Use of a Magnetic Compass for Nocturnal Homing Orientation in the Palmate Newt, *Lissotriton helveticus*

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Abstract

Previous studies have shown that migrating palmate newts (*Lissotriton helveticus*) can rely on acoustic cues for orientation to breeding ponds. Nonetheless, although acoustic cues are reliable over relatively short distances, they are unlikely to account for the long-distance homing demonstrated in several other species of newts. Most individuals of *L. helveticus* migrate only a few hundred meters (Diego-Rasilla, F. J. & Luengo, R. M. 2007: Acoustic orientation in the palmate newt, *Lissotriton helveticus*. Behav. Ecol. Sociobiol. 61, 1329—1335), raising the possibility that this species may only utilize short-distance cues (Joly, P. & Miaud, C. 1993: How does a newt find its pond? The role of chemical cues in migrating newts (*Triturus alpestris*). Ethol. Ecol. Evol. 5, 447—455; Russell, A. P., Bauer, A. M. & Johnson, M. K. 2005: Migration of amphibians and reptiles: an overview of patterns and orientation mechanisms in relation to life history strategies. In: Migration of Organisms (Elewa, M. T., ed). Springer-Verlag, Berlin Heidelberg, pp. 151—203; Sinsch, U. 2006: Orientation and navigation in Amphibia. Mar. Freshw. Behav. Phy. 39, 65—71). Therefore, experiments were carried out to investigate the use of the geomagnetic field in the nocturnal homing orientation of *L. helveticus*. Tests were carried out at night in an outdoor circular arena, under total overcast sky that prevented access to celestial compass cues. Individual newts were tested in one of four symmetrical alignments of an earth-strength magnetic field. We studied the orientation behaviour of newts from two breeding ponds located 9.05 km west-southwest and 19 km east-northeast of the testing site. The distribution of magnetic bearings from both groups of newts exhibited significant orientation in the homeward direction. These findings indicate that palmate newts are capable of long-distance homing and are able to orient in the homeward direction at night using the magnetic compass as the sole source of directional (i.e., compass) information.

Introduction

Newts have proved to be an excellent model system for studies of short-distance homing. The risk of desiccation and predation (Russell et al. 2005), as well as the high costs of locomotion in urodele amphibians (Bennett & Licht 1974; Gatten et al. 1992), coupled with the high degree of accuracy in both the map and compass components of homing required to return to woodland ponds (Freake et al. 2006), make newts an excellent model for comparison with vertebrates that home over larger spatial

scales (e.g., birds and sea turtles). In earlier experiments, it has been shown that migrating palmate newts (*Lissotriton helveticus*) can use the calls of anurans with which they share a breeding pond as reference cues for orientation (Diego-Rasilla & Luengo 2007). Newts can discriminate the calls of a sympatric anuran species and these calls can help newts to orient towards breeding sites during dispersal and homing to breeding ponds (Diego-Rasilla & Luengo 2004, 2007; Pupin et al. 2007). However, even though acoustic cues are reliable over short distances, they are unlikely to account for the long-distance homing of newts (Diego-Rasilla & Luengo 2004, 2007), although they might improve the accuracy of orientation during the final approach of palmate newts to their breeding ponds (Diego-Rasilla & Luengo 2007). Similarly, olfactory cues may be used for short-distance homing, contributing to both the map and compass components of homing (McGregor & Teska 1989; Joly & Miaud 1993; Sinsch 2007). However, the utility of olfactory cues emanating from the breeding ponds is strongly influenced by wind direction, distance from the pond and turbulence at ground level and, for inhabitants of the forest floor, olfactory cues do not provide a reliable source of map or compass information for homing from unfamiliar sites (Baldocchi 1989). Like auditory cues, olfactory cues might improve the accuracy of orientation during the final approach of palmate newts to their breeding ponds, but most studies of newt homing orientation suggest that magnetic (Phillips 1986a, 1987; Phillips & Borland 1994; Diego-Rasilla 2003; Diego-Rasilla et al. 2005) and celestial cues (Landreth & Ferguson 1967; Diego-Rasilla & Luengo 2002; Diego-Rasilla 2003) are primary sources of compass information used for homing. Because both the map and compass components of homing may involve multiple cues (previous references) and amphibians have been shown to use alternate cues if the preferred cue is unavailable (Sinsch 1987; Diego-Rasilla et al. 2005; Russell et al. 2005), palmate newts are likely to rely on other sensory mechanisms for homing orientation in addition to the acoustic sense.

Although amphibian migrations may not encompass vast distances, they nonetheless require sophisticated behavioral and navigational mechanisms to undertake these repeated movements. Thus, orientation mechanisms are essential for migrant animals as following a direct course towards the goal decreases expenditure of energy and also the risk of desiccation and predation (Russell et al. 2005).

Long-distance homing ability (i.e., actual homing and/or homeward orientation after long-distance displacement) has been documented in five species of newts representing three different genera and, thus, appears to be wide spread in this group (*Taricha rivularis, Taricha granulosa, Notophthalmus viridescens, Triturus alpestris* and *Triturus marmoratus*; e.g., Twitty 1959; Twitty et al. 1966; Phillips 1986a, 1987; Phillips et al. 1995; Diego-Rasilla & Luengo 2002, 2004; Diego-Rasilla 2003; Diego-Rasilla et al. 2005). In addition, there is evidence for a magnetic sense in newts and other amphibians. Diverse amphibians can detect the geomagnetic field, and use the earth's magnetic field for orientation and navigation (Sinsch 2006). The use of the geomagnetic field would be essential in situations where other sources of positional (map) and directional (compass) cues, like olfactory (Joly & Miaud 1993) and celestial cues (Diego-Rasilla 2003; Diego-Rasilla et al. 2005), are unavailable.

The geomagnetic field has been shown to provide amphibians with both map and compass information; the magnetic vector provides a compass, and magnetic intensity and/or inclination play a role as a component of the navigational map (Fischer et al. 2001; Phillips et al. 2002a). For example, the eastern red-spotted newt, *N. viridescens*, has been shown to have two distinct magnetoreception mechanisms: (i) a light-dependent mechanism mediated by extraocular photoreceptors located in the pineal organ that provides a source of compass information (Phillips & Borland 1992a; Deutschlander et al. 1999a), and (ii) a non-light-dependent mechanism involved in the map component of homing (Phillips 1986a; Phillips & Borland 1994; Brassart et al. 1999; Phillips et al. 2002b).

Nonetheless, although magnetic compass orientation may be wide spread in urodeles, the use of the magnetic compass for the compass component of homing by urodeles has only been demonstrated in the eastern red-spotted newt, *N. viridescens* (Phillips 1986a, 1987; Phillips & Borland 1994; Phillips et al. 1995), and the alpine newt, *T. alpestris* (Diego-Rasilla 2003; Diego-Rasilla et al. 2005). In toads (*Bufo*), the relative importance of different sensory modalities (vision, audition and magnetic) varies considerably in different species (Sinsch 1987, 1990). As the palmate newt is the second urodele amphibian shown to use auditory cues for homing (Diego-Rasilla & Luengo 2004, 2007), and neither species shown to use auditory cues has been tested for the use of magnetic compass cues, it is interesting to determine whether auditory cues are used instead of magnetic

cues in *L. helveticus*, or whether both auditory and magnetic cues are used for homing, perhaps over different spatial scales.

Tests of alpine newts at night under overcast and partly cloudy skies have provided evidence for the use of a magnetic compass for the compass component of homing. Thus, alpine newts are able to orient in the homeward direction at night using the magnetic compass as the sole source of directional information (Diego-Rasilla et al. 2005). Experiments reported here were designed to determine whether palmate newts are also capable of long-distance homing using magnetic compass cues in the absence of celestial and auditory cues.

Methods

Adult palmate newts were collected for the experiments in 2005 and 2006. In 2005, newts were collected from a pond located 9.05 km southwest (232°) of the testing site, at the Saja-Besaya Natural Park (Cantabria, northern Spain; 43°13′56″N, 4°09′45″W; 382 m a.s.l.); this pond is situated in a mountainous area and surrounded by a thick forest of *Quercus robur* and *Fagus sylvatica*, as well as less abundant and dispersed bushes of *Ilex aquifolium*. In 2006, newts were collected from a pond located 19.0 km northeast (54°) of the testing site, in an agricultural landscape and surrounded by a meadow, at the locality of Escobedo de Camargo (Cantabria, northern Spain; 43°23′31″N, 3°53′41″W; 151 m a.s.l.). Newts were collected by dip netting from breeding ponds during their seasonal migratory periods. In the lowland area, palmate newts begin their migration to their breeding ponds in February, but large numbers of newts have not been found in the ponds until late March, whereas in the mountainous area their seasonal migratory period usually extends from late March to early May (Diego-Rasilla & Luengo 2007).

Twenty-four adult newts (18 males and 6 females) were captured in 2005 (7 May) between 16:00 and 16:30 (GMT). Thirty-eight adult newts (34 males and 4 females) were captured between 13:30 and 14:15 (GMT) in 2006 (10 April).

Newts were then placed in completely covered, air-tight plastic containers (31 × 21 × 17 cm) in which the water depth was 1 cm, kept inside an opaque polyamide backpack, ensuring total darkness and transported to the testing site by car. At the testing site, animals were held in open tanks (54 × 35 × 21 cm), in which the water depth was 1 cm, aligned on the north–south geomagnetic axis.

Water used in all the phases of the experiments came from the home ponds. In both years, tests began about 2 h after nightfall and newts were tested under total overcast sky, where the moon and stars were not visible at all. This ensured dim nocturnal light levels, which impeded the clear observation of newts inside the arena for a human observer, although not total darkness. Newts were kept in captivity for about 5 h in 2005 and for 7 h in 2006 between catching and the starting of tests. All of them were returned to their ponds after testing.

Testing protocols described by Diego-Rasilla et al. (2005) were used. Newts were tested individually in a visually symmetrical test arena (circular plastic container, 44 cm diameter, 24 cm high). After each trial, the arena was thoroughly cleaned to eliminate directional olfactory cues and then wiped dry using paper towels (Diego-Rasilla et al. 2005).

Just prior to testing, individual newts were placed for 5 min in opaque plastic containers (34 × 24 × 16 cm) in which the water depth was 1 cm. They were then put in the center of the arena beneath an opaque, cylindrical plastic container (9.5 cm diameter, 14.5 cm high) that served as a release device. They were held for 1 min to overcome the effects of handling before the release device was lifted, allowing them to move freely about the arena. To minimize disturbance during the experiments, the observers moved away from the arena, leaving each animal undisturbed for 5 min. Trials were discontinued when the observer returned to the arena if the newt had not yet reached the edge of the arena. The directional response of each newt was recorded by the moist trails that it left on the floor of the arena. In all cases, newts that left the central area moved directly from their initial position to the arena wall, tapped against the wall, and then clinging to the wall, proceeded to circle around the arena. Directional responses were recorded to 5° accuracy at the point where an animal first made contact with the wall.

Each palmate newt was tested only once in one of the four magnetic field conditions: the ambient magnetic field (magnetic north at North) and three altered fields (magnetic north rotated to East, South or West; Phillips 1986b; Diego-Rasilla et al. 2005). The three altered fields were produced by means of a doubly-wrapped cube surface coil (Rubens 1945; for a complete description see Phillips 1986b) surrounding the outside of the arena. An approximately equal number of newts were tested in each of the four magnetic field alignments. In both years, the order of the four horizontal fields (magnetic N = N,

S, E or W) was determined using a random number sequence. In 2005, the first individual was tested in magN = S, the next individual in magN = W, followed by one in magN = E and one in magN = N, whereas in 2006 the first individual was tested in magN = N, the next individual in magN = W, followed by one in magN = E and one in magN = S.

Testing was carried out double blind. These sequences were repeated until the tests were completed. One experimenter set the horizontal alignment of the field using remote switches, whereas the second experimenter carried in each newt from the tanks and recorded its directional response without knowing the alignment of the magnetic field. Thus, the same sequence of four magnetic field alignments was used for successive groups of four newts without the observer being aware of the magnetic field alignment. The sequence of fields was not revealed to the observer recording the newts' directional responses until after the experiment was completed.

To determine the relative role of magnetic and non-magnetic cues in the newts' orientation, the absolute or 'topographic' bearings were plotted without regard to the alignment of the magnetic field; the use of four symmetrical magnetic field alignments caused any non-magnetic contribution to the newts' orientation to cancel out. To examine the magnetic component of the newts' orientation, the distributions of bearings obtained in the four magnetic field alignments were plotted after first rotating the distributions so that the directions of magnetic north coincided, canceling out any non-magnetic contribution (Phillips 1986b; Diego-Rasilla et al. 2005). Pooling the magnetic bearings from an approximately equal number of newts tested in each of the four magnetic field alignments made it possible to factor out any consistent non-magnetic bias and retain only that component of the newts' orientation that was consistent response to the magnetic field (see Phillips 1986b).

Distributions of bearings were analysed using standard circular statistics (Batschelet 1981; Fisher 1995). Mean vector length was calculated by vector addition and tested for departure from a random distribution using the Rayleigh test.

Results

The distribution of topographic bearings of newts from the Natural Park of Saja-Besaya failed to show significant homeward orientation (235°, r = 0.011, n = 21, p = 0.998, Rayleigh test; Fig. 1a, Table 1). In contrast, the magnetic bearings were significantly homeward oriented (235°, r = 0.398, n = 21, p = 0.034, Rayleigh test), and the 95% confidence interval (CI) for the mean vector included the home pond direction of 232° (Fig. 1b, Table 1).

The topographic bearings of newts from Escobedo de Camargo were randomly distributed (247°, r = 0.201, n = 37, p = 0.226, Rayleigh test; Fig. 1c, Table 1). However, the magnetic bearings were significantly homeward oriented (40°, r = 0.305, n = 37, p = 0.031, Rayleigh test), and the 95% CI for the mean vector included the pond direction of 54° (Fig. 1d, Table 1).

Discussion

In a recent study of alpine newts (Diego-Rasilla et al. 2005), we showed that the relative contribution of magnetic and non-magnetic cues to the newts' nocturnal homing orientation can be assessed by testing newts in four symmetrical alignments of the magnetic field, while simultaneously allowing them to view the night time sky. In alpine newts tested under total overcast (i.e., conditions experienced by palmate newts in the present experiments) and under partly cloudy skies when the moon and large portions of the sky are obscured by clouds, the magnetic compass provided the primary source of directional information for nocturnal homing orientation (Diego-Rasilla et al. 2005). In the present experiments, the distributions of magnetic bearings from both populations of palmate newts exhibited significant orientation in the homeward direction, whereas the topographic (i.e., non-magnetic) bearings of both groups of newts were randomly distributed. These findings show that palmate newts are able to orient in the homeward direction at night using the magnetic compass as the sole source of directional information. Moreover, these newts exhibited homing orientation from testing sites 9.05 and 19 km away from their breeding ponds, distances well beyond their normal range of movement, documenting long-distance homing for the first time in *L. helveticus*.

As newts in the present study were deprived of directional information during displacements, they appear to have relied on map information, rather than path integration (i.e., route reversal), to determine the home direction. The most likely source of map information is the geomagnetic field, which has been shown to play a role in the map component of homing by another species of newt (Phillips et al. 2002b), although our experiments were not
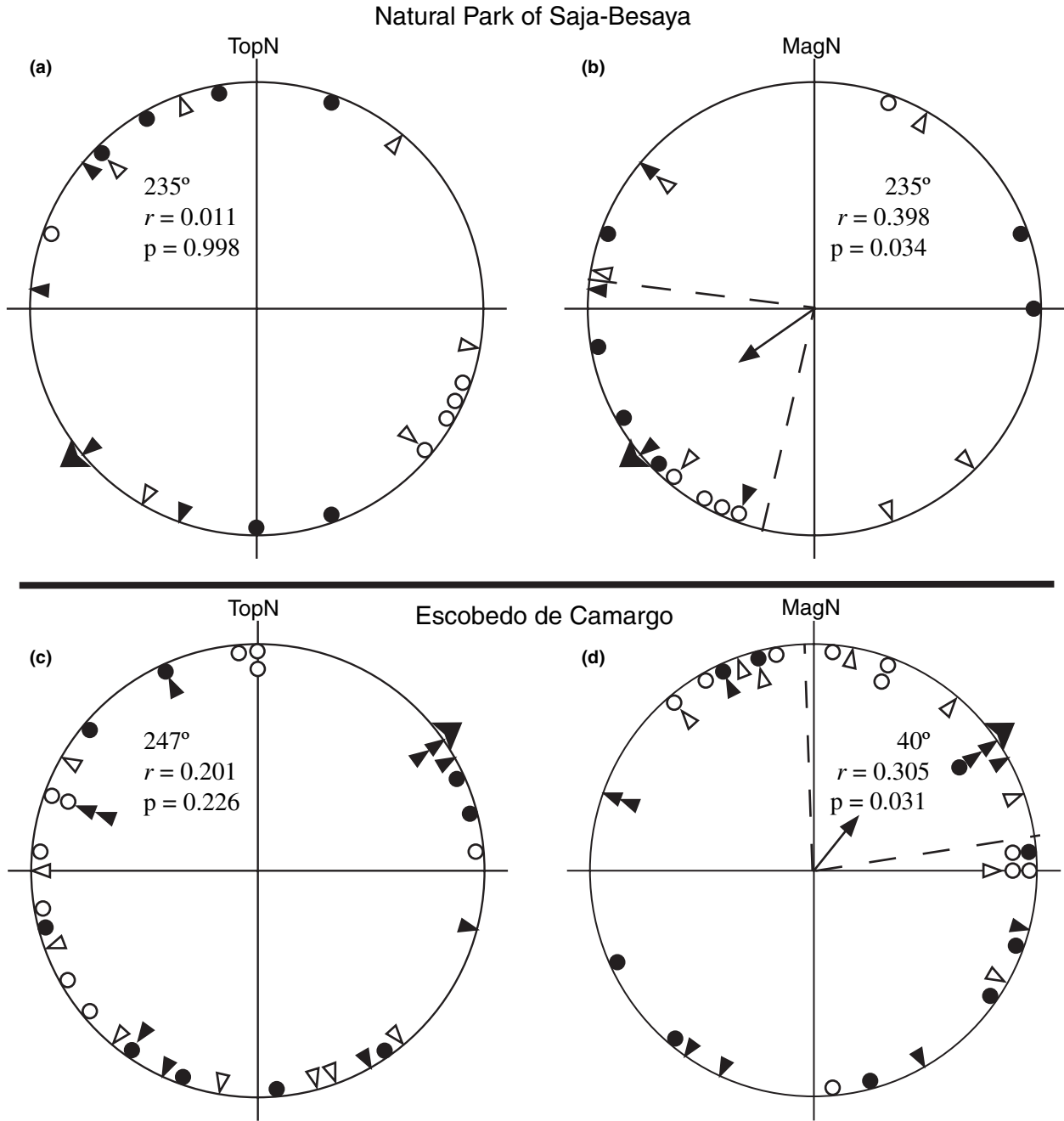
Fig. 1: Orientation responses of the palmate newts, *Lissotriton helveticus*. Each data point represents the direction of movement of an individual newt tested only once in one of four horizontal alignments of the magnetic field [i.e., magN = N (black triangles), magN = E (black circles), magN = S (open triangles), magN = W (open circles)]. Arrows at the center of each plot indicate the mean vector for each distribution. The length of each arrow is proportional to the mean vector length (r), with the radius of the circle corresponding to r = 1. Dashed lines indicate the 95% confidence intervals for the mean vectors. The arrowhead outside each circle indicates the magnetic bearing from the testing site to the home pond of the newts. Circular distributions on the left (a and c) show the topographic bearings of newts (i.e., the distribution of bearings with respect to topographic directions ignoring the alignment of the four test magnetic fields). Circular distributions on the right (b and d) show the magnetic bearings obtained in the four magnetic field alignments [i.e., bearings from the four testing fields were combined after first being rotated so magnetic north was at the top of the distribution (= 0°)].

Table 1: Directional responses of newts

	Test field (mN)	Topographic bearing	Magnetic bearing
Home direction = 232°	180°	340°	160°
	180°	100°	280°
	180°	315°	135°
	180°	210°	30°
	180°	130°	310°
	180°	40°	220°
	270°	130°	220°
	270°	110°	200°
	270°	120°	210°
	270°	115°	205°
	270°	290°	20°
	90°	20°	290°
	90°	180°	90°
	90°	330°	240°
	90°	315°	225°
	90°	350°	260°
	90°	160°	70°
	360°	275°	275°
	360°	310°	310°
	360°	200°	200°
	360°	230°	230°
Home direction = 54°	360°	290°	290°
	360°	55°	55°
	360°	205°	205°
	360°	335°	335°
	360°	55°	55°
	360°	105°	105°
	360°	60°	60°
	360°	215°	215°
	360°	290°	290°
	360°	150°	150°
	270°	230°	320°
	270°	290°	20°
	270°	260°	350°
	270°	360°	90°
	270°	360°	90°
	270°	290°	20°
	270°	275°	5°
	270°	240°	330°
	270°	85°	175°
	270°	355°	85°
	90°	75°	345°
	90°	200°	110°
	90°	255°	165°
	90°	65°	335°
	90°	310°	220°
	90°	215°	125°
	90°	335°	245°
	90°	175°	85°
	90°	145°	55°
	180°	160°	340°
	180°	250°	70°
	180°	270°	90°
	180°	140°	320°
	180°	190°	10°

Table 1: (Continued)

	Test field (mN)	Topographic bearing	Magnetic bearing
	180°	165°	345°
	180°	220°	40°
	180°	300°	120°

designed to address potential sources of map information.

The results of the present study reinforce previous findings on *T. alpestris* homing behavior. In both species, the magnetic compass seems to operate under dim nocturnal light levels (Diego-Rasilla et al. 2005), because heavily overcast skies not only eliminate potential sources of celestial compass information (e.g., stars, moon), but also decrease the overall light. A number of studies have shown that the mechanism of magnetoreception underlying the magnetic compass in newts involves a light-dependent process (Phillips & Borland 1992a, 1994; Deutschlander et al. 1999a; Ritz et al. 2002) and our present findings with *L. helveticus* provide additional evidence that nocturnal light levels, even in the absence of direct moon light, are sufficient for the magnetic compass to operate (see also Diego-Rasilla et al. 2005). It has been shown that the magnetic compasses used in homing orientation by alpine newts (Diego-Rasilla 2003) and in shoreward orientation by eastern red-spotted newts (Phillips & Borland 1992b) do not operate in total darkness, as also appears to be the case in migratory birds (Wiltschko & Wiltschko 2002). Even so, two recent studies have shown spontaneous alignment of alpine newts (Schlegel & Renner 2007) and eastern red-spotted newts (Schlegel 2007) with respect to the earth's magnetic field in total darkness, providing further evidence for a second, non-light-dependent magnetoreception mechanism in newts (Phillips et al. 2002b). This non-light-dependent mechanism appears to involve a permanent magnetic material, probably magnetite, and has been shown to play a role in the map (rather than compass) component of homing in the eastern red-spotted newt (Phillips 1986a; Phillips & Borland 1994; Brassart et al. 1999; Phillips et al. 2002b). It is important to emphasize that neither of the recent studies showing responses to the magnetic field in total darkness (Schlegel 2007; Schlegel & Renner 2007) were analyzing shoreward orientation or the compass component of homing orientation, as we did in the present work and a number of earlier studies in which

light-dependent magnetic compass orientation has been observed (Phillips & Borland 1992a; Deutschlander et al. 1999b; Phillips et al. 2001). Finally, although migratory birds have a light-dependent magnetic compass, they have recently been shown to respond to magnetic cues in the dark using a second, non-light-dependent magnetoreception mechanism with properties distinct from the magnetic compass (Stapput et al. 2008).

In summary, the findings reported here provide the first direct experimental support for the use of the geomagnetic field for the compass component of homing *L. helveticus*, providing additional evidence that magnetic compass orientation is wide spread in urodeles, and show for the first time a urodele amphibian that uses both auditory and magnetic cues for homing. Further studies are needed to determine whether *L. helveticus* uses celestial compass cues (i.e., polarized light and/or sun/moon position), as shown in other species of newts (Ferguson 1971; Taylor & Auburn 1978), and how the multiple sources of directional information are integrated in this species.

Acknowledgements

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