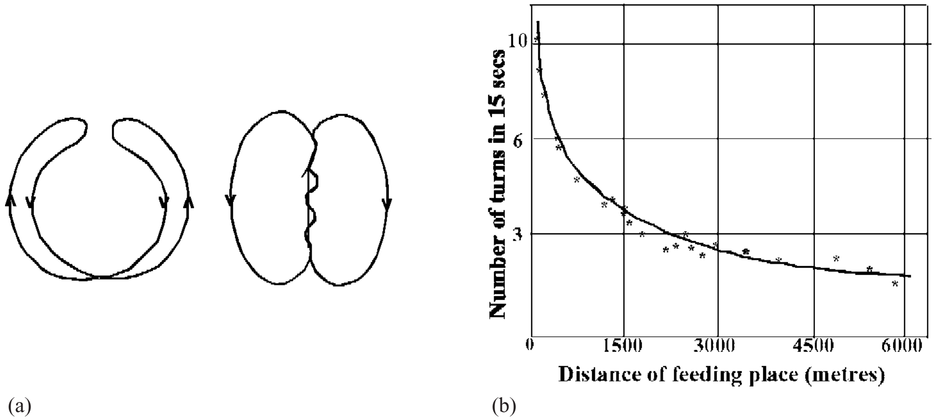

Figure 3. (a) Bee dances. (b) Relationship turns: distance.

Professor Karl von Frisch discovered that a number of special dances are used to convey the navigational information on the location of nectar to forager worker bees, two of which are now considered. When food is within 50–75 metres of the hive, the scouts dance the 'round dance' on the surface of the comb (Figure 3(a) Left). But when the food is farther than 75 metres from the hive, the scouts dance the 'waggle dance' (Figure 3(b) Right). The waggle dance has two components:

(a) A central straight run – the direction of which indicates the angular measurement of the food location relative to the Sun. On this straight run the dancer vigorously vibrates (waggles) her abdomen back and forth laterally and emits strong substrate and airborne vibrations in addition to audible buzzes. This buzzing is produced by the flight muscles and has a frequency range between 200–300 cycles per second. The direction of the straight run is corrected for changing azimuth of the Sun, i.e. for clock-shift.

(b) The speed at which the dance is repeated indicates the distance of the food from the hive, (Figure 3(b)). Bees have two compound eyes and three simple eyes. These give little information about depth but are very sensitive to 'flicker effect'. Bees use this motion of images received by their eyes as they fly to measure distance.

The importance of 'flicker effect' has been demonstrated by training honeybees to visit food placed on cards with patterns (see Figure 4(a)). For example, bees can distinguish any figure in the top row from any figure in the bottom row more easily than they can distinguish between any of the figures in either row. To test that bees use the 'flicker effect' to measure distance, a team at the Australian National University, built three tunnels (Figure 4(b)). The interior walls of the tunnels were decorated with patterns to create flicker. The bees were first fed in the middle of Tunnel 1 of standard diameter. Then the food was removed. Using the same tunnel, foragers came to the same spot in the tunnel. Using the narrower Tunnel 2, foragers began searching for food near its entrance. Forced to fly closer to the vertical stripes, the images moved by faster. Using Tunnel 3 with a larger diameter, foragers searched for food at its far end. Flying farther from the stripes, the images moved by more slowly. Thus a foraging

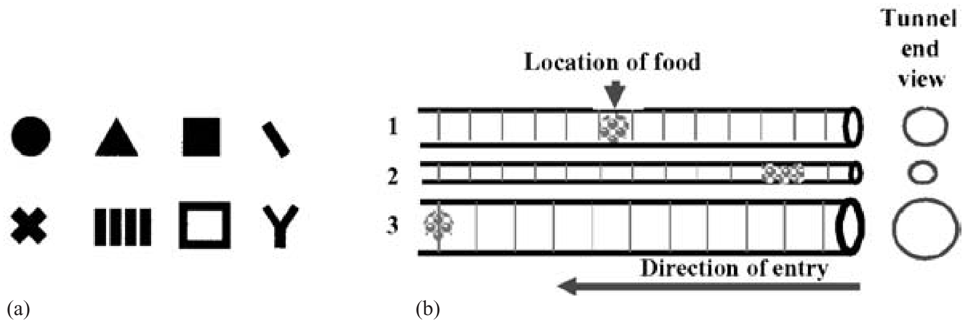

Figure 4. (a) Flicker patterns. (b) Tunnels to test 'flicker effect'.

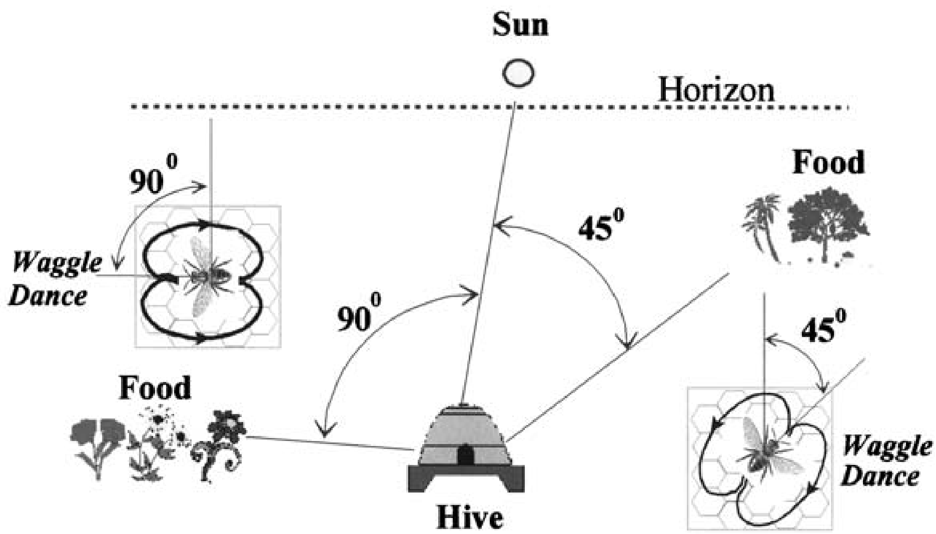

Figure 5. Interpretation of the 'waggle dance'.

worker bee is given a 'flight-plan' bearing and distance to go to the foraging area. Once embarked on the journey, which for some bees and wasps could be in excess of 10 km, a dead reckoning track made good can be maintained using observed direction from the Sun and distance from the 'flicker effect'.

The question then, is does the bee have a spatial map to update the dead reckoning track? Tests indicate that bees like ants store landmarks. We know that all landmarks are referenced back to the hive and may be regarded as a set of disconnected strip maps radiating from the hive. These strip maps provide the information required for positional updates. But, to the best of my knowledge, there is no evidence to support the idea that a bee has a complete topographical map stored in its head. Figure 5 shows how the foraging worker bee uses the information conveyed to him by the scout worker through the waggle dance on the surface of the comb. The food at the left of the figure is 90° to the left of the Sun's azimuth and the food at the right of the figure is 45° to the right of the Sun's azimuth. Distance of the two food supplies would be obtained from the speed of the dance on the front of the comb.

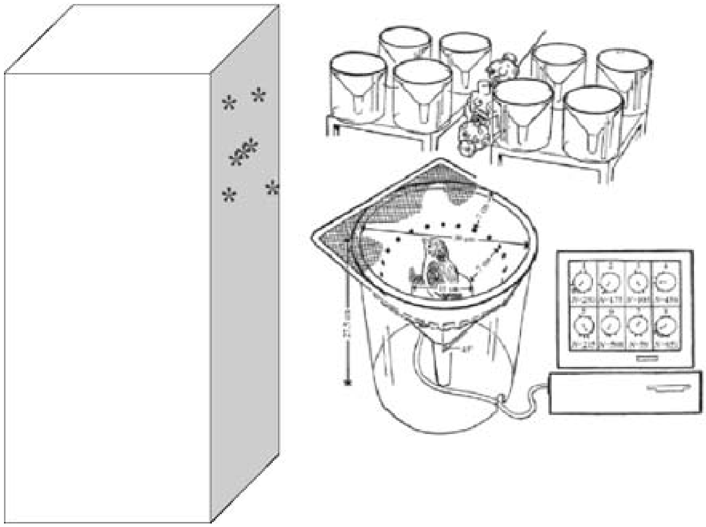

Figure 6. Computer-controlled version of Emlen funnel in a planetarium.

3.3. *Pied Flycatcher* (*Ficedula hypoleuca*). The pied flycatcher is a night-migrating bird. It is therefore reasonable to assume that the bird uses the night sky as an aid to navigation. But how? Do pied flycatchers recognize the pattern of stars constellations? Do they, like Boy Scouts, determine direction from the constellation Orion, conveniently placed for migration southward? Or from the Great Bear/The Plough conveniently placed for migration northwards? Or do they watch the sky for a long period and observe circles of light, the focus of which is the axis of rotation?

It was noted in 1949 that the migratory urge of passerines is so strong that at the time of migration birds will jump in their migratory direction. This led Professor Stephen Emlen in 1960 to develop the Emlen funnel. He placed migrating indigo buntings in the funnels lined with white plasterboard under starry skies (the modern equivalent is to use typewriter correction paper). Emlen noted that the indigo buntings (*Passerine cranea*) left most of their ink marks on the sides of the funnels pointing in the direction of their migratory path. Under overcast skies, however, the ink markings were randomly spread throughout the funnels, indicating the birds' inability to determine direction.

When Emlen brought his cages into a planetarium, the birds performed as if outdoors, using the projected star patterns to determine their direction. When he reversed the sky 180 degrees – turning the projector so the northern sky became south, and the southern sky was now north – the buntings changed their orientation by 180 degrees.

A research team from Odense University Denmark, intent on determining how pied flycatchers actually use the information from stars, developed a computer-controlled version of the Emlen funnel (Figure 6). First, they showed that like Emlen's indigo buntings the birds use a star compass. Then, further tests showed that birds use a time-independent star compass based on learned geometrical star configurations to pinpoint the rotational point of the starry sky (north). This is analogous to a human orientating a map to the direction of travel. There was no evidence to suggest that pied flycatchers could perform true astro navigation. Neither was there evidence to suggest the use of a time-compensated star compass. As a footnote, Professor W. Wiltschko determined

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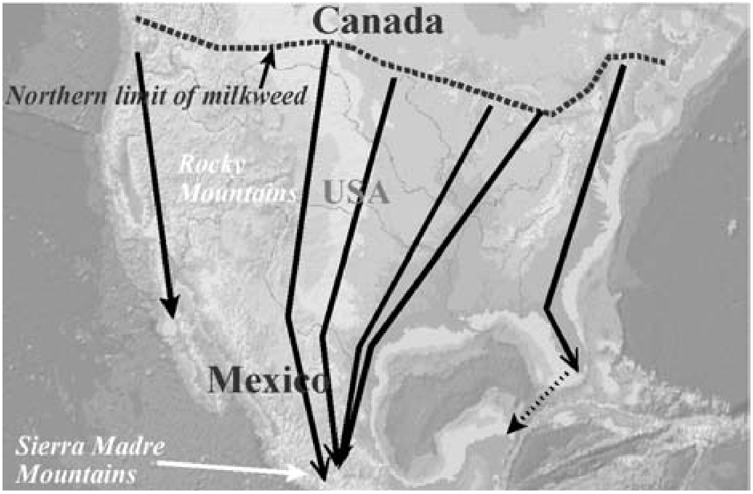

Figure 7. Autumn migration routes of the monarch butterfly.

in 1976 that young nocturnal migrants must orientate and calibrate their celestial compass to an innate magnetic compass. He also led a team in 1981 which found that birds using a sun-compass must also calibrate it to the innate magnetic compass.

3.4. *Monarch butterfly* (*Danaus plexippus*). In all the world, no butterflies migrate like the monarch butterfly of North America. They are of medium size – about 7 cm in wingspan – and they travel up to three thousand miles, which is much farther than all other tropical butterflies. Amazingly, they fly in masses from the Northern USA and Canada to the same winter roosts in Mexico, often to the exact same trees. Their migration is more the type we expect from birds or whales. However, unlike birds and whales, individuals only make the trip once. It is their children's grandchildren or great grandchildren that return. The majority of monarchs from the east side of the Rocky Mountains over-winter in the Sierra Madre mountains of Mexico, but those from west of the Rockies over-winter in groves of Monterey pines or eucalyptus trees at sites along the California coast, from San Francisco to Los Angeles.

It was not until 1975 that an over-wintering site was found in the Sierra Madre Mountains of Mexico. Now tour groups visit to see tens of millions of butterflies at 12 sites, the density being an estimated 4 million butterflies per acre. The monarchs simply hang on the Oyamel trees throughout the winter months at about 3000 m elevation. One interesting fact about the location in the Sierra Madre mountains is that the magnetic readings near the centre of the main over-wintering areas is 100 times higher than normal.

The monarchs move north and south with their favourite source of nectar – the milkweed, a wild flower associated with prairies and relatively dry areas. How do the monarchs navigate? They do not fly from Canada and New England to Mexico flapping their wings all the way. They certainly take advantage of thermals to gain height and then convert this height into distance by gliding. As far as direction is concerned, a sun-compass has been demonstrated in every animal, vertebrate or invertebrate that has ever been tested. And researchers have evidence that monarchs change orientation with the Sun's changing azimuth during clear days – in other words they have an in-built clock (Figure 7). Monarchs also fly by night and when it is

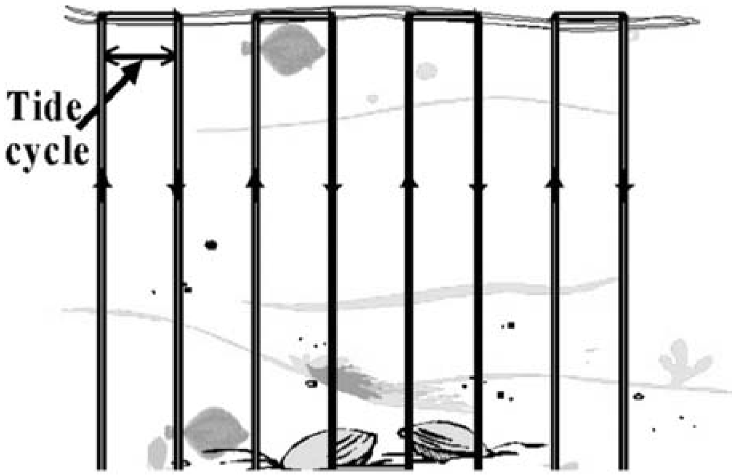

Figure 8. Plaice sensing the tidal flow.

cloudy. Particles of magnetite are located in the thorax of a monarch and it is believed that they use a magnetoclinic system similar to that suggested for birds. In effect this direction is the projection of the true magnetic dip on a plane vertical to the direction of heading.

We are discussing a butterfly that weighs no more than a few grams. So we cannot strap a GPS collar around its neck. Instead, hordes of them are marked with a lightweight tag mounted on the centre of gravity. In 1997, students at one single school – Wamego (Kansas) High School – tagged an amazing 12 397 monarchs.

Next, there are observers across the USA who are prepared to track individual butterflies from the overhead position to the point where they vanish from sight and to record the data in a particular format. This data is then fed into a computer at Kansas University to provide mean track directions across the USA. But that is not the end of it. Individual researchers on land and in boats monitor and record when monarchs fly, sun or no sun, tail-wind, head-wind or no wind, willingness or reluctance to cross the coast. Similarly, whether they fly high or low, along the lee or windward side of mountains or over the top. From all the data available on the monarch butterfly, it would appear that the monarch has a hybrid navigation system, the key elements being a compensated sun-compass, a magnetic compass, and a means of determining the wind component. There is no evidence to support the use of spatial maps.

3.5. *Plaice* (*Pleuronectes platessa*). I turn now to a fish – the plaice. Plaice in the North Sea have feeding grounds in the vicinity of the Dogger Bank. While feeding in this area, they tend to stay near the seabed by day, rising occasionally at night. But in November and December, they have been observed by scientists at Lowestoft to migrate towards their spawning grounds in the Southern Bight and eastern English Channel, a distance of about 300 km. To monitor the movement of the plaice, scientists attached acoustic tags to a number of plaice and tracked them using a research vessel's sonar. They also attached data logs to some plaice, which fishermen turned in for a reward. The monitoring revealed that plaice were able to sense the tidal streams (Figure 8), rising towards the surface when the tidal flow was towards the south and settling back on the seabed when the tidal pattern reversed. The directions followed

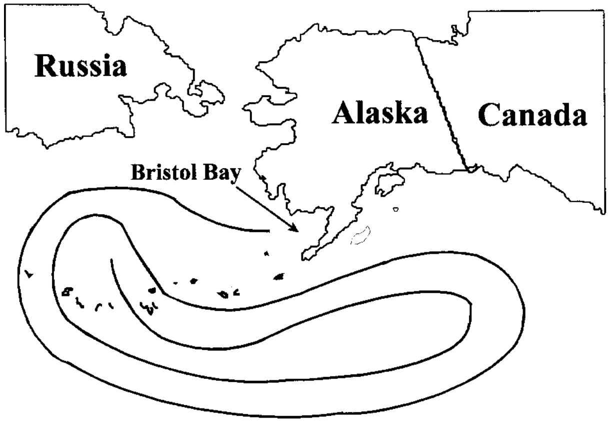

Figure 9. Alaska Gyre.

by the plaice showed a remarkable correlation with the mean direction between the Dogger Bank and the spawning grounds, as did the correlation between the tidal pattern changes and the depth of the plaice. Moreover, the sum of the tidal streams was less than the distance between the Dogger Bank and the spawning grounds, showing that the plaice actually swam towards their goal, i.e. they navigated.

3.6. *Salmon* (*Salmo salar*) *and Sea trout* (*Salmo trutta trutta*). Salmon navigation is one of the marvels of nature. While we do not know all the answers, a number of mechanisms appear likely. Highest on the list is the location of receptors sensitive to local differences in the earth's magnetic field and to observation of the Sun and stars. It is known that salmon do not follow meandering paths back to their natal river to answer the spawning instinct. They travel directly to their spawning grounds by the most direct route when sexual maturity occurs. As salmon near the coast and enter river estuaries, they are guided by a chemical memory – an olfactory imprint – that was made on smolts as they left their home stream. This allows them to recognise and home in on substances such as pheromones present in the water in very minute traces.

The Alaska Science Forum states that sockeye salmon leave their freshwater origins in the streams entering Bristol Bay and make their way to the Alaska Gyre (Figure 9) in the North Pacific and western Bering Sea. They then complete one or several circumnavigations of the gyre before starting their spawning migrations back through the Aleutians. The migration pattern is abruptly interrupted at any point in the circuit where the fish may find themselves when they attain the sexual maturity which induces spawning. There are no road signs pointing out the way back to their stream from the open ocean, so the fish must have some internal 'map sense' by which to navigate.

Salmon are remarkably perceptive of the Sun's azimuth and altitude, and are sensitive to the time of day. Under ideal conditions, this would permit a method of determining geographic north. But in a region where overcast conditions predominate (as they do in the North Pacific and Bering Sea), and because the fish move at night and in deeper water during the day, a second navigational system is required. It has been demonstrated that salmon fry will change their orientation when subjected to an artificially applied magnetic field; therefore it is likely that the earth's magnetic field will play some part in the navigation process. The magnetic field may influence a fish's

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nervous system in two ways. First, the ferromagnetic mineral magnetite in the creature's brain may function as a biological compass which is 'set' at the time of entry into the ocean. Secondly, the vertical and horizontal components of the earth's magnetic field may be stored at that point, and the declination of the horizontal component, which is the difference between magnetic and true north, presumably determined by the Sun. These factors taken together provide a combination that is unique for any geographic location.

Researchers have long been aware that magnetite existed in salmon and salmon trout, but they had not located magneto-receptors in the olfactory nerve area that could be traced along a nerve to the brain. At least, not until scientists at Auckland University traced the neural network from grains of magnetite along a branch of the trigeminal nerve that runs behind the eye to the brain in salmon and sea trout. This branch innervates much of the 'face' of the fish. Extrapolating all of these findings to the migration process, the likelihood is that, after the salmon fry have grown to smolts and entered salt water, chemical and hormonal changes occur that imprint upon the fishes' nervous system a 'memory' of its magnetic latitude and longitude at the time that it enters the ocean. When the spawning urge occurs, the salmon's computer has its present magnetic position and its home magnetic position. The Sun or stars, if available would provide confirmatory information.

3.7. *Aquatic warbler* (*Acrocephalus paludicola*). The Aquatic warbler rates a mention if only because it introduces a new scientific technique. Scientists anxious to track the movements of this bird – a globally endangered species chiefly confined to Eastern Europe – say atomic analysis of its feathers may reveal its migration route. They are concentrating on a study of stable isotopes – atoms of the same type but with different masses – and trace elements in the birds' feathers.

The warblers breed mainly in Poland, Belarus and Ukraine, with smaller numbers in Lithuania and Hungary. Much of Eastern Europe has lost key bird habitats since 1945, largely because of drainage schemes. Ornithologists think there may be some unknown breeding populations, possibly in Siberia. The birds are believed to winter in the wetlands of West Africa south of the Sahara desert.

When this story was posted on the RIN animal forum, Dr Anders Hedenstrom of Lund University, Sweden, commented that in 1987 he and three friends were ringing birds at Navrongo, N. Ghana. He went on to say that on 15 November the team caught an aquatic warbler in a suitable habitat. Since aquatic warblers are quite rare in the breeding range, the population density in their wintering grounds is presumably also quite low which he thought might explain the scarcity of wintering records.

3.8. *Clark's nutcrackers* (*Nucifraga columbiana*). In the breeding season, Clark's nutcrackers live at high altitude (2000 to 3000 m) in the Rocky Mountains. Beginning in about mid-July these birds start to collect conifer seeds, which they bury in caches of 1–20 seeds, about 3 cm below the surface, and in crevices. Researchers have calculated that each nutcracker buries between 7000 and 22 000 seeds, depending mainly on the cone crop size and length of the season. From about mid-February, the nutcrackers use spatial memory to relocate and retrieve the large number of food caches. In effect, the spatial map (Figure 10) is based on the relationship of caches to nearby, relatively large objects (e.g., rock, log, tree). Thus, only the caching bird has sufficient information for retrieval. When recovering a particular cache, the nutcrackers tend to approach from the same direction as they used when creating the cache. However, when they approached from a different direction, the cache was located with equal

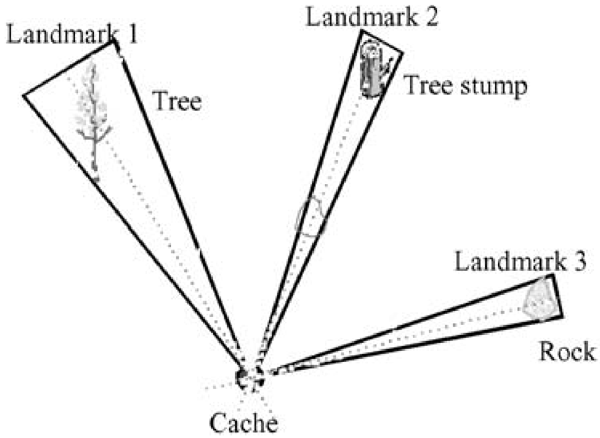

Figure 10. Use of multiple landmarks to locate a cache.

accuracy. The results of several studies indicate that the nutcrackers use multiple landmarks and directional information to relocate food caches. The same studies confirmed that nutcrackers used neither dead reckoning nor snapshots.

3.9. *Loggerhead turtle* (*Caretta caretta*). I now turn to the long distance traveller called the loggerhead turtle, which frequents the Atlantic and Pacific oceans. Loggerhead turtles have a remarkable start to life. All hatch on the same night, are programmed to go downhill and to swim for 24 hours. This is to ensure that they reach the ocean as soon as possible and get away from the many predators on or near the shore. If you pick up one of these baby turtles and put it into a bucket of seawater, the young turtle will start its 24-hour swim.

A team from the University of North Carolina recently reported that when young loggerhead turtles (*Caretta caretta*) were placed in a magnetic field that corresponded to a particular location on the North Atlantic gyre, they would swim in the appropriate direction. This was despite the fact that the young turtles in the experiment had just hatched and had not yet been to sea. The gyre forms a huge circular ocean current, moving clockwise from the US East Coast, across the North Atlantic and then south along the coasts of Spain and Africa, before turning west to complete the circle. Baby loggerhead turtles swim out into this current and flow with it, nudged along by warm waters rich in food. Their migration, lasting for years, carries them on an 8000 mile path around the Atlantic Ocean. If they leave the gyre, the turtles die, killed by the surrounding frigid waters.

Pacific Ocean loggerhead sea turtles have one of the most interesting developmental migrations of all marine turtles (Figure 11). Hatchling loggerheads emerge on the eastern coast of Asia and make a transoceanic migration to developmental habitats on the opposite shores of the ocean. For example, those hatching on nesting beaches in Japan leave those waters as 3·5 cm long turtles and swim to the west coast of North America. There they reside for an unknown number of years, before leaving to return to Japan when about 40 cm (carapace) in length. While this developmental scenario was suspected for the Atlantic basin for some time, it was only when Hubb's Sea World took DNA samples in the late 90's that identification of loggerheads in the Pacific indicated that turtles captured off the coast of California and those taken by commercial longliners operating from Hawaii, were of Japanese origin.

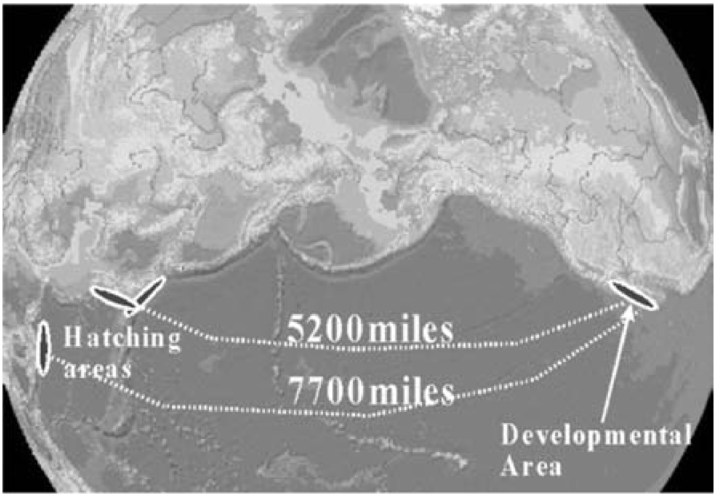

Figure 11. Migration of Pacific loggerhead turtles.

In 1996 *Adelita*, a long-term captive, was released from San Diego, equipped with a satellite transmitter, and was tracked back to Japan over a period of 14 months (J. Nichols). A preliminary analysis of data suggests that the turtle navigated by using a combination of magnetism and tracking a mean surface isotherm to navigate. It is interesting that the last section of the route into Japan was carried out at relatively high speed – not thanks to *Adelita*, but to Japanese fisherman who were taking her home on board a trawler.

Three loggerhead turtles that had been in captivity for 20 years were released into the Pacific Ocean on 1 October 2000. They were equipped with satellite transmitters that transmitted position and surface temperature. Members of the RIN animal forum followed their progress month by month up to September 2001, by which time two turtles had reached Japan. *Mihali* the slowcoach who hung around a good jellyfish feeding area (the seamounts) reached Japan in May 2002.

3.10. *Nocturnal petrels* (*Order Procellariiformes, birds*). Many burrowing petrels return to their nesting burrows in complete darkness. They have the largest olfactory bulbs among birds, leading researchers to think that a sense of smell played some part in their homing skills. Although several experiments in 1999 and 2000 provided evidence that some species of petrels are attracted by food-related odour cues, other members of the *Procellariiformes* families – notably albatrosses – are not so attracted. A team from the French National Centre of Scientific Research (CNRS-CEFE), under Dr F. Bonadonna, recently conducted tests to examine the role of olfaction in burrow recognition by nine species of petrel with different nesting habits (burrowing, crevice-nesting and surface-nesting). They concluded that nocturnal petrels appear to rely mainly on their sense of smell to find their nests, while diurnal petrels appear to disregard olfactory clues, preferring to rely on visual clues. The nocturnal petrels use a strong generic petrel odour issuing from the colony to localise the colony position. As most petrels were able to land in close proximity to their actual burrow, the researchers suggest that the returning petrels first localise the colony, then change the homing strategy to one of following the specific odour of their burrow. Further tests are required to prove this point.

3.11. *Pigeons*. Dr Hagstrum of the US Geological Survey reports that some species of pigeons can hear infrasound down to 0·05 Hz, a couple of orders below the hearing level for humans. He proposes an avian acoustic map consisting of infrasonic cues radiated from steep-sided topographical features. The source of the infrasonic signals is microseisms continuously generated by interfering oceanic waves.

4. CONCLUSION. Throughout this paper, reference has been made to snapshots, landmarks and multiple landmarks. Collectively, these amount to memorized visual panoramas. The key question is whether these visual panoramas qualify to be termed as spatial memory or spatial maps.

Maps used by humans are available in many formats. Physical, political, geological, environmental, and outline, readily spring to mind. So when we consider whether animals other than humans use spatial maps, we should not be surprised if they use map formats with which we are not familiar. Like military aviators, animals maintain a general plot using some or all of the basic navigation techniques, such as dead reckoning, magnetism, and observation of the stars and planets. And they refine their position by using their own stored strip maps and target area maps.

Humans can recall accurately the layout of their home and garden. They can recall less accurately the layout of their neighbour's house and garden. As they get further from their home, humans recall only landmarks and precious little detail between landmarks. There is one significant difference between humans and other animals. Most humans can be given a map and can navigate precisely to a designated spot. But, of course, someone must have been to that spot before in order to draw up the map. We should bear this in mind when we reflect on the monarch butterfly migrating from Canada to Mexico and a cuckoo chick navigating from Europe to Africa after the parent has departed, both using only the innate knowledge stored in the brain. Does that stored knowledge qualify to be termed a spatial map or spatial memory? I leave you to decide.

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