BIOLOGY LETTERS

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Cite this article: Bianco G, Ilieva M, Åkesson S. 2019 Magnetic storms disrupt nocturnal migratory activity in songbirds. *Biol. Lett.* **15**: 20180918.
http://dx.doi.org/10.1098/rsbl.2018.0918

Received: 2 January 2019
Accepted: 18 February 2019

Subject Areas:
behaviour, ecology

Keywords:
animal navigation, bird migration, magnetic compass, migratory restlessness, compass orientation, geomagnetic field

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Electronic supplementary material is available online at https://dx.doi.org/10.6084/m9.figshare.c.4414691.

THE ROYAL SOCIETY PUBLISHING

Animal behaviour

Magnetic storms disrupt nocturnal migratory activity in songbirds

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Birds possess a magnetic sense and rely on the Earth's magnetic field for orientation during migration. However, the geomagnetic field can be altered by solar activity at relative unpredictable intervals. How birds cope with the temporal geomagnetic variations caused by solar storms during migration is still unclear. We addressed this question by reproducing the effect of a solar storm on the geomagnetic field and monitoring the activity of three songbird species during autumn migration. We found that only the European robin reduced nocturnal migratory restlessness in response to simulated solar storms. At the same time, robins increased activity during early morning. We suggest that robins reduced activity at night when the perception of magnetic information would be strongly disrupted by temporal variations of the magnetic field, to extend their migration during daytime when several visual cues become available for orientation. The other two species, chiffchaff and dunnock, showing low or no nocturnal migratory activity, did not respond to the solar storm by changing activity.

1. Background

The Sun's energy flux shows periodic variations with longer intervals of low energy and shorter intervals with high energy that are defined as solar storms [1]. The high-energy ions emitted during solar storms interact with the ionosphere causing temporary alterations of the geomagnetic field with stronger effects at higher latitudes [1,2]. Songbirds possess the ability to detect and use the geomagnetic field for orientation during migration [3,4], but it is not clear if they are able to tell apart the spatial characteristics and the temporal variations of the magnetic field [5]. A magnetic map based on the combination of geomagnetic intensity and inclination may affect orientation [3], ecophysiology [6,7] and activity [8,9] in bird migrants. Furthermore, local geomagnetic anomalies caused by the characteristics of the Earth's crust can disrupt birds' navigation ability [10,11]. Effects of temporal variability caused by solar activity on the geomagnetic field have already received some attention in different organisms (see references in [2]), but less is known about the effects on birds [12–14]. We tested three species of migratory songbirds, two of which are expected to migrate at night (chiffchaff *Phylloscopus collybita*; European robin *Erithacus rubecula*) and one that migrates during the day (dunnock *Prunella modularis*). We monitored their activity in cages for several days while exposed to geomagnetic displacements using either constant values or variable magnetic parameters that simulated the effect of a solar storm.

2. Material and methods

(a) Experimental birds and testing facility

We captured juvenile dunnocks ($n = 8$), chiffchaffs ($n = 8$) and European robins ($n = 8$), near Stensoffa Ecological Field Station (55°41′ N 13°26′ E) in southwestern

royalsocietypublishing.org/journal/rsbl *Biol. Lett.* **15**: 20180918

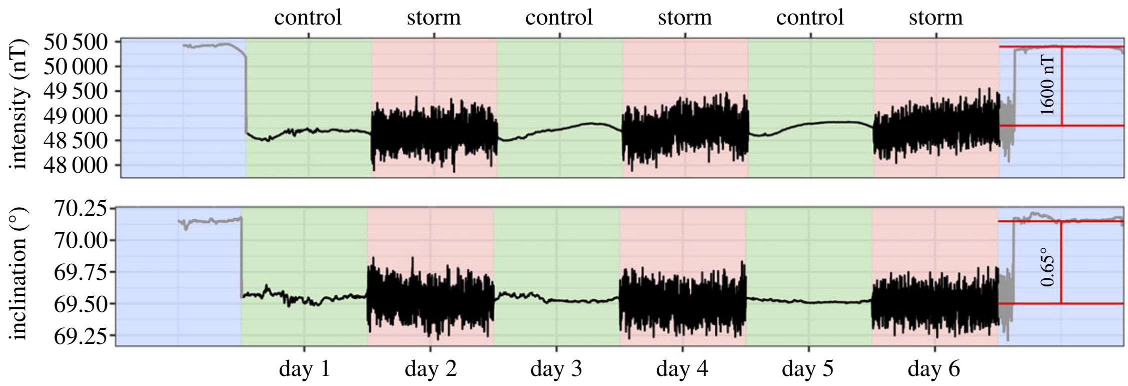

Figure 1. Example of geomagnetic parameters recorded at 1 min average during the experimental procedure alternating 24 h (from 12.00 to 12.00 of next day, local time) with constant magnetic displacement (control, green) with simulated solar storm (storm, red). Differences with the local geomagnetic field are shown before and after the experimental sequence (blue).

Sweden in October 2017. At the time of capture, all birds had finished their post-juvenile moult and, with one exception, had started to accumulate fat. Birds were kept indoors in individual cages for a few days until the start of the experiments, at which time they were provided with food and water ad libitum.

We randomly divided each species in two groups of four individuals. Each group was assigned to one of six identical experimental houses [7], and introduced in the cages in the afternoon of the day preceding the start of the experiment. The houses were built in non-magnetic material with semi-transparent roofs that exposed the birds to natural light conditions without providing any external visual cues (i.e. Sun position, stars motion or the skylight polarization pattern) [7]. All experiments were carried out 13–27 October 2017, after which all birds were released nearby.

(b) Experimental procedure

The geomagnetic field was altered using a Merritt three square-coil system large enough to accommodate four 550 mm × 700 mm (diameter × height) circular cages with perches and a constantly recording Honeywell HMR2300 magnetometer [7]. Each house was equipped with an Axis P1427-LE network camera that continuously recorded the four cages from above [9]. All birds were exposed to the same sequence of magnetic parameters (6 days in total) alternating 1 day with constant geomagnetic parameters with 1 day where the geomagnetic parameters where subject to a temporal variation resembling the effects of a solar storm (figure 1; electronic supplementary material, figure S1). The constant geomagnetic change was created by feeding a constant current (25 mA) to the vertical axis of the coil system that generated a weak magnetic field in the opposite direction of gravity that caused the local geomagnetic intensity (F) and inclination (DIP) change from the local experimental location ($F = 50\ 400$ nT, DIP $= 70.15°$) to smaller values ($F = 48\ 800$ nT, DIP $= 69.5°$; figure 1), and thus a geographical displacement towards south (approx. 700 km and 100 km for F and DIP, respectively). The solar storm was simulated applying a temporal variation to the current (random generated values at 3–4 Hz from a normal distribution with 25 mA mean) to produce a temporal variation of the magnetic parameters, but keeping the mean F and DIP equal to the same values of the constant geomagnetic change above (cf. figure 1). This procedure allowed us to test the temporal variation of the magnetic field excluding the effect of geomagnetic displacement alone [3,6–9].

(c) Analysis of activity and departure data

The computer vision analysis implemented by Ilieva *et al.* [9] was used to obtain the fraction of time spent in flights by individual birds in 20 min intervals (electronic supplementary material, figure S2; figure 2). If the birds were in flight for more than 1 min in a 20 min interval, we consider the bird active [9]. We analysed the activity data for the full day (12:00–12:00 local time, +2:00 UTC), and for three periods during evening (17:00–19:00), night (19:00–07:00) and morning (07:00–12:00) (electronic supplementary material, figure S2; figure 2). The onset of daily activity after sunset (18:00 local time, for the nocturnally migrating species) or sunrise (08:00, for the diurnal migrant) was calculated as the 10th percentile of the cumulative activity for each bird, and was used as a proxy for departure time [15].

Activity data and departure time were analysed in R v. 3.5.0 [16] with a series of mixed-effect linear models using the packages *lme4* [17] and *lmerTest* [18]. We set up a null model with species and experimental day and their interaction as fixed effects and bird ID as random effect. We compared the null model against a more complete model including storm as a fixed effect and any possible combination of interaction. If the complete model was better, we examined the fixed effect estimates of the model to evaluate the relative contribution of the fixed effects to the model.

3. Results

All three species kept a well-defined daily activity schedule with higher activity at night for the nocturnally migrating chiffchaff and robin, and higher activity during morning for the diurnally migrating dunnock (electronic supplementary material, figure S2; figure 2). We found an effect of the simulated solar storm on the activity only for the night and morning periods. In particular, the models including the storm as a fixed effect with complete interactions represented the best model compared with the simpler one, both for the night (likelihood ratio test against the null model: $\chi^2_{(5)} = 16.853$, $p < 0.01$) and the morning ($\chi^2_{(5)} = 11.215$, $p < 0.05$) activity. However, only for the robin, the interaction of fixed effect estimates of the model including the interaction with the storm was significant. Although the robins' activity level was increasing over the experimental period (i.e. positive model estimates; cf. figure 2), the effect of the storm caused a decrease in activity (mean ± s.e. $= -1.9 \pm 0.8$ h; $p = 0.001$) at night, and conversely an increase in activity during daytime (3.6 ± 0.1 h; $p = 0.01$). Furthermore, the best model for departure time did not include the storm effect, and thus the onset of migratory activity (see above) did not change under simulated solar storm in any of the three species.

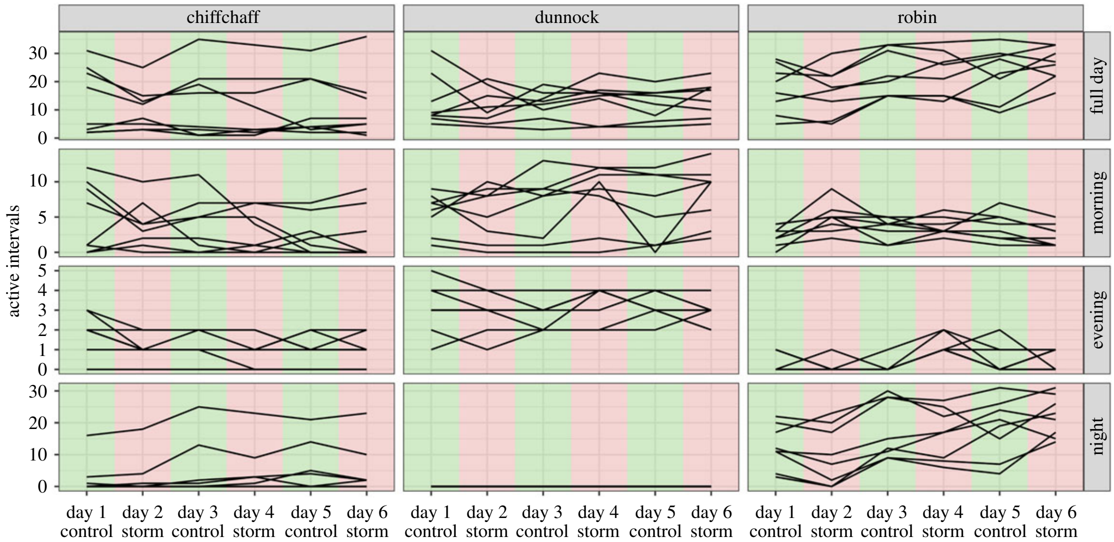

Figure 2. Activity levels for three species of first-year migratory songbirds during the experimental procedure alternating 24 h with constant magnetic displacement (control, green) with simulated solar storm (storm, red). Full data for individual birds are available as electronic supplementary material, appendix SA1.

4. Discussion

The effect of a solar storm can affect different aspects of animal biology, including behaviour [2], and potentially compromising migratory performances. Birds might be able to retrieve information of their geographical location using the unique combination of geomagnetic intensity and inclination [4,5,19], but during a solar storm, the intensity and inclination combination can vary substantially [1,2]. If the pair values correspond to locations familiar or predicted during migration, birds may be fooled to identify their position at a different location and change their behaviour accordingly [8,9]. Therefore, if the combination of intensity and inclination substantially deviate from the expected along an inherited migration route, birds may become disoriented [9]. Here, we asked if the temporal variation of the magnetic field can affect migratory activity of three species of birds with different migration strategies. Therefore, in our experimental set-up, we introduced variability in the magnetic field parameters, but maintained the same mean magnetic intensity and inclination throughout the experiment. We expected that if the temporal variation may disturb the birds' behaviour, we might also expect consequences on migratory performances during natural solar storm occurrences [12,13].

We found that only one of the two tested nocturnal migrants, the European robin, changed its activity level in response to the simulated solar storm. The changes were detected at night, when robins reduced activity, and during the morning, when they increased their activity. We propose that the reduced activity at night was used to reduce the orientation and/or navigation errors that may accumulate during migration in a disturbed magnetic field, and may have been performed as an energy-saving strategy to be able to extend the migratory schedule during the day. In daytime, alternative navigation cues become available, and any cue conflict involving the magnetic compass could be more easily resolved [3,4].

The chiffchaffs and dunnocks showed low or no nocturnal migratory activity when compared with the robins, and did not change their activity level in our experiments under simulated magnetic storms. Previous works suggest that the diurnally migrating dunnocks use geomagnetic field information for orientation and compass calibration [20], as well as for location of wintering areas [9]. It is, however, still possible that dunnocks and chiffchaffs pay less attention to geomagnetic cues, or use alternative cues, for orientation on migration [4]. Future studies should investigate the importance of geomagnetic when compared with celestial cues for orientation in both diurnal and nocturnal bird migrants, and systematically investigate how the temporal components of magnetic storms [2] affect birds' behaviour. Focusing on a single target species, it would be possible to increase the sample size and using alternative analysis procedures measure other behavioural features, e.g. orientation. Finally, responses to geomagnetic cues are sometimes difficult to interpret, and therefore, alternative explanations should be carefully considered [3,19] with special attention to the species investigated [21].

Ethics. Permissions were given by the Malmö/Lund Ethical Committee for scientific work on animals (no. M33-13), the Swedish Board of Agriculture for housing facilities (Dnr 5.8.18-12719/2017) and the Swedish Nature Protection Agency and the Swedish Ringing Centre (no. 440).

Data accessibility. Activity data for the birds are provided as electronic supplementary material.

Authors' contributions. G.B., M.I. and S.Å. conceived the study; M.I. performed the fieldwork with support from G.B. and S.Å. G.B. analysed the data; G.B., M.I. and S.Å. discussed the outcome of the results and wrote the manuscript. All authors agree to be held accountable for the content therein and approve the final version of the manuscript.

Competing interests. The authors have no competing interests.

Funding. The project received financial support from the Swedish Research Council to S.Å. (621-2013-4361 and 2016-05342) and the Centre for Animal Movement Research (CAnMove) financed by a Linnaeus grant (349-2007-8690) from the Swedish Research Council and Lund University.

Acknowledgements. We are grateful to Christoffer Sjöholm for assistance during fieldwork, and to three anonymous referees for their constructive comments on an early version of this manuscript.

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