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Use of a magnetic compass for *Y*-axis orientation in premetamorphic newts (*Triturus boscai*)

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Abstract Experiments were carried out to investigate whether premetamorphic larvae of Bosca's newt (*Triturus boscai*) are capable of using the geomagnetic field for *Y*-axis orientation (i.e., orientation toward and away from shore). Larvae were trained outdoor in two different training configurations, using one training tank aligned along the magnetic north–south axis, with shore facing north, and another training tank positioned with its length along the east–west axis, with shore located west. After training, premetamorphic newts were tested in an outdoor circular arena surrounded by a pair of orthogonally aligned cube-surface coils used to alter the alignment of the Earth's magnetic field. Each newt was tested only once, in one of four magnetic field alignments: ambient magnetic field (i.e., magnetic north at North), and three altered fields (magnetic north rotated to East, West, South). Distributions of magnetic bearings from tested larvae indicated that they oriented bimodally along the magnetic direction of the trained *Y*-axis. These findings demonstrate that *T. boscai* larvae are sensitive to the geomagnetic field and can use it for orienting along a learned *Y*-axis. This study is the first to provide evidence of *Y*-axis orientation, accomplished by a magnetic compass, in larval urodeles.

Key words Magnetic compass · Magnetoreception · Newts · Orientation · *Triturus boscai*

Introduction

Although the traditional study of animal orientation has focused on birds and other long distance migrants (Dingle 1996), amphibians have been demonstrated to be excellent

models for orientation studies (Phillips 1986a; Sinsch 1990a, 1991, 1992). Amphibians perform two major types of oriented movements: (1) homing behaviour (i.e., the ability to return home after displacement), well documented in several species of anurans (Sinsch 1990a, b) and urodeles (Phillips 1986a; Phillips and Borland 1994; Diego-Rasilla and Luengo 2002; Diego-Rasilla 2003) and (2) *Y*-axis orientation, a term coined by Ferguson and Landreth (1966) to describe local movements, oriented toward land or deep water, shown by aquatic organisms. The *Y*-axis is defined as the compass course perpendicular to the shoreline and movements along this axis have a great importance in the ecology of amphibians, since many species live near the land–water boundary (Ferguson and Landreth 1966). Whether the animals move in a direction corresponding to shore or deeper water depends on the species involved, season and stage in their life cycle (Able 1980). Deep water may provide a refuge to larvae and aquatic adults from predators and temperature variation, whereas shallow water may provide food and it is also likely to be important during seasonal migrations of amphibians in and out of breeding ponds (Freake et al. 2002). Amphibians can learn to orient in a fixed compass direction with respect not only to its natural shoreline, but also to artificial shorelines (Deutschlander et al. 2000). Thus, *Y*-axis orientation of amphibians is a useful tool to investigate the sensory basis of orientation because individuals can be trained to an artificial shoreline in controlled conditions (Adler 1970).

Many different sensorial cues are used by amphibians to learn the *Y*-axis direction, including the use of a sun compass (Ferguson and Landreth 1966; Ferguson et al. 1967; Landreth and Ferguson 1968; Adler 1976), sky polarization patterns (Taylor and Ferguson 1970; Taylor 1972; Adler and Taylor 1973; Taylor and Adler 1973; Auburn and Taylor 1979) and a magnetic compass (Phillips 1986b; Deutschlander et al. 2000; Freake et al. 2002). Like in most groups of vertebrates (Wiltshcko and Wiltshcko 1995; Diego-Rasilla 2004), the use of the geomagnetic field for orientation seems to be a widespread capability among amphibians (Sinsch 1991). However, magnetic orientation in urodeles has been only documented in three species

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(*Euricea lucifuga*, *Notophthalmus viridescens*, *Triturus alpestris*; e.g., Phillips 1977, 1986b; Diego-Rasilla 2003). In particular, newts have been shown to rely on magnetic cues for both *Y*-axis orientation and homing (Phillips 1986a, b; Phillips and Borland 1994; Deutschlander et al. 2000; Diego-Rasilla 2003; Diego-Rasilla et al. 2005). Also, only eastern red-spotted newts, *N. viridescens*, has been found to use the geomagnetic field for *Y*-axis orientation (Phillips 1986a, b), being able to learn the direction of the *Y*-axis with respect to the geomagnetic field within 12–16 h (Deutschlander et al. 2000).

The experiments presented here constitute an initial approach for understanding the orientation behaviour of Bosca's newt (*T. boscai*). The present experiments were designed to determine whether premetamorphic larvae of *T. boscai* are capable of using the geomagnetic field for *Y*-axis orientation.

Materials and methods

Subjects and study site

T. boscai is a small salamandrid newt endemic to the occidental half of Iberian Peninsula. Bosca's newt mainly inhabits small and temporary ponds with abundant vegetation and is also common in watering places for cattle, such as drinking troughs (Barbadillo et al. 1999; Díaz-Paniagua 2004).

Although *T. boscai* shows varying patterns of annual activity (Caetano and Leclair 1999), individuals in the study area spend a large part of the year in the water and active adults can be observed in all seasons. The breeding period in our study area starts in winter, with the first larvae appearing in spring. Metamorphosis mainly occurs from July to September (Lizana et al. 1989; Díaz-Paniagua 2004).

The Bosca's newt larvae used in this experiment were collected from a drinking trough located in a mountainous area near the town of Linares de Riofrío (Salamanca province, central-west Spain; 40°34'21" N, 5°57'03" W, elevation 920 m), where the vegetation mainly consists of forest of *Quercus pyrenaica* and *Castanea sativa*.

Forty-one larval newts were captured in mid-summer (20 August 2004). All individuals collected showed a similar

stage of development and were assigned to stage VI (i.e., premetamorphic stage, with regression of dorsocaudal crest and gills; Braña 1980). Their snout–vent length varied over 15–19 mm (mean = 17.5 ± 0.22 mm).

The experiments (training, testing) took place in Vegas del Condado (León province, north-western Spain; 42°40'55" N, 5°21'52" W, elevation 860 m), located 238 km north of the capture site. The collected premetamorphic newts were kept in plastic containers filled with water from the capture site and transported by car to the testing site. Special care was taken in transport, with water temperature being checked every 20 min so as to maintain it at 13–14°C.

Both training and testing were conducted outdoors, under natural conditions and natural light–dark cycle. Larvae used in the experiment were returned to their home drinking trough after testing.

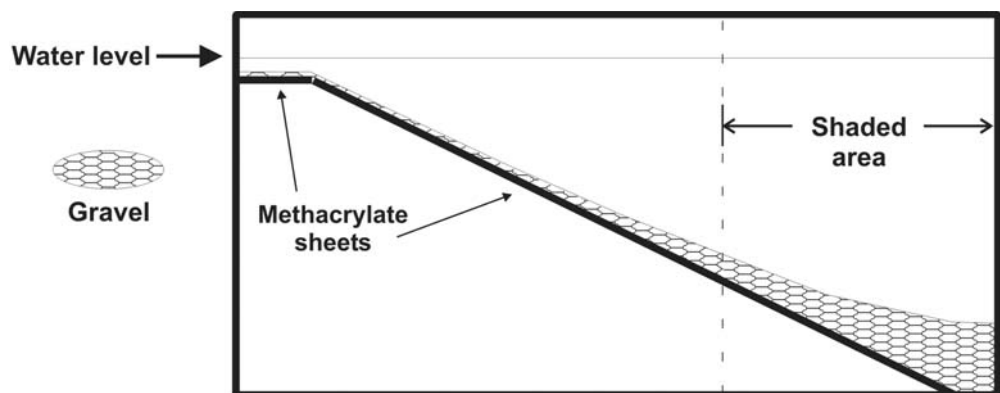
Training

The *Y*-axis training tanks consisted of two 100-l (80 × 40 × 30 cm) all-glass aquaria, each with a sloping bottom (over 25° sloop) in order to provide a deep end, and a shallow end (Fig. 1). In each aquarium, the deep end was shaded by means of a wooden board placed over the last 30 cm of the glass covering the tank. In addition, black cardboard was stuck on the aquarium exterior walls around the deep end. The rest of the aquarium glasses (top and sides, except parts near the deep end) remained unblocked, so that premetamorphic newts had free access to the sky and surroundings during training. The shaded deep end was thought to reinforce *Y*-axis orientation of larvae, acting like a “shelter zone” or hiding place.

Tap water was used, treated with aquarium water conditioners (Stress-coat from Aquarium Pharmaceutical; Sera pH-Plus). The water pH was maintained at the same value as the water from the drinking trough where specimens were collected (pH 8). Training tanks were filled with treated water so that the water depth at the shore end was 1 cm.

A partial water change, with the addition of fresh treated water, was performed every day coinciding with the hours of maximum temperature (i.e., 14:00–16:00 GMT). Thus, the water temperature in the training tanks was maintained between 13°C and 21°C. This daily fluctuation of water

Fig. 1. Training tank design (side view). The sloping bottom was constructed by means of one methacrylate sheet, pasted onto the aquarium walls with a specific silicone (Quilosa Orbasil K95). A small horizontal shore (8 cm length) was added to the shallow end with an additional methacrylate sheet. The bottom of the tank, including the horizontal shore, was completely covered with gravel that sloped up towards the shore



temperature approximately resembled the natural conditions in the home drinking trough, where the water temperature was measured to oscillate daily between 13°C and 18°C.

Two different training configurations, with perpendicular shore directions, were used for the experiment. One training tank was aligned along the magnetic north–south axis, with shore facing north, whereas the other training tank was positioned with its length along the east–west axis, with shore located west. Training tanks were placed at least 8 m from any ferrous metal, ferromagnetic materials or other possible sources of electromagnetic disturbances.

Two groups of 20 and 21 premetamorphic newts were introduced into the shallow end of each training tank and allowed 6 days (i.e., from 21 to 27 August) to learn the Y-axis direction before testing. During training, larvae were fed frozen bloodworms and lyophilized *Tubifex* once a day.

Testing procedure

After training, premetamorphic newts were tested outdoors for magnetic orientation individually. All tests were conducted on a single day (27 August 2004) during daylight hours (09:16–18:37 GMT).

Testing protocols employed here followed the design principles used by Phillips et al. in their successful series of experiments with the eastern red-spotted newt, *N. viridescens* (Phillips 1986b; Deutschlander et al. 2000). In this type of experimental design, four different magnetic field conditions are used: the ambient magnetic field and three altered fields (magnetic north rotated to east, west, south) produced by means of a doubly wrapped cube-surface coil or “Rubens coil” (Rubens 1945). The advantage of this design is that the resulting data can be pooled by rotating the four magnetic distributions so that the direction of magnetic north coincides in each to factor out any non-magnetic bias (for a more detailed explanation, see Phillips 1986b).

The testing apparatus used here was a circular, visually symmetrical, test arena (circular plastic container, 43 cm diam., 24 cm high) enclosed within a cube-surface coil (1 m side) powered by a DC regulated power supply (HQ Power model PS23023) that altered the alignment of the Earth’s magnetic field. The sides of the apparatus were covered with a black cotton curtain and, prior to tests, the arena was filled with treated tap water to a depth of 1 cm. This arena configuration afforded a view of the sky but not the horizon during tests. The temperature of arena water was maintained between 15°C and 20°C, by means of replacing some of the arena water with fresh water as soon as the temperature reached 20°C.

Prior to its individual testing session, each larva was removed from the training tank with a small dip net and placed in a rectangular plastic container with 1 cm water depth and its length along the same alignment as the training tank (N–S or W–E). After 5 min in this individual isolation tank, the premetamorphic newt was carried to the testing arena, located outdoor 5 m away from the training

tank’s position and previously levelled (since inclination cues have been shown to play an important role in the orientation responses of newts; e.g., Omland 1998). Larvae were then put in the arena centre beneath a release device consisting of an opaque, cylindrical plastic container (12 cm diam., 14 cm high) and were left in the cylindrical container for 1 min to overcome the effects of handling. After this container was lifted, the larva was allowed to move freely within the testing arena. Larval movements were observed through tiny holes in the black curtain that covered the test apparatus. The criterion for direction of movement was established as the vector of the first point where the test specimen tapped against the arena wall. Directional bearings were recorded to 10° accuracy by means of symmetrical radial marks drawn on the exterior edge of the arena walls.

Bearings of larvae that contacted the arena wall in less than 10 s were not recorded. These individuals, which moved immediately as soon as the release device was lifted, were considered to exhibit a randomly oriented escape response and were excluded from the analyses. In addition, trials were abandoned if the larva failed to score within 10 min.

Each premetamorphic newt was tested only once in one of the four magnetic field alignments, testing groups of larvae from different training configurations (N–S or E–W training tanks) alternately. The first larva to be tested was taken from N–S training tank and tested in the ambient field, [i.e., magnetic north (magN) = geographic north (gN)]. Then, another N–S larva was tested, now in a condition with magnetic north rotated to the east (magN = gE), followed by two more N–S larvae tested in magN = gW and magN = gS conditions, respectively. Once this first group of four alignments was completed, the next four larvae to be tested were taken from the E–W training tank and tested magN = gN, magN = gE, magN = gW and magN = gS. Then, four more larvae from the N–S tank were tested, then four more from the E–W tank and so on.

Through the 6 days of training, some larvae completed metamorphosis and, at the moment of testing, nine individuals (five from N–S tank, four from E–W tank) were actually metamorphs with completely reabsorbed gills. These recently metamorphosed newts were tested in the same way as the other larvae (premetamorphic newts) but their bearings were analysed separately.

Data analyses

All topographic bearings recorded were normalized with respect to magnetic north during testing. That is, data from the four magnetic field conditions (magN = gN, magN = gE, magN = gW, magN = gS) were combined by rotating the bearings so that magnetic north direction coincided at 0°, resulting in a pooled distribution of magnetic bearings (Phillips 1986b).

Data were analysed using standard circular statistics (Batschelet 1981). Mean vectors were calculated and tested for significance using the Rayleigh test. Statistics for bimodal distributions were calculated by doubling each data

value and reducing any greater than 360 using modulo arithmetic and 95% confidence intervals were used to test for orientation along the Y-axis.

Data from the two different training directions were analysed separately and the Watson U^2 -test was used to test for significant differences between the two distributions of magnetic bearings. All magnetic bearings were pooled with respect to the magnetic direction of the shore in training and similar analyses were performed. Finally, the absolute or “topographic” bearings (i.e., the distribution of bearings with respect to topographic directions ignoring the alignment of the four test magnetic fields) were also examined for any evidence of an effect of non-magnetic directional cues on the newts’ orientation, by the Rayleigh test. Statistics were calculated using Oriana ver. 2.0 (Kovach Computing Services).

Results

Premetamorphic newts trained in the tank that was aligned along the north–south axis, with the deep end towards the south, exhibited a highly significant bimodal orientation relative to the direction of the magnetic field (8–188°, $r = 0.69$, $n = 10$, $P = 0.006$, Rayleigh test; Fig. 2a). In addition, the 95% confidence interval calculated for the mean vector included the trained Y-axis.

Premetamorphic newts held in the training tank aligned east–west with the deep end towards the east also showed significant bimodal orientation (90–270°, $r = 0.54$, $n = 11$, $P = 0.037$, Rayleigh test; Fig. 2b). Again, the 95% confidence limits included the respective Y-axis.

The two distributions of magnetic bearings (north–south, east–west training configurations) were significantly different ($U^2 = 0.372$, $P < 0.001$, Watson U^2 -test) and their mean axes of orientation differed by approximately 90°.

When the two distributions of magnetic bearings were normalized with respect to the magnetic direction of the shore (i.e., pooling all bearings so that the shore direction rotated to 360°), the resulting distribution (Fig. 2c) showed a highly significant bimodal distribution in which the mean axis of orientation coincided with the Y-axis (4–184°, $r = 0.60$, $n = 21$, $P < 0.001$, Rayleigh test).

The topographic bearings from both training configurations were randomly distributed (north–south tank: 51°, $r = 0.11$, $P = 0.90$; east–west tank: 69°, $r = 0.39$, $P = 0.20$).

As mentioned above, some larvae completed metamorphosis during training. Bearings from these metamorphs were analysed separately, resulting in random distributions (9°, $n = 7$, $r = 0.28$, $P = 0.6$, for the distribution of magnetic bearings normalized with respect to the shore).

Discussion

This study demonstrates that larval *T. boscai* is able to orient along a previously learned Y-axis by using a magnetic

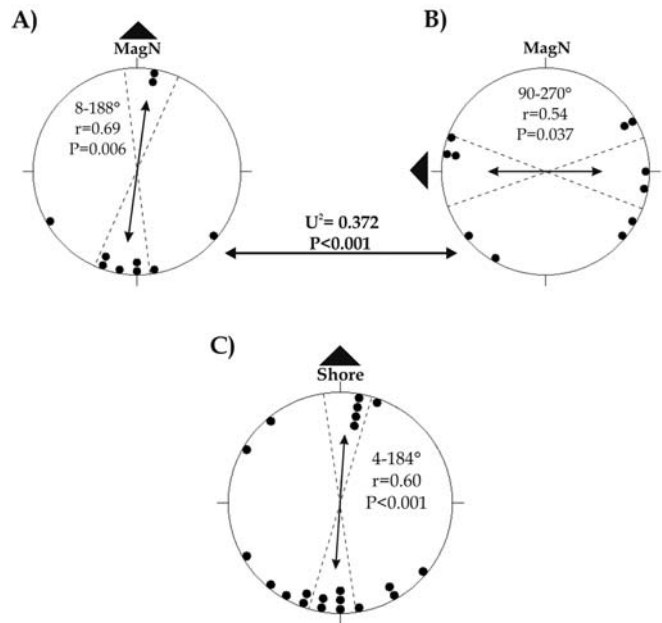


Fig. 2. Magnetic orientation responses of premetamorphic newts. Each dot represents the magnetic bearing of an individual tested only once in one of the four magnetic field alignments (i.e., magN = gN, magN = gE, magN = gW, magN = gS). Double-headed arrows at the centre of each circle indicate the mean bimodal axis of each distribution. The length of each arrow is proportional to the mean vector length (r), with the diameter of the circle corresponding to $r = 1$. Dashed lines represent the 95% confidence intervals for the mean vector. Black triangles outside the plots indicate the magnetic direction of the shore (shallow end of the Y-axis). **a** Magnetic bearings of premetamorphic newts trained in the tank with the Y-axis aligned north–south (shore towards north). **b** Magnetic bearings of premetamorphic newts from the east–west tank (shore towards west). **c** Combined distribution of magnetic bearings from **a** and **b** plotted with respect to the magnetic direction of the shore in training

compass. Results reported here suggest that perception of the geomagnetic field may play an important role in the orientation behaviour of this species and expand the diversity of animals known to have a magnetic compass (Wiltschko and Wiltschko 1995; Diego-Rasilla 2004). In addition, this study is the first to provide evidence of Y-axis orientation accomplished by a magnetic compass in larval urodeles. Previously, in urodeles this capability had been only demonstrated in adult eastern red-spotted newts, *N. viridescens* (Phillips 1986b; Deutschlander et al. 2000). With this new finding, up to four species of urodeles (Phillips 1977, 1986b; Diego-Rasilla 2003; Diego-Rasilla et al. 2005) have been proved to rely on magnetic cues for orientation; and this increasing evidence seems to point out that magnetic field perception is a wide-spread sensory capability among urodeles. The Earth’s magnetic field is likely to be a valuable source of directional information for amphibians under natural conditions, because it can be available when other types of orientation cues (e.g., celestial cues) are impaired by water turbidity, vegetation or clouds (Freake et al. 2002).

Premetamorphic *T. boscai* larvae oriented bimodally toward both ends of the Y-axis (i.e., some individuals oriented toward shore, others toward deep water) and this

behaviour can be caused by multiple factors. The stage of development might be involved in this behaviour, because several studies have shown a clear, apparently highly adaptive, direction reversal in the *Y*-axis orientation of amphibians at the moment of metamorphosis (Goodyear and Altig 1971; Tomson 1972; Adler and Taylor 1980). In experiments carried out with salamanders of the genus *Ambystoma* (Tomson 1972; Taylor 1972; Adler and Taylor 1980), larvae oriented initially towards deep water but when metamorphosis took place they reversed their directional preferences to landward.

Results presented here may be explained in relation to these developmental differences in *Y*-axis orientation. Because larval *T. boscai* were tested in a premetamorphic stage, during gill reabsorption, the resulted bimodal distributions may be caused by a mix of individuals in water-driven and land-driven conditions.

During the training period, we observed clear differences in the habitat preferences of individuals, which segregated along the training tanks in a way related to their stage of development. Initially, premetamorphic larvae occupied preferentially the shaded deep end of the aquarium, whereas newts that completed metamorphosis during training tended to move toward the shore and occupy the shallow area, where newts were sometimes observed attempting to leave the water by climbing over the aquarium walls. However, these observed differences between premetamorphic larvae and fully metamorphosed newts were not shown in the results of the magnetic tests. Although premetamorphic larvae, the main group of tested individuals, oriented bimodally along the *Y*-axis, recently metamorphosed newts did not show a significant orientation. Presumably, this random distribution of metamorphs was a result of the small sample size ($n = 4$ and 3 metamorphosed newts for N–S and E–W training tanks, respectively) and it should not be considered as a conclusive result.

The training procedure could be an additional factor responsible for bimodal orientation. Larvae might have exhibited a bimodal orientation because of an inability to learn the direction of the two ends of the *Y*-axis (Deutschlander et al. 2000). Experiments carried out with *N. viridescens* showed that, although adult newts can oriented bimodally along the *Y*-axis after a few hours of training, they need longer times to be able to learn on which end of the *Y*-axis the shore is located, exhibiting unimodal orientation toward shore after 5–7 days of training (Phillips 1986b; Deutschlander et al. 2000). In our study, the 6 days of training might have allowed larval *T. boscai* to learn the *Y*-axis but it might not have been enough time to learn to distinguish between the location of the two ends of the axis. Intensive training may also increase the motivation of amphibians to orient unimodally (Adler and Taylor 1980; Freake et al. 2002). We employed a passive training procedure, leaving larvae undisturbed during the training period. However, other types of experimental designs, based on active training of individuals, such as netting larvae from the water once a day, placing them on the shore and allowing them to return to deep water, might result in unimodal orientation of larvae.

We can conclude that, although further research is needed to distinguish between the above explanations, the findings reported here provide the first direct experimental support for the use of a magnetic compass for *Y*-axis orientation in larval urodeles.

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References

- Able KP (1980) Mechanisms of orientation, navigation and homing. In: Gauthreaux SA (ed) *Animal migration, orientation and navigation*. Academic, New York, pp 283–373
- Adler K (1970) The role of extraoptic photoreception in amphibian rhythms and orientation: a review. *J Herpetol* 4:99–112
- Adler K (1976) Extraocular photoreception in amphibians. *Photochem Photobiol* 23:275–298
- Adler K, Taylor DH (1973) Extraocular perception of polarized light by orienting salamanders. *J Comp Physiol* 87:203–212
- Adler K, Taylor DH (1980) Melatonin and thyroxine: influence on compass orientation in salamanders. *J Comp Physiol A* 136:235–241
- Auburn JS, Taylor DH (1979) Polarized light perception and orientation in larval bullfrogs *Rana catesbeiana*. *Anim Behav* 27:658–668
- Barbadillo LJ, Lacomba JI, Pérez-Mellado V, Sancho V, López-Jurado LF (1999) *Anfibios y reptiles de la Península Ibérica, Baleares y Canarias*. GeoPlaneta, Barcelona
- Batschelet E (1981) *Circular statistics in biology*. Academic, London
- Braña F (1980) Notas sobre el género *Triturus*, Rafinesque 1815 (Amphibia, Caudata) I-Observaciones fenológicas y sobre el desarrollo larvario de *T. marmoratus*, *T. alpestris* y *T. helveticus*. *Bol Ci Nat IDEA* 26:211–220
- Caetano MH, Leclair R (1999) Comparative phenology and demography of *Triturus boscai* from Portugal. *J Herpetol* 33:192–202
- Deutschlander ME, Phillips JB, Borland SC (2000) Magnetic compass orientation in the eastern red-spotted newt, *Notophthalmus viridescens*: rapid acquisition of the shoreward axis. *Copeia* 2:413–419
- Díaz-Paniagua C (2004) Tritón ibérico – *Triturus boscai*. In: Carrascal LM, Salvador A (eds) *Enciclopedia Virtual de los Vertebrados Españoles*. Museo Nacional de Ciencias Naturales, Madrid, <http://www.vertebradosibericos.org>
- Diego-Rasilla FJ (2003) Homing ability and sensitivity to the geomagnetic field in the alpine newt, *Triturus alpestris*. *Ethol Ecol Evol* 15:251–259
- Diego-Rasilla FJ (2004) El sentido magnético y su uso en la orientación de los animales. In: Pereira D, Bárcena MA, Rubio I, Sesma J (eds) *Aproximación a las ciencias planetarias*. Aquilafuente 74. Ediciones Universidad de Salamanca, Salamanca, pp 269–297
- Diego-Rasilla FJ, Luengo RM (2002) Celestial orientation in the marbled newt (*Triturus marmoratus*). *J Ethol* 20:137–141, DOI 10.1007/s10164-002-0066-7
- Diego-Rasilla FJ, Luengo RM, Phillips JB (2005) Magnetic compass mediates nocturnal homing by the alpine newt, *Triturus alpestris*. *Behav Ecol Sociobiol* 58:361–365, DOI 10.1007/s00265-005-0951-5
- Dingle H (1996) *Migration: the biology of life on the move*. Oxford University Press, New York
- Ferguson DE, Landreth HF (1966) Celestial orientation of the fowler's toad *Bufo fowleri*. *Behaviour* 26:105–123
- Ferguson DE, Landreth HF, McKeon JP (1967) Sun compass orientation of the northern cricket frog, *Acris crepitans*. *Anim Behav* 15:45–53

- Freake MJ, Borland SC, Phillips JB (2002) Use of magnetic compass for Y-axis orientation in larval bullfrogs, *Rana catesbeiana*. *Copeia* 2:466–471
- Goodyear CP, Altig R (1971) Orientation of bullfrogs (*Rana catesbeiana*) during metamorphosis. *Copeia* 362–364
- Landreth HF, Ferguson DE (1968) The sun compass of Fowler's toad, *Bufo woodhousei fowleri*. *Behaviour* 30:27–43
- Lizana M, Ciudad MJ, Pérez-Mellado V (1989) Actividad, reproducción y uso del espacio en una comunidad de anfibios. *Trebal Soc Cat Ictiol Herp* 2:92–127
- Omland KS (1998) Orientation based on ambient directional information by red-spotted newts. *Behaviour* 135:757–775
- Phillips JB (1977) Use of the earth's magnetic field by orienting cave salamanders (*Eurycea lucifuga*). *J Comp Physiol A* 121:273–288
- Phillips JB (1986a) Two magnetoreception pathways in a migratory salamander. *Science* 233:765–767
- Phillips JB (1986b) Magnetic compass orientation in the eastern red-spotted newt (*Notophthalmus viridescens*). *J Comp Physiol A* 158:103–109
- Phillips JB, Borland S (1994) Use of a specialized magnetoreception system for homing by the eastern red-spotted newt *Notophthalmus viridescens*. *J Exp Biol* 188:275–291
- Rubens SM (1945) Cube surface coil for producing uniform magnetic field. *Rev Sci Instr* 16:243–245
- Sinsch U (1990a) Migration and orientation in anuran amphibians. *Ethol Ecol Evol* 2:65–79
- Sinsch U (1990b) The orientation behaviour of three toad species (genus *Bufo*) displaced from the breeding site. *Biol Physiol Amphib* 38:73–83
- Sinsch U (1991) The orientation behaviour of amphibians. *Herpetol J* 1:541–544
- Sinsch U (1992) Amphibians. In: Papi F (ed) *Animal homing*. Chapman & Hall, New York, pp 213–233
- Taylor DH (1972) Extra-optic photoreception and compass orientation in larval and adult salamanders (*Ambystoma tigrinum*). *Anim Behav* 20:233–236
- Taylor DH, Adler K (1973) Spatial orientation by salamanders using plane-polarized light. *Science* 181:285–287
- Taylor DH, Ferguson DE (1970) Extraoptic celestial orientation in the southern cricket frog *Acris gryllus*. *Science* 168:390–392
- Tomson OH (1972) Y-Axis orientation in larvae and juveniles of three species of *Ambystoma*. *Herpetologica* 28:6–9
- Wiltschko R, Wiltschko W (1995) *Magnetic orientation in animals*. Springer, Berlin Heidelberg New York