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

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

2

3 **Author names and affiliations**

4 Oliver Lindecke<sup>1,2,\*</sup>, Christian C. Voigt<sup>1,2</sup>, Gunārs Pētersons<sup>3</sup>, Richard A. Holland<sup>4</sup>

5

6 <sup>1</sup> Leibniz Institute for Zoo and Wildlife Research, Evolutionary Ecology Research Group,  
7 Alfred-Kowalke-Str. 17, 10315, Berlin, Germany.

8 <sup>2</sup> Freie Universität Berlin, Department Animal Behaviour, Takustr. 3, 14195, Berlin,  
9 Germany

10 <sup>3</sup> Latvia University of Agriculture, Faculty of Veterinary Medicine, K. Helmaņa 8, LV-  
11 3004 Jelgava, Latvia

12 <sup>4</sup> School of Biological Sciences, Queen's University Belfast, Belfast BT9 7BL, UK.

13

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

15

16

17 **Abstract**

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

30

31 **Keywords**

32 mammalian navigation, orientation, migration, Chiroptera, sensory ecology

33

34 **Introduction**

35 Animals from a broad taxonomic background extract directional information from a  
36 variety of environmental cues [1], including the sun [2], polarized light [3], stars [4] and  
37 the Earth's magnetic field [5, 6]. In migrating passerine birds, these cues appear to be  
38 used hierarchically, in which one provides an absolute geographical reference that

39 calibrates others, which are then used as a compass to take up the desired direction of  
40 orientation [7]. Disagreement persists as to whether the magnetic field [8-12], or  
41 polarized light [3, 13] provides this absolute geographical reference.

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

54

## 55 **Material and methods**

56 *Pipistrellus nathusii* is a long-distance European migratory bat [20]. Extensive  
57 banding studies have produced evidence of southwesterly migratory movements from  
58 Northeastern Europe during autumn and distances of up to 2,000 km [21]. At the peak of  
59 the migratory season in Latvia (between 13 and 22 August 2014), we caught 16 males  
60 and 24 females (all adult) at Pape Biological Station (56°09' N 21°03' E, Rucava  
61 Municipality, Latvia), using a funnel trap. Bats were kept in wooden boxes over periods

62 of 7 to 16 days to avoid unsuitable release conditions under periods of poor weather. We  
63 did not anticipate any affect of this resting period on the outcome of our experiment,  
64 because all animals were exposed to the same conditions. Captive bats were fed  
65 individually with mealworms and had access to *ad libitum* water.

66 On the day of the experiment, any handling of test subjects was performed  
67 indoors in order to avoid exposure to polarized skylight. Prior to the treatment at dusk,  
68 bats were fed with up to 5 mealworms and water to promote activity and to counteract re-  
69 entering torpor. To test whether changing the polarization pattern of skylight affects  
70 heading of migratory flights, we fitted VHF radio transmitters (PicoPip AG379, BioTrack  
71 Ltd., Wareham, United Kingdom or LB-2N, Holohil Systems Ltd., Ottawa, Canada; 0.42  
72 g) to the back of bats, using skin glue (Manfred Sauer GmbH Hautkleber, Lobbach,  
73 Germany). We hypothesized that experimental animals exposed to a 90° rotated band of  
74 polarized light during dusk, would head in a different direction compared with control  
75 animals. Previous experiments have indicated that such a shift results in a bimodal  
76 distribution, shifted  $\pm 90^\circ$  from controls [3, 16]. During the experiment, bats were placed  
77 in the original experimental polarization boxes as described in [16], but see the  
78 supplement for a detailed description. Holding boxes were placed 50 m away from the  
79 funnel trap on a meadow offering a 360° free view of the horizon from 30 min before  
80 until 90 min after sunset, i.e. until the last visible post-sunset glow had vanished.  
81 Experimental evenings had stable weather with a light to moderate breeze (2–8 m/s) and  
82 15–60% cloud cover and always a visible sunset. Boxes were oriented either with the  
83 vertically polarized windows 90° away from the sun, corresponding to the natural  
84 polarization direction (PN, in a North-South axis) or they were shifted 90° so that

85 horizontally polarized windows were oriented North-South thus generating a shifted  
86 polarization direction (PS; Fig. 1a in [16](#)). To avoid integration of any other visual cues,  
87 bats were kept in cotton bags individually after the treatment and until release. At 23:15  
88 h, we translocated them to the release site (RS) which was about 11 km east of the  
89 capture site and the coastal migration corridor respectively. We assume that the test  
90 individuals did not know this site in the very east of the capturing site. Similar to homing  
91 studies, we hereby evade the interference of previously experienced landmarks, e.g. the  
92 seashore, which could bias any departure direction. The area chosen for RS was a flat  
93 field offering a 360° free view of the horizon. Experiments were conducted during 6  
94 nights (between 22 August and 1 September; see ESM for details).

95         At the RS, bats were fed and offered water to prompt migration instead of  
96 foraging. The person who measured the direction of vanishing bearings was blind to the  
97 treatment conditions. Before releasing bats, we surveyed the vicinity of the RS for the  
98 presence of any other bats (Echometer EM3+,  
99 Wildlife Acoustics, Inc., Maynard, United States). If any bat would have been recorded,  
100 releases of subjects would have been paused to avoid confounding via eaves-dropping.  
101 After midnight, bats were released individually from the roof of a car with a randomly  
102 chosen release direction and with a random order between treatments. Then, bats were  
103 tracked at about 4 m above ground using both a handheld 3 element yagi antenna attached  
104 to an AR8200 III receiver (AOR) and another antenna attached to an Australis 26k  
105 receiver (Titley Scientific). When the signal of the radio transmitter vanished, we noted  
106 the bearing of the fading signal and the time elapsed since the release. Two minutes after  
107 the signal disappeared, we confirmed the absence of bats by monitoring the area with the

108 radio-tracking equipment. During a given night, the last bats were released between 02:25  
109 and 04:55 h (> 1 h before sunrise, 6 nights). After having released all bats during a given  
110 experimental night, we surveyed the area for radio transmitter signals to confirm that all  
111 experimental bats had disappeared. A further complete scan for all frequencies was  
112 repeated the following day prior to further release events.

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

118

## 119 **Results**

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

130

131 **Discussion**

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

144 Our data suggests that the environmental cues used to calibrate the compass  
145 system may depend on the migratory status of bats, with non-migratory bats using cues of  
146 polarized skylight and a migratory bat not appearing to calibrate its compass system. This  
147 has parallels in bird migration, with some studies suggesting that celestial cues dominate  
148 in the pre-migratory period but not during the migratory period [9, but see 24]. However,  
149 to date the use of polarized light has only been demonstrated for a single bat species  
150 (*Myotis myotis*, [16]), and so caution is warranted in interpreting ecological differences  
151 between these two single species. Further experiments are necessary and it remains to be  
152 tested if *P. nathusii* depend on polarized light for orientation during the non-migratory  
153 period. It should also be noted that in birds, results are inconsistent, with some data



154 supporting the role of polarization as a primary calibration reference for the magnetic  
155 compass during migration [3, 13], while others do not [9-12]. A review of published  
156 literature indicated that methodological differences, namely, access to a view of the  
157 horizon at sunset, may explain these differences [24]. One recent study has also indicated  
158 an apparent difference depending upon the method by which orientation was measured  
159 [25]. Our study used the same methodology as [16] both in the view of the horizon at  
160 sunset, the nature of the experimental boxes to shift polarization and the method of  
161 measurement of orientation, and so methodological differences would seem an unlikely  
162 explanation for our results.

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

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

172

### 173 **Ethics**

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

176

177 **Data accessibility**

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

180

181 **Author contributions**

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

187

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196

197 **Competing interests**

198 We declare that we have no competing interest.

199

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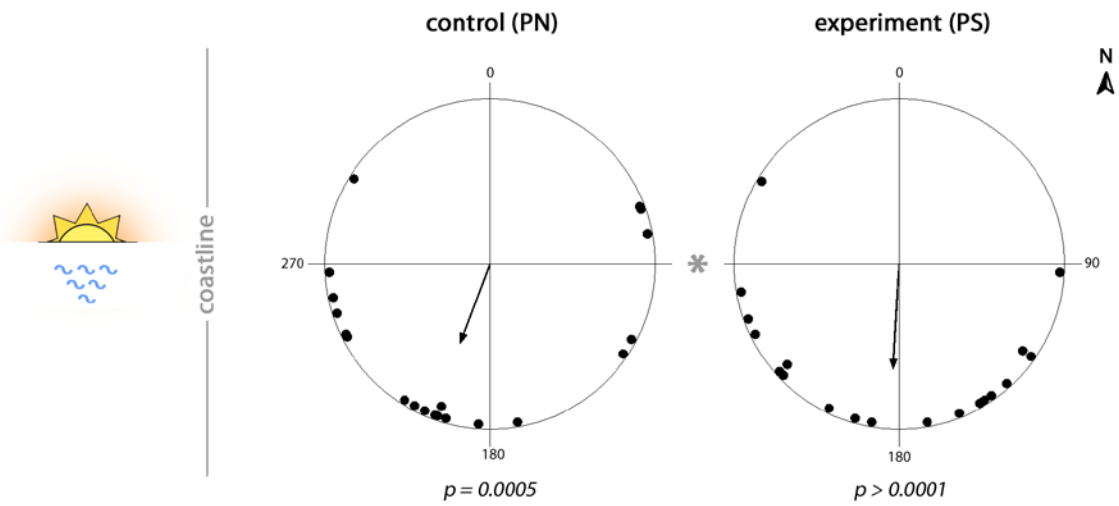
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261

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

269



270

271

272 **Supplementary material.**

273 Raw data of bat releases (.xls file).

274 Electronic supplementary materials and methods (.doc file).

275 Figure S1.