Polarized skylight does not calibrate the compass system of a migratory bat

Lindeke, O., Voigt, C. C., Ptersons, G., & Holland, R. A. (2015). Polarized skylight does not calibrate the compass system of a migratory bat. Biology Letters, 11(9).

Published in:
Biology Letters

Document Version:
Peer reviewed version

Polarized skylight does not calibrate the compass system of a migratory bat

Author names and affiliations

Oliver Lindecke[1,2,*], Christian C. Voigt[1,2], Gunārs Pētersons[3], Richard A. Holland[4]

[1] Leibniz Institute for Zoo and Wildlife Research, Evolutionary Ecology Research Group, Alfred-Kowalke-Str. 17, 10315, Berlin, Germany.

[2] Freie Universität Berlin, Department Animal Behaviour, Takustr. 3, 14195, Berlin, Germany

[3] Latvia University of Agriculture, Faculty of Veterinary Medicine, K. Helmaņa 8, LV-3004 Jelgava, Latvia

[4] School of Biological Sciences, Queen's University Belfast, Belfast BT9 7BL, UK.

*For correspondence: Oliver Lindecke (lindecke@izw-berlin.de)

Abstract

In a recent study, Greif et al. (2014) demonstrated a functional role of polarized light for a bat species confronted with a homing task. These non-migratory bats appeared to calibrate their magnetic compass by using polarized skylight at dusk, yet it is unknown if migratory bats also use these cues for calibration. During autumn migration, we equipped Nathusius' bats, *Pipistrellus nathusii*, with radio transmitters and tested if experimental animals exposed to a 90° rotated band of polarized light during dusk, would head in a different direction compared with control animals. After release, bats of both groups continued their journey in the same direction. This observation argues against the use of a polarization-calibrated magnetic compass by this migratory bat and questions that the ability of using polarized light for navigation is a consistent feature in bats. This finding matches with observations in some passerine birds that used polarized light for calibration of their magnetic compass before but not during migration.

Keywords

mammalian navigation, orientation, migration, Chiroptera, sensory ecology

Introduction

Animals from a broad taxonomic background extract directional information from a variety of environmental cues [1], including the sun [2], polarized light [3], stars [4] and the Earth’s magnetic field [5, 6]. In migrating passerine birds, these cues appear to be used hierarchically, in which one provides an absolute geographical reference that calibrates others, which are then used as a compass to take up the desired direction of orientation [7]. Disagreement persists as to whether the magnetic field [8-12], or polarized light [3, 13] provides this absolute geographical reference.

For bats, evidence from two species, one from Europe and one from North America, has indicated that non-migratory bats use a magnetic compass for orientation during homing [14]. Surprisingly for a strictly nocturnal mammal, this magnetic compass appears to be calibrated by sunset cues [15]. Also, it has been shown for one of these species that polarization cues at dusk are the crucial geographical reference for calibrating the magnetic compass [16]. A number of bat species migrate more than 1,000 km between summer and wintering areas [17, 18]. Such journeys inevitably require a suite of navigational cues to allow bats to locate their specific breeding grounds, stopover sites along the migratory route, and the preferred wintering roosts. Yet, to date studies of the navigational skills of migratory bats are lacking [19]. Here, we test for the first time the orientation of bats during autumn migration, specifically investigating whether they use the same mechanisms of compass calibration as non-migratory bats.

Material and methods

Pipistrellus nathusii is a long-distance European migratory bat [20]. Extensive banding studies have produced evidence of southwesterly migratory movements from Northeastern Europe during autumn and distances of up to 2,000 km [21]. At the peak of the migratory season in Latvia (between 13 and 22 August 2014), we caught 16 males and 24 females (all adult) at Pape Biological Station (56°09' N 21°03' E, Rucava Municipality, Latvia), using a funnel trap. Bats were kept in wooden boxes over periods of 7 to 16 days to avoid unsuitable release conditions under periods of poor weather. We did not anticipate any affect of this resting period on the outcome of our experiment, because all animals were exposed to the same conditions. Captive bats were fed individually with mealworms and had access to *ad libitum* water.

On the day of the experiment, any handling of test subjects was performed indoors in order to avoid exposure to polarized skylight. Prior to the treatment at dusk, bats were fed with up to 5 mealworms and water to promote activity and to counteract re-entering torpor. To test whether changing the polarization pattern of skylight affects heading of migratory flights, we fitted VHF radio transmitters (PicoPip AG379, BioTrack Ltd., Wareham, United Kingdom or LB-2N, Holohil Systems Ltd., Ottawa, Canada; 0.42 g) to the back of bats, using skin glue (Manfred Sauer GmbH Hautkleber, Lobbach, Germany). We hypothesized that experimental animals exposed to a 90° rotated band of polarized light during dusk, would head in a different direction compared with control animals. Previous experiments have indicated that such a shift results in a bimodal distribution, shifted +-90° from controls [3, 16]. During the experiment, bats were placed in the original experimental polarization boxes as described in [16], but see the supplement for a detailed description. Holding boxes were placed 50 m away from the funnel trap on a meadow offering a 360° free view of the horizon from 30 min before until 90 min after sunset, i.e. until the last visible post-sunset glow had vanished. Experimental evenings had stable weather with a light to moderate breeze (2–8 m/s) and 15–60% cloud cover and always a visible sunset. Boxes were oriented either with the vertically polarized windows 90° away from the sun, corresponding to the natural polarization direction (PN, in a North-South axis) or they were shifted 90° so that horizontally polarized windows were oriented North-South thus generating a shifted polarization direction (PS; Fig. 1a in 16). To avoid integration of any other visual cues, bats were kept in cotton bags individually after the treatment and until release. At 23:15 h, we translocated them to the release site (RS) which was about 11 km east of the capture site and the coastal migration corridor respectively. We assume that the test individuals did not know this site in the very east of the capturing site. Similar to homing studies, we hereby evade the interference of previously experienced landmarks, e.g. the seashore, which could bias any departure direction. The area chosen for RS was a flat field offering a 360° free view of the horizon. Experiments were conducted during 6 nights (between 22 August and 1 September; see ESM for details).

At the RS, bats were fed and offered water to prompt migration instead of foraging. The person who measured the direction of vanishing bearings was blind to the treatment conditions. Before releasing bats, we surveyed the vicinity of the RS for the presence of any other bats (Echometer EM3+, Wildlife Acoustics, Inc., Maynard, United States). If any bat would have been recorded, releases of subjects would have been paused to avoid confounding via eaves-dropping. After midnight, bats were released individually from the roof of a car with a randomly chosen release direction and with a random order between treatments. Then, bats were tracked at about 4 m above ground using both a handheld 3 element yagi antenna attached to an AR8200 III receiver (AOR) and another antenna attached to an Australis 26k receiver (Titley Scientific). When the signal of the radio transmitter vanished, we noted the bearing of the fading signal and the time elapsed since the release. Two minutes after the signal disappeared, we confirmed the absence of bats by monitoring the area with the radio-tracking equipment. During a given night, the last bats were released between 02:25 and 04:55 h (> 1 h before sunrise, 6 nights). After having released all bats during a given experimental night, we surveyed the area for radio transmitter signals to confirm that all experimental bats had disappeared. A further complete scan for all frequencies was repeated the following day prior to further release events.

Vanishing bearings were analysed using Oriana 4.0 (Kovach computing services, Pentraeth, UK). The Rayleigh test was used to test for non-uniformity of each data set and the Mardia-Watson-Wheeler test analyzed for angular differences in the groups [22]. A test for significant difference between vanishing times of groups was performed using the t-test (SigmaPlot 11.0, Systat Software Inc., Illinois, USA).

Results

The radio signals of all bats vanished after departing from the RS. Eight individuals spent a short time foraging or perching after release (t_{mean}=14 min; see ESM). Vanishing bearings of both groups were significantly oriented (Rayleigh's test, PN: $n = 20$, r=0.507, Z=5.138, $p = 0.005$; PS: $n = 20$, r=0.629, Z=7.922, $p > 0.0001$, figure 1). Mean bearing of bats with PN (control) was 200° (south-southwest) and 183° (south) in the PS group. There was no significant difference between the groups (Mardia-Watson-Wheeler test, W=2.199, p=0.333). There was no significant difference between the lengths of vanishing times of bats (PN = 15.8 min, PS = 18.4 min; t = -0.967, d.f. = 38, $p = 0.339$). Acoustic monitoring at the RS revealed no echolocation calls of any other bat during release events (see Supplementary material for details).

Discussion

Understanding of the orientation and navigation mechanisms of migratory bats has lagged behind other comparable taxa [19]. In this paper, we demonstrate that departure directions measured by VHF telemetry are comparable to the seasonally appropriate direction of migratory *P. nathusii* in a nearby migration corridor [21]. Vanishing bearings of bats treated with a 90° shifted polarization field did not differ from controls exposed to natural patterns. Thus our results contradict the hypothesis that *P. nathusii* use polarized light as their primary calibration reference. An additional observation supports the fact that a 90° shift of polarization at sunset had no effect on subjects: we did not observe any evidence of bimodality in the vanishing bearings, such as was observed in homing experiments with non-migratory greater mouse-eared bats (*Myotis myotis*) [16]. This bimodality is typical for experiments with effective PS [3, 23], since the polarization pattern is non-directional i.e. without any polarity.

Our data suggests that the environmental cues used to calibrate the compass system may depend on the migratory status of bats, with non-migratory bats using cues of polarized skylight and a migratory bat not appearing to calibrate its compass system. This has parallels in bird migration, with some studies suggesting that celestial cues dominate in the pre-migratory period but not during the migratory period [9, but see 24]. However, to date the use of polarized light has only been demonstrated for a single bat species (*Myotis myotis*, [16]), and so caution is warranted in interpreting ecological differences between these two single species. Further experiments are necessary and it remains to be tested if *P. nathusii* depend on polarized light for orientation during the non-migratory period. It should also be noted that in birds, results are inconsistent, with some data supporting the role of polarization as a primary calibration reference for the magnetic compass during migration [3, 13], while others do not [9-12]. A review of published literature indicated that methodological differences, namely, access to a view of the horizon at sunset, may explain these differences [24]. One recent study has also indicated an apparent difference depending upon the method by which orientation was measured [25]. Our study used the same methodology as [16] both in the view of the horizon at sunset, the nature of the experimental boxes to shift polarization and the method of measurement of orientation, and so methodological differences would seem an unlikely explanation for our results.

Geographic position *en route* of migration or species-specific differences could also explain varying compass calibration systems. For our experiments, we can exclude any acoustic orientation in the sense of eavesdropping as an effective cue for navigation towards the coastline. The migration corridor was more than 10 km from the RS and no bats were recorded when our test subjects were released.

We conclude that polarization of the sky is not a necessary daily calibration cue for navigation during migratory flights of bats. Further experiments are required to test for putative hierarchies of orientation cues or ecological factors influencing choice of the most reliable cues during bat migration.

Ethics

All work was conducted under the permit no. 5/2014 to the Institute of Biology, University of Latvia.

Data accessibility

All vanishing bearings and individual information used for analysis have been uploaded as the electronic supplementary material.

Author contributions

O.L. carried out the fieldwork, participated in its design, data analysis and drafted the manuscript. G.P. supported fieldwork. C.C.V. and R.A.H. supervised the project, designed the experiment, provided material and helped draft the manuscript. R.A.H. performed the statistical analysis on bearings. All authors contributed to the final form of the article.

Acknowledgements

We are grateful to Sara Troxell, Katharina Clarin and Viesturs Vintulis for their help with trapping and animal care.

Funding

This project was financially supported by the Leibniz Institute for Zoo and Wildlife Research and by DFG Vo890/22-1. Oliver Lindecke was supported by the PhD student grant of the Federal State of Berlin (Elsa-Neumann-Stipendium).

Competing interests

We declare that we have no competing interest.

References

[1] Papi, F. 1992 Animal Homing. London, Chapman and Hall.

[2] Kramer, G. 1953 Wird die Sonnehöhe bei der Heimfindeorientierung verwertet? J. Orn. 94, 201-219.

[3] Muheim, R., Phillips, J.B. & Akesson, S. 2006 Polarized light cues underlie compass calibration in migratory songbirds. Science 313, 837-839.

[4] Emlen, S.T. 1967 Migratory Orientation in Indigo Bunting Passerina Cyanea. Part I: evidence for Use of Celestial Cues. Auk 84, 309-318.

[5] Wiltschko, W. & Wiltschko, R. 1972 Magnetic compass of European Robins. Science 176, 62-64.

[6] Wiltschko, R. & Wiltschko, W. 2006 Magnetoreception. Bioessays 28, 157-168.

[7] Bingman, V.P., Budzynski, C.A. & Voggenhuber, A. 2003 Migratory systems as adaptive responses to spatial and temporal variability in orientation stimuli. In Avian Migration (eds. P. Berthold, E. Gwinner & E. Sonnenschein), pp. 457-470. Berlin, Springer.

[8] Sandberg, R., Backman, J., Moore, F.R. & Lohmus, M. 2000 Magnetic information calibrates celestial cues during migration. Anim. Behav. 60, 907-907.

[9] Wiltschko, W. & Wiltschko, R. 1975 The interaction of stars and magnetic field in the orientation system of night migrating birds. I. Autumn experiments with European Warblers (Gen. Sylvia). Z. Tierpsychol 37, 337–355.

[10] Chernetsov, N., Kishkinev, D., Kosarev, V. & Bolshakov, C.V. 2011 Not all songbirds calibrate their magnetic compass from twilight cues: a telemetry study. J. Exp. Biol. 214, 2540-2543. (doi:10.1242/jeb.057729).

[11] Wiltschko, R., Munro, U., Ford, H. & Wiltschko, W. 2008 Contradictory results on the role of polarized light in compass calibration in migratory songbirds. J. Orn. 149, 607-614. (doi:10.1007/s10336-008-0324-8).

[12] Schmaljohann, H., Rautenberg, T., Muheim, R., Naef-Daenzer, B. & Bairlein, F. 2013 Response of a free-flying songbird to an experimental shift of the light polarization pattern around sunset. J. Exp. Biol. 216, 1381-1387. (doi:10.1242/jeb.080580).

[13] Muheim, R., Phillips, J.B. & Deutschlander, M.E. 2009 White-throated sparrows calibrate their magnetic compass by polarized light cues during both autumn and spring migration. J. Exp. Biol. 212, 3466-3472.

[14] Holland, R., Thorup, K., Vonhof, M., Cochran, W. & Wikelski, M. 2006 Bat orientation using Earth's magnetic field. Nature 444, 702.

[15] Holland, R.A., Borissov, I. & Siemers, B. 2010 A nocturnal mammal calibrates a magnetic compass by the sun. Proc. Nat. Acad. Sci. U.S.A. 107, 6941-6945.

[16] Greif, S., Borissov, I., Yovel, Y. & Holland, R.A. 2014 A functional role of the sky’s polarization pattern for orientation in the greater mouse-eared bat. Nat Commun 5. (doi:10.1038/ncomms5488).

[17] Hutterer, R., Teodora, I., Meyer-Cords, C. & Rodrigues, L. 2005 Bat migrations in Europe. Bonn, Naturschutz und Biologische Vielfalt.

[18] Cryan, P.M. 2003 Seasonal distribution of migratory tree bats (Lasiurus and Lasionycteris) in North America. J. Mamm. 84, 579-593.

[19] Holland, R.A. 2007 Orientation and navigation in bats: known unknowns or unknown unknowns? Behav. Ecol. Sociobiol. 61, 653-660.

[20] Dietz, C., von Helversen, O. & Nill, D. 2009 Handbook of bats of Europe and Northwest Africa. A C Books. 400pp.

[21] Pētersons, G. 2004 Seasonal migrations of north-eastern populations of *Pipistrellus nathusii*. Myotis 41-42, 29-56.

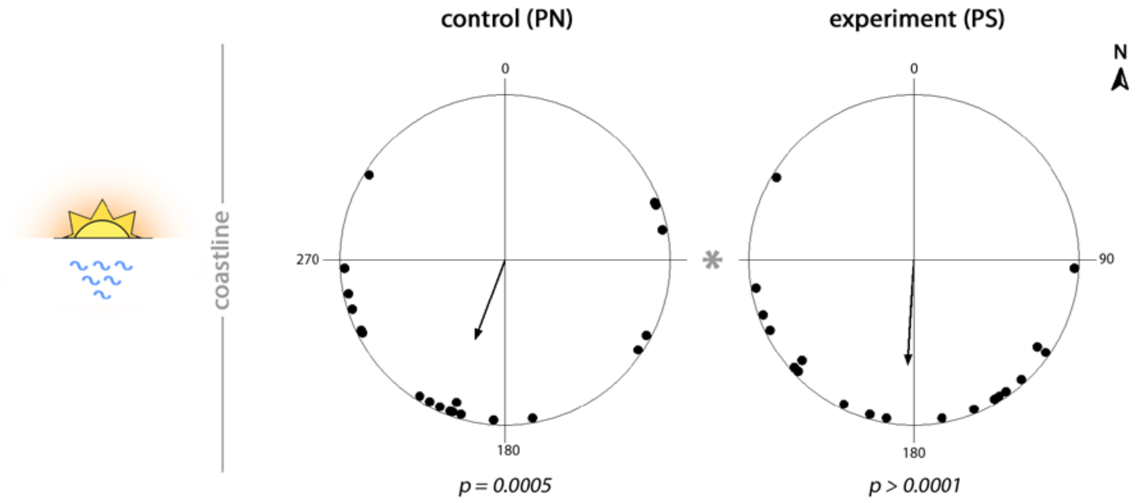
[22] Schmidt-Koenig, K., Ganzhorn, J.U. & Ranvaud, R. 1991 The sun compass. Experientia Supplementum (Basel) 60, 1-15.

[23] Beltrami, G., Bertolucci, C., Parretta, A., Petrucci, F. & Foà, A. 2010 A sky polarization compass in lizards: the central role of the parietal eye. J. Exp. Biol. 213, 2048-2054. doi: 10.1242/jeb.040246.

[24] Muheim, R., Moor, F.R. & Phillips, J.B. 2006 Calibration of magnetic and celestial compass cues in migratory birds − a review of cue-conflict experiments. J. Exp. Biol. 209, 2-17.

[25] Giunchi, D., Vanni, L., Baldaccini, N.E., Spina, F. & Biondi, F. 2015 New cue-conflict experiments suggest a leading role of visual cues in the migratory orientation of Pied Flycatchers *Ficedula hypoleuca*. J. Orn. 156, 113-121. doi: 10.1007/s10336-014-1107-z.

Figure 1. Vanishing bearings of bats translocated to the release site (asterisk) in a presumed unfamiliar area 11 km away east from the coastal migration corridor. The natural coastline, where bats were caught and treated, follows the line of longitude. North (0°) is the top of the circular plots. Arrows depict the mean and vector length of all individual migratory flights after departure of the control group tested for natural polarization direction (PN) and the experimental group (PS) treated with a 90° shifted polarization direction (n_{PN} = 20, n_{PS} = 20). P-values from the Rayleigh tests are shown.



Supplementary material.

Raw data of bat releases (.xls file).

Electronic supplementary materials and methods (.doc file).

Figure S1.