Sci Nat (2017) 104:13
DOI 10.1007/s00114-017-1439-7

ORIGINAL PAPER

Spontaneous magnetic alignment behaviour in free-living lizards

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Received: 6 November 2016 / Revised: 30 January 2017 / Accepted: 1 February 2017

Abstract Several species of vertebrates exhibit spontaneous longitudinal body axis alignment relative to the Earth's magnetic field (i.e., magnetic alignment) while they are performing different behavioural tasks. Since magnetoreception is still not fully understood, studying magnetic alignment provides evidence for magnetoreception and broadens current knowledge of magnetic sense in animals. Furthermore, magnetic alignment widens the roles of magnetic sensitivity in animals and may contribute to shed new light on magnetoreception. In this context, spontaneous alignment in two species of lacertid lizards (*Podarcis muralis* and *Podarcis lilfordi*) during basking periods was monitored. Alignments in 255 *P. muralis* and 456 *P. lilfordi* were measured over a 5-year period. The possible influence of the sun's position (i.e., altitude and azimuth) and geomagnetic field values corresponding to the moment in which a particular lizard was observed on lizards' body axis orientation was evaluated. Both species exhibited a highly significant bimodal orientation along the north-northeast and south-southwest magnetic axis. The evidence from this study suggests that free-living lacertid lizards exhibit magnetic alignment behaviour, since their body alignments cannot be explained by an effect of the sun's position. On the contrary, lizard orientations were significantly correlated with geomagnetic field values at the time of each observation. We suggest that this behaviour might provide lizards with a constant directional reference while they are sun basking. This directional reference might improve their mental map of space to accomplish efficient escape behaviour. This study is the first to provide spontaneous magnetic alignment behaviour in free-living reptiles.

Keywords Basking behaviour · Lacertidae · Lizards · Magnetic alignment · Magnetoreception

Introduction

As ectothermic animals, reptiles obtain heat from environmental sources being able to control their body temperatures within relatively narrow limits by behavioural means, even though ambient temperatures vary (Huey 1982; Stevenson 1985; Bauwens et al. 1996; Castilla et al. 1999). Behavioural thermoregulation involves microhabitat selection (Díaz 1991; Bauwens et al. 1996), adjustments in time of activity (Huey and Pianka 1977; Hertz 1992; Adolph and Porter 1993) and adoption of postures which can alter the rates of heating and cooling (Bauwens et al. 1990; Rocha and Bergallo 1990; Martín et al. 1995). Among behavioural mechanisms, adjustment of activity periods has been suggested to be the most critical in determining body temperature, whereas microhabitat selection seems to be more important than postural adjustments for controlling body temperature (Shine and Kearney 2001).

Basking in the sun is typically associated with behavioural thermoregulation in the wall lizard, *Podarcis muralis* (Braña 1991), as well as in the Balearic lizard, *Podarcis lilfordi* (Ortega et al. 2014). Most of active lacertid lizards adopt a basking posture in the sunshine during the early morning, while the occurrence of lizards basking reaches a minimum

Communicated by: Sven Thatje

Electronic supplementary material The online version of this article (doi:10.1007/s00114-017-1439-7) contains supplementary material, which is available to authorized users.

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during noon and increases again during late afternoon (Pérez-Mellado 1983; Braña 1991; Bauwens et al. 1996; Ortega et al. 2014). Otherwise, since posture and body axis orientation have an influence on heating rates and body temperatures in many species of lizards (Heath 1965; Barlett and Gates 1967; Waldschmidt 1980; Rocha and Bergallo 1990; Bauwens et al. 1996; Díaz et al. 1996), they should be expected to expose as extensive as possible an area of the body to the sun when basking. Therefore, a lizard's position should be perpendicular to the sun to maximize its exposed body surface area to gain heat, particularly in the early morning and the late afternoon but at midday as well (Muth 1977; Grant and Dunham 1988; Martín et al. 1995; Shine and Kearney 2001). For instance, lizards should be oriented east-west to maximize exposure to the midday sun's rays (Shine and Kearney 2001). Consequently, we should expect that directional body orientation (i.e., body alignment) of basking lizards is not random, although a few studies have shown that lizards' body alignment with respect to the sun does not significantly contribute to changes in body temperature (Muth 1977; Waldschmidt 1980; Martín et al. 1995; Bohórquez-Alonso et al. 2011).

Directional movements of reptiles, which are critical for locating food and mates and avoiding environmental extremes and predators (Vitt and Caldwell 2009), have been intensively studied (Ellis-Quinn and Simon 1991; Plotkin 2002; Russell et al. 2005; Vitt and Caldwell 2009; Southwood and Avens 2010). Reptiles integrate different sources of information to steer movements in space, including olfactory cues (Dundee and Miller III 1968; Chelazzi and Delfino 1986; Graham et al. 1996), celestial cues (Newcomer et al. 1974; Murphy 1981; Lawson and Secoy 1991; Freake 1999, 2001), visual landmarks (Graham et al. 1996) and the Earth's magnetic field, that has been extensively studied in turtles (Mathis and Moore 1988; Lohmann 1991; Lohmann and Lohmann 1993; Lohmann et al. 2004) and crocodiles (Rodda 1984a, b, 1985). Evidence of magnetic field sensitivity has been also found in the Philippine bent-toed gecko *Cyrtodactylus philippinicus* (Marek et al. 2010), and the diurnal agamid lizard *Pogona vitticeps* (Nishimura et al. 2010) has been proved to be sensitive to extremely low-frequency electromagnetic fields. Furthermore, *P. vitticeps* shows a light-dependent magnetoreceptive response involving the parietal eye (Nishimura et al. 2010).

It is noteworthy that amphibians (Meyer-Rochow 2014a) and reptiles (Meyer-Rochow 2014b) can use the e-vector direction of the polarized light to orient. Considerable evidence suggests that the sky polarization compass sense of amphibians and reptiles is mediated by an extraocular photoreceptor. The pineal complex itself is involved in amphibians (Taylor and Adler 1978; Taylor and Auburn 1978), while the parietal eye seems to be implicated in reptiles (Adler and Phillips 1985; Ellis-Quinn and Simon 1991; Freake 1999). Since the available evidence suggest parallels between light-dependent magnetoreception and polarized light detection in vertebrates (Phillips et al. 2001), similar photoreception mechanisms may mediate the light-dependent magnetic and polarized light compasses (Phillips et al. 2001).

Nonetheless, the study of body alignment of reptiles in diverse behavioural contexts has received little attention apart from a few studies about the orientation of the lizards' longitudinal body axis with respect to the sun (Martín et al. 1995; Bohórquez-Alonso et al. 2011), and no research has been done so far to study spontaneous magnetic alignment in free-living reptiles.

Magnetic compass orientation has been demonstrated advantageous in a wide variety of animals (Walker et al. 2002; Wiltschko and Wiltschko 2002, 2006). However, magnetic alignment, a non-goal-directed orientation of the body relative to the geomagnetic field (Begall et al. 2013), is a fixed directional response of unknown biological function and adaptive significance (Begall et al. 2013). Nevertheless, it has been suggested that magnetic alignment might play a role in increasing the accuracy of spatial orientation and/or enhancing selective attention to other sensory modalities (Phillips et al. 2010b, 2013; Červený et al. 2011; Begall et al. 2013; Landler et al. 2015).

An array of studies has shown magnetic alignment in insects (Roonwal 1958; Deoras 1960; Becker 1964; Becker and Speck 1964; Altmann 1981; Vácha et al. 2010; Painter et al. 2013) and in several species of vertebrates, including fish (Tesch and Lelek 1973; Becker 1974; Chew and Brown 1989; Hart et al. 2012), amphibians (Phillips et al. 2002; Schlegel 2007; Schlegel and Renner 2007), reptiles (Landler et al. 2015), birds (Hart et al. 2013a) and mammals (Begall et al. 2008, 2011; Burda et al. 2009; Červený et al. 2011; Hart et al. 2013b; Slaby et al. 2013). These studies offer compelling evidence for further roles of the magnetic sense apart from goal-directed orientation.

The aim of this study is to determine whether lizards exhibit spontaneous magnetic alignment behaviour when basking. Therefore, we recorded spontaneous alignment in two species of lacertid lizards (*Podarcis muralis* and *Podarcis lilfordi*) during basking periods, in diverse localities at different times of the day. We also considered sun azimuth, sun altitude and the Earth's magnetic field as possible factors affecting alignment of lizards.

Materials and methods

Subjects and study sites

Podarcis muralis (adult snout-to-vent length = 48–69 mm) is a small lacertid lizard widely distributed in Southern Europe with the north of the Iberian Peninsula being the southern edge of its range (Pérez-Mellado 1998a). Observations were gathered during 18 days from 2012 to 2014, through the months of April, July, August and October in Cantabria, northern Spain. Three study areas were selected, one in the Cieza Mountains (43° 13′ 46″ N, 4° 09′ 38″ W; elevation 308 m), one in the Valnera Mountains (43° 10′ 44″ N, 3° 40′ 36″ W; elevation 1185 m) and one in the Buelna Valley (43° 17′ 39″ N, 4° 04′ 31″ W; elevation 56 m).

Podarcis lilfordi is a medium-sized lacertid lizard endemic to the Balearic Islands (Spain). There are currently 23 subspecies of *P. lilfordi* living in the Cabrera Archipelago and coastal islets of Mallorca and Menorca (Pérez-Mellado 1998b). We studied *P. lilfordi lilfordi* from the Aire islet (39° 48′ 01″ N, 4° 17′ 26″ E; elevation 2 m), where this species attains a very high population density (3984 ± 524.1 individuals ha^{-1}) (Brown and Pérez-Mellado 1994). Aire islet is 1 n.m. apart from the SE coast of Menorca; it has a surface of 35 ha, mostly occupied by shrub halophyte vegetation (Ortega et al. 2014).

P. lilfordi is a melanistic lizard, with males (average snout-to-vent length 68.98 mm) larger than females (average snout-to-vent length 61.73 mm). The study was conducted during 11 days between April and August from 2012 to 2016.

Body temperature of lacertids depends on gaining radiative heat from the sun, either directly (heliothermy) or from a heated substrate (thigmothermy), although basking (i.e., heliothermy) is the most common mechanism for increasing body temperature in these species (Avery 1976; Braña 1991; Ortega et al. 2014). Both species are mostly active in the early morning and in the late afternoon, decreasing their activity during the hottest midday hours (Pérez-Mellado 1998a, b).

Analysis of body position of lizards

Transect lines were followed in study sites walking slowly through the area until an adult lizard basking was sighted. Recording were made by different observers in Cantabria and Balearic Islands, but all observations in a particular study site were done by the same person in the absence of wind and under a clear sky. Given the large size of the studied areas, repeated measurements of the same individual were avoided sampling each transect line only once; furthermore, *P. muralis* is a territorial species and density of *P. lilfordi* lizards was high enough to do repetition of the same individual unlikely. Observations were classified according to three different times of day: morning (sun azimuth 90–150°), noon (sun azimuth 151–210°) and afternoon (sun azimuth 211–270°).

Only head direction (angular data) of those lizards basking with their body perfectly aligned was recorded. However, since the lizards' alignments are bidirectional, we also considered data as axial in our analyses. The compass directions were estimated to the nearest 5° using a hand-held compass, and the exact time of the day (GMT) was recorded in each observation.

Geomagnetic values at the time of the observation and the lizards' orientation

Magnetic field values corresponding to the moment in which a particular lizard was observed were collected from Ebro Magnetic Observatory—Instituto Geográfico Nacional (Roquetes, Spain; 40° 49.261′, 0° 29.731′). These magnetic field values were true north component (X), true east component (Y), vertical component (Z) and total intensity (F), as well as rate of change (nT/min) of X, Y, Z and F.

To evaluate a possible relationship between the lizards' head direction (i.e., the specific direction in which one lizard's head points to when basking), as well as the lizards' body alignments (i.e., body axes) while basking, and the geomagnetic field values at the time of the observation, we performed a circular-linear correlation analysis.

The sun's position and the lizards' orientation

To evaluate a possible influence of the sun position (i.e., altitude and azimuth) on the lizards' body alignment we performed a circular correlation for these parameters. Sun altitude and azimuth data for the time of each observation were obtained from the US Naval Observatory (USNO).

Statistical procedures

The distributions of bearings were analysed using standard circular statistics (Batschelet 1981). Mean vectors were calculated by vector addition and tested for departure from a random distribution using the Rayleigh test. Watson's U^2 test and Mardia-Watson-Wheeler test were used to determine whether two or more than two distributions were identical, respectively (Batschelet 1981). Statistics for bimodal distributions were calculated by doubling each data value and reducing any greater than 360 using modulo arithmetic. Means for axial data are presented as XX°/XX°.

The circular correlation procedure and parametric significance test of Jammalamadaka and Sengupta (2001) were used to test for correlation between the sun's position and the axial directions (i.e., body alignments) of the lizards while basking. The circular-linear correlation coefficient (Mardia and Jupp 2000) was used to evaluate the correlation between the lizards' body alignment and the lizards' head direction while basking and the geomagnetic field values at the time of the observation. These circular-linear correlation coefficients range from zero to one, so there is no negative correlation. Correlation procedure and parametric significance test of Jammalamadaka and Sengupta were calculated with PAST 2.17 (Hammer et al. 2001). The remaining circular statistics were calculated with Oriana 2.0 (Kovach Computing).

Results

Common wall lizard (*Podarcis muralis*)

There were no differences between males and females in the specific direction in which a lizard's head points to when basking (i.e., angular data) (Watson's U^2 test: $U^2 = 0.149$, $P > 0.1$), and both groups were oriented randomly (Rayleigh test: males: 241°, $r = 0.108$, $P = 0.241$, $N = 134$; females: 25°, $r = 0.111$, $P = 0.189$, $N = 121$). Therefore, the mean vector of the pooled data was calculated and again, the analysis of the head direction while basking did not show a significant deviation from a random distribution (Rayleigh test: 325°, $r = 0.035$, $P = 0.737$, $N = 255$). Taken the study sites separately, lizards also showed a random distribution (Rayleigh test: Buelna Valley: 339°, $r = 0.068$, $P = 0.423$, $N = 184$; Valnera Mountains: 87°, $r = 0.059$, $P = 0.875$, $N = 39$; Cieza Mountains: 211°, $r = 0.17$, $P = 0.398$, $N = 32$). Furthermore, head direction at different times of day (i.e., morning, noon and afternoon) also showed a random distribution (Rayleigh test: morning: 343°, $r = 0.088$, $P = 0.372$, $N = 129$; noon: 275°, $r = 0.074$, $P = 0.676$, $N = 72$; afternoon: 141°, $r = 0.099$, $P = 0.589$, $N = 54$).

On the contrary, the axial data analyses showed a significant deviation from a random distribution in both males (Rayleigh test: 18°/198°, $r = 0.295$, $P = 8.33 \times 10^{-6}$, $N = 134$) and females (Rayleigh test: 25°/205°, $r = 0.284$, $P = 5.89 \times 10^{-5}$, $N = 121$). As body alignments did not differ significantly between males and females (Watson's U^2 test: $U^2 = 0.045$, $P > 0.5$), pooled data were used in subsequent analyses. Thus, the body axes of lizards showed a significant deviation from a random distribution (Rayleigh test: 21°/201° ± 9°, $P = 6.83 \times 10^{-10}$, $N = 255$; Table 1, Fig. 1a) with a preference for a north-northeast and south-southwest magnetic axis. Likewise, lizards aligned their body in a north-northeast and south-southwest axis regardless of the time of day (Mardia-Watson-Wheeler test: $W = 4.31$, $P = 0.366$; Table 1, Fig. 2). Also, there was no significant difference (Mardia-Watson-Wheeler test: $W = 1.621$, $P = 0.805$) between the lizards' body axes at different locations (Rayleigh test: Buelna Valley: 23°/203°, $r = 0.27$, $P = 1.56 \times 10^{-6}$, $N = 184$; Valnera Mountains: 18°/198°, $r = 0.3$, $P = 0.029$, $N = 39$; Cieza Mountains: 19°/199°, $r = 0.381$, $P = 0.009$, $N = 32$).

The lizards' body orientation was independent from sun position (Online Resource 1), because no significant correlation between the sun's azimuth and the lizards' body axes was found (circular correlation: $R = 0.031$, $T = 0.499$, $P = 0.618$, $N = 255$). No significant correlation was found between the sun's altitude and the lizards' body orientation (circular correlation: $R = 0.026$, $T = 0.4$, $P = 0.689$, $N = 255$; Online Resource 1). Thus, the sun can be excluded as a factor determining the alignment of lizards.

The lizards' head direction while basking was significantly correlated with the vertical component (Z) and total intensity (F) of the magnetic field, but we did not find any correlation between the geomagnetic values and the lizards' alignments (Table 2). On the contrary, the lizards' alignments were significantly correlated to the rate of change in X, Y and Z, whereas the lizards' head directions were not correlated to the rate of change in any of the geomagnetic values (Table 3).

Balearic lizard (*Podarcis lilfordi*)

Similarly to *P. muralis*, there were no differences between males and females in the specific direction in which their head points to when basking (Watson's U^2 test: $U^2 = 0.093$, $0.5 > P > 0.2$) and both groups were oriented randomly (Rayleigh test: males: 345°, $r = 0.102$, $P = 0.057$, $N = 275$; females: 49°, $r = 0.074$, $P = 0.371$, $N = 181$). Therefore, the mean vector of the pooled data was calculated and again, the analysis of the head direction while basking did not show a significant deviation from a random distribution (Rayleigh test: 4°, $r = 0.079$, $P = 0.059$, $N = 456$). In contrast, body alignments in both males (Rayleigh test: 22°/202°, $r = 0.228$, $P = 6.05 \times 10^{-7}$, $N = 275$) and females (Rayleigh test: 23°/203°, $r = 0.174$,

Table 1 Basic circular statistics for axial directions of *Podarcis muralis* and *Podarcis lilfordi* lizards (i.e., the lizards' body alignment) while basking

		α ± CI 95%	r	Circular SD	Rayleigh test, Z	Rayleigh test, P	N
Podarcis muralis	Pooled data (morning-noon-afternoon)	21°/201° ± 9°	0.288	45.222°	21.104	6.83×10^{-10}	255
	Morning (sun position 90–150°)	20°/200° ± 10°	0.351	41.476°	15.859	1.30×10^{-7}	129
	Noon (sun position 151–210°)	29°/209° ± 23°	0.206	50.915°	3.059	0.047	72
	Afternoon (sun position 211–270°)	20°/200° ± 21°	0.256	47.263°	3.551	0.029	54
Podarcis lilfordi	Pooled data (morning-noon-afternoon)	22°/202° ± 9°	0.207	50.87°	19.479	3.47×10^{-9}	456
	Morning (sun position 90–150°)	24°/204° ± 8°	0.343	41.91°	25.408	9.24×10^{-12}	216
	Noon (sun position 151–210°)	177°/357°	0.149	55.893°	1.178	0.308	53
	Afternoon (sun position 211–270°)	75° ± 41°	0.141	113.362°	3.73	0.024	187

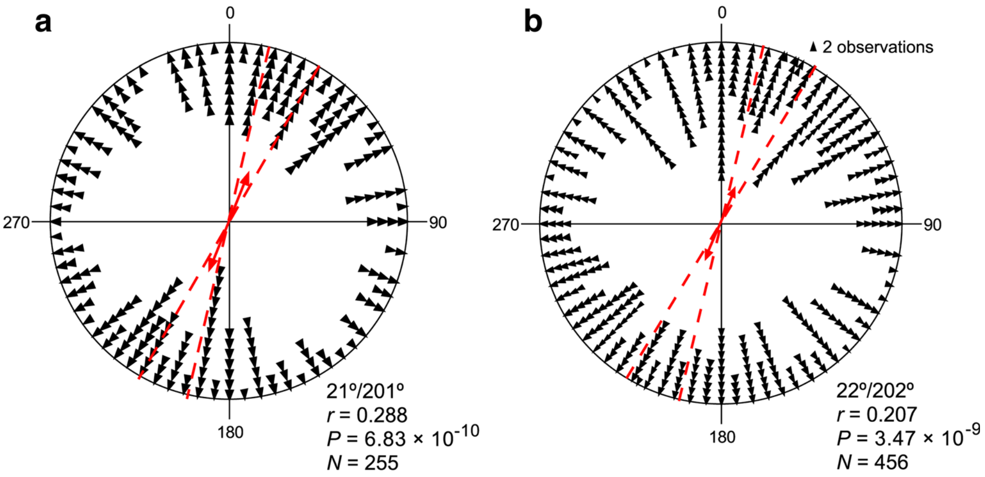

Fig. 1 Orientation of common Wall (**a**) and Balearic (**b**) lizards while basking. Each *triangle* represents the specific direction in which one common wall lizard's head (**a**) and two Balearic lizards' heads (**b**) pointed to during basking. The *double-headed arrow at the centre of the plot* indicates the mean bimodal axis for the distribution. The length of the *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

$P = 0.004$, $N = 181$) showed a highly significant bimodal orientation along the north-northeast and south-southwest magnetic axis. Body alignments did not differ significantly between both sexes (Watson's U^2 test: $U^2 = 0.062$, $P > 0.5$), and pooled data showed a highly significant north-northeast and south-southwest body alignment

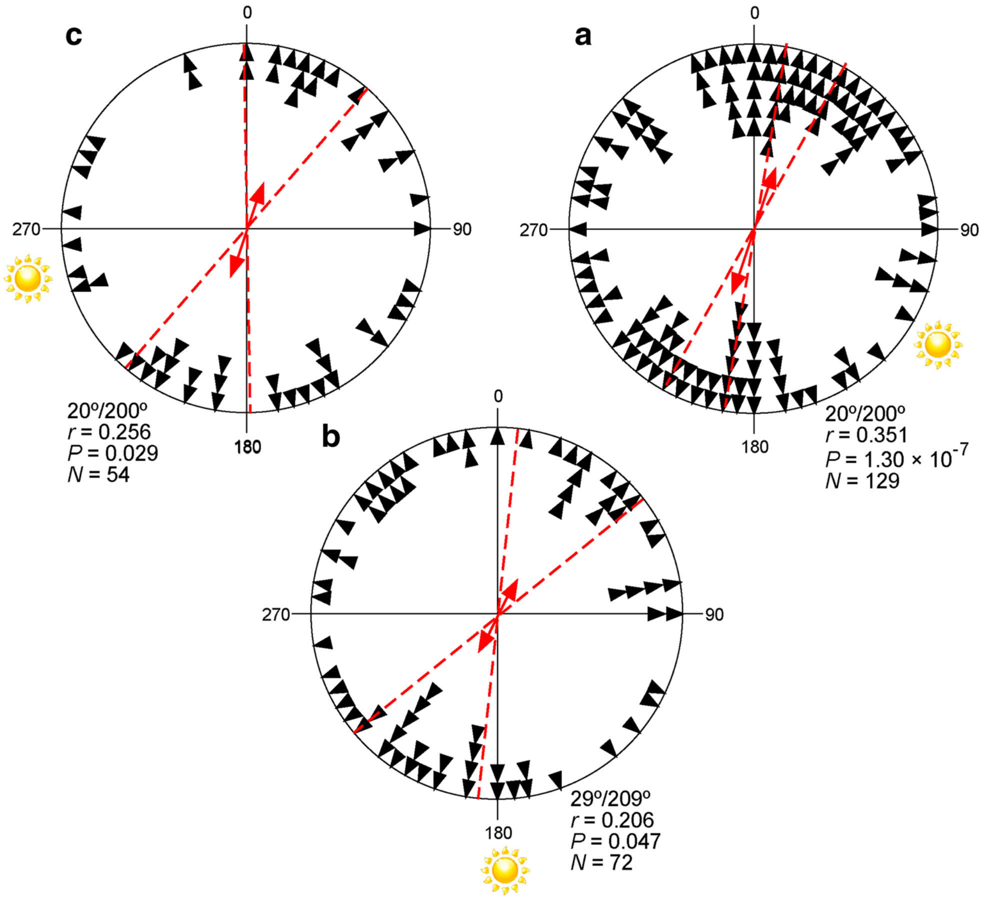

Fig. 2 Alignments of *Podarcis muralis* at different times of day. **a** Morning (sun position 90.1–149.9°; mean = 123°). **b** Noon (sun position 153.7–206.8°; mean = 179°). **c** Afternoon (sun position 211–265.3°; mean = 257°). Each *triangle* represents the specific direction in which one lizard's head points to when basking. Mean bimodal axis and its 95% confidence interval are also shown. The length of the *arrow* is proportional to the mean vector length (r), with the diameter of the *circle* corresponding to $r = 1$

Table 2 Circular-linear correlation between the lizards' axial alignment and the head direction while basking and the geomagnetic values at the time of the observations

		True north (X) component		True east (Y) component		Vertical (Z) component		Total intensity of the magnetic field (F)	
		r	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Podarcis muralis	Lizards' alignment ($N = 255$)	0.047	0.568	0.007	0.987	0.052	0.505	0.052	0.503
	Lizards' head direction ($N = 255$)	0.097	0.093	0.103	0.068	0.13	0.014	0.112	0.042
Podarcis lilfordi	Lizards' alignment ($N = 456$)	0.137	1.93×10^{-4}	0.113	0.003	0.195	3.18×10^{-8}	0.168	2.64×10^{-6}
	Lizards' head direction ($N = 456$)	0.097	0.015	0.108	0.005	0.103	0.008	0.106	0.006

(Rayleigh test: 22°/202° ± 8.9°, $P = 3.47 \times 10^{-9}$, $N = 456$; Table 1, Fig. 1b).

When considering separately different times of day, they exhibited a highly significant north-northeast and south-southwest body alignment during the morning (Table 1, Fig. 3). In contrast, Balearic lizards were randomly oriented during noon and were oriented unimodally during the afternoon with a slight preference for the eastern direction (Table 1, Fig. 3). Moreover, there were significant differences (Mardia-Watson-Wheeler test: $W = 19.933$, $P = 5.15 \times 10^{-4}$; Fig. 3) between the lizards' orientation at different times of day (i.e., morning, noon and afternoon).

We did not find any significant correlation between the sun's azimuth and a lizards' body axis (circular correlation: $R = 0.004$, $T = 0.077$, $P = 0.939$, $N = 456$; Online Resource 2) and between the sun's altitude and the lizards' body orientation (circular correlation: $R = -0.030$, $T = -0.649$, $P = 0.516$, $N = 456$; Online Resource 2),

All the correlations between the lizards' body alignment and the head direction while basking, and the geomagnetic field values at the time of the observation, were statistically significant (Table 2). Furthermore, the lizards' body alignments were significantly correlated to the rate of change in X, Y, Z and F. Similarly, the lizards' head directions were correlated with the rate of change in all geomagnetic values but X (Table 3).

Discussion

It is remarkable that the overall pattern of alignment is indistinguishable between *Podarcis muralis* (21°/201°, $N = 255$) and *Podarcis lilfordi* (22°/202°, $N = 456$) despite the complete disparity in ecological characteristics of both species (Pérez-Mellado 1998a, b). Our results show that this highly significant bimodal orientation along the north-northeast and south-southwest magnetic axis cannot be explained by an effect of solar azimuth and/or altitude, nor was it related to wind direction, since observations were carried out in the absence of wind. On the contrary, the orientation of the lizards was significantly correlated with geomagnetic field values at the time of each observation. Therefore, findings of this study indicate that basking lizards tend to align their body axis with respect to the geomagnetic field axis, thus exhibiting magnetic alignment (Wiltschko and Wiltschko 1995; Begall et al. 2013). Although magnetic alignment does not necessarily require an awareness of the geomagnetic field strength and the use of a magnetic compass for spatial long-distance orientation and navigation, it does prove magnetoreception (Begall et al. 2008). Therefore, our results provide the first evidence for spontaneous alignment behaviour in free-living reptiles and magnetoreception in lacertid lizards.

Parallel and perpendicular body orientations with respect to the sun in *Uta stansburiana* and *Sceloporus undulatus* were

Table 3 Circular-linear correlation between the lizards' body alignment and the head direction while basking and the rate of change of the geomagnetic values at the time of the observations

		Rate of change dB_X/dt (nT/min)		Rate of change dB_Y/dt (nT/min)		Rate of change dB_Z/dt (nT/min)		Rate of change dB_F/dt (nT/min)	
		r	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Podarcis muralis	Lizards' alignment ($N = 255$)	0.157	0.002	0.117	0.032	0.115	0.036	0.086	0.157
	Lizards' head direction ($N = 255$)	0.051	0.519	0.108	0.054	0.096	0.1	0.075	0.247
Podarcis lilfordi	Lizards' alignment ($N = 456$)	0.088	0.03	0.152	3.01×10^{-5}	0.121	0.001	0.126	7.11×10^{-4}
	Lizards' head direction ($N = 456$)	0.064	0.161	0.113	0.003	0.104	0.007	0.092	0.021

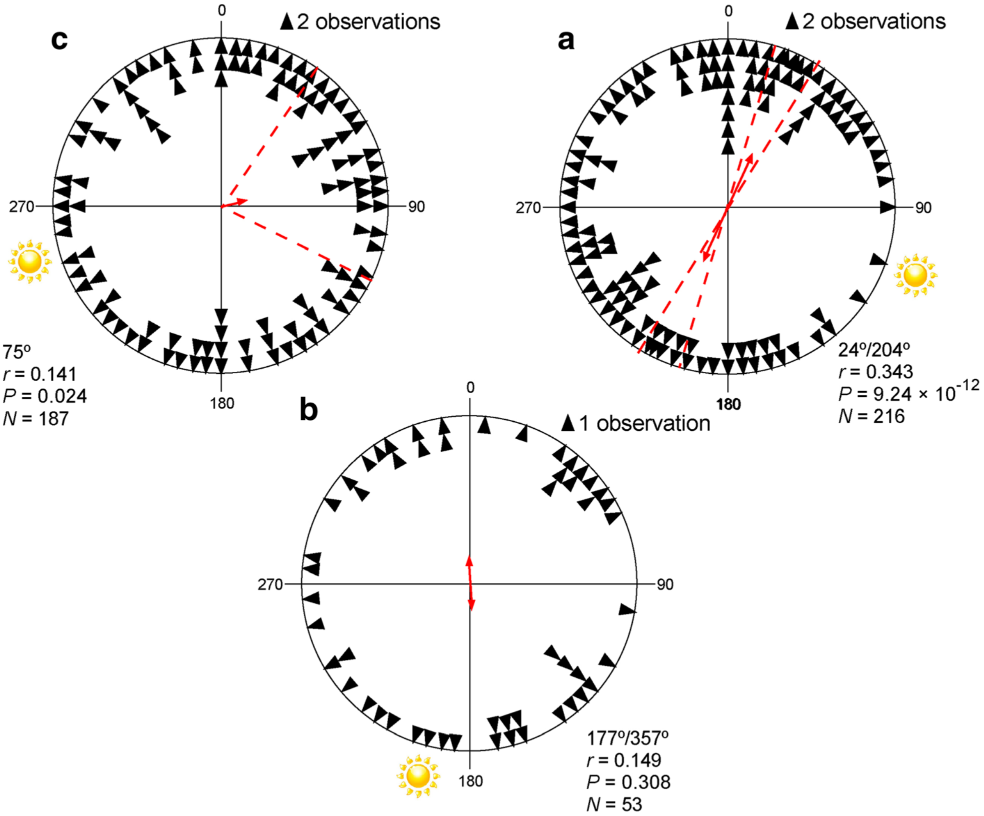

Fig. 3 Alignments of *Podarcis lilfordi* at different times of day. **a** Morning (sun position 90.5–147.2°; mean = 111°). **b** Noon (sun position 150.5–208.9°; mean = 196°). **c** Afternoon (sun position 210.5–288.5°; mean = 253°). Each *triangle* represents the specific direction in which one lizard's head points to when basking (two observations in (**a**) and (**c**) and one observation in (**b**). *Single-headed and double-headed arrows at the centre of each plot* indicate the mean vector or mean bimodal axis, respectively, 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 (*single-headed arrows*) or with the diameter of the *circle* corresponding to *r* = 1 (*doubled-headed arrow*)

suggested to be behavioural responses to the thermal environment in the early morning and the late afternoon (Waldschmidt 1980). Accordingly, perpendicular body alignment with respect to the sun increases the surface area exposed to solar radiation whereas parallel body alignment in relation to the sun might reduce the body surface exposed to the sun during the midday hours (Bohórquez-Alonso et al. 2011). However, using copper pipe models, Shine and Kearney (2001) found that operative temperatures (i.e., potential body temperatures that a reptile could achieve without thermoregulation) in the environment were not affected by orientation of the models with respect to the sun. Although, they also found that orientation to the midday sun's rays may be the least important compared to those in the morning and afternoon. Findings reported by Martín et al. (1995) in *Iberolacerta cyreni* and Bohórquez-Alonso et al. (2011) in *Gallotia galloti* fit well with those of Shine and Kearney (2001), because they found that the compass orientation of the lizards' longitudinal body axis relative to the sun did not affect their heating rates. Conversely, absorption of solar radiation may be regulated controlling the angle of incidence of solar radiation on their dorsal body surface through postural adjustments (Martín et al. 1995). Furthermore, our own results show that common wall lizards *P. muralis* and Balearic lizards *P. lilfordi* exhibited a body alignment which was independent from sun position (i.e., sun azimuth and sun altitude), thus excluding the sun as a factor determining the alignment of the lizards and indicating that the compass orientation of their body axis is not a primary factor involved in their thermoregulation process.

Body axis alignment in Balearic lizards, as well as head direction (i.e., the specific direction in which the lizards' head points to when basking), was clearly associated to the geomagnetic field values (i.e., *X*, *Y*, *Z* and *F*) at the time of each observation, whereas the relationship was not so striking in common wall lizards since only head direction while basking was significantly correlated with the vertical component (*Z*) and total intensity (*F*) of the magnetic field. On the other hand, body alignment and head direction of Balearic lizards were also noticeably associated to the rate of change in geomagnetic field values at the time of each observation, excepting the head direction and the rate of change in *X*; the common wall lizards' body alignments were associated to the rate of change in *X*, *Y* and *Z*. Taken together, these findings suggest that the lizards' magnetic alignments vary in accordance with variations in the geomagnetic field values. Obviously, this pattern of variation is stronger in *P. lilfordi* than in *P. muralis* but this might be due to the fact that Aire islet is closer to Ebro Magnetic Observatory (~342 km) than where the study sites in Cantabria are (~470 km); also, the latitude difference is only about 1° between Aire islet and Ebro Magnetic Observatory and actual geomagnetic field values experienced by *P. lilfordi* inhabiting Aire islet were more similar to those measured in

Ebro Magnetic Observatory than those at Cantabria study sites; this could explain the stronger association between orientations of Balearic lizards and geomagnetic field values.

Although the overall pattern of body alignment is neatly distributed in a north-northeast and south-southwest magnetic axis in both species of lizards, common wall lizards aligned their body according to this pattern regardless of the time of day (i.e., morning, noon and afternoon) whereas Balearic lizards were randomly oriented during the noon. It is noteworthy to mention that short-term temporal variation in the magnetic field tends to be more pronounced during the midday hours (Skiles 1985), and this could explain that Balearic lizards did not show a significant body axis alignment at noon, along with the fact that common wall lizard alignments were clustered less closely around the mean vector during the midday. Thus, temporal variations in the magnetic field increase the scatter in the lizards' body axis alignment.

Little is known about the biological meaning of magnetic alignment in vertebrates (Begall et al. 2013), but it has been suggested that magnetic alignment might assist animals in reading and organizing their mental map of space and may serve to encode their environment (Begall et al. 2008, 2013; Phillips et al. 2010b). Animals may obtain a constant directional reference maintaining a certain magnetic direction while they are performing different tasks (Begall et al. 2008, 2013; Schlegel 2008; Burda et al. 2009; Červený et al. 2011). Hence, the overall north-northeast and south-southwest magnetic alignment found in *P. muralis* and *P. lilfordi* may provide lizards with a constant directional reference while they are sun basking. A constant directional reference for spatial orientation might be useful to efficiently escape from predators (Begall et al. 2008; Obleser et al. 2016). A lizard basking to raise its body temperature exposes itself to an increased risk of predation because it exposes its whole dorsal body surface to the sun, and therefore, it becomes highly conspicuous to predators (Huey 1974; Herczeg et al. 2006). Hence, maintaining magnetic alignment while basking *P. muralis* and *P. lilfordi* get a constant directional reference which might improve their mental map of space to accomplish efficient escape behaviour.

Interestingly, both species of lacertid lizards exhibited magnetic alignment behaviour near the magnetic north-south axis but deviating significantly clockwise from magnetic north. This clockwise deviation from magnetic north is a typical feature in the vertebrates' axial magnetic alignment behaviour (Begall et al. 2013) that has been most likely attributed to a lateralization in the central nervous system processing of magnetic information (Malkemper et al. 2016). However, although a radical pair-based magnetoreceptor (radical pair mechanism) and a magnetite-based magnetoreceptor (magnetite-based mechanism) have been identified as candidates, magnetoreception mechanism underlying magnetic alignment in vertebrates is not clearly understood, and asymmetries at the receptor level should not be discarded as responsible of the clockwise deviation from magnetic north (Malkemper et al. 2016).

Although, both magnetoreception mechanisms differ in their functional properties (Ritz et al. 2000, 2004, 2010; Wiltschko and Wiltschko 2005; Rodgers and Hore 2009), the available evidence demonstrates that both mechanisms are not necessarily mutually exclusive since at least birds (Wiltschko et al. 2011; Wiltschko and Wiltschko 2013) and amphibians (Phillips 1986; Phillips and Borland 1994) use both types of mechanisms for various tasks.

The magnetite-based mechanism is involved in the fixed direction responses of birds, since they are unaffected by fields oscillating in the MHz range,and respond to the polarity of the magnetic field but not to inclination (Wiltschko et al. 2005, 2007; Wiltschko and Wiltschko 2005; Stapput et al. 2008). Likewise, magnetite-based magnetoreception mediates the fixed axis magnetic orientation in amphibians (Phillips et al. 2002). However, findings from other studies provide some evidence that a radical pair mechanism is involved in magnetic alignment behaviour (Landler et al. 2015; Malkemper et al. 2015). Yearling snapping turtles (*Chelydra serpentina*) show spontaneous alignment relative to the magnetic field that is affected by low-level radio frequency fields (i.e., fields oscillating in the MHz range), a trait indicating that a radical pair mechanism underlies magnetic alignment in this species of reptile (Henbest et al. 2004; Landler et al. 2015). Similarly, wood mice (*Apodemus sylvaticus*) have been shown to orient their nests along the north-northeast and south-southwest axis relative to the magnetic field using a magnetic sense based on a radical pair mechanism (Malkemper et al. 2015). These findings well agree with the idea that animals might use information obtained from the geomagnetic field to encode spatial information in their environment (Phillips et al. 2010b; Landler et al. 2015).

Retinal (Wiltschko et al. 2002, 2003) or pineal (Deutschlander et al. 1999a, b; Phillips et al. 2001) photoreceptors have been found to play a role in magnetoreception through a radical pair mechanism. In lizards, a light-dependent magnetoreceptive response involving the parietal eye has been shown in the Agamidae bearded dragon (*Pogona vitticeps*). The parietal eye, together with the pineal gland, forms the pineal complex of lizards. Although both the pineal gland and the parietal eye are photosensitive, the parietal eye is a complex photoreceptive structure, with a well-defined lens, cornea and retina (Tosini 1997). Reptilian parietal eye can discriminate between different wavelengths of light through chromatic antagonism; i.e., opposing responses consisting of short-wavelength-sensitive hyperpolarisation and green-sensitive depolarisation (Solessio and Engbretson 1993; Wada et al. 2012). Antagonistic spectral mechanism in photoreceptors of the parietal eye of lizards exhibits spectral features similar to those found in the pineal complex of amphibians (Dodt and Heerd 1962; Eldred and Nolte 1978; Korf et al.

1981) and is consistent with the properties of the light-dependent magnetic compass found in newts and frogs (Diego-Rasilla et al. 2010, 2013, 2015; Phillips et al. 2010a). In fact, short-wavelength and long-wavelength inputs to the magnetic compass of amphibians are mediated by extraocular photoreceptors located in the pineal complex (Deutschlander et al. 1999a, b; Phillips et al. 2001).

Considered in their entirety, previous findings suggest that spontaneous magnetic alignment in common wall lizards and Balearic lizards could be mediated by a radical pair mechanism involving the parietal eye. Further studies will need to be undertaken to examine the role of the parietal eye and the effects of wavelength of light on the lizards' magnetic alignment. In addition, further research studying separately the effect of polarity and inclination of the ambient field, using treatments with brief magnetic pulses to remagnetize magnetite particles or using magnetic fields oscillating in the low MHz range, will be useful to characterize the magnetoreception mechanism underlying magnetic alignment in lizards (Begall et al. 2013).

Acknowledgements The results presented in this paper rely on the data collected at Observatori de l'Ebre. We thank the Instituto Geográfico Nacional (Spain) for supporting its operation and the INTERMAGNET for promoting high standards of magnetic observatory practice (www.intermagnet.org). Field work in Balearic Islands was supported by the grants CGL2012-39850-CO2-02 and CGL2015-68139-C2-2-P from the Spanish Ministry of Economy and Competitivity.

Author contributions FJDR conceived the study and wrote the manuscript; FJDR, VPM and APC conducted all the experimental work and FJDR carried out the statistical analysis. All authors gave final approval for publication.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical standard statement All applicable institutional and/or national guidelines for the care and use of animals were followed.

Funding Field work in Balearic Islands carried out by VPM and APC was supported by the grants CGL2012-39850-CO2-02 and CGL2015-68139-C2-2-P from the Spanish Ministry of Economy and Competitivity. FJDR received no funding.

References

Adler K, Phillips JB (1985) Orientation in a desert lizard (*Uma notata*): time compensated compass movement and polarotaxis. J Comp Physiol A 156:547–552. doi:10.1007/BF00613978

Adolph SC, Porter WP (1993) Temperature, activity, and lizard life histories. Am Nat 142:273–295. doi:10.1086/285538

Altmann GA (1981) Untersuchung zur Magnetotaxis der Honigbiene, *Apis melliflica* L. Schadlingskd Pflanzenschutz Umweltschutz 54: 177–179

Avery RA (1976) Thermoregulation, metabolism and social behaviour in Lacertidae. In: Bellairs AA, Cox CB (eds) Morphology and biology of reptiles. Academic Press, London, pp 245–259

Barlett PN, Gates DM (1967) The energy budget of a lizard on a tree trunk. Ecology 48:315–322. doi:10.2307/1933120

Batschelet E (1981) Circular statistics in biology. Academic Press, New York

Bauwens D, Castilla AM, Damme RV, Verheyen RF (1990) Field body temperatures and thermoregulatory behavior of the high altitude lizard, *Lacerta bedriagae*. J Herpetol 24:88–91. doi:10.2307/1564296

Bauwens D, Hertz PE, Castilla AM (1996) Thermoregulation in a lacertid lizard: the relative contributions of distinct behavioral mechanisms. Ecology 77:1818–1830. doi:10.2307/2265786

Becker G (1964) Reaktion von Insekten auf Magnetfelder, elektrische Felder und atmospherics. Z Angew Entomol 54:75–88. doi:10.1111/j.1439-0418.1964.tb02917.x

Becker G (1974) Einfluss des Magnetfelds auf das Richtungsverhalten von Goldfischen. Naturwissenschaften 61:220–221. doi:10.1007/BF00599929

Becker G, Speck U (1964) Untersuchungen ueber die Magnetfeldorientierung von Dipteren. Z Vergl Physiol 49:301–340. doi:10.1007/BF00302681

Begall S, Burda H, Červený J, Gerter O, Neef-Weisse J, Němec P (2011) Further support for the alignment of cattle along magnetic field lines: reply to Hert et al. J Comp Physiol A 197:1127–1133. doi:10.1007/s00359-011-0674-1

Begall S, Červený J, Neef J, Vojtech O, Burda H (2008) Magnetic alignment in grazing and resting cattle and deer. Proc Natl Acad Sci U S A 105:13451–13455. doi:10.1073/pnas.0803650105

Begall S, Malkemper EP, Červený J, Němec P, Burda H (2013) Magnetic alignment in mammals and other animals. Mamm Biol 78:10–20. doi:10.1016/j.mambio.2012.05.005

Bohórquez-Alonso ML, Molina-Borja M, Font E (2011) Activity and body orientation of *Gallotia galloti* in different habitats and daily times. Amphibia-Reptilia 32:93–103. doi:10.1163/017353710X542994

Braña F (1991) Summer activity patterns and thermoregulation in the wall lizard, *Podarcis muralis*. Herpetol J 1:544–549

Brown RP, Pérez-Mellado V (1994) Ecological energetics and food acquisition in dense Menorcan islet populations of the lizard *Podarcis lilfordi*. Funct Ecol 8:427–434. doi:10.2307/2390065

Burda H, Begall S, Červený J, Neef J, Nemec P (2009) Extremely low-frequency electromagnetic fields disrupt magnetic alignment of ruminants. Proc Natl Acad Sci U S A 106:5708–5713. doi:10.1073/pnas.0811194106

Castilla AM, Damme RV, Bauwens D (1999) Field body temperatures, mechanisms of thermoregulation and evolution of thermal characteristics in lacertid lizards. Natura Croatica 8:253–274

Červený J, Begall S, Koubek P, Nováková P, Burda H (2011) Directional preference may enhance hunting accuracy in foraging foxes. Biol Letters 7:355–357. doi:10.1098/rsbl.2010.1145

Chelazzi G, Delfino G (1986) A field test on the use of olfaction in homing by *Testudo hermanni* (Reptilia: Testudinidae). J Herpetol 20:451–455. doi:10.2307/1564513

Chew GL, Brown GE (1989) Orientation of rainbow trout (*Salmo gairdneri*) in normal and null magnetic fields. Can J Zool 67:641–643. doi:10.1139/z89-092

Deoras PJ (1960) Some observations on the termites of Bombay. In: Termites in the humid tropics, vol Proc New Delhi Symp 1960. UNESCO, Paris, New Delhi, pp 101–103

Deutschlander ME, Borland SC, Phillips JB (1999a) Extraocular magnetic compass in newts. Nature 400:324–325. doi:10.1038/22450

Deutschlander ME, Phillips JB, Borland SC (1999b) The case for light-dependent magnetic orientation in animals. J Exp Biol 202:891–908

Díaz JA (1991) Temporal patterns of basking behaviour in a Mediterranean lacertid lizard. Behaviour 118:1–14. doi:10.1163/156853991X00166

Díaz JA, Bauwens D, Asensio B (1996) A comparative study of the relation between heating rates and ambient temperatures in lacertid lizards. Physiol Zool 69:1359–1383

Diego-Rasilla FJ, Luengo RM, Phillips JB (2010) Light-dependent magnetic compass in Iberian green frog tadpoles. Naturwissenschaften 97:1077–1088. doi:10.1007/s00114-010-0730-7

Diego-Rasilla FJ, Luengo RM, Phillips JB (2013) Use of a light-dependent magnetic compass for y-axis orientation in European common frog (*Rana temporaria*) tadpoles. J Comp Physiol A 199: 619–628. doi:10.1007/s00359-013-0811-0

Diego-Rasilla FJ, Luengo RM, Phillips JB (2015) Evidence of light-dependent magnetic compass orientation in urodele amphibian larvae. Behav Process 118:1–7. doi:10.1016/j.beproc.2015.05.007

Dodt E, Heerd E (1962) Mode of action of pineal nerve fibers in frogs. J Neurophysiol 25:405–429

Dundee H, Miller M III (1968) Aggregative behavior and habitat conditioning by the prairie ringneck snake, *Diadophis punctatus arnyi*. Tulane Stud Zool Bot 15:41–58

Eldred WD, Nolte J (1978) Pineal photoreceptors: evidence for a vertebrate visual pigment with two physiologically active states. Vis Res 18:29–32

Ellis-Quinn BA, Simon CA (1991) Lizard homing behavior: the role of the parietal eye during displacement and radio-tracking, and time-compensated celestial orientation in the lizard *Sceloporus* jarrovi. Behav Ecol Sociobiol 28:397–407. doi:10.1007/BF00164121

Freake MJ (1999) Evidence for orientation using the e-vector direction of polarised light in the sleepy lizard *Tiliqua rugosa*. J Exp Biol 202: 1159–1166

Freake MJ (2001) Homing behaviour in the sleepy lizard (*Tiliqua rugosa*): the role of visual cues and the parietal eye. Behav Ecol Sociobiol 50:563–569. doi:10.1007/s002650100387

Graham T, Georges A, McElhinney N (1996) Terrestrial orientation by the eastern long-necked turtle, *Chelodina longicollis*, from Australia. J Herpetol 30:467–477. doi:10.2307/1565689

Grant BW, Dunham AE (1988) Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami*. Ecology 69: 167–176. doi:10.2307/1943171

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: Paleontological statistics software package for education and data analysis. Palaeontol Electron 4:9 pp

Hart V, Kušta T, Němec P, Bláhová V, Ježek M, Nováková P, Begall S, Cervený J, Hanzal V, Malkemper EP, Stípek K, Vole C, Burda H (2012) Magnetic alignment in carps: evidence from the Czech Christmas fish market. PLoS One 7:e51100. doi:10.1371/journal.pone.0051100

Hart V, Malkemper EP, Kušta T, Begall S, Nováková P, Hanzal V, Pleskač L, Ježek M, Policht R, Husinec V, Cervený J, Burda H (2013a) Directional compass preference for landing in water birds. Front Zool 10:38. doi:10.1186/1742-9994-10-38

Hart V, Nováková P, Malkemper EP, Begall S, Hanzal V, Ježek M, Kušta T, Němcová V, Adámková J, Benediktová K, Cervený J, Burda H (2013b) Dogs are sensitive to small variations of the Earth's magnetic field. Front Zool 10:80. doi:10.1186/1742-9994-10-80

Heath JE (1965) Temperature regulation and diurnal activity in horned lizards. Univ Cal Pub Zool 64:97–136

Henbest KB, Kukura P, Rodgers CT, Hore PJ, Timmel CR (2004) Radio frequency magnetic field effects on a radical recombination reaction: a diagnostic test for the radical pair mechanism. J Am Chem Soc 126:8102–8103. doi:10.1021/ja048220q

Herczeg G, Gonda A, Saarikivi J, Merilä J (2006) Experimental support for the cost-benefit model of lizard thermoregulation. Behav Ecol Sociobiol 60:405–414. doi:10.1007/s00265-006-0180-6

Hertz PE (1992) Temperature regulation in Puerto Rican Anolis lizards: a field test using null hypotheses. Ecology 73:1405–1417. doi:10.2307/1940686

Huey RB (1974) Behavioral thermoregulation in lizards: importance of associated costs. Science 184:1001–1003

Huey RB (1982) Temperature, physiology, and the ecology of reptiles. In: Gans C, Pough FH (eds) Biology of the Reptilia, Physiology (C). Academic Press, London, vol 12 pp 25–91

Huey RB, Pianka ER (1977) Seasonal variation in thermoregulatory behavior and body temperature of diurnal Kalahari lizards. Ecology 58:1066–1075. doi:10.2307/1936926

Jammalamadaka SR, Sengupta A (2001) Topics in circular statistics. World Scientific Publishing Co, Singapore

Korf HW, Liesner R, Meissl H, Kirk A (1981) Pineal complex of the clawed toad, *Xenopus laevis* Daud.: structure and function. Cell Tissue Res 216:113–130

Landler L, Painter MS, Youmans PW, Wa H, Phillips JB (2015) Spontaneous magnetic alignment by yearling snapping turtles: rapid association of radio frequency dependent pattern of magnetic input with novel surroundings. PLoS One 10:e0124728. doi:10.1371/journal.pone.0124728

Lawson PA, Secoy DM (1991) The use of solar cues as migratory orientation guides by the plains garter snake, *Thamnophis radix*. Can J Zool 69:2700–2702. doi:10.1139/z91-380

Lohmann KJ (1991) Magnetic orientation by hatchling loggerhead sea turtles (*Caretta caretta*). J Exp Biol 155:37–49

Lohmann KJ, Lohmann CMF (1993) A light-independent magnetic compass in the leatherback sea turtle. Biol Bull 185:149–151. doi:10.2307/1542138

Lohmann KJ, Lohmann CMF, Ehrhart LM, Bagley DA, Swing T (2004) Geomagnetic map used in sea-turtle navigation. Nature 428:909–910. doi:10.1038/428909a

Malkemper EP, Eder SHK, Begall S, Phillips JB, Winklhofer M, Hart V, Burda H (2015) Magnetoreception in the wood mouse (*Apodemus sylvaticus*): influence of weak frequency-modulated radio frequency fields. Scientific Reports 4:9917. doi:10.1038/srep09917

Malkemper EP, Painter MS, Landler L (2016) Shifted magnetic alignment in vertebrates: evidence for neural lateralization? J Theor Biol 399: 141–147. doi:10.1016/j.jtbi.2016.03.040

Mardia KV, Jupp PE (2000) Directional statistics. Wiley, New York

Marek C, Bissantz N, Curio E, Siegert A, Tacud B, Ziggel D (2010) Spatial orientation of the Philippine bent-toed gecko (*Cyrtodactylus philippinicus*) in relation to its home range. Salamandra 46:93–97

Martín J, López P, Carrascal LM, Salvador A (1995) Adjustment of basking postures in the high-altitude Iberian rock lizard (*Lacerta monticola*). Can J Zool 73:1065–1068. doi:10.1139/z95-126

Mathis A, Moore FR (1988) Geomagnetism and the homeward orientation of the box turtle, *Terrapene carolina*. Ethology 78:265–274. doi:10.1111/j.1439-0310.1988.tb00238.x

Meyer-Rochow VB (2014a) Polarization sensitivity in amphibians. In: Horváth G (ed) Polarized light and polarization vision in animal sciences. Springer-Verlag, Berlin Heidelberg, pp 249–263. doi:10.1007/978-3-642-54718-8_10

Meyer-Rochow VB (2014b) Polarization sensitivity in reptiles. In: Horváth G (ed) Polarized light and polarization vision in animal sciences. Springer-Verlag, Berlin Heidelberg, pp 265–274. doi:10.1007/978-3-642-54718-8_11

Murphy PA (1981) Celestial compass orientation in juvenile american alligators (*Alligator mississippiensis*). Copeia 1981:638–645. doi:10.2307/1444569

Muth A (1977) Thermoregulatory postures and orientation to the sun: a mechanistic evaluation for the zebra-tailed lizard *Callisaurus draconoides*. Copeia 1977:710–720. doi:10.2307/1443171

Newcomer RT, Taylor DH, Guttman SI (1974) Celestial orientation in two species of water snakes (*Natrix sipedon* and *Regina septemvittata*). Herpetologica 30:194–200

Nishimura T, Okano H, Tada H, Nishimura E, Sugimoto K, Mohri K, Fukushima M (2010) Lizards respond to an extremely low-frequency electromagnetic field. J Exp Biol 213:1985–1990. doi:10.1242/jeb.031609

Obleser P, Hart V, Malkemper EP, Begall S, Holá M, Painter MS, Červený J, Burda H (2016) Compass-controlled escape behavior in roe deer. Behav Ecol Sociobiol 70:1345–1355. doi:10.1007/s00265-016-2142-y

Ortega Z, Pérez-Mellado V, Garrido M, Guerra C, Villa-García A, Alonso-Fernández T (2014) Seasonal changes in thermal biology of *Podarcis lilfordi* (Squamata, Lacertidae) consistently depend on habitat traits. J Therm Biol 39:32–39. doi:10.1016/j.jtherbio.2013.11.006

Painter MS, Dommer DH, Altizer WW, Muheim R, Phillips JB (2013) Spontaneous magnetic orientation in larval *Drosophila* shares properties with learned magnetic compass responses in adult flies and mice. J Exp Biol 216:1307–1316. doi:10.1242/jeb.077404

Pérez-Mellado V (1983) Activity and thermoregulation patterns in two species of Lacertidae: *Podarcis hispanica* (Steindachner, 1870) and *Podarcis bocagei* (Seoane, 1884). Cienc Biol Ecol Syst 5:5–12

Pérez-Mellado V (1998a) *Podarcis muralis* (Laurenti, 1768). In: Ramos MA et al. (eds) Fauna Ibérica. Museo Nacional de Ciencias Naturales, CSIC, Madrid, vol 10 pp 283–294

Pérez-Mellado V (1998b) *Podarcis lilfordi* (Günther, 1874). In: Ramos MA et al. (eds) Fauna Ibérica., Museo Nacional de Ciencias Naturales, CSIC, Madrid, vol 10 pp 272–282

Phillips JB (1986) Two magnetoreception pathways in a migratory salamander. Science 233:765–767

Phillips JB, Borland SC (1994) Use of a specialized magnetoreception system for homing by the eastern red-spotted newt *Notophthalmus viridescens*. J Exp Biol 188:275–291

Phillips JB, Borland SC, Freake MJ, Brassart J, Kirschvink JL (2002) 'Fixed-axis' magnetic orientation by an amphibian: non-shoreward-directed compass orientation, misdirected homing or positioning a magnetite-based map detector in a consistent alignment relative to the magnetic field? J Exp Biol 205:3903–3914

Phillips JB, Deutschlander ME, Freake MJ, Borland SC (2001) The role of extraocular photoreceptors in newt magnetic compass orientation: evidence for parallels between light-dependent magnetoreception and polarized light detection in vertebrates. J Exp Biol 204:2543–2552

Phillips JB, Jorge PE, Muheim R (2010a) Light-dependent magnetic compass orientation in amphibians and insects: candidate receptors and candidate molecular mechanisms. J R Soc Interface 7:S241–S256. doi:10.1098/rsif.2009.0459.focus

Phillips JB, Muheim R, Jorge PE (2010b) A behavioral perspective on the biophysics of the light-dependent magnetic compass: a link between directional and spatial perception? J Exp Biol 213:3247–3255. doi:10.1242/jeb.020792

Phillips JB, Youmans P, Muheim R (2013) Rapid learning of magnetic compass direction by C57BL/6 mice in a 4-armed 'plus' water maze. PLoS One 8:e73112. doi:10.1371/journal.pone.0073112

Plotkin PT (2002) Adult migrations and habitat use. In: Lutz PL, Musick J, Wyneken J (eds) The biology of sea turtles, CRC Press, vol 2. Boca Raton, FL, pp 225–241

Ritz T, Adem S, Schulten K (2000) A model for photoreceptor-based magnetoreception in birds. Biophys J 78:707–718. doi:10.1016/S0006-3495(00)76629-X

Ritz T, Ahmad M, Mouritsen H, Wiltschko R, Wiltschko W (2010) Photoreceptor-based magnetoreception: optimal design of receptor molecules, cells, and neuronal processing. J R Soc Interface 7:S135–S146. doi:10.1098/rsif.2009.0456.focus

Ritz T, Thalau P, Phillips JB, Wiltschko R, Wiltschko W (2004) Resonance effects indicate a radical-pair mechanism for avian magnetic compass. Nature 429:177–180. doi:10.1038/nature02534

Rocha CFD, Bergallo HG (1990) Thermal biology and flight distance of *Tropidurus oreadicus* (Sauria Iguanidade) in an area of Amazonian Brazil. Ethol Ecol Evol 2:263–268

Rodda GH (1984a) Homeward paths of displaced juvenile alligators as determined by radiotelemetry. Behav Ecol Sociobiol 14:241–246

Rodda GH (1984b) The orientation and navigation of juvenile alligators: evidence of magnetic sensitivity. J Comp Physiol A 154:649–658. doi:10.1007/BF01350218

Rodda GH (1985) Navigation in juvenile alligators. Z Tierpsychol 68:65–77. doi:10.1111/j.1439-0310.1985.tb00115.x

Rodgers CT, Hore PJ (2009) Chemical magnetoreception in birds: the radical pair mechanism. Proc Natl Acad Sci U S A 106:353–360. doi:10.1073/pnas.0711968106

Roonwal ML (1958) Recent work on termite research in India (1947–57). Trans Bose Res Inst 22:77–100

Russell AP, Bauer AM, Johnson MK (2005) Migration in amphibians and reptiles: an overview of patterns and orientation mechanisms in relation to life history strategies. In: Elewa AMT (ed) Migration of organisms. Climate. Geography. Ecology. Springer-Verlag, Berlin Heidelberg, pp 151–203. doi:10.1007/3-540-26604-6_7

Schlegel P (2007) Spontaneous preferences for magnetic compass direction in the American red-spotted newt, *Notophthalmus viridescens* (Salamandridae, Urodela). J Ethol 25:177–184. doi:10.1007/s10164-006-0016-x

Schlegel P, Renner H (2007) Innate preference for magnetic compass direction in the Alpine newt, *Triturus alpestris* (Salamandridae, Urodela)? J Ethol 25:185–193. doi:10.1007/s10164-006-0017-9

Schlegel PA (2008) Magnetic and other non-visual orientation mechanisms in some cave and surface urodeles. J Ethol 26:347–359. doi:10.1007/s10164-007-0071-y

Shine R, Kearney M (2001) Field studies of reptile thermoregulation: how well do physical models predict operative temperatures? Funct Ecol 15:282–288

Skiles DD (1985) The geomagnetic field: its nature, history and biological relevance. In: Kirschvink JL, Jones DS, MacFadden BJ (eds) Magnetite biomineralization and magnetoreception in organisms: a new biomagnetism. Plenum Press, New York, pp 43–102

Slaby P, Tomanova K, Vácha M (2013) Cattle on pastures do align along the north–south axis, but the alignment depends on herd density. J Comp Physiol A 199:695–701. doi:10.1007/s00359-013-0827-5

Solessio E, Engbretson GA (1993) Antagonistic chromatic mechanisms in photoreceptors of the parietal eye of lizards. Nature 364:442–445. doi:10.1038/364442a0

Southwood A, Avens L (2010) Physiological, behavioral, and ecological aspects of migration in reptiles. J Comp Physiol B 180:1–23. doi:10.1007/s00360-009-0415-8

Stapput K, Thalau P, Wiltschko R, Wiltschko W (2008) Orientation of birds in total darkness. Curr Biol 18:602–606. doi:10.1016/j.cub.2008.03.046

Stevenson RD (1985) The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. Am Nat 126:362–386

Taylor DH, Adler K (1978) The pineal body: site of extraocular perception of celestial cues for orientation in the tiger salamander (*Ambystoma tigrinum*). J Comp Physiol A 124:357–361. doi:10.1007/BF00661385

Taylor DH, Auburn J (1978) Orientation of amphibians by linearly polarized light. In: Schmidt-Koenig K, Keeton W (eds) Animal migration, navigation and homing. Springer-Verlag, Berlin, pp 334–346. doi:10.1007/978-3-662-11147-5_33

Tesch FW, Lelek A (1973) Directional behaviour of transplanted stationary and migratory forms of the eel, *Anguilla anguilla*, in a circular tank. Neth J Sea Res 7:46–52. doi:10.1016/0077-7579(73)90031-8

Tosini G (1997) The pineal complex of reptiles: physiological and behavioral roles. Ethol Ecol Evol 9:313–333. doi:10.1080/08927014.1997.9522875

Vácha M, Kvíčalová M, Půžová T (2010) American cockroaches prefer four cardinal geomagnetic positions at rest. Behaviour 147:425–440

Vitt LJ, Caldwell JP (2009) Herpetology: an introductory biology of amphibians and reptiles, 3rd edn. Academic Press, New York

Wada S, Kawano-Yamashita E, Koyanagi M, Terakita A (2012) Expression of UV-sensitive parapinopsin in the iguana parietal eyes and its implication in UV-sensitivity in vertebrate pineal-related organs. PLoS One 7:e39003. doi:10.1371/journal.pone.0039003

Waldschmidt S (1980) Orientation to the sun by the iguanid lizards *Uta stansburiana* and *Sceloporus undulatus*: hourly and monthly variations. Copeia 1980:458–462. doi:10.2307/1444522

Walker MM, Dennis TE, Kirschvink JL (2002) The magnetic sense and its use in long-distance navigation by animals. Curr Opin Neurobiol 12:735–744. doi:10.1016/S0959-4388(02)00389-6

Wiltschko R, Stapput K, Ritz T, Thalau P, Wiltschko W (2007) Magnetoreception in birds: different physical processes for two types of directional responses. HFSP J 1:41–48. doi:10.2976/1.2714294

Wiltschko R, Wiltschko W (1995) Magnetic orientation in animals. Springer-Verlag, Berlin, Heidelberg, New York. doi:10.1007/978-3-642-79749-1

Wiltschko R, Wiltschko W (2006) Magnetoreception. BioEssays 28:157–168. doi:10.1002/bies.20363

Wiltschko R, Wiltschko W (2013) The magnetite-based receptors in the beak of birds and their role in avian navigation. J Comp Physiol A 199:89–98. doi:10.1007/s00359-012-0769-3

Wiltschko W, Munro U, Ford H, Wiltschko R (2003) Lateralisation of magnetic compass orientation in silvereyes, *Zosterops lateralis*. Aust J Zool 51:1–6. doi:10.1071/ZO03022

Wiltschko W, Ritz T, Stapput K, Thalau P (2005) Two different types of light-dependent responses to magnetic fields in birds. Curr Biol 15:1518–1523. doi:10.1016/j.cub.2005.07.037

Wiltschko W, Traudt J, Gunturkun O, Prior H, Wiltschko R (2002) Lateralisation of magnetic compass orientation in a migratory birds. Nature 419:467–470. doi:10.1038/nature00958

Wiltschko W, Wiltschko R (2002) Magnetic compass orientation in birds and its physiological basis. Naturwissenschaften 89:445–452. doi:10.1007/s00114-002-0356-5

Wiltschko W, Wiltschko R (2005) Magnetic orientation and magnetoreception in birds and other animals. J Comp Physiol A 191:675–693. doi:10.1007/s00359-005-0627-7

Wiltschko W, Wiltschko R, Ritz T (2011) The mechanism of the avian magnetic compass. Procedia Chem 3:276–284. doi:10.1016/j.proche.2011.08.035