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Current Biology

***In Situ* Clock Shift Reveals that the Sun Compass Contributes to Orientation in a Pelagic Seabird**

Highlights

- First demonstration of wild birds making use of a sun compass for active navigation
- First clock shift of a wild bird *in situ*, moving from selectively bred pigeon models
- Attention to the sun compass paid even when visual landmarks available

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In Brief

Padget et al. show that a wild bird makes use of a time-compensated sun compass during active navigation. By measuring the minute-by-minute orientation of GPS-tracked Manx shearwaters homing under clock shift from distant release sites, the authors demonstrate that a sun compass is fundamental even once visual landmarks are available.



In Situ Clock Shift Reveals that the Sun Compass Contributes to Orientation in a Pelagic Seabird

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SUMMARY

Compass orientation is central to the control of animal movement from the scale of local food-caching movements around a familiar area in parids [1] and corvids [2, 3] to the first autumn vector navigation of songbirds embarking on long-distance migration [4–6]. In the study of diurnal birds, where the homing pigeon, *Columba livia*, has been the main model, a time-compensated sun compass [7] is central to the two-step map-and-compass process of navigation from unfamiliar places, as well as guiding movement via a representation of familiar area landmarks [8–12]. However, its use by an actively navigating wild bird is yet to be shown. By phase shifting an animal's endogenous clock, known as clock-shifting [13–15], sun-compass use can be demonstrated when the animal incorrectly consults the sun's azimuthal position while homing after experimental displacement [15–17]. By applying clock-shift techniques at the nest of a wild bird during natural incubation, we show here that an oceanic navigator—the Manx shearwater, *Puffinus puffinus*—incorporates information from a time-compensated sun compass during homeward guidance to the breeding colony after displacement. Consistently with homing pigeons navigating within their familiar area [8, 9, 11, 18], we find that the effect of clock shift, while statistically robust, is partial in nature, possibly indicating the incorporation of guidance from landmarks into movement decisions.

RESULTS AND DISCUSSION

61 Manx shearwaters were clock shifted (–4 hr, 0 hr, and +4 hr; Figure 1; Tables S1 and S2) for 5–7 days while undertaking typically long incubation stints [19] at their nests in underground burrows (Figure 1) before being released at sea 29–48 km from

their colony over 5 dates while equipped with miniature archival GPS loggers that recorded fixes every 1 min (Figure 2). Analyses were conducted on the flying portions ($> 2.32 \text{ ms}^{-1}$; Figure S2) of tracks from 48 birds that returned to the colony on the day of release. For orientation analyses, we excluded periods of resting on the water and short stints of flight that occurred before directed, homeward-oriented flight began, identifying the start of homeward-oriented movement using a backward path analysis as in [20]. We used linear mixed models (LMMs) to test for the effect of treatment on instantaneous deflection during homing with random (intercept-only) effects fitted to account for the effect of release trio and release date. Likelihood ratio (LR) tests between the full model and a nested, null case of the model without treatment as a predictor were used to obtain p values. Treating the clock shift as a continuous predictor (–4 hr, 0 hr, and +4 hr) revealed a highly significant effect of treatment on birds' mean instantaneous deflection to the colony during active homing flight (LR test: $\chi^2 = 21.32$, d.f. = 1, $p < 0.00001$) with an estimated effect of $13.2 \pm 0.62^\circ$ per 4-hr difference in clock-shift schedule. Modeling instantaneous deflection as a response to treatment as a factor (rather than assuming a linear response of deflection to the direction of shift) yielded similar results ($\chi^2 = 21.40$, d.f. = 2, $p < 0.0001$) with largely symmetrical estimates for the effect of fast and slow treatment relative to controls (fast: $-14.3 \pm 4.8^\circ$; control: $+0.7 \pm 8.0^\circ$; slow: $+12.1 \pm 5.3^\circ$; Figure 3). The difference among treatments was upheld at the $\alpha = 0.05$ significance level for models run pairwise for control-fast and control-slow, even after p values were doubled as a Bonferroni correction for the two-way comparison, which conservatively (and in this case, incorrectly) assumes that treatment expectations are independent (control-slow: $\chi^2 = 5.19$, d.f. = 1, Bonferroni $p = 0.04$; control-fast: $\chi^2 = 5.82$, d.f. = 1, Bonferroni $p = 0.03$). Release date explained a significant amount of variation in the instantaneous deflection to home (refitted as a fixed predictor and tested with LR test: $\chi^2 = 21.65$, d.f. = 2, $p < 0.0001$). While our concentrated directional data met the assumptions of LMMs, we nonetheless conducted a randomization to test the probability of observing our result by chance without assuming anything about the residual distribution. We calculated each treatment's overall deflection by taking, for each release separately, the mean difference of each fast and



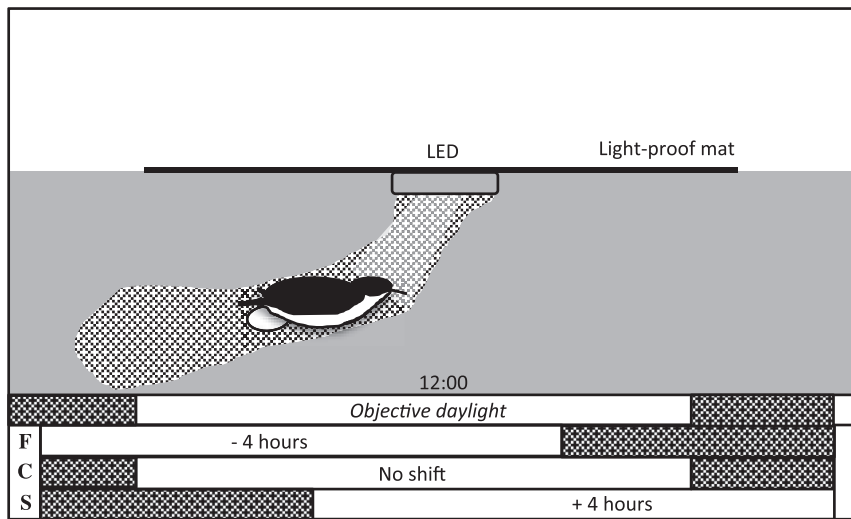


Figure 1. The *In Situ* Clock-Shift Setup at the Manx Shearwater's Burrow While It Incubates Its Egg

Schematic shows the schedule of dark and light photoperiods over the 5–7 days during which the clock shift was applied. The times shown in the figure are ~30 min earlier than in the experiment (so that they fit within the arbitrary 24-hr period between consecutive midnights).

See also [Tables S1](#) and [S2](#).

orientation was influenced consistently by the clock-shift treatment, even accounting for different starting locations and thus different beeline routes home. We observed no differences among treatments in the timing of homing or in the speed that birds flew during homeward-oriented flight, which suggests that the

slow bird from the mean control and then calculating the global weighted mean across dates. We then randomized (with replacement) the treatment identity of each bird 100,000 times and calculated the global deflections of treatments for each run. We found that fewer than 0.1% of randomizations gave deflections that were equal to or greater than observed in either the fast (F) < control (C) < slow (S) or the S < C < F directions (two-tailed $p < 0.001$). For visual comparison, tracks transformed such that they have the same start location and rotated such that the home bearing from the start is the same for each are shown in [Figure 4](#).

There was no significant difference in mean flight speed (LR test: $\chi^2 = 0.86$, d.f. = 2, $p = 0.65$) or time of departure toward the colony after release (Kruskal-Wallis $\chi^2 = 2.79$, d.f. = 2, $p = 0.25$) that might have indicated motivational differences among treatments. There was also no significant change in the magnitude of the modeled deflections for each 2.5-km bin as birds came closer to the colony (slow-control: $F = 0.17$, d.f. = 1,8, $p = 0.69$; fast-control: $F = 0.01$, d.f. = 1,8, $p = 0.93$). Measured deflections are shown as a function of distance to the colony in [Figure S3](#).

The deflections in birds' orientation relative to the goal induced by the clock shift indicate that Manx shearwaters incorporate guidance from a time-compensated sun compass into their movement decisions as they home after release from distant—but probably previously visited—areas. Our controlled experimental design—with a clock shift in both directions—precludes the possibility that the result obtained here was confounded by some aspect of the clock-shift treatment not related to a manipulation of birds' circadian rhythms. By using a mixed-modeling approach to identify differences among treatments in instantaneous deflection, we were able to disentangle directional bias across release dates from the effect of clock shift on the compass orientation of birds homing from different starting locations while accounting for our repeated measures of deflection from each bird's track. This revealed that release date strongly influenced the homing orientation of birds (most probably caused by wind direction or the intended rafting destination of birds before making landfall on the colony), but nevertheless, that

observed deflections among treatments were not caused by differences in motivation that might have been unwittingly influenced by clock shift. Navigationally, the observed deflections in this study are consistent only with sun-compass use. If birds were to use the sun's arc as a map (Matthews' sun-arc hypothesis [21]) instead of a compass—an idea discussed in much detail elsewhere [22]—then clock shifting would result in deflected homing orientations in the opposite direction to that observed in the current study. Under that hypothesis, a fast-shifted bird would perceive the later-than-expected sunset as displacement to the west (and thus should orient more clockwise in the current study), and slow-shifted birds would perceive a later sunset as displacement to the east (and thus should orient more counterclockwise). To our knowledge, these findings therefore represent the first successful attempt to clock shift an animal in the wild and the first evidence for use of sun-compass orientation in a wild bird during active navigation—an experiment only previously attempted once, unsuccessfully, and without the advantage of GPS telemetry [23].

Pure sun-compass guidance is predicted to result in deflected orientation equivalent to the angular displacement of the sun's azimuth between the actual and subjective time of day at release [24, 25]. Where pigeons are released from familiar areas, however, deflection is typically much smaller than this—around half—perhaps indicating a compromise with guidance from a magnetic compass or piloting cues from familiar visual landmarks [11]. In birds that are very familiar with their route home [8] or are released in sight of their loft [9], deflections are smaller again but still present. Thus, while the qualitative prediction of opposing deflections under slow and fast shifts indicates involvement of the sun compass in many different situations (in pigeons, at least), the way in which it is used varies between different situations, and this is reflected in the degree of deflection relative to the expectation for pure sun-compass use. In our experiment, the difference in deflection between fast and slow clock-shift treatments was ~26° of an expected ~101° under full sun-compass use for the median time of homeward-oriented flight. This represents a substantial but partial effect of clock shift on the birds' orientation

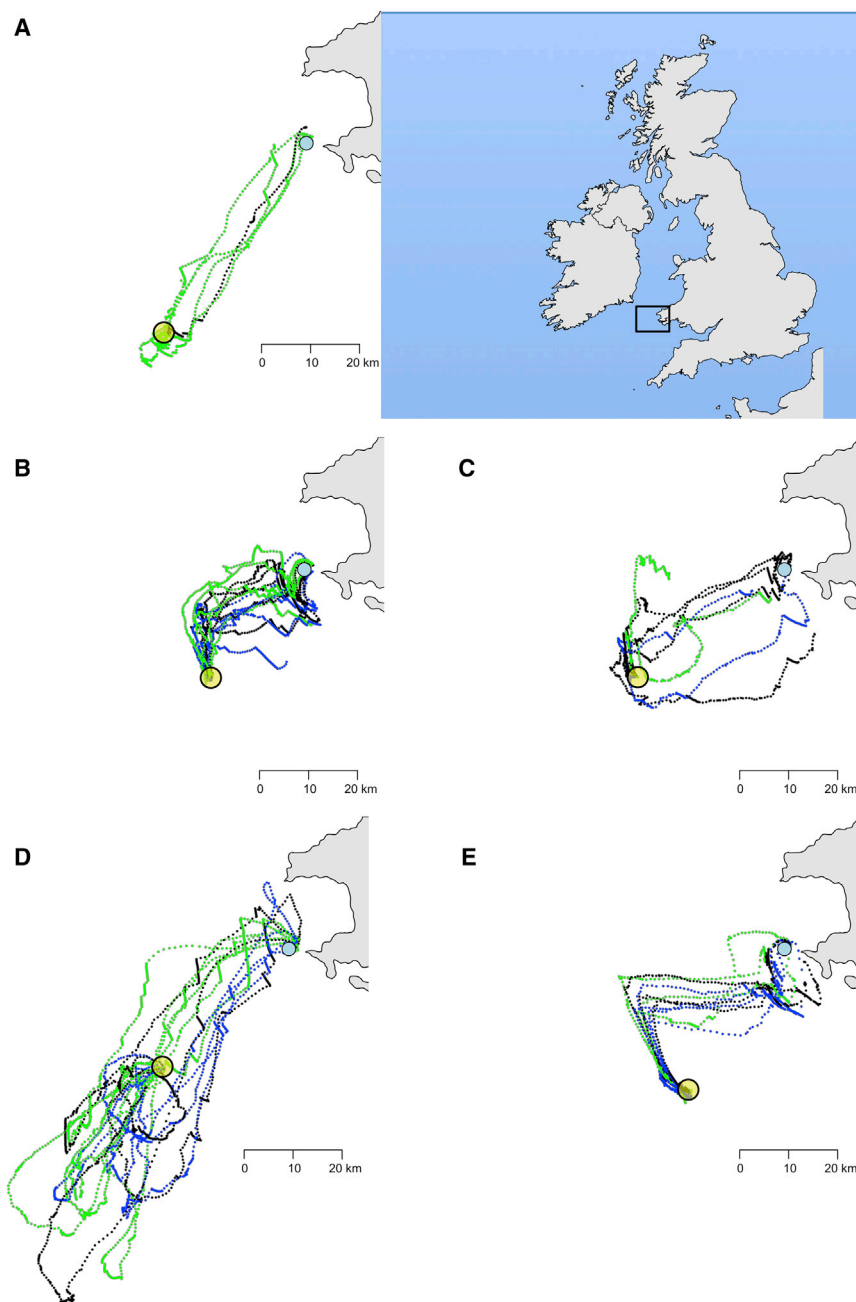


Figure 2. GPS Recording Homing Trajectories for Clock Shifted Manx Shearwaters

Individual releases in chronological order (A–E) with control (black), fast (green), and slow (blue). 2015 is shown in (A–C) and 2017 is shown in (D and E). Release site for each is shown as a yellow circle and Skomer Island as a blue circle, demonstrating the considerable movement of birds between release and homeward-oriented movement. Rafting behavior can be seen where consecutive 1-min fixes are close together, forming solid lines. Tracks from all releases are shown together in Figure S1 and raw orientation data are shown in Table S3.

See also Figure S2 and Table S1.

landmarks, a clock shift should not induce a response when landmarks are available. How compass information is relevant to the use of visual information remains unknown. It has recently been suggested [12] that landmarks themselves could be recognized in a time-compensated way because how landmarks appear might vary with the sun's movement over the course of a day. In the same vein, we speculate that for a bird such as a shearwater, being able to see a distant landmark feature with a relatively uniform shape (perhaps a mountain or a small island) might yield only information about the distance to the object from its apparent size and not its precise location if the object appeared similar from a range of directions. Recognition of the landmark alone (and the distance to it) would then provide an arc of potential locations at which the bird could be positioned at that given distance. Incorporating the time-compensated angle of the sun relative to the landmark, however, could enable birds to reduce their location uncertainty to a subset of the arc, thus enhancing the location information gained from relatively sparse and otherwise uninformative horizon-limited features. This predicts both the persistence

of clock-shift deflection and its partiality for shearwaters or pigeons navigating by reference to at least some visual cues.

that persisted as birds approached the colony—a journey taking them from areas with no or few landmark cues to 8 km from the colony, where much visual information is available from the adjacent topography.

Small deflections under clock shift are not easy to place into extant theory for bird navigation [8–10]. For example, if birds made use of a mosaic map of landmarks with known spatial relationships, sun-compass guidance between these features should be indicated by a full deflection in orientation under clock shift as measured by instantaneous deflection. Conversely, if birds navigate home by flying toward landmarks associated with getting closer to the colony (known as pilotage [10]) or calculate their desired heading by reference to the configuration of

of clock-shift deflection and its partiality for shearwaters or pigeons navigating by reference to at least some visual cues.

The partial clock-shift deflections in the current study suggest that the mechanisms guiding seabirds' movements over open ocean may conform to the same rules that have been suggested to govern navigation in the few terrestrial species tested previously where the time-compensated sun compass is implicated in the control of much oriented movement. This is perhaps surprising, given the different sensory challenge that navigation at sea represents. Our *in situ* clock shift of a wild seabird therefore opens up the potential for studying wild birds navigating in scenarios that are more ecologically relevant than those studied previously and thus might, in the

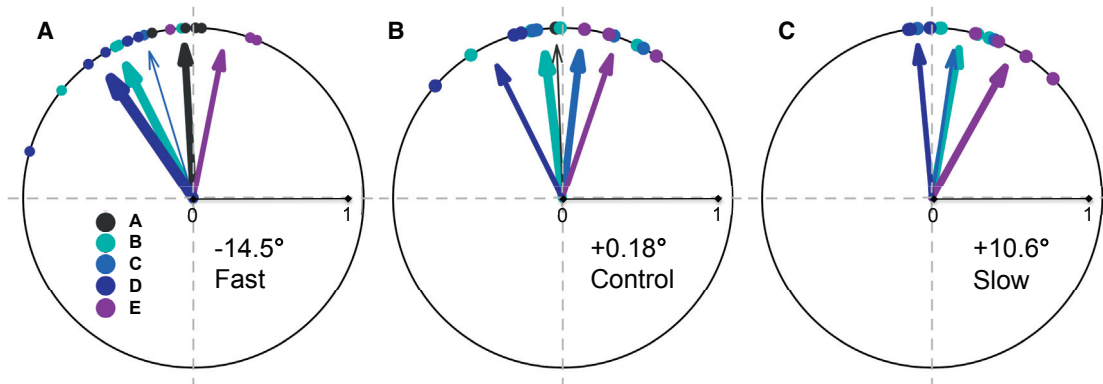


Figure 3. Orientation of Clock Shifted Manx Shearwaters Relative to the Goal

Circle plots showing the mean instantaneous deflection of each bird (on the circle perimeter) during flight as it homed to the colony for fast-shifted (A), control (B), and slow-shifted (C) treatments. The colony direction is 0° . Arrows show the second order means for each release date, which is represented by arrow color for releases (A)–(E) corresponding to Figure 2 and indicated by the color key. The weighted mean for each treatment across all releases is reported in the circle. Arrow thickness is the sample size for that release (thickest arrow = 6; thinnest = 1). Arrow length is the second-order angular dispersion of the tracks for that arrow scaling from 0 to 1 as indicated by the horizontal bar. Measured deflections from the beeline are shown. Modeled deflections are in the main text. See also Table S4.

future, yield clues about the unresolved aspects of both oceanic and terrestrial animal navigation.

STAR★METHODS

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SUPPLEMENTAL INFORMATION

Supplemental Information includes three figures and four tables and can be found with this article online at <https://doi.org/10.1016/j.cub.2017.11.062>.

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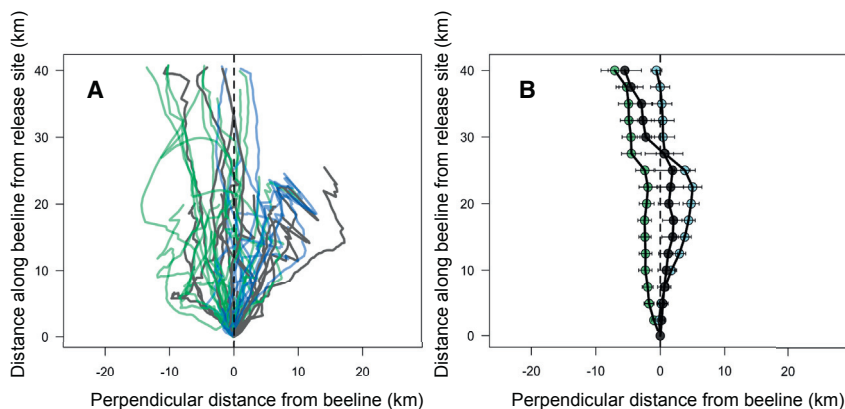


Figure 4. Manx Shearwater Homing Trajectories Transformed to the Same Starting Location

Slow (blue), fast (green), and control (dark gray) flight sections of tracks transformed from a north-south map coordinate system such that the start of directed homing flight is at $[0,0]$ and the colony location lies at $[0,n]$, where n is the distance (arbitrary units) to the colony from the start of directed homing flight and differs among tracks correspondingly. Consequently, the great circle geodesic to the colony is at a bearing of 0° from $[0,0]$, and distances and relative angles along the paths are inherited from the birds' real Universal Transverse Mercator (UTM) coordinates by the transformation, allowing for a visual comparison of all analyzed tracks (A) and their mean perpendicular distance (and standard error) (B) to the beeline for

where the path crosses each 2-km interval parallel to the beeline from the original release site. Note that since tracks are normalized from the start of homing behavior, distances to the colony are not comparable (hence the differing length of tracks in A). Instantaneous deflection as birds get closer to the colony is shown in Figure S3.

AUTHOR CONTRIBUTIONS

O.P. and T.G. conceived the experiment; O.P., T.G., S.L.B., M.M.K., M.S., M.B., and A.L.F. carried out the fieldwork; and O.P., E.v.L., and S.R. conducted the analyses. All authors contributed to writing the manuscript.

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STAR★METHODS

KEY RESOURCES TABLE

| REAGENT or RESOURCE | SOURCE | IDENTIFIER |
|--|----------------------------------|---|
| Experimental Models: Organisms/Strains | | |
| Manx shearwater <i>Puffinus puffinus</i> | Skomer Island (51°44' N, 5°19'W) | N/A |
| Software and Algorithms | | |
| R software | N/A | https://cran.r-project.org/ |

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Oliver Padget (oliver.padget@zoo.ox.ac.uk).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Adult Manx shearwaters, *Puffinus puffinus* of unknown age and sex were used in this study. The Manx shearwaters breed at the study site, on Skomer Island, in a colony with > 300,000 breeding pairs.

METHOD DETAILS

Clock-shift Procedure

The study was carried out on Skomer Island, Wales (51°44' N, 5°19'W), probably the largest Manx shearwater breeding colony globally [26], from mid-May to early July, and late May and early June 2015 and early June 2017 respectively. To clock shift wild birds *in situ*, we monitored the attendance of incubating pairs of burrow-nesting Manx shearwater at the colony. Like other Procellariiformes, the two members of the pair will alternate incubation stints, which regularly last a week [19]. Birds that switched incubation duty 6 or 7 days before a release date were alternately assigned to a fast clock shift, slow clock shift or a control treatment. “Clock-shift mats” which comprised a 35 × 35 cm sheet of 3 mm thick commercial grade rubber with a Rolson 24 LED lamp fitted in its center were placed over the entrance to each burrow and held in place using metal pegs. Photoperiods were manipulated by turning these lights on and off as in Table S2, based on the sunrise and sunset times for the release date. Our “control” (zero shift) clock-shift birds underwent the same procedure but no shift in the photoperiod was imposed. The photoperiod was then maintained with the phase-shifted dawn and dusk for 5-7 days until release, sufficient for the desired clock shift in homing pigeons [15].

Release and retrieval

61 birds were released over six dates (Table S1). Before being transported to the release site birds were fitted with I-gotU GT-120 GPS loggers using strips of TESA 4651 marine tape [27]. GPS loggers weighed 16.7 g (on average 4.1% of the birds' body mass, see Table S3), and were programmed to take fixes at 1-minute intervals. Birds were removed from their burrows while both the objective and the subjective time was ‘daytime’ for all subjects. It was ensured that birds did not see the sun’s disc during deployment and transportation. When birds were collected for GPS deployment, their eggs were moved to an incubator in which they were kept at ~37°C until dusk when they were returned to their burrows such that the adults did not arrive at an empty nest in the event that they were not caught upon landing at the colony.

Birds were translocated in individual or partitioned cardboard boxes and taken by boat at a bearing of ~225° southwest as far as possible (sea-state permitting). Releases were 30 – 49 km from the colony. Where possible, birds were released in trios with one fast-shift bird, one slow-shift bird and one control bird. When released, birds were placed on a wooden board on the side of the boat and allowed to take off into the wind in their own time.

At dusk on the night following release birds were recaptured by hand upon arrival and their GPS devices retrieved before being placed back into their burrows and allowed to resume incubation or to join their partner to complete the incubation changeover if their partner had also returned on the same night.

QUANTIFICATION AND STATISTICAL ANALYSIS

Track Processing

We identified at-sea behavior in our homing tracks by using a speed filter empirically derived by fitting a Gaussian mixture model to speed, calculated between consecutive GPS fixes, as in other studies [28] (Figure S2). Because our releases necessarily took place earlier in the day than birds would begin homing, we identified the point along the track after release where birds began directed flight toward the colony as the decision to start homing. Pre-homing behavior of shearwaters varied considerably among release dates, possibly because

of differences in wind conditions, sea state or the proximity of foraging resources, but nonetheless, the onset of homing was indicated by a switch to high-speed, oriented flight. By moving backward along the track from the colony we identified the point where each bird's beeline distance from the colony over time stopped changing linearly with respect to the length of the backward path (excluding periods of resting) and considered this point to be the start of homing, as in [20]. This was done blind with respect to treatment, but nonetheless there is some subjectivity in identifying the breakpoints. Therefore we also repeated the orientation analyses with different starting points denoted by the first time that the bird was in oriented flight for a prolonged period of time after release. The parameters for both the threshold deflection identified as 'oriented' and the time period that oriented flight was considered to represent the start of homing were varied to check for sensitivity to the identification of start points (Table S4). Tracks were analyzed either until they reached 8 km from the colony, where much socialising occurs and movement orientation is no longer related to navigation, or at the end of nautical twilight after which time sun-compass use is unlikely (whichever came first). Track-segments where birds were sitting on the water (slow speed) were removed and analysis was therefore conducted on homeward oriented flight sections of track. Instantaneous deflection, the angle between the animal's current bearing and the goal between consecutive GPS fixes, was calculated as in several other studies [9, 29]. We used instantaneous deflection since it is a measure fundamentally associated with compass orientation, unlike other metrics sometimes reported to analyze compass deflections (e.g., (virtual) vanishing bearings). A hypothetical bird that consults a deflected compass from a known location will set off at a bearing equal to the homeward direction summed with the induced deflection. If the bird rapidly updates its map, it will readjust its course to its new bearing from home plus its induced deflection. Therefore, a bird with high-resolution map updating would spiral homewards with a rate of change of course related to its map resolution and the imposed compass deflection, provided the induced deflection is less than 90° . In this hypothetical scenario, instantaneous deflection will remain constant, whereas virtual vanishing bearing will decrease as the distance between the release site (where the bearing is measured from) and the bird increases, even for a bird consulting a consistently shifted compass with constant deflection.

Statistics

Clock-shift effect on orientation

We used linear mixed models (LMM) to analyze the effect of our clock-shift treatment on the instantaneous deflection of birds as they homed to the colony. Since our data were structured in trios (individual releases) and across five dates that differed in weather, release trio and release date parameters were fitted as nested random (intercept only) effects such that model errors around the effect of treatment were independent. Because our clock-shift treatment was effectively a single treatment with three ordered levels, we fitted an LMM with clock shift as a continuous predictor (-4 , 0 or $+4$). As a conservative approach (since this tests only for a monotonic response to treatment), and to obtain estimates for each treatment, we also fitted an LMM with treatment level as a factor and conducted post hoc pairwise tests with p values adjusted with a Bonferroni correction for the two comparisons (control \sim fast; control \sim slow). For all LMMs, we obtained p values by comparing a full model including treatment with its corresponding null, nested model with only random effects using a likelihood ratio (LR) test. Instantaneous deflections were highly concentrated and thus their circularity did not cause a violation of the assumptions for LMMs of normal residuals and homogeneous variance in error. However, to ensure that circularity did not affect the outcome of our analysis, we performed an intuitive randomization test that reflected the structure of our data to confirm that the LMM assumptions did not impact our results. To calculate our observed deflections (global response), we first normalized the instantaneous deflection for each release trio as a positive or negative deflection to control, and then normalized the mean of these deflections as a positive or negative deflection for each release date. We next randomized each bird's treatment 100,000 times and re-calculated our global response and recorded the probability of the observed deflections or greater by chance, permitted in either direction (two tailed: Slow < Control < Fast; Fast < Control < Slow).

Treatment effect with distance to the colony

To assess whether the deflection induced by our clock-shift treatment changed as shearwaters came closer to the colony, we refitted our LMMs to 2.5 km binned distances from the colony from 8 km to 40 km and > 40 km. This allowed us to obtain an estimate of treatment effect for each bin but taking account of different sample sizes and data structure for different distances (for example, only birds from two releases had homing tracks within the farthest bins). We then used a linear regression to see if the magnitude of the effects varied with distance to the colony.

Analysis of secondary response variables

The effect of treatment on mean homing speed was tested using LMMs fitted with the same random effects as detailed above. A non-parametric Kruskal-Wallis test was employed to test the effect of treatment on the highly non-normal departure times (when birds first undertook a prolonged homing portion of flight).

All LMMs were fitted using the 'lme4' package [30] in R. Gaussian mixture models were fitted using the 'Mixtools' package [31].

Ethical statement

All work adheres to the ASAB/ABS guidelines for the Use of Animals in Research and was conducted after ethical approval by Natural Resources Wales, Islands Conservation Advisory Committee for Skomer and Skoholm Islands and the University of Oxford's Local Ethical Review Process. GPS deployments were approved by the British Trust for Ornithology Unconventional Methods Technical Panel (permit C/5311). Similar biologging techniques have been used on this colony since 2007 with no significant effect on reproductive success [32].