Title: Jetlagged birds lose their way: clock-shift during longitudinal flights causes sun compass error

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Abstract: Many animals use the sun compass to guide their movement, sometimes over thousands of kilometres. Consistent use of the sun compass relies on the endogenous clock to track the sun's arc, yet animals travelling east-west might experience mismatches between their internal clock and local time (clock-shift). Using GPS, we reveal that Manx shearwaters (*Puffinus puffinus*) experience such shifts during homing flights, generating predictable errors in sun compass orientation. Use of the sun compass persists even when shearwaters have access to compass-independent cues during coast-following. Our findings provide a new avenue for chronobiology research in the wild, suggest that rapid longitudinal movements may impact other processes governed by the endogenous clock, and that conserved chronobiological mechanisms impose remarkable constraints on navigation.

Main Text: Compass cues are central to navigation, allowing animals to determine the geographic direction of their heading during movements ranging from metres to thousands of kilometres. Their use is ubiquitous across animal taxa (*1-8*) and a wide array of navigational contexts (*7, 9-15*), from relatively simple vector navigation to flexible map-and-compass navigation (*16-18*). Animals use three main sources of compass information: the geomagnetic field, polar stars and the azimuth (horizontal) angle of the sun (*19-22*). To use the sun as a consistent compass cue, animals must adjust their heading relative to the sun as it moves across the sky over the course of day. This 'time-compensation' is controlled directly by an endogenous clock (*23, 24*) calibrated to local time using external cues, most notably dawn and dusk (*25*). Consequently, researchers can use artificial lights to shift the experienced light-dark cycle and induce discrepancies between an animal's endogenous clock and local solar time (*22, 24*). After this 'clock-shifting', animals using a sun compass show predictable deflections away from their intended trajectory due to error in time-compensation (*22*). Using this approach, sun compass orientation has been investigated thoroughly in homing pigeons (*Columba livia*), the main model of avian navigation (*8*), but also demonstrated in a wide variety of avian and non-avian taxa (*2, 9, 12, 15, 26-30*), including in wild Manx shearwaters homing after displacement (*13*).

As well as mitigating against the accumulation of error, calibration of the clock to light-dark cycles allows animals to adjust to changes in local solar time when they move across lines of longitude. Dawn provides a highly salient calibration cue (*25, 31*) so birds' clocks are expected to be in sync with local time at the start of each day (*32*). However, they appear unable to use other time-varying cues, such as sun elevation, to calibrate their clocks between dawn and dusk (*33*). As a result, clock-shift may be induced by longitudinal movement within a single day (*34*). Movement-induced clock-shifts might impact any behavioural or physiological processes influenced by the endogenous clock (*35, 36*), with the potential for adverse effects on migratory animals similar to those of jetlag in humans (*37-40*). Most endogenous clock research has occurred in laboratory settings (*41, 42*) but the ability to detect clock-shifts induced by longitudinal movement would create the potential to investigate the role of the clock in behaviour and physiology under natural conditions.

Due to its close link to the endogenous clock, such clock-shifts could be detected by their impacts on the sun compass and would facilitate investigations of sun compass use in the wild. Eastwards movements should cause the endogenous clock to lag behind local time, resulting in clockwise deflection from the intended direction, whilst westwards movements should cause the clock to run ahead of local time, with anticlockwise deflection. These predictions have been supported by rapid experimental displacements of Adélie penguins (*Pygoscelis adeliae*) across lines of longitude (*43, 44*) and observations that the routes of wild migratory birds in the Arctic appear, as predicted, to follow changing compass bearings (*45, 46*). However, these observations of migratory birds could not be linked directly to clock-shifts and sun compass error. To attribute orientation error to movement-induced clock-shifts via use of the sun compass without experimental manipulation, other sources of navigational error must first be excluded. Some birds use a geomagnetic compass with error caused by changes in geomagnetic declination (the angular difference between geographic and magnetic north (14, 35)), which varies across lines of longitude. Distinguishing these sources of error requires calculation of precise expected deflections under these alternate hypotheses which, for sun compass use, requires knowledge of an animal's longitudinal movement since dawn.

In this study, we used a GPS tracking dataset, comprising 3025 foraging trips from 886 free-ranging breeding Manx shearwaters to demonstrate that rapid flights across lines of longitude

induce clock-shift and sun compass error. Shearwaters from major UK colonies generally forage in the Irish Sea and Northeast Atlantic, up to around 1,000km west of their breeding islands. After foraging, they home back to these colonies, orienting with remarkable efficiency (Fig.1A; (*47*)). We isolated 2101 homing bouts by identifying periods of continuous flight which involved directed movement towards the colony (see Fig.1B and Materials and Methods for details).

Movement-induced clock-shift and sun compass use

During homing, the breeding island can be defined as the intended target of the shearwater *a priori* and the angular deflection away from the most direct (great circle beeline) route can be calculated. We can also estimate the angular deflection expected if time-compensation errors result from clock-shifts during longitudinal movement. The expected clockwise deflection increases at an average rate of 1° for every 1° of eastward longitudinal displacement but with variation depending on the time of day, due to changes in the rate of solar azimuth change. This allows us to calculate precise values of expected deflection (Fig.2).

Although shearwaters avoid flying over land, they do not anticipate landmasses until after they come within sight, and instead orient on the direct homeward beeline, using map-and-compass navigation (*47-50*). For this reason, and to exclude a variety of other spatial or directional cues available along coastlines which might mask sun compass error, we initially focused on homing behaviour out of sight of land.

For each bout of continuous homing, we calculated the mean observed and expected deflections from the beeline at each fix. We constructed a linear mixed effect model with observed angular deflection as the response, predicted by expected deflection as a fixed effect and individual as a random intercept. To account for other potential influences on orientation, such as the Coriolis effect, time of day, cumulative distance travelled that day, distance from the colony and colony identity, these terms were included in the model (see Materials and Methods for a detailed explanation of the Coriolis term). Although shearwaters are generally assumed to orient along the most direct great circle routes (*47*), they may also use a simpler strategy of following a fixed compass bearing, resulting in rhumb line routes. To ensure observed deflections from the great circle beeline did not result from rhumb line orientation, we calculated the difference between the initial great circle and rhumb line bearings towards the colony from each fix. The mean of these deflections across each bout acted as the expected deflection if shearwaters orient on rhumb lines and was included in the model. Terms with Variance Inflation Factor (VIF) > 5 were removed to avoid multicollinearity, and chi-square and P-values were estimated for each term using likelihood ratio tests on nested full and restricted models. Model fit is visualised in Fig.S1-S6.

Clockwise deflection increased with increasing expected deflection (4.62 ± 4.27° observed deflection per 1° expected deflection [mean ± 95% CI], $\chi^2_1 = 4.45$, $P = 0.035$), consistent with use of the sun compass to navigate when out of sight of land and clock-shift resulting from longitudinal movement (Fig.3). In addition, expected rhumb line deflection did not predict observed deflection ($\chi^2_1 = 0.24$, $P = 0.627$), suggesting that, in the absence of sun compass error, shearwaters orient along the most direct great circle beelines. No other covariates predicted observed orientation error (test statistics are reported in Table S1). The slope between observed and expected deflection is steeper than the expected 1:1 relationship but not significantly so. Although estimating the precise magnitude of orientation error from tracking data is difficult (see Supplementary Text), this suggests heavy reliance on the sun compass as part of a map-and-compass system, without complete correction from compass-independent mechanisms or other compass cues. This mirrors findings in homing pigeons released outside their familiar area (*51, 52*), where they are thought to

use the sun compass in combination with a map of large-scale gradients in atmospheric olfactants (*53*), perhaps similarly to wild shearwaters (*48-50*). This result also necessarily suggests that animals clock-shift themselves during their natural longitudinal movements, with a range of potential behavioural and physiological consequences.

To ensure that this result was not driven by magnetic compass error, we also calculated predicted deflections based on two magnetic compass mechanisms. First, we calculated predicted deflection if shearwaters used a magnetic compass without accounting for changes in geomagnetic declination through space (using declination at the colony as the baseline). Predicted deflection was equal to the difference in declination between a given GPS location and declination at the colony. Secondly, we calculated predicted deflection if shearwaters were able to correct their magnetic compass for changes in declination by calibration during dawn or dusk (*54*). The predicted deflection was, therefore, the difference between declination the shearwater experienced at a given GPS location and declination it experienced at sunrise. Inclusion of the former metric in the main model resulted in high multicollinearity (VIF = 29.29) so we instead constructed two models identical to the main model but with magnetic rather than sun compass predictions, to conduct non-nested model comparison. We found that the sun compass model fitted substantially better than both magnetic models (ΔAICc = -3.56 and -2.99, respectively). As the expected deflections under sun and magnetic compasses are so similar in most of the dataset, we constructed linear models using only the data where the absolute difference between the sun and both magnetic compass predictions was >2°. In this case, when the disparity between predictions was greatest (and despite the very small size of this subset: n = 14), support for the sun compass model was even stronger (ΔAICc = -7.82 and -8.62, respectively). These comparisons indicate that the observed deflections result from use of the sun compass, not a magnetic compass. This is consistent with existing research on shearwaters; although there is evidence that they are magnetosensitive (*55*), attachment of strong neodymium magnets does not appear to affect their orientation (*48-50*), unlike in species that have been robustly shown to use a geomagnetic compass (*56*). In contrast, experimentally induced clock-shift has demonstrated that shearwaters use a time-compensated sun compass (*13*) and are not able to orient accurately when it is manipulated, suggesting that the sun is their primary source of compass information.

Use of the sun compass in combination with compass-independent cues

Coastlines may provide familiar visual or spatial cues that reduce navigational error and hence reduce clock-shift effects. Following of similar linear features has been observed in pigeons released at familiar sites (*51, 52*) and attributed to learning of idiosyncratic pilotage routes (*57-59*). However, small clock-shift effects persist even when pigeons are following highly familiar routes (*14*). Inspired by this phenomenon, we investigated whether self-induced clock-shift in shearwaters resulted in similar lateral shifts during coast-following. We identified bouts of homing when shearwaters were flying along coastlines and recorded the direction of land (clockwise or anticlockwise) relative to their direction of travel, the expected deflection under sun compass-use and the mean perpendicular distance from land. We constructed a linear mixed effect model with mean distance from land as the response, predicted by an interaction between the expected deflection and the direction of land. We also included the covariates listed above as fixed effects and individual as a random intercept.

We found a significant interaction between shearwaters' predicted deflection and the relative direction of land (χ^2_1 = 9.68, P = 0.002); shearwaters fly closer to land when their expected deflection is in the same direction as the coast they are flying along (-0.64km per 1° expected clockwise deflection when land is clockwise of direction of travel and 0.56km per 1° when land is

anticlockwise, difference: 1.20 ± 0.76km; Fig.4). Distance from land was not predicted by any other term with the exception of colony ($\chi^2_5 = 42.22$, $P < 0.001$) and time since dawn; shearwaters moved closer to land later in the day (-0.09 ± 0.09 km per hour, $\chi^2_1 = 4.29$, $P = 0.038$). To ensure that values with extreme expected deflections were not driving the relationship with expected sun compass error, we conducted the same analysis on data with expected deflections between -2° and 2°, yielding the same significant relationship with very similar coefficients (Supplementary Text; Fig.S7). This suggests that shearwaters use the sun compass in combination with compass-independent mechanisms (e.g. pilotage) along coastlines even when these mechanisms conflict.

Discussion

Previous studies have used longitudinal displacement to generate clock-shift effects (*43, 44*) and theoretical work has suggested that this might occur naturally during long-distance migration (*34, 45, 46, 60*). Here, we demonstrate that rapid longitudinal movements can indeed lead to jetlag-like clock-shifts in wild animals and that these result in sun compass error. We show that shearwaters use the sun compass throughout homing. Our results provide further support for the notion that shearwaters use map-and-compass navigation when homing from distant locations beyond sight of land (*47*) with solar azimuth as the main compass cue (*13*). We also provide evidence that when shearwaters follow coastlines (*49, 50*), presumably using compass-independent pilotage, they balance this with information from the sun compass. These findings provide insight into how animals use the sun compass under natural conditions but match well to those generated from experimental displacement of homing pigeons (*14, 51, 52*), despite their relatively distant phylogenetic relationship and markedly different environment.

The angular deflections induced by this error are relatively small (up to a maximum of around 15° in shearwaters) but such errors could accumulate over long-distance migrations, especially in birds relying on clock-and-compass navigation without the ability to reorient toward a goal. For instance, Northern wheatears (*Oenathe oenathe*) making non-stop flights over the Atlantic from Baffin Island, Canada, to the British Isles traverse around 3,400km and 60° of longitude in four days (*61*). If wheatears, like shearwaters, use a time-compensated sun compass and cannot correct for clock-shifts within each day, they would be predicted to end up hundreds of kilometres from the endpoint of their initial bearing. Alternatively, if such deflections are not observed, animals relying on a sun compass must use mechanisms to account for these time-compensation errors either through calibrating their endogenous clocks against as yet unknown cues available throughout the day, monitoring their own longitudinal movement to adjust their time-compensation or combining sun compass information with other cues. By shifting the orientations of migratory animals and perhaps driving the evolution of strategies to mitigate for these shifts, this phenomenon has the potential to shape global animal movement and navigational strategies.

In this study, it was possible to detect clock-shifts through shearwaters' use of a time-compensated sun compass. Predominantly through laboratory studies, endogenous clocks are known to influence a wide array of animal physiological and behavioural processes (*35, 36*) with downstream impacts on ecological interactions (*62-64*) and adverse effects of disruption to the clock, including in humans (*37-40*). Due to its inherent reliance on the endogenous clock, with little potential for masking by other cues (*65*), sun compass orientation might be a particularly powerful way to detect clock-shifts in wild animals. We hope that this study will help bridge the gap between chronobiology and ecology (*41, 42*), opening the door to investigations into the influence of the endogenous clock on behaviour and physiology under natural conditions, the impacts of clock-shift on long-distance migratory animals, sun compass use in the wild, and perhaps how some animals might be able to cope with frequent clock-shifts. Although these clock-

shifts will be most detectable and ecologically relevant for animals travelling long distances, our findings imply that any animals moving east-west between dawn and dusk might be subject to clock-shifts, with broad implications for the ecology and chronobiology of wild animals.

References and Notes

1. A. O. D. Willows, Shoreward orientation involving geomagnetic cues in the nudibranch mollusc Tritonia diomedea. *Marine and Freshwater Behaviour and Physiology* **32**, 181-192 (1999); doi:10.1080/10236249909379046

2. K. von Frisch, Decoding the Language of the Bee. *Science* **185**, 663-668 (1974); doi:10.1126/science.185.4152.663

3. R. T. Newcomer, D. H. Taylor, S. I. Guttman, Celestial Orientation in Two Species of Water Snakes (Natrix sipedon and Regina septemvittata). *Herpetologica* **30**, 194-200 (1974); doi:10.2307/3892040

4. S. Marhold, W. Wiltschko, H. Burda, A Magnetic Polarity Compass for Direction Finding in a Subterranean Mammal. *Naturwissenschaften* **84**, 421-423 (1997); doi:10.1007/s001140050422

5. K. J. Lohmann, N. D. Pentcheff, G. A. Nevitt, G. D. Stetten, R. K. Zimmer-Faust, H. E. Jarrard, L. C. Boles, Magnetic Orientation of Spiny Lobsters in the Ocean: Experiments with Undersea Coil Systems. *Journal of Experimental Biology* **198**, 2041-2048 (1995); doi:10.1242/jeb.198.10.2041

6. K. J. Lohmann, C. Lohmann, A Light-Independent Magnetic Compass in the Leatherback Sea Turtle. *The Biological Bulletin* **185**, 149-151 (1993); doi:10.2307/1542138

7. A. D. Hasler, R. M. Horrall, W. J. Wisby, W. Braemer, Sun-Orientation and Homing in Fishes. *Limnology and Oceanography* **3**, 353-361 (1958); doi:10.4319/lo.1958.3.4.0353

8. K. Schmidt-Koenig, The sun compass. *Experientia* **46**, 336-342 (1990); doi:10.1007/BF01952166

9. C. Merlin, R. J. Gegear, S. M. Reppert, Antennal Circadian Clocks Coordinate Sun Compass Orientation in Migratory Monarch Butterflies. *Science* **325**, 1700-1704 (2009); doi:10.1126/science.1176221

10. M. Lindauer, Time-compensated sun orientation in bees. *Cold Spring Harb Symp Quant Biol* **25**, 371-377 (1960); doi:10.1101/sqb.1960.025.01.039

11. A. J. Helbig, Genetic Basis, Mode of Inheritance and Evolutionary Changes of Migratory Directions in Palearctic Warblers (Aves: Sylviidae). *Journal of Experimental Biology* **199**, 49-55 (1996); doi:10.1242/jeb.199.1.49

12. W. Wiltschko, R. P. Balda, Sun compass orientation in seed-caching scrub jays (Aphelocoma coerulescens). *Journal of Comparative Physiology A* **164**, 717-721 (1989); doi:10.1007/BF00616744

13. O. Padget, S. L. Bond, M. M. Kavelaars, E. van Loon, M. Bolton, A. L. Fayet, M. Syposz, S. Roberts, T. Guilford, In situ clock shift reveals that the sun compass contributes to orientation in a pelagic seabird. *Current Biology* **28**, 275-279. e272 (2018); doi:10.1016/j.cub.2017.11.062

14. D. Biro, R. Freeman, J. Meade, S. Roberts, T. Guilford, Pigeons combine compass and landmark guidance in familiar route navigation. *Proceedings of the National Academy of Sciences* **104**, 7471-7476 (2007); doi:10.1073/pnas.0701575104

15. M. Müller, R. Wehner, Path integration in desert ants, Cataglyphis fortis. *Proceedings of the National Academy of Sciences* **85**, 5287-5290 (1988); doi:10.1073/pnas.85.14.5287

16. V. Bingman, K. Cheng, Mechanisms of animal global navigation: comparative perspectives and enduring challenges. *Ethology Ecology & Evolution* **17**, 295-318 (2005); doi:10.1080/08927014.2005.9522584

17. G. V. T. Matthews, Navigation in the Manx shearwater. *Journal of Experimental Biology* **30**, 370-396 (1953); doi:10.1242/jeb.30.3.370

18. G. V. T. Matthews, The Experimental Investigation of Navigation in Homing Pigeons. *Journal of Experimental Biology* **28**, 508-536 (1951); doi:10.1242/jeb.28.4.508

19. S. T. Emlen, Migratory orientation in the Indigo Bunting, Passerina cyanea. Part II: Mechanism of celestial orientation. *The Auk* **84**, 463-489 (1967);

20. S. T. Emlen, The stellar-orientation system of a migratory bird. *Scientific American* **233**, 102-111 (1975);

21. W. Wiltschko, R. Wiltschko, Magnetic compass of European robins. *Science* **176**, 62-64 (1972);

22. K. Schmidt-Koenig, in *Cold Spring Harbor Symposia on Quantitative Biology*. (Cold Spring Harbor Laboratory Press, 1960), vol. 25, pp. 389-393.

23. R. E. Mistlberger, B. Rusak, in *The Behavior of Animals, 2nd Edition*. (2021), pp. 78-110.

24. K. Hoffmann, Versuche zu der im Richtungsfinden der Vögel enthaltenen Zeitschätzung. *Zeitschrift für Tierpsychologie*, (1954); doi:10.1111/j.1439-0310.1954.tb02169.x

25. C. Hirschie Johnson, J. A. Elliott, R. Foster, Entrainment of Circadian Programs. *Chronobiology International* **20**, 741-774 (2003); doi:10.1081/CBI-120024211

26. L. Pardi, Innate components in the solar orientation of littoral amphipods. *Cold Spring Harb Symp Quant Biol* **25**, 395-401 (1960); doi:10.1101/sqb.1960.025.01.042

27. S. L. Fluharty, D. H. Taylor, G. W. Barrett, Sun-Compass Orientation in the Meadow Vole, Microtus pennsylvanicus. *Journal of Mammalogy* **57**, 1-9 (1976); 10.2307/1379508

28. S. J. Duff, L. A. Brownlie, D. F. Sherry, M. Sangster, Sun compass and landmark orientation by black-capped chickadees (Parus atricapillus). *Journal of Experimental Psychology: Animal Behavior Processes* **24**, 243 (1998); doi:10.1037/0097-7403.24.3.243

29. P. H. Zimmerman, S. J. Pope, T. Guilford, C. J. Nicol, Involvement of the sun and the magnetic compass of domestic fowl in its spatial orientation. *Applied Animal Behaviour Science* **116**, 204-210 (2009); doi:10.1016/j.applanim.2008.09.006

30. D. M. Kelly, K. Cheng, R. Balda, A. C. Kamil, Effects of sun compass error on spatial search by Clark's nutcrackers. *Integrative Zoology* **14**, 172-181 (2019); doi:10.1111/1749-4877.12302

31. G. Kramer, Recent experiments on bird orientation. *Ibis* **101**, 399-416 (1959); doi:10.1111/j.1474-919X.1959.tb02396.x

32. R. Wiltschko, M. Walker, W. Wiltschko, Sun-Compass Orientation in Homing Pigeons: Compensation for Different Rates of Change in Azimuth? *Journal of Experimental Biology* **203**, 889-894 (2000); doi:10.1242/jeb.203.5.889

33. K. Schmidt-Koenig, J. U. Ganzhorn, R. Ranvaud, in *Orientation in Birds,* P. Berthold, Ed. (Birkhäuser Basel, Basel, 1991), pp. 1-15.

34. T. Alerstam, S.-G. Pettersson, Orientation along great circles by migrating birds using a sun compass. *Journal of Theoretical Biology* **152**, 191-202 (1991); doi:10.1016/S0022-5193(05)80452-7

35. S. Krittika, P. and Yadav, Circadian clocks: an overview on its adaptive significance. *Biological Rhythm Research* **51**, 1109-1132 (2020); doi:10.1080/09291016.2019.1581480

36. V. Pilorz, C. Helfrich-Förster, H. Oster, The role of the circadian clock system in physiology. *Pflügers Archiv - European Journal of Physiology* **470**, 227-239 (2018); doi:10.1007/s00424-017-2103-y

37. G. Costa, Shift work and occupational medicine: an overview. *Occupational medicine* **53**, 83-88 (2003); doi:10.1093/occmed/kqg045

38. A. J. Davidson, M. T. Sellix, J. Daniel, S. Yamazaki, M. Menaker, G. D. Block, Chronic jet-lag increases mortality in aged mice. *Current Biology* **16**, R914-R916 (2006); 10.1016/j.cub.2006.09.058

39. V. Rafnsson, H. Tulinius, J. G. Jónasson, J. Hrafnkelsson, Risk of breast cancer in female flight attendants: a population-based study (Iceland). *Cancer Causes & Control* **12**, 95-101 (2001); doi:10.1023/a:1008983416836

40. T. Roenneberg, M. Merrow, The Circadian Clock and Human Health. *Current Biology* **26**, R432-R443 (2016); doi:10.1016/j.cub.2016.04.011

41. B. Helm, M. E. Visser, W. Schwartz, N. Kronfeld-Schor, M. Gerkema, T. Piersma, G. Bloch, Two sides of a coin: ecological and chronobiological perspectives of timing in the wild. *Philosophical Transactions of the Royal Society B: Biological Sciences* **372**, 20160246 (2017); doi:10.1098/rstb.2016.0246

42. W. J. Schwartz, B. Helm, M. P. Gerkema, Wild clocks: preface and glossary. *Philosophical Transactions of the Royal Society B: Biological Sciences* **372**, 20170211 (2017); doi:10.1098/rstb.2017.0211

43. J. Emlen, R. Penney, Distance navigation in the Adelie Penguin. *Ibis* **106**, 417-431 (1964); doi:10.1111/j.1474-919X.1964.tb03724.x

44. R. L. Penney, J. Emlen, Further experiments on distance navigation in the Adelie penguin Pygoscelzs Adelzae. *Ibis* **109**, 99-109 (1967); doi:10.1111/j.1474-919X.1967.tb00006.x

45. T. Alerstam, J. Bäckman, R. Strandberg, G. A. Gudmundsson, A. Hedenström, S. S. Henningsson, H. Karlsson, M. Rosén, Great-circle migration of Arctic passerines. *The Auk* **125**, 831-838 (2008); doi:10.1525/auk.2008.07142

46. T. Alerstam, G. A. Gudmundsson, M. Green, A. Hedenstrom, Migration along orthodromic sun compass routes by arctic birds. *Science* **291**, 300-303 (2001); doi:10.1126/science.291.5502.300.

47. O. Padget, G. Stanley, J. K. Willis, A. L. Fayet, S. Bond, L. Maurice, A. Shoji, B. Dean, H. Kirk, I. Juarez-Martinez, Shearwaters know the direction and distance home but fail to encode intervening obstacles after free-ranging foraging trips. *Proceedings of the National Academy of Sciences* **116**, 21629-21633 (2019); doi:10.1073/pnas.1903829116

48. A. Gagliardo, J. Bried, P. Lambardi, P. Luschi, M. Wikelski, F. Bonadonna, Oceanic navigation in Cory's shearwaters: evidence for a crucial role of olfactory cues for homing after displacement. *Journal of Experimental Biology* **216**, 2798-2805 (2013); 10.1242/jeb.085738

49. O. Padget, G. Dell'Ariccia, A. Gagliardo, J. González-Solís, T. Guilford, Anosmia impairs homing orientation but not foraging behaviour in free-ranging shearwaters. *Sci.Rep.* **7**, 9668 (2017); doi:10.1038/s41598-017-09738-5

50. E. Pollonara, P. Luschi, T. Guilford, M. Wikelski, F. Bonadonna, A. Gagliardo, Olfaction and topography, but not magnetic cues, control navigation in a pelagic seabird: displacements with shearwaters in the Mediterranean Sea. *Scientific reports* **5**, 1-10 (2015); doi:10.1038/srep16486

51. A. Gagliardo, F. Odetti, P. Ioalè, Factors reducing the expected deflection in initial orientation in clock-shifted homing pigeons. *Journal of experimental biology* **208**, 469-478 (2005); doi:10.1242/jeb.01383

52. R. Wiltschko, R. Kumpfmüller, R. Muth, W. Wiltschko, Pigeon homing: the effect of a clock-shift is often smaller than predicted. *Behavioral Ecology and Sociobiology* **35**, 63-73 (1994); doi:10.1007/BF00167061

53. H. G. Wallraff, *Avian navigation: pigeon homing as a paradigm*. (Springer Science & Business Media, 2005).

54. R. Muheim, F. R. Moore, J. B. Phillips, Calibration of magnetic and celestial compass cues in migratory birds-a review of cue-conflict experiments. *Journal of Experimental Biology* **209**, 2-17 (2006); doi:10.1242/jeb.01960

55. J. Wynn, O. Padget, H. Mouritsen, C. Perrins, T. Guilford, Natal imprinting to the Earth's magnetic field in a pelagic seabird. *Current Biology* **30**, 2869-2873.e2862 (2020); doi:10.1016/j.cub.2020.05.039

56. F. Packmor, D. Kishkinev, F. Bittermann, B. Kofler, C. Machowetz, T. Zechmeister, L. C. Zawadzki, T. Guilford, R. A. Holland, A magnet attached to the forehead disrupts magnetic compass orientation in a migratory songbird. *Journal of Experimental Biology* **224**, jeb243337 (2021); doi:10.1242/jeb.243337

57. D. Biro, J. Meade, T. Guilford, Familiar route loyalty implies visual pilotage in the homing pigeon. *Proceedings of the National Academy of Sciences* **101**, 17440-17443 (2004); doi:10.1073/pnas.0406984101

58. D. Biro, J. Meade, T. Guilford, Route recapitulation and route loyalty in homing pigeons: pilotage from 25 km? *The Journal of Navigation* **59**, 43-53 (2006); doi:10.1017/S0373463305003541

59. J. Meade, D. Biro, T. Guilford, Homing pigeons develop local route stereotypy. *Proc Biol Sci* **272**, 17-23 (2005); doi:10.1098/rspb.2004.2873

60. J. D. McLaren, H. Schmaljohann, B. Blasius, Predicting performance of naïve migratory animals, from many wrongs to self-correction. *Communications Biology* **5**, 1058 (2022); doi:10.1038/s42003-022-03995-5

61. F. Bairlein, D. R. Norris, R. Nagel, M. Bulte, C. C. Voigt, J. W. Fox, D. J. T. Hussell, H. Schmaljohann, Cross-hemisphere migration of a 25 g songbird. *Biology Letters* **8**, 505-507 (2012); doi:10.1098/rsbl.2011.1223

62. G. Bloch, N. Bar-Shai, Y. Cytter, R. Green, Time is honey: circadian clocks of bees and flowers and how their interactions may influence ecological communities. *Philosophical Transactions of the Royal Society B: Biological Sciences* **372**, 20160256 (2017); doi:10.1098/rstb.2016.0256

63. N. Kronfeld-Schor, M. E. Visser, L. Salis, J. A. van Gils, Chronobiology of interspecific interactions in a changing world. *Philosophical Transactions of the Royal Society B: Biological Sciences* **372**, 20160248 (2017); doi:10.1098/rstb.2016.0248

64. A. Rijnsdorp, S. Daan, C. Dijkstra, Hunting in the kestrel, Falco tinnunculus, and the adaptive significance of daily habits. *Oecologia* **50**, 391-406 (1981); 10.1007/BF00344982

65. N. Mrosovsky, Masking: history, definitions, and measurement. *Chronobiology international* **16**, 415-429 (1999); doi:10.3109/07420529908998717

66. J. Beuchert, A. Matthes, A. Rogers, SNAPPERGPS: open hardware for energy-efficient, low-cost wildlife location tracking with snapshot GNSS. *Journal of Open Hardware* **7**, (2023); doi:10.5334/joh.48

67. T. C. Guilford, J. Meade, R. Freeman, D. Biro, T. Evans, F. Bonadonna, D. Boyle, S. Roberts, C. M. Perrins, GPS tracking of the foraging movements of Manx Shearwaters Puffinus puffinus breeding on Skomer Island, Wales. *Ibis* **150**, 462-473 (2008); doi:10.1111/j.1474-919X.2008.00805.x

68. R Core Team, R: A Language and Environment for Statistical Computing, (2024); https://www.R-project.org/

69. T. Barrett, M. Dowle, A. Srinivasan, J. Gorecki, M. Chirico, T. Hocking, B. Schwendinger, I. Krylov, data.table: Extension of 'data.frame', R package version 1.17.99 (2025); https://r-datatable.com

70. G. Grolemund, H. Wickham, Dates and Times Made Easy with lubridate. *Journal of Statistical Software* **40**, 1-25 (2011);

71. H. Wickham, stringr: Simple, Consistent Wrappers for Common String Operations, R package version 1.5.1 (2023); https://github.com/tidyverse/stringr

72. H. Wickham, R. François, L. Henry, K. Müller, D. Vaughan, dplyr: A Grammar of Data Manipulation. , R package version 1.1.4 (2023); https://github.com/tidyverse/dplyr

73. D. Dunnington, ggspatial: Spatial Data Framework for ggplot2, R package version 1.1.9.9000 (2025); https://github.com/paleolimbot/ggspatial

74. J. Fox, S. Weisberg, Visualizing Fit and Lack of Fit in Complex Regression Models with Predictor Effect Plots and Partial Residuals. *Journal of Statistical Software* **87**, 1-27 (2018); 10.18637/jss.v087.i09

75. J. Fox, S. Weisberg, *An R Companion to Applied Regression*. (Sage, Thousand Oaks CA, ed. 3, 2019).

76. P. Massicotte, A. South, rnaturalearth: World Map Data from Natural Earth, R package version 1.1.0 (2025); https://docs.ropensci.org/rnaturalearth/

77. A. South, S. Michael, P. Massicotte, rnaturalearthdata: World Vector Map Data from Natural Earth Used in 'rnaturalearth', R package version 1.0.0.9000 (2025); https://docs.ropensci.org/rnaturalearthdata/

78. A. South, S. Michael, P. Massicotte, rnaturalearthhires: High Resolution World Vector Map Data from Natural Earth used in rnaturalearth, R package version 1.0.0.9000 (2025); https://docs.ropensci.org/rnaturalearthhires

79. H. Wickham, *ggplot2: Elegant Graphics for Data Analysis*. (Springer-Verlag, New York, 2016).

80. J. Beuchert, A. Rogers, in *Proceedings of the 19th ACM Conference on Embedded Networked Sensor Systems*. (2021), pp. 165-177.

81. R. J. Hijmans, geosphere: Spherical Trigonometry, R package version 1.5-10. (2019); https://CRAN.R-project.org/package=geosphere

82. H. Borchers, pracma: Practical Numerical Math Functions. R package version 2.4.4, (2023); https://CRAN.R-project.org/package=pracma

83. T. Benaglia, D. Chauveau, D. R. Hunter, D. S. Young, mixtools: An R Package for Analyzing Mixture Models. *Journal of Statistical Software* **32**, 1 - 29 (2009); 10.18637/jss.v032.i06

84. B. Thieurmel, A. Elmarhraoui, suncalc: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase. R package version 0.5.2, (2025); https://github.com/datastorm-open/suncalc

85. P. Alken, E. Thébault, C. D. Beggan, H. Amit, J. Aubert, J. Baerenzung, T. N. Bondar, W. J. Brown, S. Califf, A. Chambodut, A. Chulliat, G. A. Cox, C. C. Finlay, A. Fournier, N. Gillet, A. Grayver, M. D. Hammer, M. Holschneider, L. Huder, G. Hulot, T. Jager, C. Kloss, M. Korte, W. Kuang, A. Kuvshinov, B. Langlais, J. M. Léger, V. Lesur, P. W. Livermore, F. J. Lowes, S. Macmillan, W. Magnes, M. Mandea, S. Marsal, J. Matzka, M. C. Metman, T. Minami, A. Morschhauser, J. E. Mound, M. Nair, S. Nakano, N. Olsen, F. J. Pavón-Carrasco, V. G. Petrov, G. Ropp, M. Rother, T. J. Sabaka, S. Sanchez, D. Saturnino, N. R. Schnepf, X. Shen, C. Stolle, A. Tangborn, L. Tøffner-Clausen, H. Toh, J. M. Torta, J. Varner, F. Vervelidou, P. Vigneron, I. Wardinski, J. Wicht, A. Woods, Y. Yang, Z. Zeren, B. Zhou, International Geomagnetic Reference Field: the thirteenth generation. *Earth, Planets and Space* **73**, 49 (2021); 10.1186/s40623-020-01288-x

86. R. Hijmans, raster: Geographic Data Analysis and Modeling, R package version 3.6-32 (2025); https://rspatial.org/raster

87. P. E, Simple Features for R: Standardized Support for Spatial Vector Data. *The R Journal* **10**, 439-446 (2018); 10.32614/RJ-2018-009

88. E. Pebesma, R. Bivand, *Spatial Data Science: With applications in R*. (Chapman and Hall/CRC, 2023).

89. C. Agostinelli, U. Lund, R package 'circular': Circular Statistics, R package version 0.5-1 (2024); https://CRAN.R-project.org/package=circular

90. D. Lüdecke, M. S. Ben-Schachar, I. Patil, P. Waggoner, D. Makowski, performance: An R Package for Assessment, Comparison and Testing of Statistical Models. *Journal of Open Source Software* **6**, (2021); doi:10.21105/joss.03139

91. M. J. Mazerolle, AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c), R package version 2.3.3 (2023); https://cran.r-project.org/package=AICcmodavg

92. H. Jacqmin-Gadda, S. Sibillot, C. Proust, J.-M. Molina, R. Thiébaut, Robustness of the linear mixed model to misspecified error distribution. *Computational Statistics & Data Analysis* **51**, 5142-5154 (2007); doi:10.1016/j.csda.2006.05.021

93. H. Schielzeth, N. J. Dingemanse, S. Nakagawa, D. F. Westneat, H. Allegue, C. Teplitsky, D. Réale, N. A. Dochtermann, L. Z. Garamszegi, Y. G. Araya-Ajoy, Robustness of linear mixed-effects models to violations of distributional assumptions. *Methods in Ecology and Evolution* **11**, 1141-1152 (2020); doi:10.1111/2041-210X.13434

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Supplementary Materials

Materials and Methods

Supplementary Text

Figs. S1 to S7

Table S1

References (*66–93*)

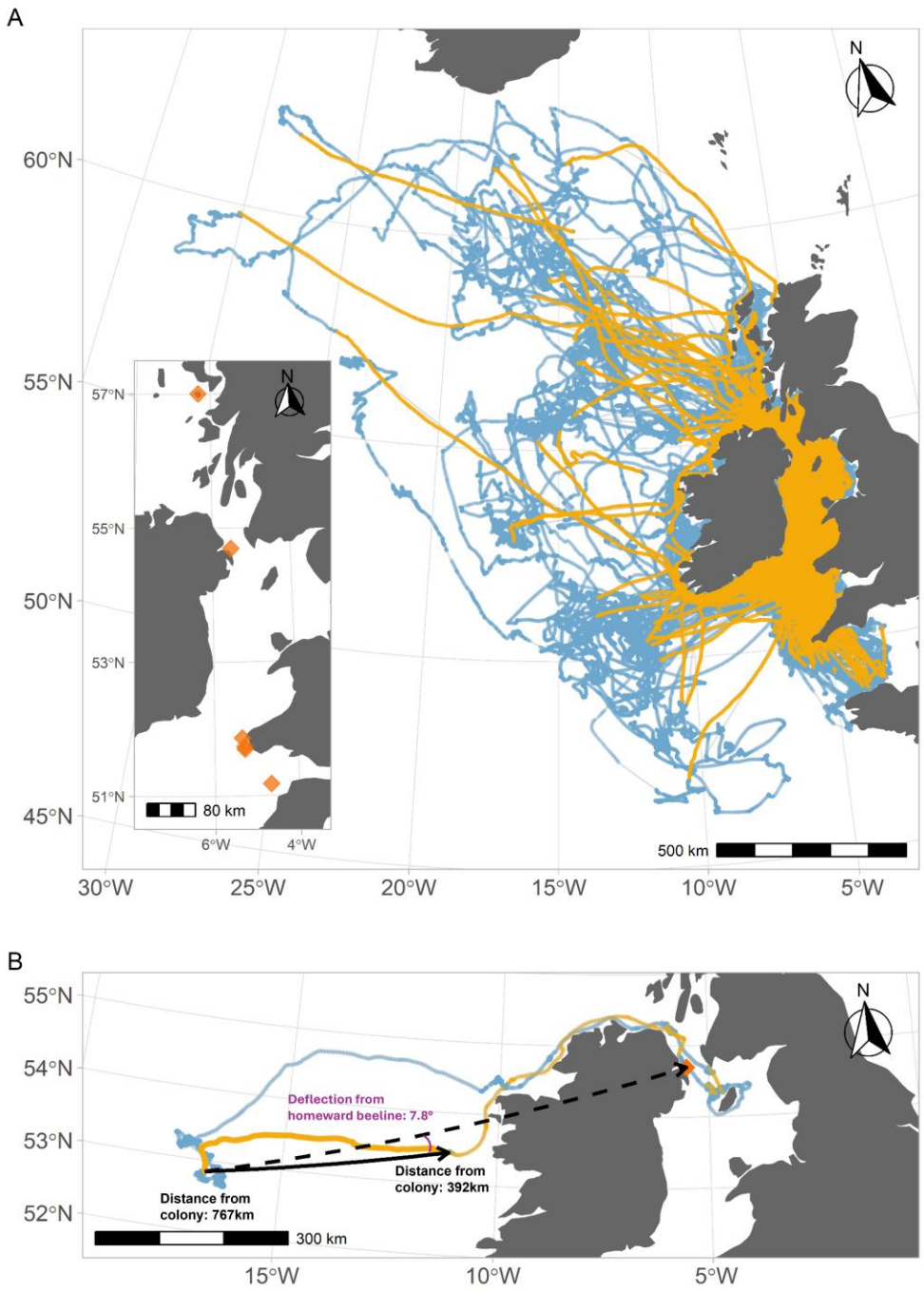


Fig.1. 20 years of tracking data from adult Manx shearwaters breeding on islands across the western coasts the UK. (**A**) Full tracking dataset with outbound flight and foraging in blue, and homing flights highlighted in orange. The positions of breeding colonies (orange diamonds) are shown in the inset. (**B**) Schematic detailing identification of homing. Outbound travel and foraging are shown in blue and homing in orange. A single continuous homing bout is highlighted in brighter orange. Homing was identified as bouts with bearings within 75° of the homeward direction and which end at least 25% closer to the colony than they started. For this bout, deflection from the homeward beeline is 7.5° and the bout ends around 50% closer to the colony.

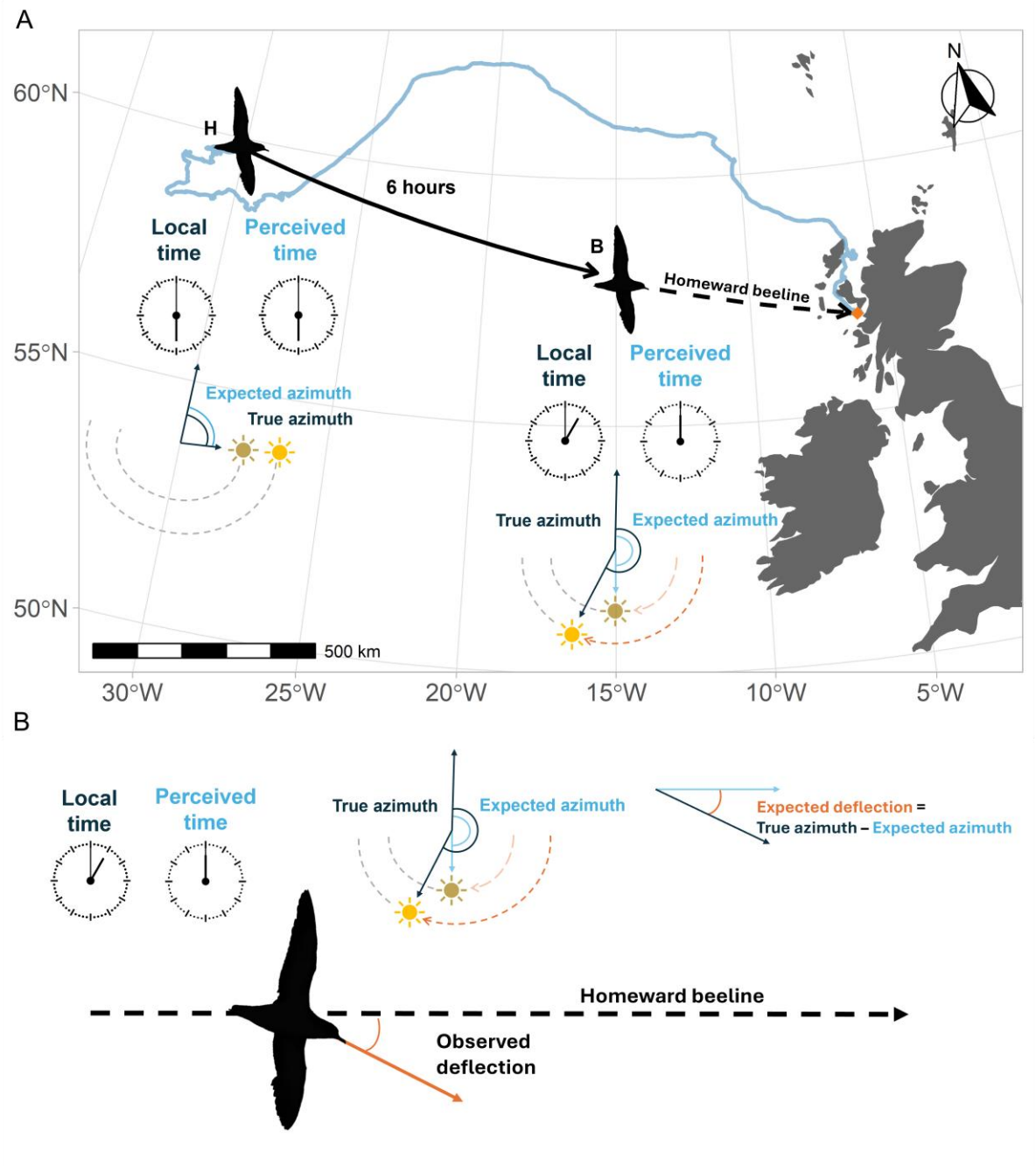


Fig.2. Schematic of expected clock-shift during longitudinal homing flights of shearwaters. (**A**) An example foraging trip with outbound flight and foraging in blue. The bird begins to home at point H. On the first day of homing, its endogenous clock is calibrated to local time at 30°W. However, the shearwater travels eastwards to 15°W over 6 hours to point B. Here, sunrise happened an hour earlier, so the shearwater's perceived time lags local time by an hour and the sun is roughly 20° further clockwise than the shearwater expects. (**B**) At point B, this discrepancy causes the shearwater to orient roughly 20° clockwise of the correct direction. Clock images were reproduced without modification under CC BY-SA 4.0 from https://commons.wikimedia.org/wiki/File:Clock_12-00.svg and https://commons.wikimedia.org/wiki/File:Clock_01-00.svg.

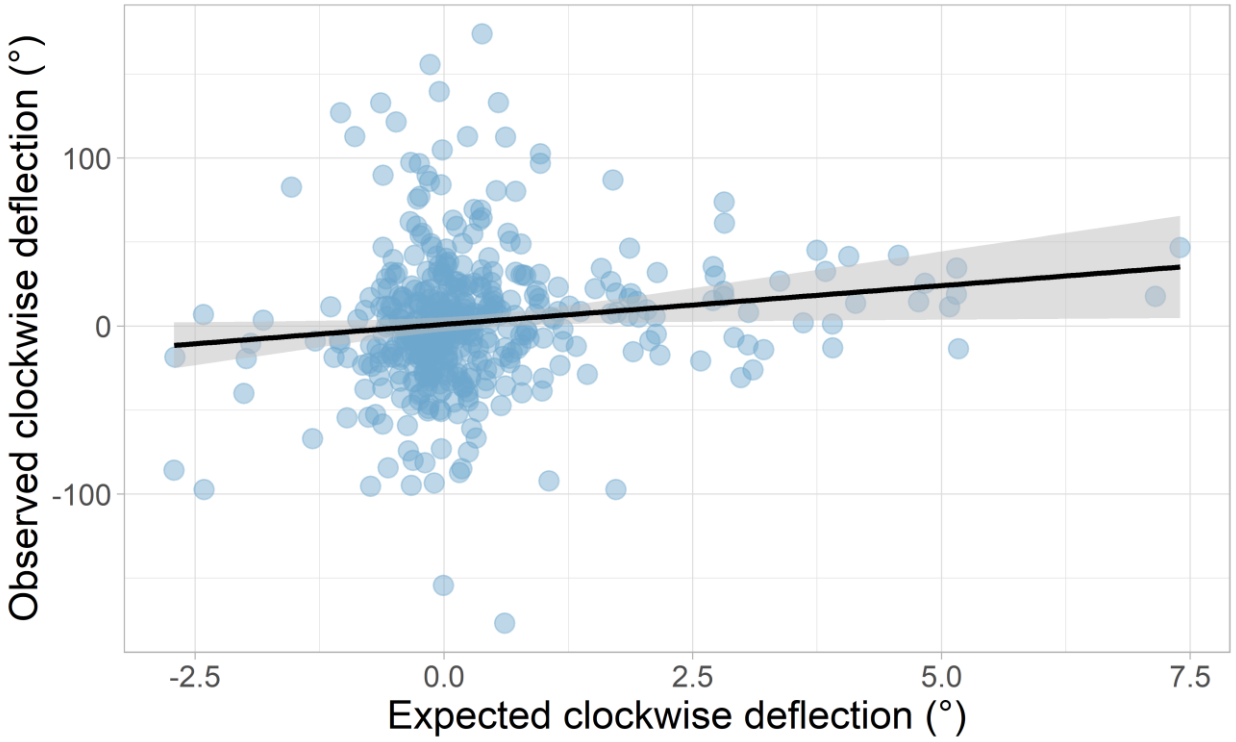


Fig.3. The relationship between expected and observed deflection, based on use of the sun compass and clock-shift during longitudinal movement. The fitted slope is a marginal effect derived from the linear mixed effects model.

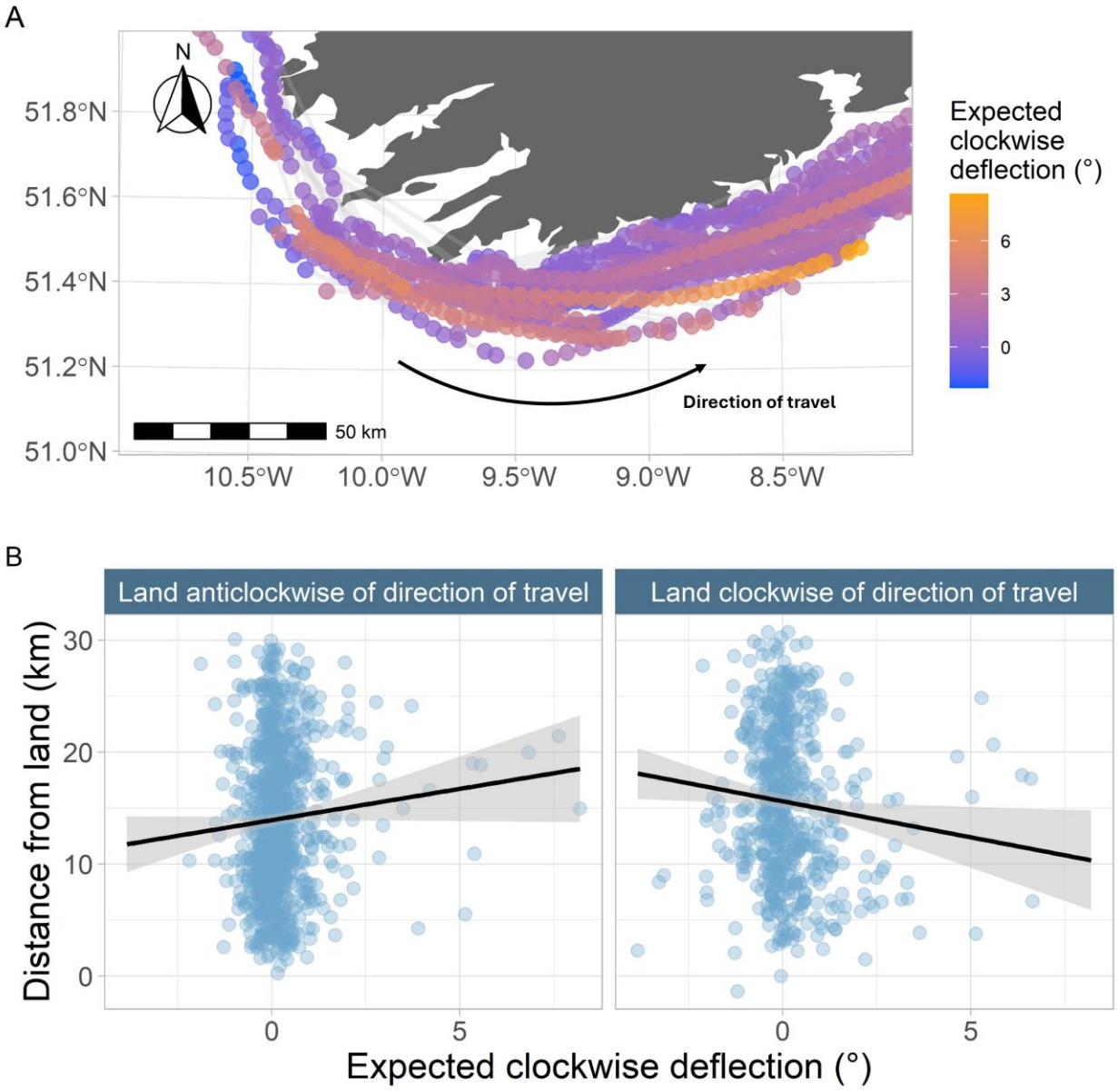


Fig.4. The relationship between expected deflection and distance from land. (**A**) An example set of homing bouts following the southern coastline of Ireland. Land is anticlockwise of the direction of travel and those birds with the most clockwise predicted deflection are furthest from the coast. (**B**) Marginal effect plot showing the relationship between expected clockwise deflection and perpendicular distance from land whilst coast-following. Shearwaters fly closer to land when the expected deflection aligns more strongly with the relative direction of land. See Fig.S7 for a detailed view of the relationship within the cluster of points around expected deflection = 0°.

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Supplementary Materials for

Jetlagged birds lose their way: clock-shift during longitudinal flights causes sun compass error

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The PDF file includes:

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Materials and Methods

Data collection

Breeding adult Manx shearwaters were tracked between 2004 and 2023 on breeding colonies around the UK: Skomer Island (n = 2831 trips; 51°44′15.7″N, 5°16′58.8″W), Ramsey Island (n = 196 trips; 51° 51' 58.3"N, 5° 20' 20.9”W) and Skokholm Island (n = 307 trips; 51°41′38.6″N, 5°17′7.5″W), Pembrokeshire, Wales; Lighthouse Island (n = 3142 trips; 51° 41′ 38.5″N, 5°31′32.9″W), Copeland Islands, Northern Ireland; Rum (n = 89 trips; 56°58′59.4″N, 6°17′41.3″W), Hebrides, Scotland; Lundy (n = 368 trips; 51°10′7.6″N, 4°40′7.8″ W), Bristol Channel, England. Shearwaters were tracked with Mobile Action Igot-U GT-120 (17g), TechnoSmart AxyTrek Marine (13g), TechnoSmart AxyTrek Gypsy 6 (11g), SnapperGPS (11g, see(*66*)) or custom-built (17g, see (*67*)) archival loggers that were attached dorsally using Tesa tape and superglue following the protocol laid out in (*67*). Devices weighed no more than 5% of each bird's total body mass and smaller devices used later in the study weighed < 3% body mass. All tracking was conducted under Special Methods licence from the British Trust for Ornithology and approved by the University of Oxford Animal Welfare Ethical Review Body.

Data processing

Data processing and statistical analysis were conducted in R version 4.4.2 (*68*), using the packages 'dplyr,' 'data.table,' 'stringr' and 'lubridate' (*69-72*). The full dataset is composed of 1477 GPS tracks. Figures were created using 'ggplot2,' 'effects,' 'ggspatial,' 'rnaturalearth,' 'rnaturalearthdata' and 'rnaturalearthhires' (*73-79*).

Filtering and interpolation

Tracks were first filtered to remove any unrealistic positions (< 45° or > 75° N, < 35° W or > 6° E) or duplicate fixes. The median fix interval was calculated and gaps between fixes longer than 10 median fix intervals were identified. These represent periods where the GPS was occluded and did not receive sufficient satellite signal to estimate position. Positional data from SnapperGPS loggers are generated through a post-processing algorithm (*80*) which assigns each fix a value of 'confidence' (arbitrary units), with 0 representing failure to estimate a location; fixes with values of 0 were removed. For remaining fixes, we calculated the great circle distance between each fix and the preceding fix using the 'distHaversine' function from the package 'geosphere' (*81*) and calculated the speed between fixes. We iteratively removed fixes associated with unrealistic speeds ($> 80 km h^{-1}$). We then again identified gaps of greater than 10 fixes. To ensure consistent measures of orientation error, we interpolated to 5-minute resolution within each continuous section of track (i.e. not across gaps), using a cubic polynomial approach via the 'pchip' function from the package 'pracma' (*82*). After interpolation, speeds were recalculated and filtered again. Finally, we calculated distance from the colony at each fix and considered to the bird to have returned to the colony when it was within 3km. Using this rule, we split tracks into separate trips, ignoring periods when the bird was more than 3km from the colony for less than 2 hours. After this processing, we retained 3,025 trips from 1,370 tracks for analysis.

Homing identification

Homing is sometimes identified as the final period of rapid, directed movement during a trip, where this ends at or near the breeding colony (*13, 47*). However, due to the distance of many shearwater trips, necessitating homing over multiple bouts or even days, and the fact that they detour around landmasses, both of which we wished to capture, we used a broader approach. We aimed to identify periods of continuous travel which were, overall, directed towards the colony

and resulted in substantial movement towards it, even if they involved detours around obstacles and did not actually end at the colony. To identify periods of continuous travel, we calculated mean speed over a rolling 15-minute window. Rolling mean speed was bimodally distributed and we used a Gaussian mixture model (via the 'normalmixEM' function from 'mixtools' (*83*)) on the natural logarithm of rolling mean speed to identify bouts of commuting (> 15.6kmh^{-1}), ignoring bouts which were less than 15 minutes long and ignoring gaps within bouts which were up to 60 minutes long. To quantify whether each bout involved substantial, directed movement towards the colony, we measured the initial distance from the colony, the final distance from the colony and the great circle bearing from the start to the end. We identified homing bouts as those with bearings within 75° of the homeward direction (threshold derived from a Gaussian mixture model on the natural logarithms of the absolute deflections), that started at least 50km from the colony, and ended at least 25% closer to the colony. Within each of the bouts, only those fixes when the bird was in flight over the 5-minute fix interval (raw speed > 15.5kmh^{-1}, as identified by a Gaussian mixture model) were identified as being actively homing.

Orientation data and expected deflection predictors

For each fix, we calculated the great circle bearing to the next fix, as well as the great circle and rhumb bearings to the colony using the 'bearing' and 'bearingRhumb' functions from 'geosphere' (*81*). The difference between the instantaneous bearing and the great circle bearing to the colony was the measured instantaneous deflection (orientation error). We used the difference between the great circle and rhumb bearings to the colony as the expected deflection from the great circle beeline if the birds followed rhumb, rather than great circle orientations. To generate predictions for orientation error under sun compass use, we identified when the bird could see the sun directly by extracting local sunrise and sunset times for each fix and the azimuth angle of the sun a shearwater would have observed at each fix using the 'sunCalc' package (*84*). We calculated the difference between this azimuth and the solar azimuth the bird would have experienced at the same time if it had remained at its sunrise location, which gives the expected deflection if shearwaters use a time-compensated sun compass. To generate predictions for orientation error under geomagnetic compass use, we also extracted the geomagnetic declination angle at each fix and the declination at each colony on the 1st July in each year of the study from the International Geomagnetic Reference Field 13 via the GEOMAG70 program (*85*). We then calculated the difference between the local declination and the colony's declination, which represents the expected orientation error if shearwaters rely on a geomagnetic compass calibrated to magnetic declination at the colony. To generate expected error if shearwaters use a geomagnetic compass that is corrected for changes in declination during dawn or dusk, we calculated change in geomagnetic declination since the bird experienced sunrise. We also calculated a metric for the expected deflection generated by the Coriolis effect acting on flying shearwaters. For periods of continuous flight, we calculated the distance travelled from the start of the period in both longitudinal and latitudinal components. The sum of these components multiplied by the sine of the bird's latitude constituted the Coriolis predictor.

Coast-following and distance from land

We identified whether any landmass in the British Isles was visible from each fix using a grid of steradians of visible land around the British Isles ('raster' package (*86*)), whether the home colony was visible and whether the fix was within 30km of any major landmass (area greater than 20km^2, using the package 'sf' (*87, 88*)). We determined whether, from each fix, there was a clear beeline to the colony, without intervening landmasses. For fixes within 30km of land, we calculated the clockwise and anticlockwise bearings perpendicular to the instantaneous bearing.

We then identified whether any land was present within 30km along these bearings and calculated the distance from the fix to the nearest land.

Identification of continuous diurnal periods out of sight of land and land-following

For analysis of orientation, we identified periods of continuous homing that occurred between sunrise and sunset, out of sight of land (including the colony), ignoring periods shorter than 15 minutes and ignoring gaps within periods of less than 30 minutes. For each of these bouts, including only fixes where the bird was in flight, we calculated the mean orientation error expected under sun compass use, and both geomagnetic compass predictions, as well as the mean observed orientation error, using the 'mean.circular' function from the package 'circular' (*89*). We also calculated the mean angular deflection expected if shearwaters followed a rhumb, rather than great circle bearing. For each bout, we calculated a number of covariates that might predict changes in orientation: mean time since dawn, mean cumulative distance travelled so far that day and mean distance from the colony.

Using the same procedure, we also identified bouts of homing between sunrise and sunset where birds were flying with a coastline perpendicular clockwise or anticlockwise to their direction of travel within 30km, where either the bird was beyond the maximum distance at which their colony was visible or where the beeline to their colony was blocked by an intervening landmass. For each bout, we recorded the expected orientation error under the three compass predictions, as well as the same covariates listed above. In addition, we calculated the mean perpendicular distance from the coastline and recorded whether that coastline was clockwise or anticlockwise of the direction of travel.

Statistical analysis

We constructed linear mixed effects models to test whether (a) orientation error and (b) distance from land were predicted by compass error. The first model included mean orientation error as the response, and expected sun compass error, colony, mean time since dawn, mean cumulative distance travelled and mean distance from the colony as fixed effects. The second model included mean distance from the coastline as the response, and the same fixed effects, as well as an additional effect of the interaction between predicted sun compass error and direction of land (clockwise or anticlockwise of direction of travel). Both models included individual as a random intercept. For each term in each model we calculated VIF using the 'check_collinearity' function from the 'performance' package (*90*). Terms with VIF > 5 were excluded from the model. This applied only to distance from the colony in the first model. Model fit was assessed via diagnostic plots (Supplementary Materials). Coefficients for each variable were extracted from the model and are presented ± 95% confidence intervals (CI). The significance of each predictor was assessed using a likelihood ratio test on nested full and restricted models. In the second model, the significance of the additive effects of relative distance from land and expected deflection were not assessed because, in the absence of the interaction, these terms are not expected to predict distance from land. Non-nested comparisons between models with orientation error from a) sun compass use, b) geomagnetic compass use calibrated at the colony and c) geomagnetic compass use calibrated each day were conducted using the corrected Akaike Information Criterion (AICc) from the 'AICcmodavg' package (*91*).

Supplementary Text

Model fit

Model fit for both linear mixed effects models is visualised in Fig.S1-S6. Both models show significant deviation from the assumption of normally distributed residuals (Kolmogorov-Smirnov $D = 0.107$, $P < 0.001$ and $D = 0.055$, $P < 0.001$, respectively) but, given the robustness of linear mixed effects models to such violations (*92, 93*), these were not considered to jeopardise inference.

Full model results

Full results from both linear mixed effects models are presented in Table S1.

Accounting for high leverage of extreme values in land-following model

In the analysis of distance from land in relation to the relative direction of expected clock-shift, 95.7% of expected deflections were between -2° and 2°. However, the largest values were up to around 8°, so the roughly 4% of data beyond the -2° to 2° range potentially had extreme leverage in this model. We therefore conducted the same analysis but using only data from the -2° to 2° range (n = 1366). The coefficients of the model were very similar to those of the full model (-0.93km per 1° when land was clockwise of direction of travel and 0.52km per 1° when land was anticlockwise, difference: 1.46 ± 1.24km) and the interaction between the relative direction of land and the expected clockwise deflection remained significant ($\chi^2 = 5.34$, $P = 0.021$). The results of this model are shown in Fig.S7, with the slopes from the full model overlaid for comparison.

Measuring the magnitude of orientation error from tracking data

Although the direction and relative magnitude of angular orientation error can be assessed within tracking datasets, the absolute magnitude of such error is difficult to measure if animals are able to reorient towards a goal (i.e. if they are using map-and-compass navigation). The measured angular orientation error will only correspond to the true decision error if the frequency of location estimates matches the frequency with which the animal makes orientation decisions. When an animal makes an orientation decision with some error and moves along that bearing, the angular difference between its movement direction and the goal increases monotonically. Therefore, if multiple location estimates are taken along the course of that path, the average measured angular error from the goalward direction will be greater than the true error of the orientation decision. However, if the animal re-estimates its location after some time, it will reorient towards the goal and its deflection will reduce again to equal the true angular error of its orientation decision. As the animal moves along this new path, the angular difference between the bearing from its original location to its current location and the bearing from the original location to the goal decreases. Therefore, if location estimates are taken only after the animal has reoriented at least once, the measured angular deflection of the implied path will be less than the animal's true orientation error. This effect means that the exact magnitude of the slope between observed and expected orientation error should be interpreted with caution.

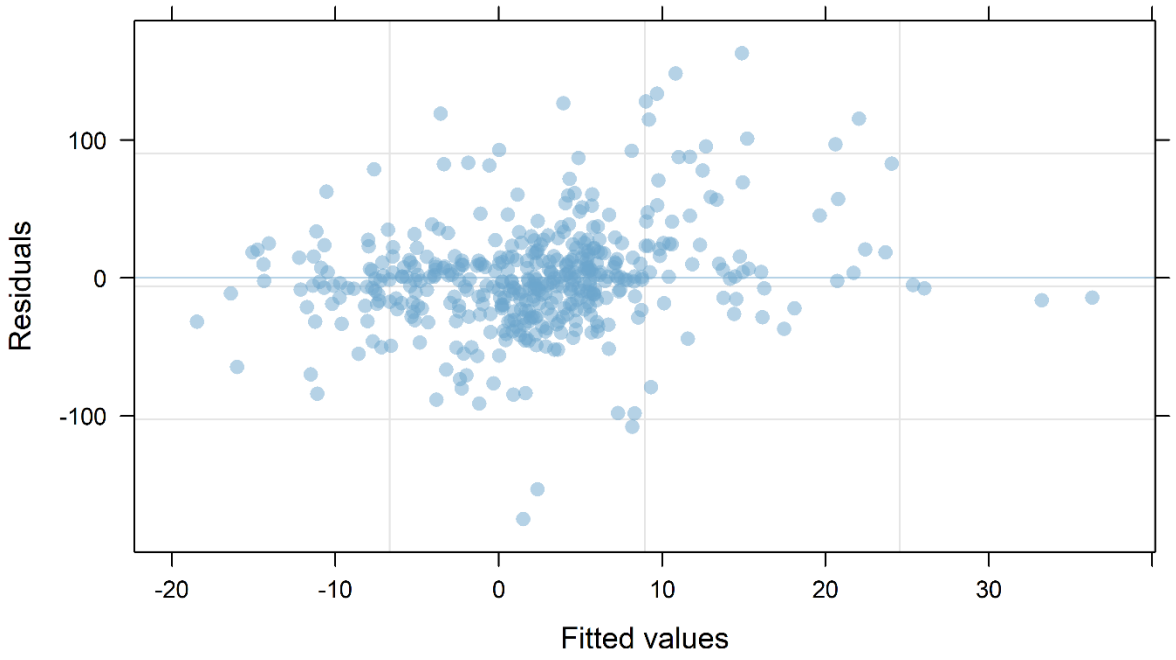


Fig.S1. Model fit for the model with observed deflection as the response, showing residuals against fitted values.

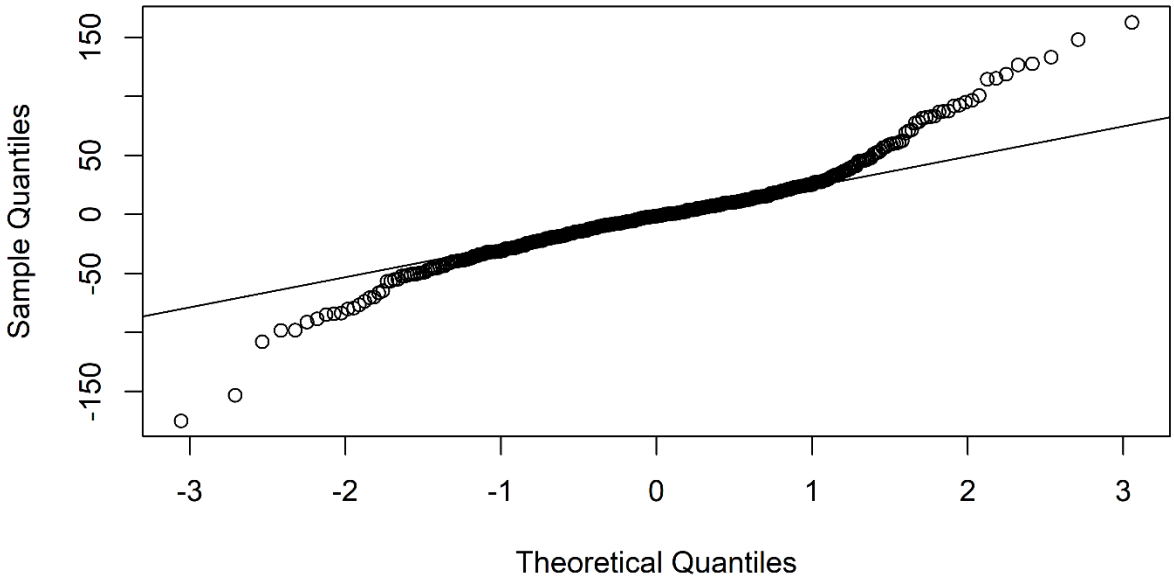


Fig.S2. Observed quantiles for the residuals in the model with observed deflection as the response, fitted against quantiles expected under the assumption of normality.

5

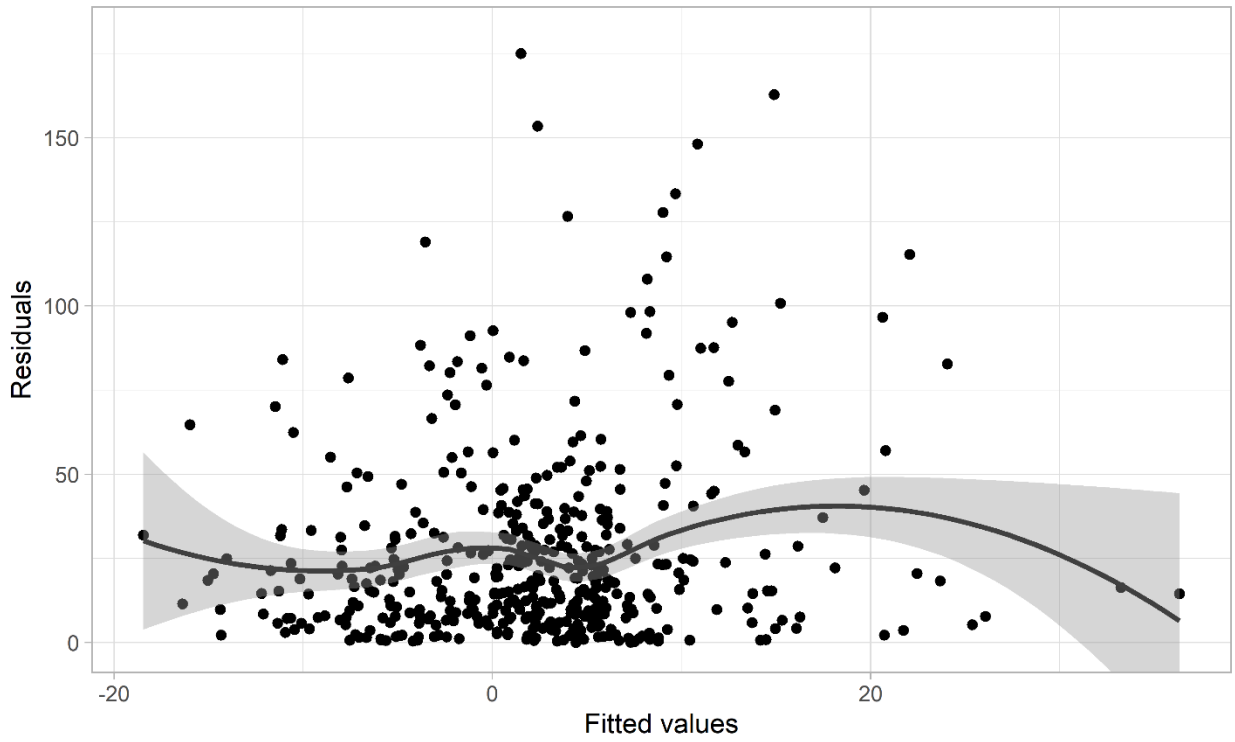


Fig.S3. Magnitude of absolute residuals across fitted values in the model with observed deflection as the response. Fitted line is a Loess smooth.

5

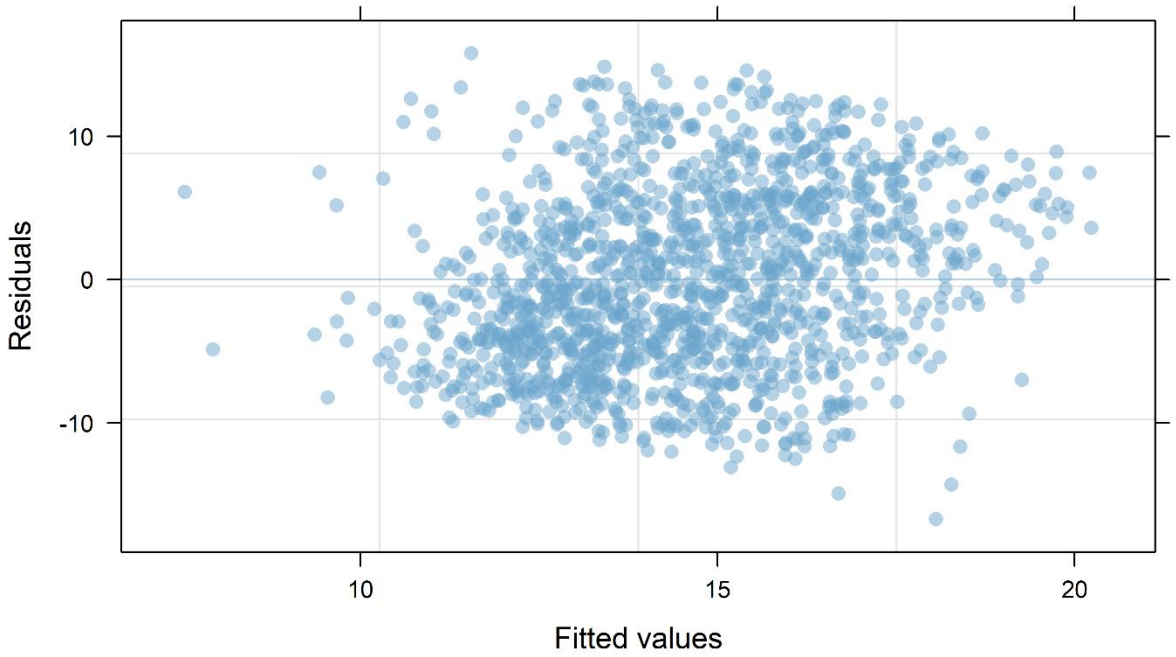


Fig.S4. Model fit for the linear mixed effects model with distance from land as the response, showing residuals against fitted values.

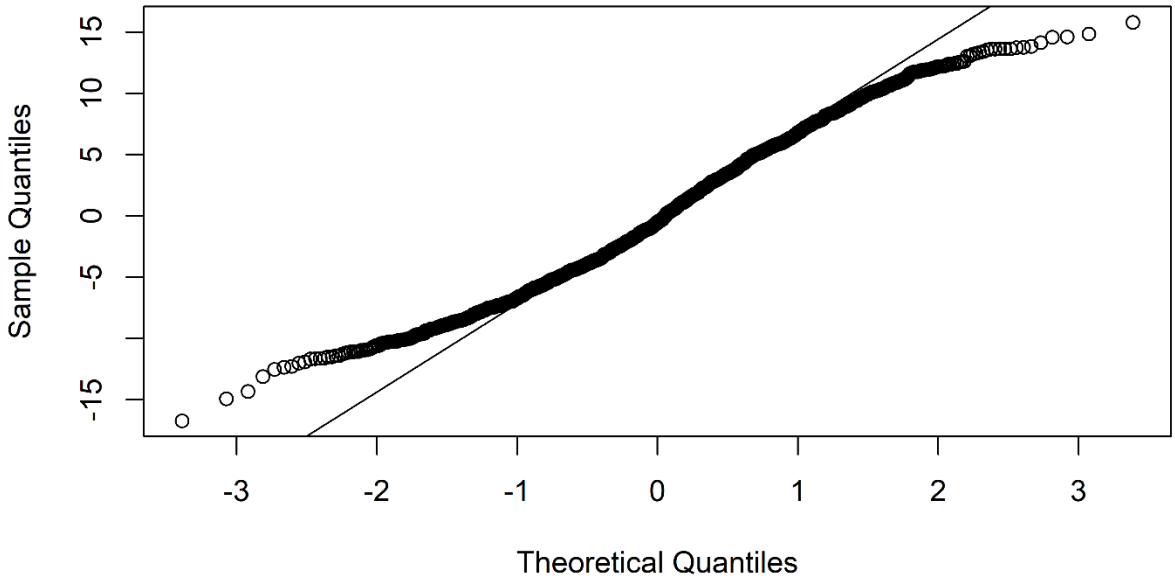


Fig.S5. Observed data quantiles for the residuals in the model with distance from land as the response, fitted against quantiles expected under the assumption of normality.

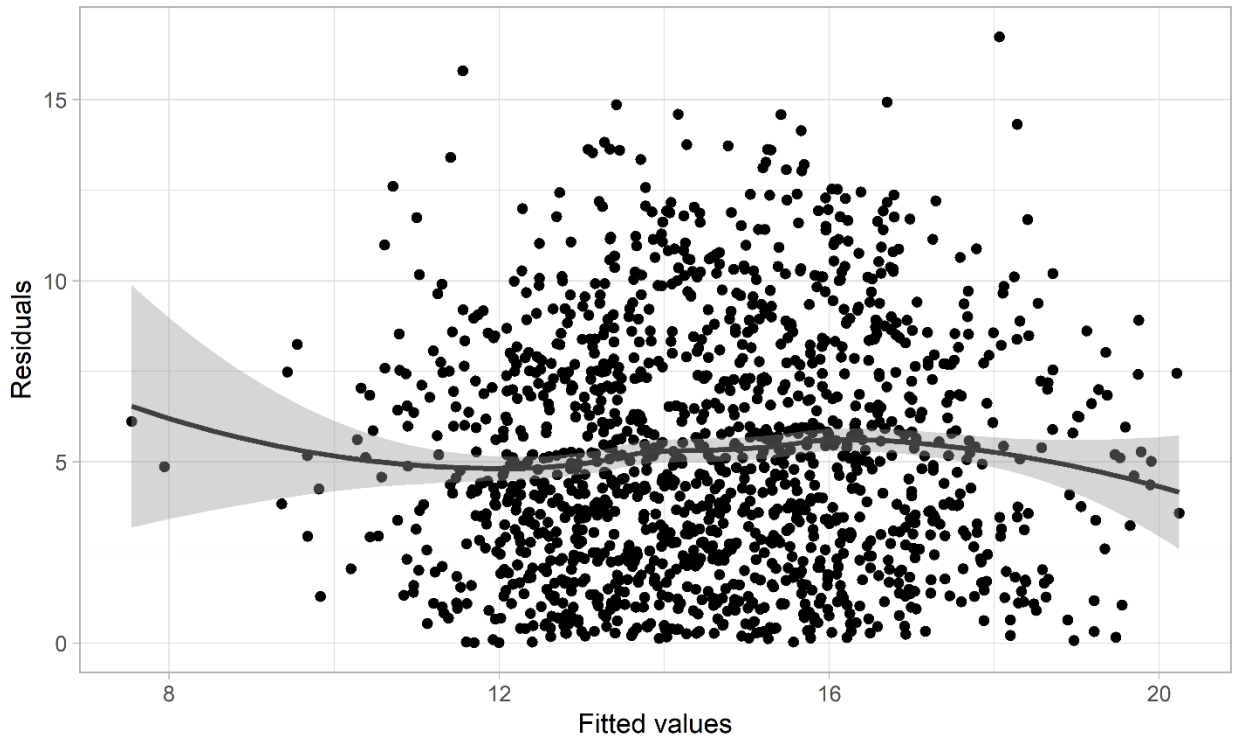


Fig.S6. Magnitude of absolute residuals across fitted values in the model with distance from land as the response. Fitted line is a Loess smooth.

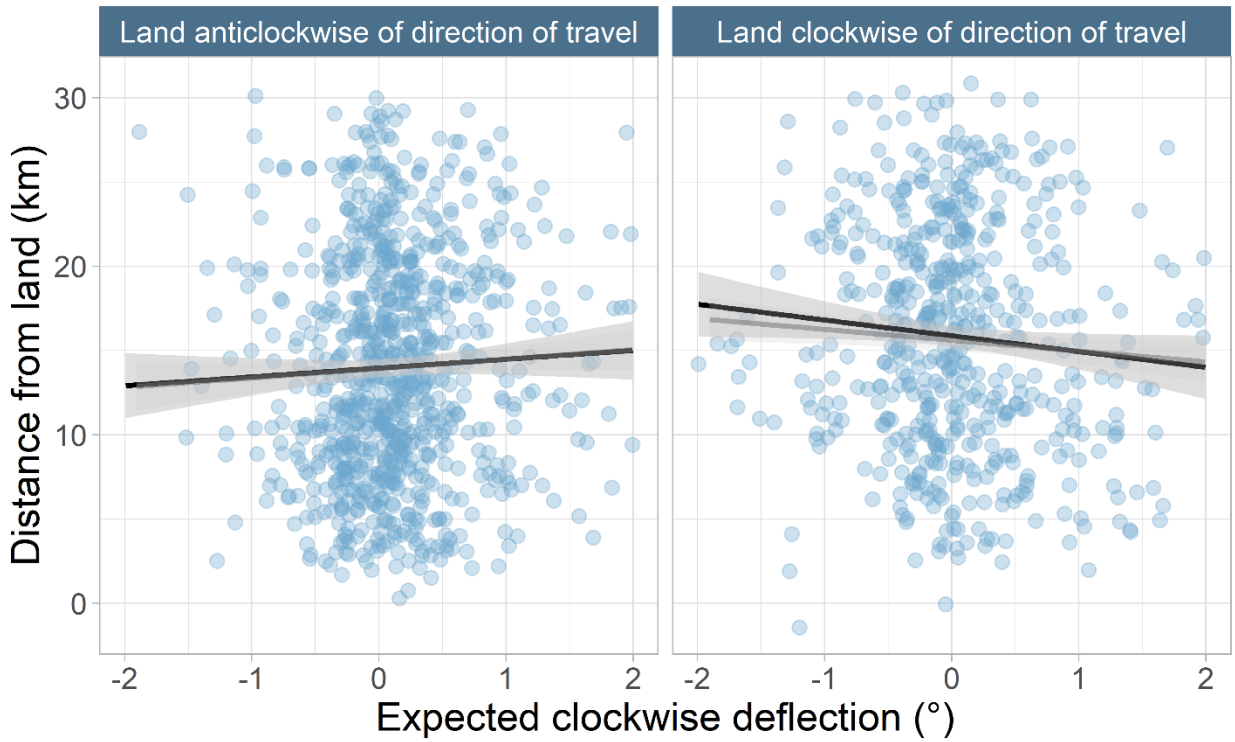


Fig.S7. The relationship between expected clockwise deflection and distance from land for values of expected deflection between -2° and 2°. The marginal effect of expected deflection on distance from land in this model are shown with black lines and the marginal effect from the full model is overlaid for comparison using grey lines.

Response [Sample size]	**Predictor**	**Coefficient [95% CI]**	**DF**	**χ^2**	**P**
Mean orientation error (°) [n = 445]	Intercept (colony = Copeland)	-8.73 [-31.30, 13.99]	-	-	-
	Mean expected deflection (°)	4.62 [0.33, 8.90]	1	4.463	**0.035***
	Mean expected rhumb deflection (°)	-1.34 [-6.73, 4.07]	1	0.236	0.627
	Colony	Lundy: 15.89 [-10.18, 42.19] Ramsey: 30.91 [-5.02, 67.04] Rum: -7.79 [-59.23, 43.56] Skomer: 15.73 [-5.01, 36.64] Skokholm: 7.59 [-16.24, 31.51]	5	5.873	0.319
	Mean Coriolis deflection (°)	-0.05 [-0.18, 0.07]	1	0.750	0.387
	Mean time since dawn (hours)	-0.15 [-1.21, 0.91]	1	0.076	0.783
	Mean cumulative distance travelled (km)	0.01 [-0.04, 0.05]	1	0.077	0.782
Mean distance from land (km) [n = 1,427]	Intercept (colony = Copeland, land clockwise)	15.95 [14.44, 17.45]	1	-	-
	Mean expected deflection (°) : Relative direction of land	1.20 [0.45, 1.96]	1	9.681	**0.002****
	Mean expected deflection	-0.64 [-1.19, -0.10]	1	NA	NA
	Relative direction of land = anticlockwise	-1.68 [-2.46, -0.90]	1	NA	NA
	Colony	Lundy: 3.99 [1.33, 6.66] Ramsey: 3.33 [0.80, 5.85] Rum: -1.97 [-5.63, 1.70] Skomer: 2.46 [1.49, 3.42]	5	42.215	**<0.001*****

		Skokholm: -1.32 [-3.48, 8.29]			
	Time since dawn (hours)	-0.09 [-0.18, -0.01]	1	4.287	**0.038***
	Mean cumulative distance travelled (km)	-0.00 [-0.01, 0.00]	1	3.694	0.054
	Mean distance from the colony (km)	0.00 [-0.01, 0.01]	1	0.012	0.913

Table S1. Full statistical results for linear mixed effects models. Degrees of freedom, χ^2 and P-values relate to likelihood ratio tests between full and restricted models for each term. The significance of the additive terms 'Mean expected deflection' and 'Relative direction of land' was not assessed due to their strong interaction.