

LABORATORY STUDIES OF HOMING ORIENTATION IN THE EASTERN RED-SPOTTED NEWT, *NOTOPHTHALMUS VIRIDESCENS*

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SUMMARY

The orientation behaviour of adult male eastern red-spotted newts (*Notophthalmus viridescens*) was studied in laboratory tests. Newts were collected from ponds located 10–30 km from the laboratory, and housed in water-filled, all-glass aquaria located in a greenhouse or outdoors adjacent to the laboratory building. The aquaria were aligned on the magnetic north–south axis. Newts were tested in a dry, enclosed arena in four magnetic fields: the ambient magnetic field (magnetic north at North) and three altered fields (magnetic north rotated to East, West or South). Newts tested during January–March exhibited weak *bimodal* magnetic orientation along the axis of the holding tank. However, during the spring migratory period (April until early May), the bimodal response shifted to coincide with the direction of the pond from which the newts had been collected. Much stronger *unimodal* orientation was elicited by elevating the water temperature to 33–34°C immediately prior to testing. If newts were held in a training tank with an artificial shoreline at one end and exposed to elevation of water temperature after several days of stable water temperatures, they exhibited unimodal shoreward orientation and did not show the seasonal switch to homing behaviour observed in the earlier tests. If, however, the elevation of water temperature followed a period of fluctuating water temperature (over a 20°C range), the newts exhibited strong unimodal orientation in the direction of the pond from which they had been collected. These results suggest that newts possess a navigational system that enables them to home from distances in excess of 20 km. Moreover, these experiments provide the first opportunity to examine the sensory basis of navigational ability in any animal under controlled laboratory conditions.

INTRODUCTION

True navigation, defined as homeward or goalward orientation in the absence of familiar landmarks or goal-emanating cues (Griffin, 1952), has been demonstrated in relatively few species, primarily birds (for a review see Able, 1981). However, navigational ability is thought to be important in a variety of vertebrates that migrate

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over very great distances (e.g. salmon, Quinn & Groot, 1984; Quinn, 1982; sea turtles, Carr, 1964). Moreover, a few studies have provided evidence for navigational ability in cold-blooded vertebrates whose movements encompass at most a few kilometres (Twitty, Grant & Anderson, 1966; Rodda, 1984a,b, 1985). Thus, navigational ability appears to be widespread in vertebrates. Until the present study, however, evidence for true navigation had only been obtained under natural or semi-natural field conditions where directional cues thought to underlie the navigational map and environmental factors suspected of playing a role in triggering homing orientation were difficult to control. The present study provides evidence of true navigation in male eastern red-spotted newts (*Notophthalmus viridescens*) under controlled laboratory conditions. The orientation behaviour of adult male newts was studied in an enclosed indoor arena after displacements of 10–30 km from their home pond. These experiments made use of the fact that this species will orient using an earth-strength magnetic field as a directional cue (Phillips, 1985, 1986).

The eastern newt is widely distributed in the eastern United States (Conant, 1975). Its eggs are laid on submerged vegetation in still water, and larvae remain fully aquatic for several months after hatching. At the end of the larval period, the larva metamorphoses into a terrestrial juvenile stage, the red eft. The eft stage may last for as long as 5–8 years, during which the newt is an inhabitant of the forest floor. At the end of the juvenile period, the eft undergoes a second transformation and returns to the water as an adult; most return to their natal pond, while 20–30% are recaptured in ponds 1–2 km away (Gill, 1978, 1979 and personal communication; Healey, 1973, 1974). Although adult newts are normally aquatic, they may leave the water seasonally to avoid extreme temperatures (Gill, 1978 and personal communication). The movement of adults to and from ponds occurs primarily during two migratory periods of 4–6 weeks in the spring and autumn (Hurlbert, 1969; D. Gill, personal communication). However, there is no evidence that adults move between ponds. Most adults return to their home pond, even if displaced to another pond with a viable population of newts (Gill, 1979).

Field observations have shown that newts respond to elevated water temperatures by leaving the water and seeking shelter in cooler microhabitats on shore (D. Gill, personal communication). In laboratory experiments, elevation of training tank water temperature just prior to testing caused newts to exhibit strong unimodal magnetic orientation in the direction of an artificial shoreline (Phillips, 1985).

MATERIALS AND METHODS

Training procedures

All experiments were carried out at Liddell Laboratory, Cornell University, Ithaca, New York.

Test series I

Groups of adult male newts were collected in September. One group was collected from a pond located 20.5 km east (100°, all directions are magnetic) and a second

group from a pond 27 km southwest (230°) of the laboratory (E group and SW group, respectively). The newts were transported to the laboratory in 2-l translucent plastic containers filled with 10 cm of pond water. The plastic containers were placed inside a styrofoam cooler that admitted only diffuse light and were transported by car. The newts were maintained in water-filled 110-l all-glass aquaria ($30 \times 45 \times 90$ cm) aligned along the geomagnetic north–south axis, located in a greenhouse attached to the south wall of the laboratory building. These tanks were featureless, except for a weak current generated by an external filtration system that flowed along the long axis of the tanks from north to south.

In test series I, each group of newts was tested repeatedly at approximately 1-week intervals from January until May. A given individual was tested only once in each test. The testing format (described below) ensured that if individual newts failed to make a new assessment of direction relative to the magnetic field in each test, this would only *increase* the scatter in the pooled distribution of magnetic bearings.

Test series II

In September and October, new groups of newts were collected from two ponds located 20.5 km east (100°) and 21.5 km southeast (125°) of the laboratory. Newts from these two ponds were combined and designated the E groups for testing. The mean direction of the two ponds (113°) was used as the expected home direction. Additional groups were collected from the two easterly ponds and from a pond located 12 km south (190°) of the laboratory (S groups) in the spring and summer of the following year. Prior to being placed in specially designed training tanks (Fig. 1 and see below), the groups of 30–60 adult male newts were maintained in aquaria aligned along the north–south axis with shelter at the north end. Tanks were located

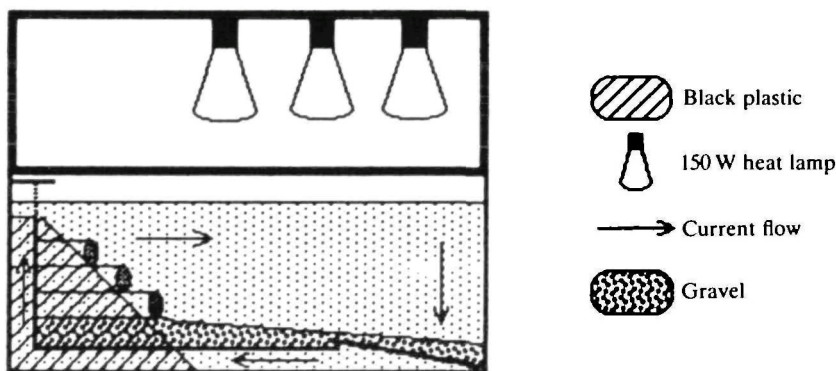


Fig. 1. Training tank design (from Phillips, 1985). Training tanks used in series II consisted of 110-l, all-glass aquaria with one end partially enclosed in black plastic. Four rows of progressively shorter 5-cm diameter plastic tubes provided an artificial shoreline at the enclosed end. The bottom of the tank was covered with coarse gravel that sloped up towards the shore. Heat lamps (150 W) located above the tank were used to elevate water temperature. An air-driven circulation system prevented a thermal gradient from forming, and produced a current flowing from the shallow to the deep end of the tank.

group from a pond 27 km southwest (230°) of the laboratory (E group and SW group, respectively). The newts were transported to the laboratory in 2-l translucent plastic containers filled with 10 cm of pond water. The plastic containers were placed inside a styrofoam cooler that admitted only diffuse light and were transported by car. The newts were maintained in water-filled 110-l all-glass aquaria ($30 \times 45 \times 90$ cm) aligned along the geomagnetic north–south axis, located in a greenhouse attached to the south wall of the laboratory building. These tanks were featureless, except for a weak current generated by an external filtration system that flowed along the long axis of the tanks from north to south.

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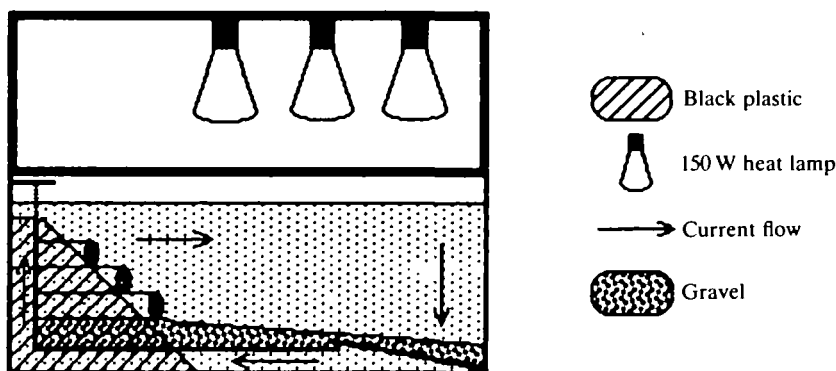


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in the greenhouse or, during the warmer months, outdoors adjacent to the laboratory building.

Approximately 1 week prior to testing, a group of newts was placed in a training tank aligned on the north-south axis (Fig. 1). On the day of testing, a bank of 150-W heat lamps (3-5, depending on air temperature) was turned on in the morning (06.00-07.00 h, Eastern Standard Time). Testing was initiated once the temperature reached 32°C (2-4 h after the lights had been turned on). When the tank reached 33°C, the voltage to the heat lamps was turned down and adjusted periodically to maintain the water temperature at 33-34°C for the duration of the test.

While in the training tanks *prior* to the day of testing, each group of newts was exposed to one of two temperature regimes. *Stable water temperatures*: variation in training tank water temperature was kept to less than 10°C (and usually less than 5°C). In these tests, the maximum temperature during *any* of the days prior to testing was 24-27°C and the minimum was 17-23°C. Tests were carried out from February until August. *Fluctuating water temperatures*: fluctuations of training tank water temperature of approximately 20°C were produced by turning off the greenhouse heat on the night before a test and turning on ventilation fans to bring in cold outside air. This lowered the water temperature in the training tanks to 2-7°C. During the day, the ventilation fans were turned off and the heat was turned back on, raising the water temperature to 25-27°C. On the morning of the test, the greenhouse heating system was turned on and supplemented with 2-4 1500-W radiant heaters. The bank of heat lamps was then turned on, rapidly elevating the water temperature to 33-34°C for testing. Tests which involved fluctuating water temperature required outside air temperatures near freezing and were carried out in March-May (four tests) and in September-December (four tests). A group of newts was tested only once after exposure to each of the temperature regimes (i.e. stable or fluctuating water temperature), and an individual newt was tested only once in each test.

Testing procedures

Tests were carried out in the laboratory building adjacent to, and directly north of, where the holding and training tanks were located. The newts were tested in a dry enclosed circular arena (70 cm high \times 80 cm in diameter). The walls and roof of the arena were constructed of aluminium and wood and were painted matt black. The floor was made of frosted Plexiglas. The arena was illuminated by a single light source consisting of a 12-V, 100-W quartz/halogen bulb and two frosted Pyrex diffusers positioned above a 4.5-cm diameter opening centrally located in the roof of the arena. A newt's movements were observed by means of its silhouette which was visible through the arena floor and reflected in a mirror located underneath. The legs of the arena rested on a flagstone base that was isolated from vibrations. The arena was also enclosed in aluminium screening, which shielded the interior from alternating electromagnetic fields, but did not affect the d.c. magnetic field of the earth. In addition, fluorescent lights in adjacent rooms were turned off to decrease electromagnetic noise.

For testing, a newt was removed individually from a tank and placed in a clear plastic container that had been freshly rinsed with tank water. The newt was carried 2–3 m North away from the tank along the tank axis with the plastic box held so that the newt faced in the direction of movement. The plastic container was then placed inside a light-tight bag made out of four layers of heavy black cloth and carried into the laboratory. The room used for testing was located approximately 10 m North of the location of the tanks in the greenhouse and 20 m North of the outdoor tanks used during the summer.

In the test room, the newt was removed from the carrying container in total darkness and placed into a release device consisting of a small (8 cm high \times 5 cm in diameter) Plexiglas cylinder in the centre of the arena floor. After closing the top of the arena, the arena light was turned on. The newt was released using a hydraulic mechanism controlled by the observer. In test series I, the newt was released following a delay of 60 s and its directional response recorded to 5° accuracy where it first contacted a 30 cm radius circle. In series II, because newts exposed to elevated water temperatures were reluctant to leave the release area and took much longer to score than in the previous series, the criterion distance was reduced to 10 cm and the delay to 30 s (see Phillips, 1985). Preliminary tests showed that newts exposed to elevated water temperatures prior to testing exhibited similar orientation when scored at the 10 and 30 cm radius circles. Even using the 10 cm criterion, however, on average only 40–50 % of the newts tested reached the criterion distance within the 15 min allotted. Because unimodal orientation was observed only when newts were exposed to elevated water temperatures after residing in a training tank for at least a week, the data obtained from each group were limited by the number of bearings that could be obtained during a single test (usually lasting from 4 to 6 h).

In both test series, the arena surface was wiped with a damp sponge between trials to disrupt any olfactory cues left by the previous animal. As in Phillips (1985), data from newts reaching the 30 cm circle in less than 1 min were not used, since such rapid movement often indicates that an animal had been disturbed by the release device, resulting in a rapid, randomly oriented escape response. Observation was discontinued if a newt did not reach the circle within 15 min. The paths of newts generally consisted of a series of short segments, usually circling one or more times under the release device before leaving the centre of the arena and reaching the criterion. A newt would characteristically move 3–4 cm tangential to the centre of the arena and then pause for a variable period of up to several minutes. It would then turn its head and, after a brief pause, move along this new heading, again travelling only a short distance before pausing.

Individual newts were tested in one of four magnetic fields: the ambient magnetic field (magnetic north at North) and three altered fields (magnetic north rotated to East, South or West). The three altered fields were produced by means of a doubly wrapped cube-surface coil (Rubens, 1945; see Fig. 2), and they closely resembled the natural fields in dip angle and total intensity ($\pm 5\%$). The first individual was tested in magnetic north ($\text{magN} = \text{N}$), the next individual in $\text{magN} = \text{E}$, followed by one in $\text{magN} = \text{W}$ and one in $\text{magN} = \text{S}$. This sequence of magnetic field conditions was

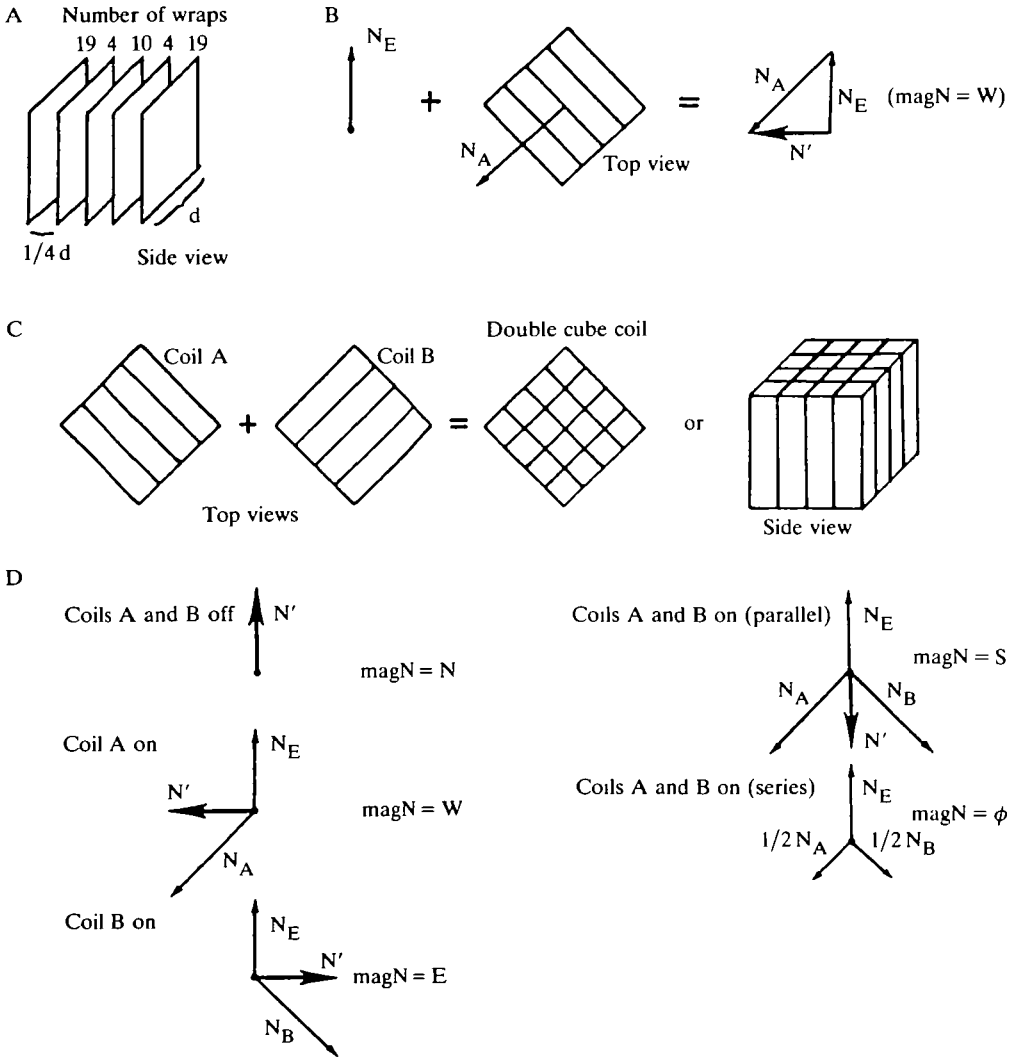


Fig. 2. Production of altered magnetic fields (from Phillips, 1985). (A) Schematic design of cube-surface-coil of Rubens (1945). The number of wraps in each coil element and their relative spacing is shown. The coil alignment necessary to shift the horizontal magnetic component 90° counterclockwise is shown in B. The coil is aligned to produce an artificial field N_A 135° from geomagnetic north N_E . Increasing the artificial field strength until the resultant field (N') is rotated 90° reproduces the horizontal intensity of the earth's magnetic field. Because the vertical component is unchanged, the vertical and horizontal magnetic vectors sum to produce the same inclination (or dip-angle) and total intensity as the natural field. (C) Double cube-coil, consisting of two perpendicularly aligned cube-coils wrapped on the same structural frame. (D) Equal resistances of the two coils (A and B) permit a constant setting of a voltage-regulated power supply to be used to produce four altered horizontal magnetic components (including cancelling the horizontal component) in addition to the natural field. $\text{mag}N$, magnetic north.

repeated with new individuals until the test was terminated (approximately 1 h prior to sunset). In test series II, because of the newts' reluctance to leave the release area (apparently because it was cooler than the training tank), it was not always possible to obtain an even multiple of four bearings in each test. When the next group of newts was tested, the sequence of magnetic fields was started where the previous test had left off. Consequently, data pooled from the entire test series included approximately equal numbers of bearings from each of the four alignments of the magnetic field.

The advantage of the symmetrical design used in these experiments is that data from the four alignments of the magnetic field can be combined, by rotating the distributions until the magnetic norths coincide, to retain only the component of orientation that is a consistent response to the magnetic fields (Fig. 3, and see Phillips, 1985, 1986). Thus, it is unlikely that the orientation evident in the pooled distribution of magnetic bearings is an artifact of a non-magnetic directional cue. This method of analysis is similar to the technique used in field studies of pigeon homing (e.g. Wallraff, 1986), in which directional bearings are pooled from four release sites symmetrically located around the home loft in order to distinguish the 'homeward component' of the birds' orientation from a 'preferred compass direction' that is not in the homeward direction.

The testing format used in the present experiments also eliminates the possibility that retesting individual newts in successive tests (as occurred in test series I) will increase the clustering of data in the pooled distribution of magnetic bearings. A newt might, for example, use some irregularity in the arena as a landmark enabling it

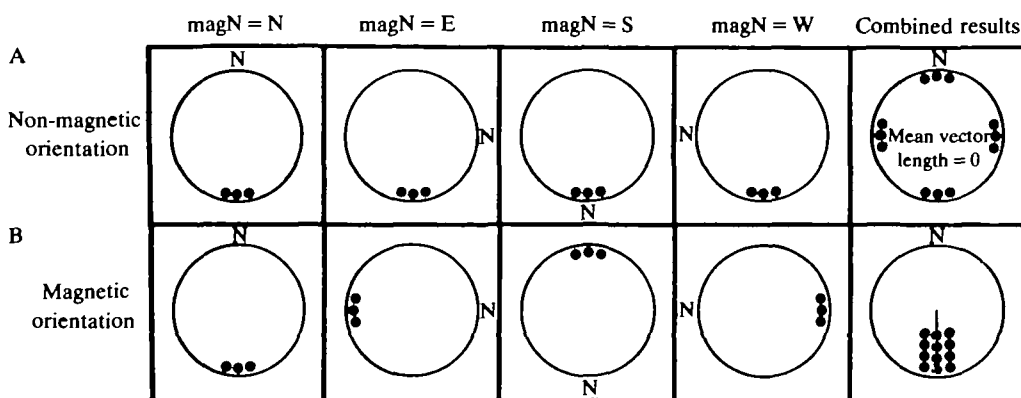


Fig. 3. Magnetic testing format (from Phillips, 1985). Equal numbers of newts are tested in each of the four horizontal alignments of the magnetic field (i.e. the first newt in magnetic north ($\text{magN} = \text{N}$), the second newt in $\text{magN} = \text{E}$, the third in $\text{magN} = \text{S}$, the fourth in $\text{magN} = \text{W}$, and then this sequence is repeated with four new animals). In subsequent analysis, data from the four conditions are combined by rotating the bearings so that the magnetic norths coincide (i.e. 90° is subtracted from the actual headings of newts tested in $\text{magN} = \text{E}$, 180° from the headings of newts tested in $\text{magN} = \text{S}$ and 270° from the headings of newts tested in $\text{magN} = \text{W}$). If the newts are orienting with respect to a geographically fixed (non-magnetic) cue, the pooled data will be uniformly distributed (A). However, if the newts are exhibiting a consistent directional response relative to the magnetic fields, the pooled data will be non-randomly distributed (B).

to orient in the same absolute direction as in a previous test, i.e. not make a new assessment of compass direction relative to the magnetic field in each test. However, because the individual will have an equal likelihood of being tested in any one of the four alignments of the magnetic field in subsequent tests, the result would be a uniform response, rather than an oriented, distribution of *magnetic* bearings.

Analysis and statistical procedures

For analysis, the data from series I are divided into two groupings. The 'winter' period includes data from tests carried out in January–March, prior to the spring migratory period. The 'spring' period incorporates data from the beginning of April until the first week of May, coinciding with the period during which newts migrate into ponds in the Ithaca, New York area (Hurlbert, 1969).

The pooled distribution of magnetic bearings was analysed according to the statistical procedures described in Batschelet (1981). Bimodal distributions obtained in series I were first converted to unimodal distributions by doubling the angles. The V-test was used to test for departure from a random distribution with respect to a predicted direction or, in the case of a bimodal distribution, a predicted axis. A 95 % confidence interval for the mean bearing or mean axis of each distribution was determined from Batschelet (1981: table 5.2.1). To test for a significant difference between two distributions, the Watson U^2 test was used (carried out on doubled angles when comparing bimodal distributions).

RESULTS

Series I

Both the SW and E groups exhibited weak bimodal orientation relative to the tank axis of 0–180° during the winter months (January until March; Fig. 4A,B). The distributions of magnetic bearings for the two groups were not significantly different ($P > 0.05$; Watson U^2 test), and the 95 % confidence intervals for both distributions included the tank axis, but did not include either group's respective home axis (i.e. the axis coinciding with the magnetic direction of the home pond from the laboratory building).

In contrast, during the spring migratory period (April until early May), the weak bimodal orientation exhibited by the SW group was significantly oriented with respect to their home axis of 50/230° (Fig. 4C). Because of the scatter in the bearings, however, this response was not significantly different from the distribution of magnetic bearings exhibited by this group during the winter ($P > 0.05$, Watson U^2 test). Newts in the E group were also significantly oriented with respect to their home axis of 100/280° during the spring migratory period (Fig. 4D), and their orientation differed significantly from that exhibited during the winter months ($P < 0.005$, Watson U^2 test). During the spring migratory season, the 95 % confidence intervals for *both* groups included their respective home axes, but not the axis of the training tank. In addition, a comparison of the E and SW groups found no difference in their

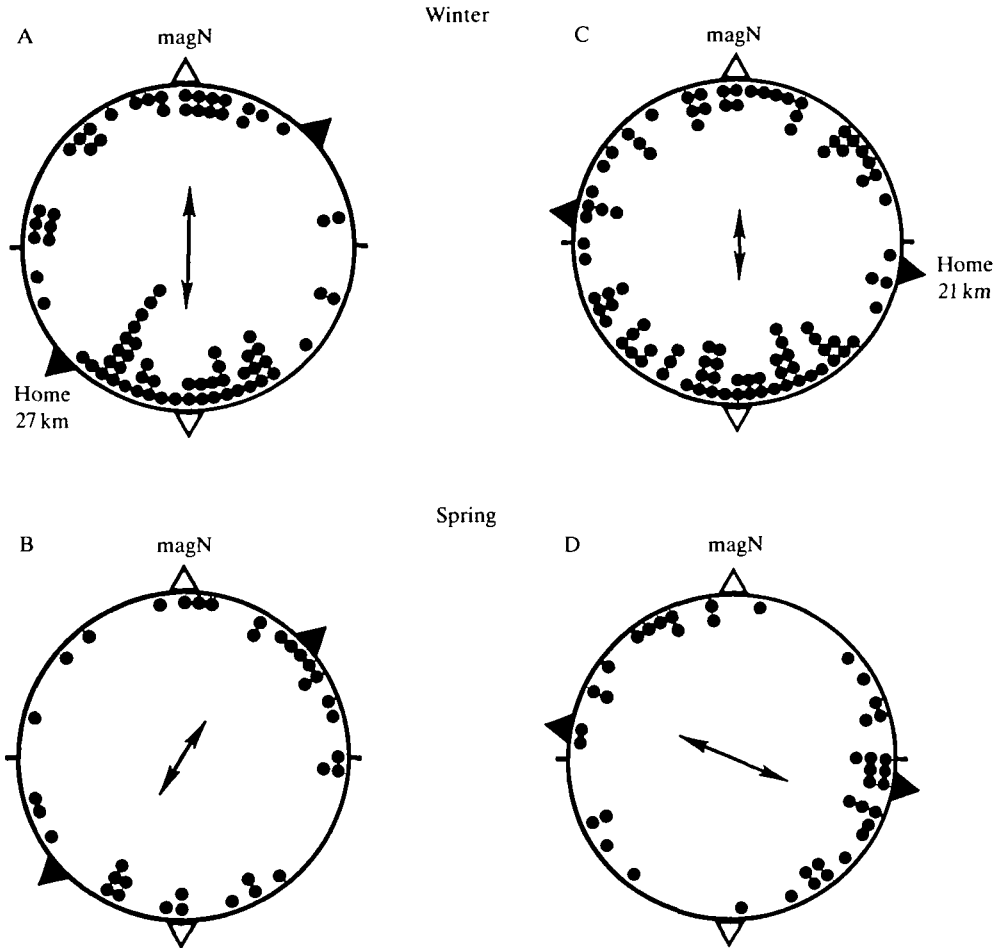


Fig. 4. Seasonal change in magnetic compass orientation. Each distribution pools data from approximately equal numbers of newts tested in each of four horizontal magnetic field conditions [magnetic north (magN) = N, E, W or S]. Each data point is the magnetic bearing of a single newt. The mean axis of orientation is indicated by the double-headed arrow in the centre of each distribution; the length of the arrow is proportional to the mean vector length 'r' which varies from 0 to 1 and indicates the degree of clustering in the distribution (the circle's diameter corresponds to $r = 1$). The open arrowheads at the edge of each circle indicate the alignment of the training tank, while the solid arrowheads indicate the magnetic axis coinciding with the compass direction from the laboratory to the pond in which the newts were collected. (A) During the winter, the SW group was bimodally oriented with respect to the tank axis [$1-181^\circ$, $r = 0.37$, $N = 77$, $P < 0.0001$, V-test (expected axis = $0-180^\circ$)]. (B) During the spring migratory period, this group shifted to an axis that was oriented with respect to the home axis [$33-213^\circ$, $r = 0.27$, $N = 35$, $P = 0.03$, V-test (expected direction = $50-230^\circ$)]. (C) The E group also oriented with respect to the tank axis during the winter [$1-181^\circ$, $r = 0.22$, $N = 92$, $P = 0.002$, V-test (expected axis = $0-180^\circ$)], and (D) to the home axis during the spring migratory period [$112-292^\circ$, $r = 0.37$, $N = 41$, $P = 0.002$, V-test (expected axis = $100-280^\circ$)].

orientation during the winter months: the two groups differed in orientation during the spring migratory period ($P < 0.005$, Watson U^2 test).

Series II

Groups exposed to elevation of water temperature just prior to testing after a period of stable, moderate water temperatures exhibited unimodal northward orientation (Fig. 5A,B). The distributions of data obtained from newts collected to the east and south of the laboratory did not differ significantly ($P > 0.05$, Watson U^2 test), and the 95 % confidence intervals for both groups included the direction of shore in the training tank, but not the home direction. Preliminary tests indicated that the newts' shoreward orientation was a consequence of the elevation of water temperature, i.e. the presence of an artificial shoreline alone did not result in unimodal orientation.

In contrast, after exposure to wide fluctuations in water temperature prior to testing (see Materials and Methods) the newts were significantly oriented with respect to the compass direction of their home pond (Fig. 5C,D). The distribution of magnetic bearings from newts collected to the east and south differed significantly ($P < 0.05$, Watson U^2 test). The 95 % confidence interval for the S group, but not the E group, included the home direction, and in neither case included the trained direction. The counterclockwise deviation from the home direction exhibited by the E group may represent the type of bias in initial homeward orientation that is observed at some release sites in field studies of pigeon homing (e.g. Windsor, 1975; Wallraff, 1986).

DISCUSSION

Series I

Newts tested during the winter exhibited weak bimodal orientation that coincided with the tank axis. Since the tanks used in this test series did not contain an artificial shoreline, the newts may have been orienting with respect to the current flowing along the axis of the tank, or to the initial direction of displacement away from the tank which was along the tank axis (see Materials and Methods). This response was independent of the direction of the pond in which they had been captured. During the spring migratory period, however, the newts that had been captured the previous autumn switched from the trained axis to an axis coinciding with the direction of their home pond (Fig. 4). This seasonal occurrence of homing parallels the behaviour of this species under natural conditions. Gill (1979) found that adult *Notophthalmus* displaced from their home pond to a nearby pond containing newts remained in the new pond until the next spring. Prior to the spring breeding season, however, most of the adult males abandoned the new pond and returned to the pond from which they originated. A smaller percentage of adult females also returned to the home pond. The correspondence between laboratory and field observations suggests that male newts that have been displaced from their home pond or have left

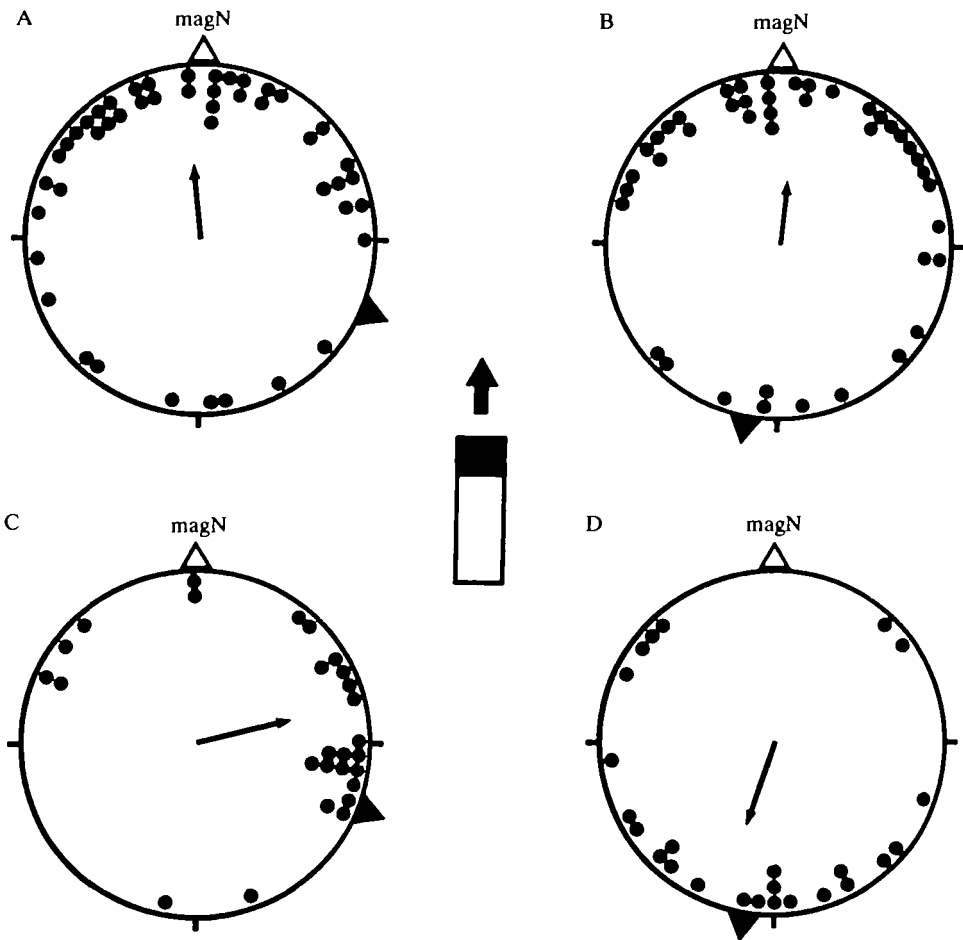


Fig. 5. Unimodal compass and homing orientation after exposure to elevated water temperatures. Data are presented as in Fig. 4, with the exception that the *radius* of each circle corresponds to a mean vector length (r) of 1. The alignment of the training tank is shown in the centre of the figure. The darkened end indicates the position of the artificial shoreline, and the solid arrow indicates the direction to the laboratory building. magN, magnetic north. (A) The E group responded to elevation of water temperature after several days of stable temperatures by orienting unimodally in a compass direction corresponding to the direction of the shoreline in the training tank [354° , $r = 0.42$, $N = 46$, $P < 0.0001$, V-test (expected angle = 360°)]. (B) The S group also responded to elevation of water temperature following exposure to stable water temperatures by orienting in a shoreward direction [7° , $r = 0.37$, $N = 43$, $P = 0.0004$, V-test (expected angle = 360°)]. In contrast, when the same groups were tested after exposure to fluctuating water temperatures, they responded to elevation of water temperature by orienting in the direction of their respective home ponds. (C) The E group was oriented with a mean bearing of 78° [$r = 0.54$, $N = 27$, $P = 0.0007$, V-test (expected angle = 113°)], and (D) the S group was oriented with a mean bearing of 198° [$r = 0.45$, $N = 25$, $P = 0.0009$, V-test (expected angle = 190°)].

the pond to overwinter on land, actively home to ponds at the onset of the breeding season.

Series II

Newts exposed to elevation of water temperature after a period of stable temperatures exhibited unimodal shoreward orientation throughout the period of testing (February–August; see also Phillips, 1985). The absence of seasonality in the response to elevated water temperature is presumably due to the overriding importance of responding to conditions that pose an immediate threat to survival. In contrast to the trained compass response evident after a period of stable water temperature, wide fluctuation in water temperature prior to testing caused newts to orient in the direction of their home pond. This finding suggests that newts switch to homing facultatively, when local conditions are unfavourable for long-term survival and reproduction (see below). In conjunction with the findings of test series I, these results indicate that newts possess a navigational system that enables them accurately to determine the home direction at distances in excess of 20 km.

Influence of fluctuating water temperatures

Notophthalmus occurs primarily in permanent bodies of water (Gates & Thompson, 1982), which are less subject to fluctuations in temperature than are smaller temporary bodies of water. Consequently, temperature variation may provide one means of assessing habitat quality. Rapid changes in water temperature indicate that the volume of water is small and, as a consequence, the prospects for long-term survival and reproduction in the pond are low (because the pond is likely to dry up during the summer, or freeze during the winter). For a newt that has dispersed from the natal pond as an eft and entered a new pond as an adult, a facultative homing response would make it possible to return directly to the natal pond, if factors such as the rate of change in water temperature indicate that the new pond is unsuitable. Thus, navigational ability may play an important role in dispersal by providing a fall-back strategy of returning to the natal area when a new habitat encountered by dispersing individuals proves to be unsuitable. Unfortunately, a facultative response of this kind is difficult to observe under natural conditions because, unlike seasonal migration, it will not occur predictably or synchronously within a population.

Facultative versus seasonal migratory orientation

The contrast between the weak bimodal homing orientation exhibited by newts during the spring migratory season (Fig. 4C,D) and the stronger unimodal homing response exhibited following exposure to rapidly fluctuating water temperatures (Fig. 5C,D) suggests an important difference between seasonal and facultative migration. A general feature of seasonally programmed migration is that its timing anticipates changing environmental conditions (Terrill, 1987). Thus, during seasonal migration an individual has some flexibility in selecting favourable conditions for movement. As a consequence, seasonal migratory orientation may be much more easily disrupted by the highly unnatural surroundings in laboratory

studies of orientation behaviour. In contrast, when migratory orientation is triggered facultatively by rapidly deteriorating or unstable local conditions, an organism may not have the luxury of waiting for conditions that are optimal for migration. Thus, facultative migratory orientation may be less 'context specific' and, therefore, less subject to disruption by experimental conditions used in laboratory studies.

Interestingly, behaviour very similar to that observed in newts has been reported in recent studies of a migratory bird, the dark-eyed junco (*Junco hyemalis*). Terrill (1987) has shown that female juncos exposed to competition for a limited food resource exhibit nocturnal migratory restlessness ('Zugunruhe') outside the normal migratory season. In preliminary experiments, these socially stressed individuals exhibited much stronger species-appropriate migratory orientation than is normally exhibited by this species during seasonal migration. As the findings in both newts and juncos suggest, the facultative triggering of migratory behaviour by appropriate manipulation of conditions prior to testing provides the experimenter with a useful tool for studies of migratory orientation.

Sensory basis of the navigational map

The present study demonstrates that the migratory orientation of newts involves true navigation, i.e. orientation in the direction of the home pond from distances well beyond the newt's normal range of movement. To home from unfamiliar territory, an animal must be able to determine its geographical position relative to home (the 'map step'); only then can it orient in the appropriate homeward direction (the 'compass step') (reviewed in Able, 1981). There are two ways in which an animal can derive 'map' information beyond its area of familiarity. Map information may be derived by integrating simple compass information regarding the direction and distance over which it has moved or been displaced. This 'route-based' map information enables an animal to 'retrace its steps' by using the same compass mechanism. Alternatively, an organism may determine its position by means of a bicoordinate (or multicoordinate) map sense that requires learning the spatial relationship of geographically varying gradients of two or more cues relative to the home pond.

In the present experiments, newts had to have derived the home direction (i.e. carried out the map step of homing) *prior* to testing, either during the earlier displacement from the home pond or while residing in the training or holding tanks. Map information was not available in the test arena, because all potential map cues except the magnetic field were excluded. Moreover, the intensity and alignment of the magnetic field within the test arena were sufficiently variable ($\pm 5\%$) that detection of the natural geographical variation in the earth's field (suggested as a possible basis for the map; Gould, 1980, 1982; Moore, 1980; Walcott, 1980, 1982) was almost certainly impossible. [Note, however, the test fields were well within the range of intensity that can be used for compass orientation (Wiltschko, 1972).] Thus, newts in the test arena were using the magnetic field to carry out the compass step of homing. Future experiments will examine whether magnetic cues also play a role in the map step, and determine whether newts use route-based or site-specific (bicoordinate) map information to determine the home direction.

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REFERENCES

- ABLE, K. P. (1981). Mechanisms of orientation, navigation and homing. In *Animal Migration, Orientation and Navigation* (ed. S. A. Gauthreaux). Berlin, Heidelberg, New York: Springer-Verlag. pp. 283–373.
- BATSCHLET, E. (1981). *Circular Statistics in Biology*. New York: Academic Press.
- CARR, A. (1964). Transoceanic migration of the green turtle. *Bioscience* **14**, 49–52.
- CONANT, R. (1975). *A Field Guide to Reptiles and Amphibians of Eastern and Central North America*. Boston: Houghton Mifflin.
- GATES, J. E. & THOMPSON, E. L. (1982). Small pool habitat selection by red-spotted newts in Western Maryland. *J. Herp.* **16**, 7–15.
- GILL, D. E. (1978). The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). *Ecol. Monogr.* **48**, 145–166.
- GILL, D. E. (1979). Density dependence and homing behavior in adult red-spotted newts *Notophthalmus viridescens* (Rafinesque). *Ecology* **60**, 800–813.
- GOULD, J. L. (1980). The case for magnetic sensitivity in birds and bees (such as it is). *Am. Scient.* **68**, 256–267.
- GOULD, J. L. (1982). The map sense of pigeons. *Nature, Lond.* **296**, 205–211.
- GRIFFIN, D. R. (1952). Bird navigation. *Biol. Rev.* **27**, 359–400.
- HEALEY, W. R. (1973). Life history variation and the growth of juvenile *Notophthalmus viridescens* from Massachusetts. *Copeia* **1973**, 641–647.
- HEALEY, W. R. (1974). Population consequences of alternative life histories in *Notophthalmus viridescens*. *Copeia* **1974**, 221–229.
- HURLBERT, S. H. (1969). The breeding migrations and interhabitat wandering of the vermilion-spotted newt *Notophthalmus viridescens* (Rafinesque). *Ecol. Monogr.* **39**, 465–488.
- MOORE, B. R. (1980). Is the homing pigeons's map geomagnetic? *Nature, Lond.* **285**, 69–70.
- PHILLIPS, J. B. (1985). Magnetic compass orientation in the Eastern red-spotted newt (*Notophthalmus viridescens*). *J. comp. Physiol.* **158**, 103–109.
- PHILLIPS, J. B. (1986). Two magnetoreception pathways in a migratory salamander. *Science* **233**, 765–767.
- QUINN, T. P. (1982). A model for salmon navigation on the high seas. In *Salmon and Trout Migratory Behavior Symposium* (ed. E. L. Brannon & E. O. Salo). Seattle, Washington: University of Washington School of Fisheries.
- QUINN, T. P. & GROOT, C. (1984). Pacific salmon (*Onchorhynchus*) migrations: Orientation versus random movement. *Can. J. Fish. aquat. Sci.* **41**, 1319–1324.
- RODDA, G. H. (1984a). Orientation and navigation of juvenile alligators: Evidence for magnetic sensitivity. *J. comp. Physiol.* **154**, 649–658.
- RODDA, G. H. (1984b). Homeward paths of displaced juvenile alligators as determined by radiotelemetry. *Behav. Ecol. Sociobiol.* **14**, 241–246.
- RODDA, G. H. (1985). Navigation in juvenile alligators. *Z. Tierpsychol.* **68**, 65–77.
- RUBENS, S. M. (1945). Cube surface coil for producing uniform magnetic field. *Rev. Sci. Instr.* **16**, 243–245.

- TERRILL, S. B. (1987). Relative importance of proximate factors in bird migration. *XIXth Intern. Ornith. Congr.* (in press).
- TWITTY, V. C., GRANT, D. & ANDERSON, O. (1966). Course and timing of the homing migration in the newt *Taricha rivularis*. *Proc. natn. Acad. Sci. U.S.A.* **56**, 864–869.
- WALCOTT, C. (1980). Magnetic orientation in homing pigeons. *I.E.E.E. Trans. Mag.* **16**, 1008–1013.
- WALCOTT, C. (1982). Is their evidence for a magnetic map in homing pigeons? In *Avian Navigation* (ed. F. Papi & H. G. Wallraff), pp. 99–108. Berlin: Springer-Verlag.
- WALLRAFF, H. G. (1986). Directional components derived from initial-orientation data of inexperienced homing pigeons. *J. comp. Physiol.* **159**, 143–159.
- WILTSCHKO, W. (1972). The influence of magnetic total intensity and inclination on directions chosen by migrating European robins. In *Animal Orientation and Navigation* (ed. S. R. Galler, K. Schmidt-Koenig, G. J. Jacobs & R. E. Belleville). Washington, D.C.: NASA SP-262, U.S. Govt Print. Off.
- WINDSOR, D. M. (1975). Regional expression of directional preferences by experienced homing pigeons. *Anim. Behav.* **23**, 335–343.