Effects of blood parasite infections on spatiotemporal migration patterns and activity budgets in a long-distance migratory passerine

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Abstract

How blood parasite infections influence the migration of hosts remains a lively debated issue as past studies found negative, positive or no response to infections. This particularly applies to small birds, for which monitoring of detailed migration behaviour over a whole annual cycle has been technically unachievable so far.

Here, we investigate how bird migration is influenced by parasite infections. To this end, we tracked great reed warblers (*Acrocephalus arundinaceus*) with multi-sensor loggers, characterized general migration patterns as well as detailed flight bout durations, resting times and flight heights and related these to the genus and intensity of their avian haemosporidian infections.

We found migration distances to be shorter and the onset of autumn migration to be delayed with increasing intensity of blood parasite infection, in particular for birds with *Plasmodium* and mixed-genus infections. Additionally, the durations of migratory flight bout were prolonged for infected compared to uninfected birds. But since severely infected birds and particularly birds with mixed genus infections had shorter resting times, initial delays seemed to be compensated for and the timing in other periods of the annual cycle was not compromised by infection.

Overall, our multi-sensor logger approach revealed that avian blood parasites have mostly subtle effects on migratory performance and that effects can occur in specific periods of the year only.

**Keywords:** activity, biologging, bird migration, flight height, great reed warbler, *Haemoproteus*, migration timing, parasites, *Plasmodium*, resting
Introduction

Infection-related deviations in host migration performance have already been described for a variety of parasite and host taxa: Monarch butterflies migrated slower when infected by ectoparasites (Bradley & Altizer, 2005), reindeer herds with more ectoparasites performed shorter migrations (Folstad, Nilssen, Halvorsen, & Andersen, 1991) and the timing of arrival at the breeding site was delayed for blood parasite infected compared to uninfected passerines (Rätti, Dufva, & Alatalo, 1993). A recent meta-analysis suggested movement capacity and phenology of migratory animals to be moderately affected by the status and intensity of infections, while body condition and survival were only weakly associated with infection (Risely, Klaassen, & Hoye, 2018). Nevertheless, the magnitude of parasite effects on migratory hosts and, particularly, how effects depend on the taxon and severity of infection, remain unresolved.

In migratory birds, parasites might affect host migration via several mechanistic pathways: Parasites could (i) directly reduce physiological performance and thereby lead to slower flight. Early seminal works indicated that *Plasmodium* infections decreased the oxygen consumption rates of experimentally infected canaries during nocturnal rest (Hayworth, Riper, & Weathers, 1987) and naturally infected lizards during exercise (Schall, Bennett, & Putnam, 1982). In contrast, the metabolic rates of a migratory passerine were not significantly influenced by infection neither during resting nor during exercise both for natural haemosporidian infections and experimental *Plasmodium* infections (Hahn et al., 2018).

Alternatively, parasites could (ii) indirectly impair host migration e.g. by slowing down fuelling, prolonging stopovers or increasing the need for resting after endurance flights. For instance, benign avian influenza infections lowered the feeding rates and prolonged stop-over durations in
migratory swans (van Gils et al., 2007) and infections with multiple intestinal parasites were correlated with delayed spring migration timing in passerines (López, Muñoz, Soriguer, & Figuerola, 2013).

Yet, regardless of the mechanisms behind parasite-effects on host migration, such changes are thought to cascade through to breeding, with delayed arrivals and late onset of breeding lowering individual fitness (Kokko, 199). However, so far, the insight into infection-related changes of host migration had been restricted to i) basic migration parameters measurable by standard methods (e.g. geolocation, telemetry and satellite tracking) and ii) snapshots of certain periods of the annual cycle. A full-migration approach relating detailed migration behaviour to individual infection parameters is still missing for wild birds.

Therefore, we used multisensor loggers to describe detailed migration patterns of great reed warblers (Acrocephalus arundinaceus) and related these patterns to the hosts’ blood parasite infections (genera Plasmodium and Haemoproteus within Haemosporida). Multisensor loggers do not only enable geolocation by recording light, but also allow compiling individual activity and behaviour by recording accelero- and barometric data (Liechti et al., 2018). The recorded patterns were then related to the parasite genus and the individual intensities of avian haemosporidian parasite infections assessed by real-time quantitative PCR. Specifically, we related these infection parameters measured at the deployment and retrieval of the loggers to several key migration traits: distance, duration and speed of migration, the timing of autumn and spring migration, the duration of migratory flight bouts and resting periods, and flight height.

If infections affect migration throughout on a broad scale, we expect infected individuals to migrate shorter distances or to take longer for the same distance. If migration distance would vary
for infections with different parasite genera, this could both signify a parasite effect on migration performance and a differential probability of getting infected with different parasites in various regions of the non-breeding range. Depending on how infections affects migration timing, we may expect the following outcomes: If blood parasites hamper the preparation for migration, we expect that infected individuals to depart with delays. If, in contrast, blood parasites affect the progression of migration, we rather expect arrivals to be delayed. By using multisensor loggers, we also expect insights into the mechanisms behind parasite on migration patterns on a finer scale: If blood parasites impair flight, we expect infected birds to fly slower and their migratory flight bouts to be shorter (if fuel is limiting) or longer (if infected birds compensate for slower flight). If, in turn, blood parasites impair fuelling rates or increase energy expenditure, infected individuals are expected to need longer resting times. Finally, if partial oxygen pressures experienced aloft are limiting for migrating birds, we expect infected individuals to fly at lower altitudes. All these potential effects are expected to increase with growing intensity of infection and are to some degree expected to differ between parasite genera, as *Haemoproteus* and *Plasmodium* infections are known to differ in their average pathogenicity and co-infections with several genera are known to be most virulent (Valkiūnas, 2005).

**Material & Methods**

Study species and field sites

We investigated great reed warblers (*Acrocephalus arundinaceus*) breeding at three study sites in Bulgaria (BG, Kalimok Biological Station, 44.00°N 26.45°E), in the Czech Republic (CZ, Mutěnice, 48.90°N, 17.05°E) and in western Russia (RU, Rybachy, 55.15°N, 20.85°E). Great reed warblers breed in reed beds along fresh or brackish standing water and spend the non-breeding season in
sub-Saharan Africa (Koleček et al., 2016 and Figure 1a). They often harbour haemosporidian parasites – a widespread group of blood parasites which are transmitted by dipteran vectors – and within the two genera *Plasmodium* and *Haemoproteus* 29 genetic lineages have been recorded for great reed warblers (MalAvi database; Bensch, Hellgren, & Pérez-Tris, 2009; accessed on the 13.06.2019). The two parasite genera and their lineages can greatly vary in their virulence. While many infections are benign, some infected hosts can show fatigue and lose appetite during the acute phase or rarely even die (Lapointe, Atkinson, & Samuel, 2012). Most avian blood parasites infections become chronic and the minor effects of chronic infections are known to accumulate, e.g. resulting in reduced life-time reproductive success in great reed warblers (Asghar, Hasselquist, & Bensch, 2011).

Additionally, we found the maximum, but not the mean, resting durations to be reduced by infection, suggesting that, regardless of infection status, migrating birds need a certain minimum recovery period between consecutive migratory flight bouts. But extensive stop-over periods can be shortened to compensate for delays – may they be caused by infections or other factors. This also implies that focussing on a single migration variable (e.g. the arrival at a stopover or breeding site) may be insufficient, as parasite effects on timing in one phase of the annual cycle can be compensated with adjustments in other phases. Whether these adjustments come with the drawback of being more exposed to predators due to compensatory feeding activity or of continuing migration in worse condition as shorter resting times cannot be compensated by extended feeding, cannot be tested with our data set.

In conclusion, using multi-sensor loggers enabled to describe detailed patterns in individual migration behaviours and how infections with parasites affect these. We found that chronic
infections with avian blood parasites have diverse, but relatively weak effects on the migration performance of great reed warblers. Our results also indicate that birds can compensate some effects of parasites arising in certain periods of the annual cycle, which thus might not be detectable anymore in subsequent periods. This indicates that hosts can cope with a broad range of chronic infection intensities, maintaining most of their migratory capacity and thus also their potential for spreading parasites (Bauer & Hoye, 2014).

Authors' contributions

TE, SH and SBa developed the conceptual framework of this study. DK, PP and PZ organized the field work and took care of permissions for their study sites. TE, DK, PP and SH carried out the field work. TE and SBe planned and conducted the lab work. TE and SBa analysed the data and drafted the manuscript. All co-authors contributed to writing of the manuscript, approved the final version and declared not to have any competing interests.

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Data accessibility statement

The datasets analysed and generated for this study are available on Zenodo (raw logger data: 10.5281/zenodo.4017739; migration variables and infection data: 10.5281/zenodo.4022516).
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Figure 1: The breeding sites and site-specific non-breeding ranges of the tracked great reed warblers (a) as well as the individual genus and intensity of haemosporidian infections prior to and after the tracked migrations (b). Birds breeding in Bulgaria (closed square), Czech Republic (closed circle) and Russia (closed triangle) spent the non-breeding period in sub-Saharan Africa (open symbols = site-specific median, ± 25-75% quantiles of the individual non-breeding sites). The haemosporidian infections were generally more intense after than prior to the tracked migrations, and *Plasmodium* infections (blue) tended to be less intense than *Haemoproteus* infections (red) and mixed-genus infections (purple). Note that for some samples parasite genus is unknown (grey) and some points are unconnected as the pre-migration blood sample was missing (n = 3).
Figure 2: Effects of parasite infection on basic parameters of great reed warblers’ migration.

While the total migration distance (a) and the total migration duration (b) of infected great reed warblers were significantly related to the intensity, but not the genus (open symbols: Plasmodium = blue, Haemoproteus = red, mixed-genus = purple) of their haemosporidian infections, the resulting average migration speed (c) was statistically unrelated to both infection parameters.
Figure 3: The timing of departures (a+c) and arrivals (b+d) of great reed warblers in autumn (a+b) and spring (c+d) as dependent on the haemosporidial infection. Only the departure for autumn migration was significantly related to genus (LM fit ± CrI; closed symbols: Plasmodium = blue, Haemoproteus = red, mixed-genus = purple) and intensity of infections. All other timing events were statistically unrelated to infection parameters (open symbols).
Figure 4: The interrelations between the haemosporidian infections of tagged great reed warbler with the mean (a) and the maximum (b) of individual flight bout durations as well as the median (c) and the maximum (d) individual resting durations. While mean flight times were merely related to infection intensity (LME fit ± CrI; open symbols: Plasmodium = blue, Haemoproteus = red, mixed-genus = purple), the maximal resting times were significantly related to both the intensity and the genus of the hosts’ haemosporidian infections (LME fit ± CrI; closed symbols).
Appendix

Table S1: Overview on logger data and type of blood samples available from the tracked birds - sorted by logger ID.

| logger id | ring id | study site | deployment year | general information | light data | multi-sensor data | blood smear | blood in SET |
|-----------|---------|------------|-----------------|---------------------|------------|-------------------|-------------|--------------|
|           |         |            |                 | autumn | spring | autumn | spring | before migration | after migration |
| 14AZ      | 1-545764 | bg | 2015 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 14ES      | 1-545798 | bg | 2015 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 14FF      | 1-545865 | bg | 2015 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 14GD      | 1-545690 | bg | 2015 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 14GF      | 1-545842 | bg | 2015 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 14GG      | 1-545679 | bg | 2015 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 14GH      | 1-545683 | bg | 2015 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 14GS      | 1-545673 | bg | 2015 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 14GW      | 1-545859 | bg | 2015 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 14HA      | 1-545681 | bg | 2015 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 14HB      | 1-545703 | bg | 2015 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 14HC      | 1-545680 | bg | 2015 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 14HT      | 1-545817 | bg | 2015 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 14SD      | za35988  | cz | 2016 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 14SF      | za60716  | cz | 2016 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 14TC      | za48338  | cz | 2016 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 14TF      | za32371  | cz | 2016 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 14TS      | 1-545674 | bg | 2016 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 |
| 14TZ      | 1-545971 | bg | 2016 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 16BR      | 1-555140 | bg | 2016 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 16EA      | fs27400  | ru | 2016 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 |
| 16ER      | fs27378  | ru | 2016 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 |
| 16ET      | fs27417  | ru | 2016 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 |
| 16EY      | 1-545791 | bg | 2016 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 16FB      | 1-545785 | bg | 2016 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 16FI      | 1-545777 | bg | 2016 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 16FT      | 1-545683 | bg | 2016 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 16GA      | za59713  | cz | 2016 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Code  | ID         | Type | Year | Length1 | Length2 | Length3 | Length4 | Length5 | Length6 | Length7 | Length8 |
|-------|------------|------|------|---------|---------|---------|---------|---------|---------|---------|---------|
| 16HB  | 1-545761   | bg   | 2016 | 1       | 1       | 1       | 1       | 1       | 1       | 1       | 1       |
| 16HL  | 1-545679   | bg   | 2016 | 1       | 1       | 1       | 1       | 1       | 1       | 1       | 1       |
| 16HM  | 1-555134   | bg   | 2016 | 1       | 1       | 1       | 1       | 1       | 1       | 1       | 1       |
| 18HA  | ZA76610    | cz   | 2017 | 1       | 0       | 1       | 0       | 1       | 1       | 1       | 1       |
| 18HY  | ZA76621    | cz   | 2017 | 1       | 1       | 1       | 1       | 1       | 1       | 1       | 1       |
| 18IC  | ZA48339    | cz   | 2017 | 1       | 1       | 1       | 1       | 1       | 1       | 1       | 1       |
| 18IJ  | ZA69547    | cz   | 2017 | 1       | 1       | 1       | 1       | 1       | 1       | 1       | 1       |
| 18IQ  | ZA76620    | cz   | 2017 | 1       | 0       | 1       | 0       | 1       | 1       | 1       | 1       |
| 18KA  | ZA69517    | cz   | 2017 | 1       | 1       | 1       | 1       | 1       | 1       | 1       | 1       |
| 18LD  | ZA44432    | cz   | 2017 | 1       | 1       | 1       | 1       | 1       | 1       | 1       | 1       |
| 18LX  | ZA45656    | cz   | 2017 | 1       | 1       | 1       | 1       | 1       | 1       | 1       | 1       |
| 18LZ  | ZA62192    | cz   | 2017 | 1       | 1       | 1       | 1       | 1       | 1       | 1       | 1       |
Table S2: The variables used in the models (also see Table S3). We list the abbreviations along with a full description, the units/levels and an annotation whether a variable was used as a response variable (RV), an explanatory variable (EV) or a random factor (RF).

| Variable   | Description                                | Unit/Levels           | Used as? |
|------------|--------------------------------------------|-----------------------|----------|
| am.start² | departure for autumn migration             | day of the year       | RV       |
| am.end²   | arrival from autumn migration              | day of the year       | RV       |
| sm.star²  | departure for spring migration             | day of the year       | RV       |
| sm.end²   | arrival from spring migration              | day of the year       | RV       |
| dist³     | total migration distance                   | kilometres            | RV       |
| migdur³   | total migration duration                   | days                  | RV       |
| speed³    | total migration speed                      | kilometers/day        | RV       |
| durFB³    | flight bout duration                       | hours                 | RV       |
| durSO³    | duration of resting period                 | hours                 | RV       |
| FH³       | flight height                              | meters a.s.l.         | RV       |
| int⁴      | intensity of infection                     | relative qPCR intensity| EV       |
| season⁴   | migration season                           | am = autumn, sm = spring| EV       |
| numSex⁴   | numerical sex of the host                  | 0 = female, 0.5 = NA  | EV       |
| indi⁴     | individual geolocator id                   | 40 different IDs      | RF       |

¹ Unless stated otherwise, we centred this variable within study site by subtracting the site-specific mean from every individual value (indicated by the suffix '.pc').

² For this variable we calculated the mean, median, max and/or sum per individuum to be used in the models.

³ This variable was used as unitless log-transformed values.

⁴ We used ‘int1’ when we involved the intensity from the sample before to the tracked migration, ‘int2’ for the sample after or ‘int’ when we used either of the two samples.
Table S3: List of model formulas and parameter estimates from models with (A) parasite genus as the only focal explanatory variable, (B) parasite genus and infection intensity as two focal explanatory variables and (C) infection intensity as the only focal explanatory variable (from top to right), and the models with (1) basic migration parameters, (2) migration timing parameters, (3) flight times, (4) resting times and (5) flight heights as response variables (from top to the bottom).

Significant estimates and the accoring variables are shown in bold. The suffix ‘.pc’ indicates that a variable has been centred within each site by subtracting the site-specific mean from the individual values. See Table S2 for a glossary of the variables used in the models.

| (A) GENUS ONLY | (B) LOGST(INT) + GENUS | (C) LOGST(INT) ONLY |
|----------------|------------------------|---------------------|
|                |                        |                     |
| (1) Basic migration parameters |             |                     |
| dist_pc = genus + season + sex + (1 | Indo) |                     |
| Fixed effects: |             |                     |
| (Intercept) | 136.55 | 108.99 | 1.25 | 0.21 |
| genus | 0.56 | 0.44 | 1.29 | 0.20 |
| season | 0.40 | 0.22 | 1.83 | 0.07 |
| sex | 6.32 | 1.74 | 3.63 | 0.0002 ** |
|        | 24.85 | 5.26 | 4.74 | 0.0000 ** |
|        | 14.92 | 4.12 | 3.59 | 0.0005 ** |
| ginusb | 0.39 | 0.19 | 2.00 | 0.04 |
| genusc | 0.72 | 0.25 | 2.92 | 0.0039 ** |
| genusd | 0.39 | 0.19 | 2.00 | 0.04 |
| genuse | 0.72 | 0.25 | 2.92 | 0.0039 ** |
| sex | 6.32 | 1.74 | 3.63 | 0.0002 ** |
|        | 24.85 | 5.26 | 4.74 | 0.0000 ** |
|        | 14.92 | 4.12 | 3.59 | 0.0005 ** |
|        | 0.39 | 0.19 | 2.00 | 0.04 |
|        | 0.72 | 0.25 | 2.92 | 0.0039 ** |
|        | 0.39 | 0.19 | 2.00 | 0.04 |
|        | 0.72 | 0.25 | 2.92 | 0.0039 ** |

(2) Migration timing

| am_start_pc = genus + maines |             |                     |
| Fixed effects: |             |                     |
| (Intercept) | 136.55 | 108.99 | 1.25 | 0.21 |
| genus | 0.56 | 0.44 | 1.29 | 0.20 |
| season | 0.40 | 0.22 | 1.83 | 0.07 |
| sex | 6.32 | 1.74 | 3.63 | 0.0002 ** |
|        | 24.85 | 5.26 | 4.74 | 0.0000 ** |
|        | 14.92 | 4.12 | 3.59 | 0.0005 ** |
|        | 0.39 | 0.19 | 2.00 | 0.04 |
|        | 0.72 | 0.25 | 2.92 | 0.0039 ** |
|        | 0.39 | 0.19 | 2.00 | 0.04 |
|        | 0.72 | 0.25 | 2.92 | 0.0039 ** |

| sm_start_pc = logst + genus + season + sex + (1 | Indo) |                     |
| Fixed effects: |             |                     |
| (Intercept) | 0.49 | 0.21 | 2.30 | 0.021 |
| genus | 0.02 | 0.02 | 1.25 | 0.21 |
| season | 0.07 | 0.03 | 2.43 | 0.015 ** |
| sex | 0.08 | 0.02 | 4.74 | 0.0000 ** |
|        | 0.09 | 0.02 | 4.74 | 0.0000 ** |
|        | 0.09 | 0.02 | 4.74 | 0.0000 ** |
|        | 0.09 | 0.02 | 4.74 | 0.0000 ** |
|        | 0.09 | 0.02 | 4.74 | 0.0000 ** |

(3) Flight times

| durh_mean_pc = genus + season + sex + (1 | Indo) |                     |
| Fixed effects: |             |                     |
| (Intercept) | 17.14 | 12.38 | 1.38 | 0.17 |
| genus | 0.82 | 0.34 | 2.42 | 0.016 ** |
| season | 0.82 | 0.34 | 2.42 | 0.016 ** |
| sex | 0.82 | 0.34 | 2.42 | 0.016 ** |
|        | 0.82 | 0.34 | 2.42 | 0.016 ** |
|        | 0.82 | 0.34 | 2.42 | 0.016 ** |
|        | 0.82 | 0.34 | 2.42 | 0.016 ** |
|        | 0.82 | 0.34 | 2.42 | 0.016 ** |

** indicates significance at p < 0.01.
### Flight height

| orangutans | Estimate | Std. Error | t value | Pr(>|t|) |
|------------|----------|------------|---------|----------|
| Intercept  | -0.094   | 0.004      | -23.1   | 0.000    |
| season     | 0.198    | 0.004      | 49.0    | 0.000    |
| genus      | 0.138    | 0.004      | 34.8    | 0.000    |

### Flight height vs. Season

| orangutans | Estimate | Std. Error | t value | Pr(>|t|) |
|------------|----------|------------|---------|----------|
| season     | 0.198    | 0.004      | 49.0    | 0.000    |
| genus      | 0.138    | 0.004      | 34.8    | 0.000    |
Figure S1: A sample data set for the period 16-31 August 2015 from a great reed warbler with the multi-sensor logger ID 14AZ. The panels depict data from the different sensors (from top to the bottom): light intensity, air pressure, ambient temperature, locomotor activity and pitch (i.e. mean body position). The colours in the pressure and activity panels show behaviours categorised as ‘resting’ (black), ‘active’ (green), ‘flight’ (blue) and ‘migratory flight’ (red).
