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Research article

Effects of immune status on stopover departure decisions are subordinate to those of condition, cloud cover and tailwind in autumn-migrating common blackbirds *Turdus merula*

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Migratory birds encounter a large variety of parasites and pathogens en route and invest in immune defences to limit the risk and fitness costs of infection. Since both migration and immune defences carry costs, individuals on tight budgets may face trade-offs between migratory progress and immune status. Many species alternate legs of strenuous migratory flight with stopovers during which birds refuel, rest, and recover physiologically. Despite this, most time and energy consumed during migration are actually spent on stopovers. As a result, identifying what determines stopover duration is key in understanding how migratory birds balance investments in immune defences and migration. Yet, it is unknown under what conditions an individual's immune status may affect migratory progress through the duration of stopovers. We explored whether immune status at arrival affects stopover duration by radio-tagging and blood-sampling common blackbirds *Turdus merula* during autumn stopovers on the Dutch island of Vlieland. To measure immune status, we quantified levels of bacterial killing ability, natural antibodies, complement, and haptoglobin, as well as heterophil–lymphocyte ratios. We show that stopover departures peaked during periods with low cloud cover and strong tailwinds. While lean birds prolonged stopovers, we only found a weak tendency of prolongation in birds with elevated haptoglobin levels. We conclude that effects of immune status on minimum stopover durations are subordinate to those of condition, cloud cover, and tailwinds in autumn-migrating common blackbirds. Hence, future studies on the link between immune defences and stopover durations should take weather conditions into account.

Keywords: cloud cover, common blackbird, eco-immunology, stopover ecology, wind selectivity

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Introduction

To help ensure a well-timed, energetically efficient, and safe migration, birds can adjust their migratory schedules in response to a variety of extrinsic and intrinsic factors. For example, migrants are well known to avoid unfavourable weather conditions and to adequately recover fuel stores on stopovers so they can complete the next leg of migration (Deppe et al. 2015). Partly because of these stopovers, migratory birds encounter a greater abundance and diversity of pathogens and parasites compared to non-migratory birds (Figuerola and Green 2000, Leung and Koprivnikar 2016, De Angeli Dutra et al. 2021, Xu et al. 2024). Consequently, physiological functions important to self-maintenance, such as immune defences that limit the risks and fitness costs of these pathogens or parasites, may affect migratory movement decisions, investments, or both (Hegemann et al. 2018a). Whether and how avian migration, and in particular stopover decision-making, is constrained by aspects of immunological function while simultaneously taking into account the weather conditions en route is poorly understood.

Higher exposure of migratory birds to pathogens may suggest that immune defences should be upregulated during migratory journeys to avoid infection (Møller and Erritzøe 1998). However, maintaining and deploying an immune system involves energetic and immunopathological costs (Klasing 2004, Hasselquist and Nilsson 2012). As migratory birds travel on a tight budget (Wikelski et al. 2003), resource trade-offs are imposed on migrating individuals (Sheldon and Verhulst 1996, Norris and Evans 2000). For example, to fuel skeletal muscles in propelling migratory flight, energy may be diverted away from immune defences (Norris and Evans 2000, Lee 2006, Guglielmo 2018). In addition, strenuous physical activity required for flight may result in damage to muscles (Bordel and Haase 2000, Guglielmo et al. 2001) or other tissues (Larcombe et al. 2010), the expression of heat-shock proteins (Bounas et al. 2024), and the production of reactive oxygen species (Costantini et al. 2008, Jenni-Eiermann et al. 2014, McWilliams et al. 2021). Due to this expansion of an individual's 'self-antigen' repertoire, the risk of autoimmune responses and ensuing immunopathological costs may increase (Tidball 2005). Consequently, downregulation of immune defences during migration may result (Råberg et al. 1998). In line with energetic trade-offs or immunopathology avoidance, several studies report lower immune indices during migration compared to those in other annual-cycle stages (Owen and Moore 2006, Eikenaar and Hegemann 2016). While immune defences might vary seasonally (Owen and Moore 2008), experimental work suggests that immune functions may also be impacted by strenuous flight on a much finer temporal scale (Matson et al. 2012a, Nebel et al. 2012; but see Hasselquist et al. 2007).

Although migration is often viewed as one large investment in a single experience or behaviour, most migratory birds alternate migratory flights with stopovers. Yet, the role these stopovers play in mitigating physiological challenges of migration is poorly understood. During stopovers, fuel for the next leg of migration is accumulated (Schmaljohann and Eikenaar 2017): individuals carrying small fuel loads upon arrival often make longer stopovers to refuel than those arriving with large fuel stores (Deppe et al. 2015, Dossman et al. 2016, Packmor et al. 2020, Herbert et al. 2022; but see Salewski and Schaub 2007). Since refuelling occurs at a much lower rate than fuel is burned during flight, stopover duration rather than flight speed determines total duration of, and energy expenditure during, migration (Hedenström and Alerstam 1997, Wikelski et al. 2003, Schmaljohann et al. 2012, Nilsson et al. 2013, Schmaljohann and Both 2017). Both the energy and time it takes to migrate can carry over into subsequent annual-cycle stages to affect an individual's fitness, for example through reduced reproductive output (Kokko 1999, Smith and Moore 2005, Lameris et al. 2018, Tomotani et al. 2021). Consequently, how immune defences may shape migration is best understood by exploring whether immune status can impact stopover durations.

Recently, the interest in functions of stopovers beyond refuelling has grown (Eikenaar et al. 2020b, Linscott and Senner 2021, Schmaljohann et al. 2022). One of these additional functions of stopover may be physiological recovery, in which individuals restore some physiological function or state over time on stopover. Although the relations to refuelling have not fully been elucidated (Eikenaar et al. 2020b), physiological recovery has been suggested to occur in the context of oxidative balance (Skrip et al. 2015, Eikenaar et al. 2020c, 2023c, Cooper-Mullin and McWilliams 2022) and may extend to the recovery of immune functions (Eikenaar and Hegemann 2016, Eikenaar et al. 2020a, b). Such a recovery may be needed after arrival on a stopover, as indices of immune function can be impacted by flight (Matson et al. 2012a, Nebel et al. 2012; but see Hasselquist et al. 2007), especially in birds that are mounting an acute phase response (Nebel et al. 2013). Indeed, immune indices have been found to increase over time since arrival on a stopover (Buehler et al. 2010a, Eikenaar et al. 2020a, 2023a), suggesting that this process takes time. Yet, to what extent the recovery of immune function may prolong stopover durations is not clear, especially against a background of other intrinsic and extrinsic determinants of stopover duration.

Evidence linking an individual's immune status to the decision to continue migration is mixed. The magnitude of a primary antibody response in red knots *Calidris canutus* (Hasselquist et al. 2007), as well as acute phase protein concentrations (haptoglobin: Quaye 2008) and bacterial killing ability in western sandpipers *Calidris mauri* (Nebel et al. 2013) were all found to be positively correlated to flight duration in a wind tunnel. In contrast, an immune challenge that elicits an acute phase response did not affect wind tunnel flight performances of western sandpipers (Nebel et al. 2013), nor did immune challenges or experimental infections reduce migratory restlessness in several caged songbird species (Owen et al. 2006, Kelly et al. 2023). In free-flying songbirds, however, several studies report correlations between immune status and time to departure from a stopover location. For example, experimental immune challenges (Hegemann et al.

2018a) as well as natural blood parasite infections and physiological markers of inflammation (Hegemann et al. 2018b; but see Eikenaar et al. 2019) are associated with longer stopovers. Indices of immune function have also been found to explain variation in stopover durations: higher complement-mediated lysis activity (Hegemann et al. 2018b), bacterial killing capacity, natural antibody, and total immunoglobulin levels (Brust et al. 2022) have all been found associated with prolonged stopovers, but in a variety of species studied in different contexts.

While no clear pattern emerges across immune indices from these studies, they indicate that at least under some circumstances, stopover departure may be constrained by an individual's immune status. Critically, however, the true relevance of immune status for stopover duration remains elusive since statistical associations between the two are often reported in the absence of the broader ecological context. For example, birds often depart from stopovers when favourable winds support flights towards their migratory goal (Åkesson and Hedenström 2000, Packmor et al. 2020) and when weather conditions allow for high visibility to aid navigation (Åkesson et al. 2001, Zehnder and Karlsson 2001, Packmor et al. 2020). The importance of these extrinsic factors in determining stopover duration is widely acknowledged, but studies on the effect of immune status on stopover duration rarely take them into account.

In a single-year, correlative study, we explored the importance of immune status in explaining stopover durations by investigating the association between time to stopover departure and indices of immune function in autumn-migrating common blackbirds *Turdus merula* (hereafter: blackbirds) that stop over on the Dutch island of Vlieland. Whereas the local blackbird breeding population in the Netherlands is non-migratory (van Vliet et al. 2009), ring recoveries indicate that most autumn-migrating blackbirds that stop over on Vlieland breed in Scandinavia and cross the North Sea to winter in the UK (Spina et al. 2022). Fuel loads as well as supportive winds likely factor into the stopover departure decisions of birds, especially prior to the crossing of large bodies of open water, which may represent geographic barriers to migratory birds (Shamoun-Baranes and van Gasteren 2011, Bradarić et al. 2020).

We hypothesized that the need for physiological recovery during migration would influence migratory movement decisions in tandem with considerations related to weather conditions. We expected minimum stopover duration to be correlated with the arrival-related levels of our measured indices of immune defences. As explained above, these indices can differ in their responsiveness to infection- and non-infection-related physiological challenges and the resulting shifts away from 'baseline' levels associated with homeostatic conditions. Indices that increase with migration, flight, and physical activity more generally (e.g. heterophil–lymphocyte ratio: Matson et al. 2012a, van Dijk and Matson 2016) are expected to correlate positively with stopover duration, as higher values take longer to be brought down. Those that decrease, e.g. as a consequence of either increased use or decreased production, are expected to correlate negatively with stopover duration, as lower values take longer to be restored. At the same time, we expected birds to depart from stopover during periods of supportive winds, and clear skies that may facilitate the use of celestial cues for navigation. Alternatively, avoiding unsuitable weather conditions for migratory flights or taking advantage of favourable ones may be more important than physiological recovery for migratory progress and, ultimately, for fitness. In this case, stopover duration would be primarily (or only) related to atmospheric conditions.

Material and methods

Study site and population

From 30 October to 9 November 2022, we captured (n = 385), sampled (n = 90), and radio-tagged (n = 38) blackbirds at the 'V.R.S. 3e Kroon's polders' ringing station on the Dutch island of Vlieland (53°15′17″N, 4°57′03″E). Autumn migration of blackbirds over the Netherlands spans a period from early October to late November, with a peak at the end of October (Lensink et al. 2002). We used a standardised set-up consisting of 250 m of mist net and a two-door clap net. Blackbirds were lured to the nets using conspecific song playback from 30 minutes before sunrise to two hours after sunrise. Individuals caught using the clap net were lured using apples. We sexed and aged birds following Svensson (1992). The body mass of each bird was measured to the nearest 0.1 g on a digital scale (Pesola PTS1000-BS). We recorded two measures of structural body size: tarsus length (to the nearest 0.01 mm) and maximum wing chord (to the nearest 0.5 mm). Subcutaneous fat (range: 0–3) and pectoral muscle size (all 3) were scored, but showed limited variation and were excluded from our analyses. The same was done for moult scores, as no individuals in our sample were moulting body or flight feathers. Birds were not examined for ectoparasites. All measurements were taken by the same person (TM).

Stopover ecology

Radio tracking

To quantify variation in minimum stopover durations between individuals, we equipped and released blackbirds with a 1.3 g 150.1 MHz VHF transmitter (NTQB2-4-2S Motus tag with reinforced antenna, Lotek, ON, Canada) that was glued onto the shafts of clipped rump feathers (Loctite Super Glue-3). Once activated, these tags emit uniquely coded VHF signals at regular intervals (range: 4.1–4.9 s), resulting in an expected lifespan of 265–310 days. We reduced the risk of the tag aliasing by activating tags shortly before deployment while listening to and avoiding overlap with signals of previously deployed tags using a handheld receiver. We selectively tagged newly ringed blackbirds and aimed to spread tags equally over different sexes and age classes, while maximising variation in tagging date. We thus used a staggered entry design: on each of 11 successive mornings, we aimed to tag two to five birds, ideally one of each sex–age class combination. Due to the limited availability of newly ringed birds of the desired sex and age that we could blood-sample within 30 minutes after netting (see under 'blood samples') not every sex–age class combination was possible on all days. In total, we tagged 11 first calendar year (1 cy) males, eight 1 cy females, nine older (> 1 cy) males and 10 > 1 cy females (Supporting information).

Receiver network

A local receiver station was installed on the meteorological tower at the Netherlands Royal Airforce base on Vlieland (53°15′14″N, 4°56′30″E), 620 m from the tagging site. On this tower, four Yagi-type antennas (SIRIO WY140-6N, 6-element, 25 cm length) were mounted at 10–12 m above ground level, covering four different compass bearings (77°, 169°, 216°, and 312°). Detection ranges depend on various factors, including a tag's position relative to the antenna bearing, weather conditions, and signal attenuation by vegetation and the terrain. Other studies with similar technical infrastructure have shown detection ranges of 1–7 km of tagged animals close to ground level (< 40 m; Lagerveld et al. 2017), and up to 20 km of birds in flight (Brust et al. 2022). We used data from the local receiver and two other receivers on the island (Flidunen, and Strandhotel) as a primary source of information to establish minimum stopover duration. In addition, we used detection data from nearby receivers (most importantly those on Texel, the Afsluitdijk, and around Den Helder, Supporting information) to confirm the identified departure moments (below).

Quantifying minimum stopover duration using detection data

To assess when blackbirds ended their stopover on the island we downloaded individual tag's detection data by the Motus receiver network (Taylor et al. 2017) using the 'motus' package (Brzustowski et al. 2024). The Motus network provided dense coverage along the Dutch coast in 2022 and 2023. For each detected signal, a receiver logs a tag's and antenna's unique ID, time of detection, and signal strength (in dB). The Motus system is conservative in omitting detections. As a result, radio noise or code collisions of multiple tags in the vicinity of the same receiver occasionally result in false positives. We discarded false positives following Brust et al. (2019; as described in the Supporting information). For each tag, we inspected the remaining detections by plotting signal intensity over time at the three receivers on the island, as well as more remote receivers. Following departure from the stopover site, birds usually ascend quickly, resulting in a sudden increase in signal strength due to reduced signal attenuation by terrain elements, followed by a gradual decrease in signal strength as tagged birds move away from the receiver. We identified the last peak in signal strength visually on all receivers on the island, and defined this time point as an individual's departure moment. Although daily captures started well before the onset of tagging (16 August), and no recaptured birds were tagged, the time an individual was already present before tagging could not be ascertained. We use the moment of tagging as a surrogate for arrival time to quantify minimum stopover durations.

Ecological immunology

Blood samples

To measure variation in innate immune defences between individuals, we collected 93 blood samples of 90 different individual blackbirds (three individuals were recaptured and sampled twice). Shortly after capture, we bled birds by brachial venipuncture using sterile bleeding techniques (Owen 2011) and sterile supplies (BD Microlance 25G needles, Brand 749311 heparinised capillaries) to collect ca 300 µl blood per individual. Immunological indices can change over time following capture, suggesting a role for stress from capture, handling, or both (Scope et al. 2002, Matson et al. 2006, Millet et al. 2007, Buehler et al. 2008, Zylberberg 2015). To limit these effects on our baseline measures, we bled tagged birds as soon as possible after collection from the net (mean ± SD = 12 ± 7, range 3–29 minutes, n = 38). Nets were checked at least every 30 minutes to ensure that all birds were bled within one hour after flying into the net. Between collection and centrifugation (10 minutes, 7000 rotations per minute, Eppendorf Minispin), samples were stored on ice (for 30 ± 23 minutes, range 4–101, n = 93). Plasma was pipetted into a separate 0.5 ml tube and stored on frozen ice packs in a cool box for up to seven hours, until we transferred these samples into a freezer. Samples were transported to the mainland in a cool box filled with frozen ice packs. Once on the mainland, we confirmed that no samples had thawed and then further transported the samples on dry ice to the Netherlands Institute of Ecology, where samples were stored as single aliquots at −20°C until further analysis. Assays were performed in the same order for all samples (assay dates are given under the relevant sections).

Haemolysis and haemagglutination

We used a haemolysis and haemagglutination (HL-HA) assay to gain insight in levels of non-specific (i.e. 'natural') antibodies and lytic enzymes (e.g. complement), both of which represent dimensions of the innate immune system (Matson et al. 2005, assay date 13 July 2023). We blocked microtiter plates with a 2% milk powder solution, and we based the assay on 20 µl dilution series (instead of 25 µl as originally described). We incubated the serially diluted plasma samples (1:1 to 1:1024 in PBS) with 20 µl of a 1% rabbit erythrocyte suspension (Fiebig Animal blood Products, Düsseldorf, Germany) for 90 minutes at 37°C. Assay plates were scanned 20 minutes post-incubation for haemagglutination (driven by natural antibodies) and 90 minutes post-incubation for haemolysis (driven by an interaction between natural antibodies and lytic enzymes). All samples were scored at least twice (by TM, blind to sample identity). When the two scores differed more than 0.5 titres, a sample was scored another time and the median titre was used as a final score. When scores fell within 0.5 titres, the average titre was used as a final score.

Haptoglobin

We measured the concentration of an acute phase protein (haptoglobin or a functional equivalent) as a biomarker relevant to inflammation, infection, and trauma, using a commercially available kit that quantifies the haem-binding capacity of plasma (TP801; Tri-Delta Diagnostics, NJ, USA, assay date 21 April 2023). We used 7.5 µl samples and followed the 'manual method' described in the manufacturer's instructions with two additional scans following (Matson et al. 2012b). We measured absorbances at 450 nm and 630 nm before adding the last reagent. Absorbance at 450 nm was used as a covariate to account for differences in plasma redness since haemolysis is known to impact the assay. Absorbance at 630 nm was used to deduct background absorbance (e.g. due to sample cloudiness) from final absorbance at the same wavelength after adding the second reagent. We corrected concentrations calculated from the standard curves for variation between plates using duplicated samples (coefficients of variation [CV]: $CV_{between} = 14.8\%$, $CV_{within} = 10.0\%$).

Bacteria killing ability

To obtain an integrative measure of innate immune function, we quantified the capacity of plasma to control a standard bacterial challenge in vitro. We followed the basic protocol for plasma and *E. coli* described in Matson et al. (2006, assay dates 7–8 April 2023). For each reaction, we mixed 20 µl of a daily-prepared working solution of *E. coli* (ATCC 8739, Epower, 0483E7) with a dilution of 7.5 µl plasma in 192.5 µl PBS (Sigma-Aldrich P4417) in a sterile 2 ml tube. The working solution was made from stock (both kept at 4°C) and regularly monitored so that 20 µl of the working solution contained ca 585 colony forming units (CFUs), and that 75 µl of reaction mixture (i.e. an aliquot spread onto an agar plate) contained approximately 200 CFUs at the start of incubation. We incubated reaction mixtures for 45 minutes at 41°C while shaking at 250 rotations per minute. After incubation, each reaction mixture (including negative controls) was spread in duplo on two agar plates, and the plates were inverted and incubated overnight at 37°C. Colonies were counted manually on each plate. Average colony counts for each sample were subtracted from, and subsequently divided by the average colony counts for the control plates that preceded and followed a given sample within each batch, to give a killing ability (BKA) proportion. A positive BKA value indicates net bacterial killing; a negative BKA value indicates bacterial growth in a sample exceeds growth in the corresponding negative controls. Based on seven samples that we assayed in duplo, we estimated a CV of 20.3%.

Blood smears and leukocyte quantification

Immediately after collecting a blood sample, a small drop of blood was smeared onto a glass slide. Smears were air-dried and then fixed in 96% ethanol for 10 minutes within 12 hours after collection. Slides were stained for 5 minutes in pure May-Grünwald solution (Sigma Aldrich MG-500), rinsed in deionized water, and stained again for 45 minutes in a 1:20 dilution of Giemsa solution (Sigma Aldrich GS-500) in deionized water. After a final rinse, slides were air-dried and stored until use. From the smears, we quantified leukocyte profiles and derived heterophil-to-lymphocyte ratios (hereafter: HL-ratios). A single observer inspected blood smears under oil immersion at a 1000× magnification (Olympus BX40). For each slide, the number of lymphocytes, heterophils, eosinophils, basophils, monocytes, and thrombocytes were recorded per field of view (classified following Campbell 1995), and new fields were included until a total of 100 leukocytes were counted. The HL-ratio (number of heterophils divided by the number of lymphocytes) can be interpreted as a measure of stress (Gross and Siegel 1983, Davis et al. 2008) including in an immunological context (Owen and Moore 2006).

Weather variables

Tailwind components

As wind assistance is known to affect departure decisions of wild birds during migration (Åkesson and Hedenström 2000), we quantified the tail wind component ($m\ s^{-1}$) into our model on minimum stopover duration. Tailwind components are the projection of the wind vector onto the flight vector (which is defined by flight speed and endogenous migratory heading: Kemp et al. 2012b). We used gridded data on wind vectors (decomposed into westerlies: u, and southerlies: v) from the NCEP-R1 data set (Kalnay et al. 1996)) using the 'RNCEP' package (Kemp et al. 2012a). By linear spatial and temporal interpolation we computed local values of wind vectors for each day at sunset (calculated from the 'suntools' package: Bivand et al. 2023) and at all departure moments. Using these local u and v wind components, we computed the tailwind component using the *NCEP.Tailwind* function. To compute the flight vector, we assumed an optimal air speed of 10 $m\ s^{-1}$ (Bruderer and Boldt 2001) and an endogenous flight departure bearing of 247.05°. This bearing is based on locations of 73 blackbirds that were captured on Vlieland in the years 1997 to 2023, and recaptured or recovered in the subsequent winter (from November to February), at least 50 km away from the study site. We calculated an initial departure bearing for flights to each recovery or recapture location. From these individual-level bearings, we computed a circular mean initial departure bearing (mean ± SD: 247.05 ± 47.31°) using the 'circular' package (Agostinelli and Lund 2023). This circular mean departure bearing was robust to omitting 25 records from January (244.34°), nine records from February (248.10°), or records from both months (244.86°). As birds may dynamically change flight altitudes to maximise wind support (Kemp et al. 2013), we used the maximum tailwind component computed for the 1000 hPa (near surface), 925 hPa (760 m), and 850 hPa (1500 m above sea level) pressure bands for each time point (as in Kelsey et al. 2021).

Cloud cover

As birds are often found to depart from stopovers during high visibility weather conditions (Packmor et al. 2020), we retrieved hourly cloud cover scores (0–8, indicating no cloud cover to completely overcast skies) from the local meteorological tower via the KNMI (Royal Dutch Meteorological Institute) data portal.

Statistics

We tested whether the minimum stopover duration of tagged birds on Vlieland was related to variation in immune status using a time-dependent Cox-proportional hazard model (Therneau and Grambsch 2013) fitted in the 'survival' package (Therneau 2024a). This model enables the inclusion of time-variant predictors (here: cloud cover and tailwind component) on the probability of overnight departure for each day the individual is tagged and present. We included the day of tagging as the origin in our model, while including one row for each day an individual was at risk of departure (coded by the event column taking a value of 1). For each potential departure night, we used the tailwind component and cloud cover as time-dependent predictors. Specifically, we used tailwind values at time of sunset when an individual did not depart, and at the exact time of departure when the individual departed overnight (as in Packmor et al. 2020). We included cloud cover scores at the same time points by using the most recent hourly logged value. Tailwind components and cloud cover were not significantly correlated and could therefore be included as predictors in a single model ($\rho = 0.11$, 95% CI: −0.14–0.34, $t_{63} = 0.86$, $p = 0.39$). We also included all immune indices measured at first capture of the 29 tagged birds in the full model. However, since in the full data set of 93 samples haemolysis and haemagglutination scores were highly correlated ($\rho = 0.81$, 95% CI: 0.72–0.87, $t = 13.06$, $df = 91$, $p < 0.001$) these two were scaled, centred, and combined into a single principal component $PC1_{HLHA}$ that explained 89.4% of the variation (eigenvalues: $\lambda_{PC1} = 1.81$ and $\lambda_{PC2} = 0.19$; loadings: HL = 0.71, HA = 0.71). To avoid collinearity of lysis and agglutination scores as predictors within the same model, the principal component was included as a predictor instead. The minimal adequate model did not change when we included either haemolysis score (haemolysis: $\beta \pm SE = 0.05 \pm 0.14$, $\chi^2_1 = 0.12$, $p = 0.73$) or haemagglutination scores (haemagglutination: $\beta \pm SE = 0.18 \pm 0.16$, $\chi^2_1 = 1.26$, $p = 0.26$) in the full model instead of $PC1_{HLHA}$. To exclude variation in haptoglobin concentration resulting from plasma redness and cloudiness, we regressed haptoglobin concentration over the sample's 450 nm pre-assay (i.e. pre-colour-change) value and used the residuals as predictors in the departure model. Including haptoglobin concentration without a correction for pre-assay values did not alter our conclusions ($HP_{uncorrected}$: $\beta \pm SE = -3.01 \pm 1.53$, $\chi^2_1 = 4.30$, $p = 0.038$). Finally, the full model included each individual's sex, age, and scaled mass index (Peig and Green 2009) as predictors. We computed the latter using each individual's body mass at first capture over its tarsus length (which was more strongly correlated to body mass than was wing chord: $\rho_{tarsus} = 0.49$, 95%-CI = 0.29–0.64, $t_{74} = 4.80$, $p = 8.17 \times 10^{-6}$; $\rho_{wing} = 0.33$, 95%-CI = 0.11–0.52, $t_{74} = 3.03$, $p = 0.0034$). None of the included explanatory variables were significantly correlated (Supporting information). In addition to the model described above we fitted a full model that, apart from these fixed effects, includes a random intercept term for tagging date to account for non-independence of birds that were tagged on the same day (using the 'coxme' package: Therneau 2024b). Although our model preferably includes a random structure, this comes with a cost of higher model complexity which, on small data sets like ours, may hamper inference of fixed effect parameters (Gomes 2022). We therefore include both alternatives to evaluate the consequences for fixed parameter estimates and the uncertainty around those.

We selected a minimal adequate model from a full model by stepwise deletion of least significant terms in a likelihood ratio test, sequentially excluding terms with non-significant terms until the resulting model only included significant terms. Given our modest sample size, we did not include interaction terms between weather variables and immune indices in the full model. However, to test whether the departure probability for an individual was influenced by weather variables in a way that depended on its immune status, we separately introduced interactions between the bird-related variables and both atmospheric variables into the minimal adequate model. We validated that model assumptions of constant proportionality of hazards were met with the *cox.zph* function.

Results

For 29 out of 38 tagged individuals, a departure moment could be identified based on radio signal detections. Individuals departed from the island between 0.40 and 28.28 days (mean ± SD = 6.71 ± 5.70, n = 29) after tagging. For one individual, the departure moment could not be determined. Another individual lost its tag or may have died on the capture site (constant signal strength for some hours during daytime, followed by signal loss). Seven individuals (five young females and one male of each age class) did not depart before 16 January after which the receiver was inactive until it was activated again on 9 March. Three of these seven individuals that presumably overwintered at or near the study location were detected several times between 9 March and 21, 23, and 24 March, respectively, when these individuals departed towards the east on their presumed spring migration.

Testing for statistical associations between immune status, condition, weather, and stopover departure

Individuals were more likely to depart on nights with lower cloud cover and when stronger tailwinds prevailed, and had lower minimal stopover durations if they had a higher scaled mass index at first capture (Table 1, Fig. 1, 2). Minimal stopover durations were slightly longer for individuals with high haptoglobin concentrations at first capture (Table 1, Fig. 2), although this weak positive effect was not significant in a random intercept model that accounted for non-independence of individuals that were tagged on the same day ($\beta \pm SE = -2.06 \pm 1.59$, $\chi^2(1) = 1.48$, $p = 0.22$, Supporting information). Bacterial killing ability, haemolysis-haemagglutination ($PC1_{HLHA}$), and HL-ratios did not explain variation in

Table 1. Minimal adequate model on time to departure as obtained through stepwise backward selection by sequential deletion of non-significant terms from a full model. Cox proportional hazard regression, with 29 events for 29 individuals over 212 nights at risk of departure. β: estimate of coefficient, SE: standard error, e^{β}: hazard ratio, 95%CI (L-U): lower and upper bound of 95% confidence interval, z: z score, $p(>\lvert z\rvert)$: p-value of a z-test (with H_0: $\beta = 0$), $\chi^2(1)$: likelihood ratio test statistic (single degree of freedom), $p(>\chi)$: p-value of likelihood ratio test. Significant p-values are indicated in bold.

Predictor	β ± SE	e^{β}	e^{β} 95%CI (L-U)	z	$p(>\lvert z\rvert)$	$\chi^2(1)$	$p(>\chi)$
Minimal adequate model							
Cloud cover	−0.37 ± 0.09	0.69	0.58–0.82	−4.25	2.18×10^{-5}	19.89	$\mathbf{8.18 \times 10^{-6}}$
Tailwind component	0.16 ± 0.04	1.17	1.07–1.27	3.56	0.00037	14.37	**0.00015**
Scaled mass index	0.13 ± 0.04	1.14	1.06–1.22	3.40	0.00065	13.41	**0.00025**
Haptoglobin (450 nm corr.)	−3.03 ± 1.37	0.05	0.00–0.71	−2.21	0.027	5.20	**0.023**
Dropped terms							
HL-ratio	2.18 ± 1.74	8.88	0.29–269.45	1.25	0.21	1.43	0.23
Sex (male)	−0.54 ± 0.46	0.58	0.24–1.43	−1.18	0.24	1.39	0.24
$PC1_{HLHA}$	0.17 ± 0.20	0.84	0.57–1.23	−0.88	0.38	0.77	0.38
Bacterial killing ability	0.32 ± 1.72	1.38	0.05–40.14	0.19	0.85	0.04	0.85
Age (1cy)	−0.11 ± 0.64	0.90	0.25–3.16	−0.17	0.87	0.03	0.87

time to departure (Table 1). Two-way interactions between bird-related variables and tailwind component (all $p > 0.41$) or cloud cover (all $p > 0.29$) did not explain variation in minimum stopover duration when these were added back into the minimal model (Supporting information), and this did not change when we included interactions into the minimal model that included a random intercept for tagging date (Supporting information).

Discussion

We hypothesised that the need for physiological recovery during migration would result in correlations between minimum stopover durations and indices of immune function. Our results indicate that the three indices of innate immune function and HL-ratio do not explain variation in minimum stopover durations of short-distance migrating blackbirds that stop over on Vlieland during autumn. Only at best, a weak positive effect of haptoglobin concentration on minimum stopover duration was found. Rather, our study suggests that autumn-migrating blackbirds stop over on Vlieland to refuel (since body condition predicted minimum stopover durations), and that individuals depart under supportive tailwinds and low cloud cover. Immune status is apparently of lower importance in these departure decisions.

Effects of immune status on minimum stopover duration

Blackbirds with higher haptoglobin concentrations at first capture tended to make longer stopovers than those with lower haptoglobin concentrations. This result was only significant in a model that did not account for non-independence of blackbirds that were tagged on the same day and should therefore be interpreted with caution. In line with the observed positive trend, a previous study found that elevated haptoglobin levels in short- and long-distance migrants were associated with prolonged stopovers at Falsterbo (Hegemann et al. 2018b). In contrast, haptoglobin concentrations of northern wheatears *Oenanthe oenanthe* explained no variation in autumn stopover durations on Helgoland (Eikenaar et al. 2019). The tendency for individuals with elevated haptoglobin to prolong stopovers is in line with our hypothesis, but revealing the mechanism underlying this result requires further study. We see three mutually non-exclusive explanations for our result.

First, individuals might trade off investments in (certain) immune defences and migration. Blackbirds might prolong stopovers to maintain or recover immunoregulatory and bacteriostatic functions associated with high-haptoglobin levels on stopover (Quaye 2008). Although maintaining high-haptoglobin levels may not be particularly costly (Klasing 1998), even small savings may be worthwhile on a budget that is tightened by thermoregulatory and flight costs (Wikelski et al. 2003, Hasselquist and Nilsson 2012, Guglielmo 2018). Second, haptoglobin levels may reflect variation in infection status or intensity. During an acute infection, haptoglobin levels increase steeply (van de Crommenacker et al. 2010, Matson et al. 2012a, b, but see Hegemann et al. 2013), while food intake is reduced (Hegemann et al. 2012). In other species, high-haptoglobin levels, blood parasite infections, and immune challenges were associated with prolonged stopovers (Hegemann et al. 2018a, b). Although the haptoglobin levels we measured (range: 0.04–0.86 mg ml^{-1}) are not uncommon in blackbirds (Norte et al. 2018), and may signal chronic rather than acute infections (e.g. with blood parasites: Ellis et al. 2014, Biard et al. 2015, Agliani et al. 2023, Figuerola et al. 2024), possibly infected individuals made up for lost refuelling opportunities and higher energetic demands by extending stopovers. Third, the tendency of individuals with high-haptoglobin levels to prolong stopovers might result from physiological impacts of flight. Prolonged flight shifts the oxidative balance towards damaging pro-oxidants (Costantini et al. 2008, Jenni-Eiermann et al. 2014, McWilliams et al. 2021). Through haptoglobin's antioxidant properties (Gutteridge 1987, Tseng et al. 2004, Quaye 2008) blackbirds with high-haptoglobin levels may have

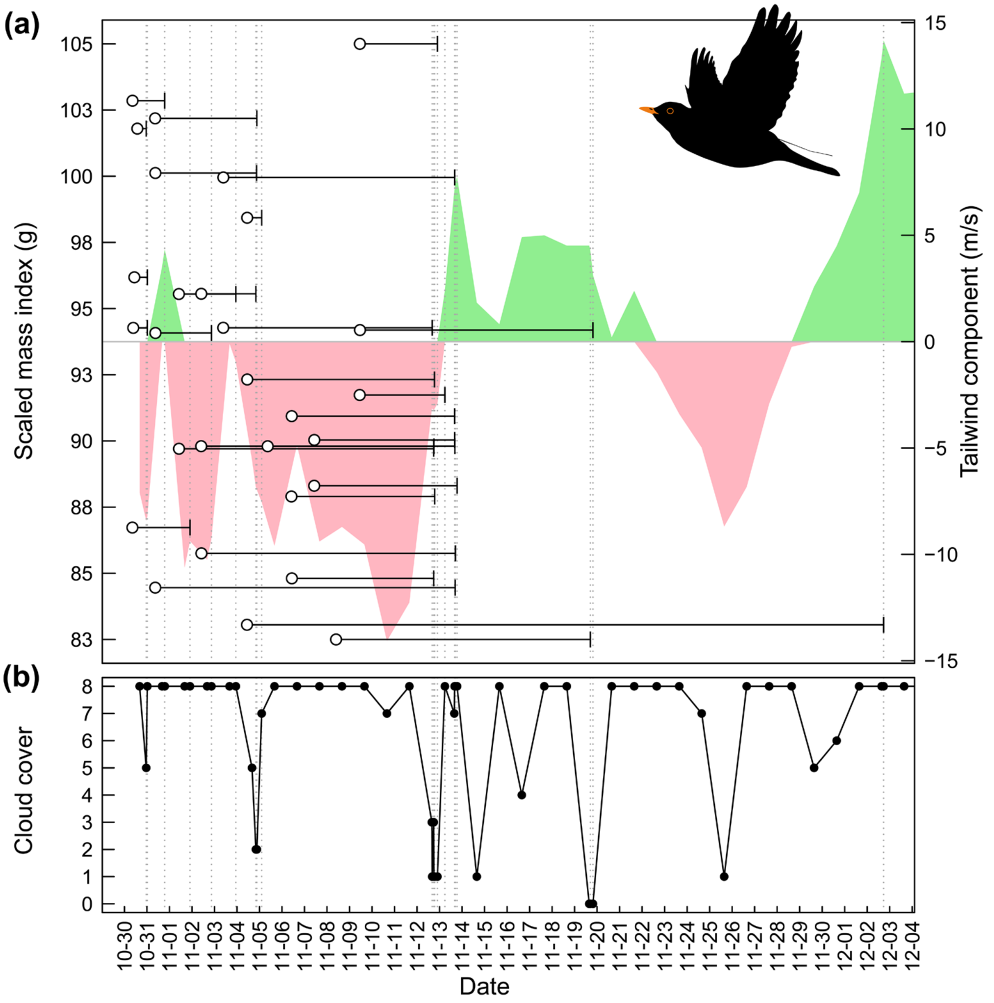

Figure 1. Departure moments of blackbirds on Vlieland were associated with positive tailwinds, low cloud cover scores, and low scaled mass indices at arrival. In panel (a), horizontal lines represent the time each individual spent on the stopover location since the moment of first capture (open plotting symbols) until the moment of departure (vertical end line). Individuals are positioned on a vertical axis corresponding to their scaled mass index at their first capture. Shaded areas represent the tailwind component, with green indicating positive tailwinds towards the expected wintering grounds, and red indicating negative tailwinds (i.e. headwinds). In panel (b), cloud cover at sunrise or the moment of an individual's departure are plotted over date. Dotted vertical lines indicate the moment individuals departed from the stopover location. All times are in UTC.

been restoring their oxidative balance. However, how flight impacts haptoglobin levels is poorly understood (Nebel et al. 2012, Matson et al. 2012a), and although oxidative lipid damage was found to decrease during stopover (Skrip et al. 2015, Eikenaar et al. 2020c, 2023b, Cooper-Mullin and McWilliams 2022), the evidence linking it to stopover durations is mixed (Cooper-Mullin and McWilliams 2022, Eikenaar et al. 2023b).

Apart from the weak positive correlation involving haptoglobin, we found no other correlations between immune indices and minimum stopover duration. Values of immune indices reported in literature vary greatly within and among species, and values we measured did not fall outside the range of variation observed for blackbirds in any surprising way (Norte et al. 2018, Brust et al. 2022). In line with our result, minimum stopover durations and immune indices measured in blackbirds and four other short- to medium-distance migrants were correlated in spring, when migrants are more time-constrained (Nilsson et al. 2013), but not in autumn (Brust et al. 2022). While this suggests that time-constrained migrants are more likely to trade-off immune defences against total migration speed, no observational evidence of these trade-offs has been found in long-distance migrants (Hegemann et al. 2018b, Eikenaar et al. 2019) for which time constraints are especially stringent (Nilsson et al. 2014). After being immune-challenged, however, correlations between stopover duration and immune indices appeared in both short- and long-distance migrants (Hegemann et al. 2018a). Migrants under contrasting time constraints thus appear to trade-off immune defences and migratory progress differently, depending on the nature of the immune response (Buehler et al. 2010b). Although the lack of correlation

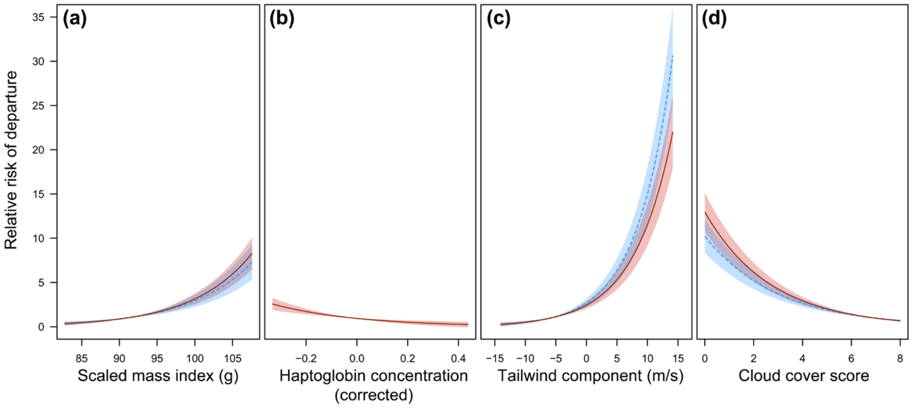

Figure 2. Minimal adequate model fits with (dotted blue line), and without (solid red line) a random intercept for the day of tagging, with corresponding 95% confidence intervals (shaded blue and red areas, respectively). Lines show the ratio between the risk of departure, relative to an individual with all other covariates set at the sample's mean, for (a) scaled mass index, (b) haptoglobin level (the residual concentration over pre-scan absorbance at 450 nm), (c) tailwind component, and (d) cloud cover score.

between autumn stopover duration and immune defences contrasts with previous work on short-distance migrants (Hegemann et al. 2018b), the weak correlation between haptoglobin levels and minimum stopover duration we observed is in line with the view that, in migrants without strong time constraints, recovery from even mild inflammation can take priority over migratory progress (Hegemann et al. 2018a, b).

An important caveat in light of the above complications is that the links between recovery of immune defences, oxidative balance, and replenishment of fuel stores are poorly understood. Immune functions may trade off against more than just stopover duration (e.g. antioxidant defences: Eikenaar et al. 2018a). Likely, priorities between immune functions and competing physiological functions differ across contexts. For example, in free-flying but not in ad libitum-fed, captive northern wheatears, refuelling appeared to be incompatible with oxidative recovery (Eikenaar et al. 2023a). Hermit thrushes *Catharus guttatus* show something of an opposite pattern: dietary antioxidants reduced stopover durations when birds were food-limited but not when they were allowed to refuel (Cooper-Mullin and McWilliams 2022). Since these contextual differences can induce physiological reallocations, trade-offs between immune function and stopover duration may sometimes be obscured. Given the growing body of evidence for trade-offs between physiological systems, an integrative approach to studying physiology on stopovers may be required to understand the (lack of) correlations between stopover duration and individual physiological functions.

An absence of strong correlations between immune status and minimum stopover duration does not demonstrate that immune status does not influence stopover duration. The full stopover duration and immune status immediately upon arrival could not be ascertained in our study. Hence, no firm conclusions can be drawn on their associations. In addition, the prolonged episodes of prevailing headwinds that occurred during our study may have masked effects of arrival immune status on minimum stopover durations. That is, if weather constraints on departure possibilities persist, individuals that have arrived with varying immune status may all have recovered before weather conditions have improved, and therefore may depart at the same time. In that case, no correlation between arrival immune status and stopover duration will be found. This masking effect is especially concealing when immune status is rapidly restored on stopover, since immune recovery then is more likely to be completed before the weather changes. In caged northern wheatears with ad libitum food, bacterial killing abilities increased steeply over the course of two days (Eikenaar et al. 2020c). Even though the recovery of immune defences in free-flying songbirds may be slower (Eikenaar et al. 2023a), periods of unsuitable weather for departure on Vlieland may still have masked the effects of recovery processes on stopover durations.

Other factors related to minimum stopover duration

Blackbirds with low scaled mass indices at first capture had longer minimum stopover durations than birds with high scaled mass indices. Since scaled mass indices increase with fuel loads, this result suggests that blackbirds needed to refuel before resuming migration. Relationships between body condition and stopover duration have been documented in a variety of species (Schmaljohann and Eikenaar 2017), including autumn-migrating blackbirds (Packmor et al. 2020). Refuelling may be particularly important near geographic barriers, such as open waters which offer little opportunity for stopovers (Deutschlander and Muheim 2009, Sjöberg et al. 2015). Although a previous study indicated that arrival fuel loads of the vast majority (91%) of autumn-migrating blackbirds that stopped over on Helgoland were sufficient to have reached the nearest coastal destination, this proportion dropped significantly when accounting for wind conditions (Kelsey et al. 2021).

In our study, strong tailwinds and low cloud cover scores were associated with overnight stopover departures. Both tailwinds and low cloud cover have previously been identified as a predictor for the onset (Linek et al. 2021) and resumption of autumn migration in blackbirds (Packmor et al. 2020). Similar wind selectivity has been documented in a large variety of species (Åkesson and Hedenström 2000, Åkesson et al. 2002, Schaub et al. 2004, Tsvey et al. 2007), and the same is true for effects of cloud cover on departures (Åkesson et al. 2001, Brust et al. 2019, Rüppel et al. 2023; but see Bolshakov et al. 2007). Tailwinds can reduce the energetic and time costs of migratory flight (Deppe et al. 2015) and are therefore expected to lower thresholds for departure (Weber and Hedenström 2000). What causally links supportive winds to stopover departures is largely unexplored, and hence it is unknown whether physiology plays a mediating role. Yet, in autumn-migrating blackbirds on Helgoland, strong tailwinds were associated with elevated corticosterone levels (Eikenaar et al. 2018b). This association is intriguing, since in other species elevated corticosterone predicted stopover departures (Eikenaar et al. 2014, 2017) while it is also known to downregulate immune defences (Gao et al. 2016). Wind selectivity is especially relevant near geographic barriers (Bulte et al. 2014), as the risk of mortality in traversing these likely increases when birds face unfavourable winds that can rapidly deplete fuel stores (Loonstra et al. 2019). Similarly, blackbirds may have avoided overcast departures to reduce energetic costs or risks of barrier-crossing. Migrants use celestial cues to navigate (Emlen 1970, Mouritsen and Larsen 2001), and in overcast or associated weather conditions (e.g. precipitation: Rüppel et al. 2023) these cues may become inaccessible. Although the use of celestial cues for navigation has not been demonstrated in blackbirds, departure bearings of reed warblers *Acrocephalus scirpaceus* were more scattered under overcast than cloudless skies (Åkesson et al. 2001), and under total cloud cover white-throated sparrows *Zonotrichia albicollis* performed more tortuous flight paths than under clear skies (Emlen and Demong 1978). Possibly because of suboptimal navigation, autumn migrants took longer to cover ca 50 km distance over sea after an overcast than after a cloudless departure from Falsterbo (Sjöberg et al. 2015). By hampering orientation, low-visibility weather thus may result in longer barrier-crossing flights that incur higher energetic costs and mortality risks.

Our results should be interpreted with some caution: due to the relatively short study period within a single year, the observed variation in weather conditions, energetic condition, and immune status was limited. Nonetheless, the peaked departure we observe for blackbirds matched observations from radar studies above the North Sea. Such studies show that, especially in autumn, migrants cross the North Sea en masse, since easterly winds that support flights to the UK are comparatively rare in autumn (Buurma 1987, Shamoun-Baranes and van Gasteren 2011, Bradarić et al. 2020, 2024). We find that individual blackbirds on Vlieland awaited supportive winds and cloudless nights for considerable time periods. Instead of having minimised total migration time or energy by reducing stopover durations, blackbirds may therefore have prioritised minimising other currencies, such as the energetic costs and possibly mortality risks, of resuming migration and crossing the North Sea. However, to identify whether individuals that prolong stopovers indeed experience fitness costs would require further study.

Conclusion

We conclude that immune status does not always impact minimum stopover durations. Instead, our results suggest that fuel loads at arrival, and atmospheric conditions at departure, are of overriding importance. Ideally, future studies on the role of immune status in stopover departure decisions should account for weather variability.

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Author contributions

Tjomme van Mastrigt: Conceptualization (lead), Data curation (lead), Formal analysis (lead), Funding acquisition (supporting), Investigation (lead), Methodology (lead), Project administration (lead), Resources (equal), Software (lead), Validation (lead), Visualization (lead), Writing - original draft (lead), Writing - review and editing (equal). **Kevin D. Matson**: Methodology (equal), Supervision (equal), Writing - review and editing (equal). **Sander Lagerveld**: Resources (equal), Writing - review and editing (equal). **Xinrou S. Huang**: Methodology (supporting), Writing - review and editing (supporting). **Willem F. de Boer**: Funding acquisition (supporting), Supervision (equal), Writing - review and editing (equal). **Henk P. van der Jeugd**: Conceptualization (supporting), Funding acquisition (lead), Supervision (equal), Writing - review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.ffbg79d3q (van Mastrigt et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Agliani, G., Giglia, G., De Bruin, E., van Mastrigt, T., Blom, R., Sikkema, R. S., Kik, M., Koopmans, M. P. G., Gröne, A. and Van Den Brand, J. M. A. 2023. The pathology of co-infection with Usutu virus and *Plasmodium* spp. in naturally infected Eurasian blackbirds (*Turdus merula*). – One Health 16: 100534.

Agostinelli, C. and Lund, U. 2023. circular: circular statistics. – https://cran.r-project.org/web/packages/circular/index.html.

Åkesson, S. and Hedenström, A. 2000. Wind selectivity of migratory flight departures in birds. – Behav. Ecol. Sociobiol. 47: 140–144.

Åkesson, S., Walinder, G., Karlsson, L. and Ehnbom, S. 2001. Reed warbler orientation: initiation of nocturnal migratory flights in relation to visibility of celestial cues at dusk. – Anim. Behav. 61: 181–189.

Åkesson, S., Walinder, G., Karlsson, L. and Ehnbom, S. 2002. Nocturnal migratory flight initiation in reed warblers *Acrocephalus scirpaceus* : effect of wind on orientation and timing of migration. – J. Avian Biol. 33: 349–357.

Biard, C., Monceau, K., Motreuil, S. and Moreau, J. 2015. Interpreting immunological indices: the importance of taking parasite community into account. An example in blackbirds *Turdus merula*. – Methods Ecol. Evol. 6: 960–972.

Bivand, R., Dokter, A. M., Huybrechts, P., Luque, S., Pelletier, G. and Tedeschi, A. 2023. suntools: calculate sun position, sunrise, sunset, solar noon and twilight. – https://cran.r-project.org/web/packages/survival/index.html.

Bolshakov, C. V., Chernetsov, N., Mukhin, A., Bulyuk, V. N., Kosarev, V., Ktitorov, P., Leoke, D. and Tsvey, A. 2007. Time of nocturnal departures in European robins, *Erithacus rubecula*, in relation to celestial cues, season, stopover duration and fat stores. – Anim. Behav. 74: 855–865.

Bordel, R. and Haase, E. 2000. Influence of flight on protein catabolism, especially myofilament breakdown, in homing pigeons. – J. Comp. Physiol. B 170: 51–58.

Bounas, A., Komini, C., Toli, E.-A., Talioura, A., Sotiropoulos, K. and Barboutis, C. 2024. Expression patterns of heat-shock genes during stopover and the trade-off between refueling and stress response in a passerine migrant. – J. Comp. Physiol. B 194: 1–6.

Bradarić, M., Bouten, W., Fijn, R. C., Krijgsveld, K. L. and Shamoun-Baranes, J. 2020. Winds at departure shape seasonal patterns of nocturnal bird migration over the North Sea. – J. Avian Biol. 51: 1–11.

Bradarić, M., Kranstauber, B., Bouten, W. and Shamoun-Baranes, J. 2024. Forecasting nocturnal bird migration for dynamic aeroconservation: the value of short-term datasets. – J. Appl. Ecol. 61: 1147–1158.

Bruderer, B. and Boldt, A. 2001. Flight characteristics of birds: I. Radar measurements of speeds. – Ibis 143: 178–204.

Brust, V., Michalik, B. and Hüppop, O. 2019. To cross or not to cross – thrushes at the German North Sea coast adapt flight and routing to wind conditions in autumn. – Movem. Ecol. 7: 32.

Brust, V., Eikenaar, C., Packmor, F., Schmaljohann, H., Hüppop, O. and Czirják, G. Á. 2022. Do departure and flight route decisions correlate with immune parameters in migratory songbirds? – Funct. Ecol. 36: 3007–3021.

Brzustowski, J., Lepage, D., LaZerte, S., Bernard, J., Berrigan, L., Crewe, T., Crysler, Z.Hussell, J., Jardine, C., MacDonald, A., Mackenzie, S., Morrill, P., Sayers, J. and Taylor, P. 2024. motus: fetch and use data from the Motus Wildlife Tracking System. – https://motuswts.github.io/motus/.

Buehler, D. M., Bhola, N., Barjaktarov, D., Goymann, W., Schwabl, I., Tieleman, B. I. and Piersma, T. 2008. Constitutive immune function responds more slowly to handling stress than corticosterone in a shorebird. – Physiol. Biochem. Zool. 81: 673–681.

Buehler, D. M., Tieleman, B. I. and Piersma, T. 2010a. Indices of immune function are lower in red knots (*Calidris canutus*) recovering protein than in those storing fat during stopover in Delaware Bay. – Auk 127: 394–401.

Buehler, D. M., Tieleman, B. I. and Piersma, T. 2010b. How do migratory species stay healthy over the annual cycle? A conceptual model for immune function and for resistance to disease. – Integr. Comp. Biol. 50: 346–357.

Bulte, M., McLaren, J. D., Bairlein, F., Bouten, W., Schmaljohann, H. and Shamoun-Baranes, J. 2014. Can wheatears weather the Atlantic? Modeling nonstop trans-Atlantic flights of a small migratory songbird. – Auk 131: 363–370.

Buurma, L. S. 1987. Patronen van hoge vogeltrek boven het Noordzeegebied in oktober. – Limosa 60: 363–370.

Campbell, T. W. 1995. Avian hematology and cytology. – Iowa State Univ. Press.

Cooper-Mullin, C. and McWilliams, S. R. 2022. Fat stores and antioxidant capacity affect stopover decisions in three of four species of migratory passerines with different migration strategies: an experimental approach. – Front. Ecol. Evol. 10: 762146.

Costantini, D., Dell'Ariccia, G. and Lipp, H.-P. 2008. Long flights and age affect oxidative status of homing pigeons (*Columba livia*). – J. Exp. Biol. 211: 377–381.

Davis, A. K., Maney, D. L. and Maerz, J. C. 2008. The use of leukocyte profiles to measure stress in vertebrates: a review for ecologists. – Funct. Ecol. 22: 760–772.

De Angeli Dutra, D., Fecchio, A., Martins Braga, É. and Poulin, R. 2021. Migratory birds have higher prevalence and richness of avian haemosporidian parasites than residents. – Int. J. Parasitol. 51: 877–882.

Deppe, J. L., Ward, M. P., Bolus, R. T., Diehl, R. H., Celis-Murillo, A., Zenzal, T. J., Moore, F. R., Benson, T. J., Smolinsky, J. A., Schofield, L. N., Enstrom, D. A., Paxton, E. H., Bohrer, G., Beveroth, T. A., Raim, A., Obringer, R. L., Delaney, D. and Cochran, W. W. 2015. Fat, weather, and date affect migratory songbirds' departure decisions, routes, and time it takes to cross the Gulf of Mexico. – Proc. Natl Acad. Sci. USA. 112: E6331–E6338.

Deutschlander, M. E. and Muheim, R. 2009. Fuel reserves affect migratory orientation of thrushes and sparrows both before and after crossing an ecological barrier near their breeding grounds. – J. Avian Biol. 40: 85–89.

Dossman, B. C., Mitchell, G. W., Norris, D. R., Taylor, P. D., Guglielmo, C. G., Matthews, S. N. and Rodewald, P. G. 2016. The effects of wind and fuel stores on stopover departure behavior across a migratory barrier. – Behav. Ecol. 27: 567–574.

Eikenaar, C. and Hegemann, A. 2016. Migratory common blackbirds have lower innate immune function during autumn migration than resident conspecifics. – Biol. Lett. 12: 20160078.

Eikenaar, C., Klinner, T. and Stöwe, M. 2014. Corticosterone predicts nocturnal restlessness in a long-distance migrant. – Horm. Behav. 66: 324–329.

Eikenaar, C., Müller, F., Leutgeb, C., Hessler, S., Lebus, K., Taylor, P. D. and Schmaljohann, H. 2017. Corticosterone and timing of migratory departure in a songbird. – Proc. R. Soc. B 284: 20162300.

Eikenaar, C., Isaksson, C. and Hegemann, A. 2018a. A hidden cost of migration? Innate immune function versus antioxidant defense. – Ecol. Evol. 8: 2721–2728.

Eikenaar, C., Ballstaedt, E., Hessler, S., Klinner, T., Müller, F. and Schmaljohann, H. 2018b. Cues, corticosterone and departure decisions in a partial migrant. – Gen. Comp. Endocrinol. 261: 59–66.

Eikenaar, C., Packmor, F., Schmaljohann, H. and Hegemann, A. 2019. Stopover departure decisions in autumn are not associated with constitutive immune function in northern wheatears *Oenanthe oenanthe*. – J. Ornithol. 160: 813–817.

Eikenaar, C., Hessler, S. and Hegemann, A. 2020a. Migrating birds rapidly increase constitutive immune function during stopover. – R. Soc. Open Sci. 7: 192031.

Eikenaar, C., Hegemann, A., Packmor, F., Kleudgen, I. and Isaksson, C. 2020b. Not just fuel: energy stores are correlated with immune function and oxidative damage in a long-distance migrant. – Curr. Zool. 66: 21–28.

Eikenaar, C., Winslott, E., Hessler, S. and Isaksson, C. 2020c. Oxidative damage to lipids is rapidly reduced during migratory stopovers. – Funct. Ecol. 34: 1215–1222.

Eikenaar, C., Ostolani, A., Hessler, S., Ye, E. Y. and Hegemann, A. 2023a. Recovery of constitutive immune function after migratory endurance flight in free-living birds. – Biol. Lett. 19: 20220518.

Eikenaar, C., Ostolani, A., Brust, V., Karwinkel, T., Schmaljohann, H. and Isaksson, C. 2023b. The oxidative balance and stopover departure decisions in a medium- and a long-distance migrant. – Movem. Ecol. 11: 7.

Ellis, V. A., Kunkel, M. R. and Ricklefs, R. E. 2014. The ecology of host immune responses to chronic avian haemosporidian infection. – Oecologia 176: 729–737.

Emlen, S. T. 1970. Celestial rotation: its importance in the development of migratory orientation. – Science 170: 1198–1201.

Emlen, S. T. and Demong, N. J. 1978. Orientation strategies used by free-flying bird migrants: a radar tracking study. – In: Schmidt-Koenig, K. and Keeton, W. T. (eds), Animal migration, navigation, and homing, Proceedings in Life Sciences. Springer, pp. 283–293.

Figuerola, J. and Green, A. J. 2000. Haematozoan parasites and migratory behaviour in waterfowl. – Evol. Ecol. 14: 143–153.

Figuerola, J., La Puente, J. M., Díez-Fernández, A., Thomson, R. L., Aguirre, J. I., Faivre, B. and Ibañez-Alamo, J. D. 2024. Urbanization correlates with the prevalence and richness of blood parasites in Eurasian blackbirds (*Turdus merula*). – Sci. Tot. Environ. 922: 171303.

Gao, S., Sanchez, C. and Deviche, P. J. 2016. Corticosterone rapidly suppresses innate immune activity in the house sparrow (*Passer domesticus*). – J. Exp. Biol. 220: 322–327.

Gomes, D. G. E. 2022. Should I use fixed effects or random effects when I have fewer than five levels of a grouping factor in a mixed-effects model? – PeerJ 10: e12794.

Gross, W. B. and Siegel, H. S. 1983. Evaluation of the heterophil/lymphocyte ratio as a measure of stress in chickens. – Avian Dis. 27: 972.

Guglielmo, C. G. 2018. Obese super athletes: fat-fuelled migration in birds and bats. – J. Exp. Biol. 221: jeb165753.

Guglielmo, C. G., Piersma, T. and Williams, T. D. 2001. Muscle damage in migrant birds. – J. Exp. Biol. 204: 2683–2690.

Gutteridge, J. M. C. 1987. The antioxidant activity of haptoglobin towards haemoglobin-stimulated lipid peroxidation. – Biochim. Biophys. Acta 917: 219–223.

Hasselquist, D. and Nilsson, J.-Å. 2012. Physiological mechanisms mediating costs of immune responses: what can we learn from studies of birds? – Anim. Behav. 83: 1303–1312.

Hasselquist, D., Lindström, A., Jenni-Eiermann, S., Koolhaas, A. and Piersma, T. 2007. Long flights do not influence immune responses of a long-distance migrant bird: a wind-tunnel experiment. – J. Exp. Biol. 210: 1123–1131.

Hedenström, A. and Alerstam, T. 1997. Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. – J. Theor. Biol. 189: 227–234.

Hegemann, A., Matson, K. D., Versteegh, M. A. and Tieleman, B. I. 2012. Wild skylarks seasonally modulate energy budgets but maintain energetically costly inflammatory immune responses throughout the annual cycle. – PLoS One 7: e36358.

Hegemann, A., Matson, K. D., Versteegh, M. A., Villegas, A. and Tieleman, B. I. 2013. Immune response to an endotoxin challenge involves multiple immune parameters and is consistent among the annual-cycle stages of a free-living temperate zone bird. – J. Exp. Biol. 216: jeb.083147.

Hegemann, A., Alcalde Abril, P., Sjöberg, S., Muheim, R., Alerstam, T., Nilsson, J. Å. and Hasselquist, D. 2018a. A mimicked bacterial infection prolongs stopover duration in songbirds – but more pronounced in short- than long-distance migrants. – J. Anim. Ecol. 87: 1698–1708.

Hegemann, A., Alcalde Abril, P., Muheim, R., Sjöberg, S., Alerstam, T., Nilsson, J.-Å. and Hasselquist, D. 2018b. Immune function and blood parasite infections impact stopover ecology in passerine birds. – Oecologia 188: 1011–1024.

Herbert, J. A., Mizrahi, D. and Taylor, C. M. 2022. Migration tactics and connectivity of a Nearctic–Neotropical migratory shorebird. – J. Anim. Ecol. 91: 819–830.

Jenni-Eiermann, S., Jenni, L., Smith, S. and Costantini, D. 2014. Oxidative stress in endurance flight: an unconsidered factor in bird migration. – PLoS One 9: e97650.

Kalnay, E. et al. 1996. The NCEP/NCAR 40-year reanalysis project. – Bull. Am. Meteor. Soc. 77: 437–471.

Kelly, T. R., Butnari, A. C., MacDougall-Shackleton, E. A. and MacDougall-Shackleton, S. A. 2023. Rising to the challenge: mounting an acute phase immune response has no long-term negative effects on captive sparrow migratory body composition or migratory restlessness. – Integr. Comp. Biol. 63: 1182–1196.

Kelsey, N. A., Hüppop, O. and Bairlein, F. 2021. Days to visit an offshore island: effect of weather conditions on arrival fuel load and potential flight range for common blackbirds *Turdus merula* migrating over the North Sea. – Movem. Ecol. 9: 53.

Kemp, M. U., Emiel Van Loon, E., Shamoun-Baranes, J. and Bouten, W. 2012a. RNCEP: global weather and climate data at your fingertips. – Methods Ecol. Evol. 3: 65–70.

Kemp, M. U., Shamoun-Baranes, J., Van Loon, E. E., McLaren, J. D., Dokter, A. M. and Bouten, W. 2012b. Quantifying flow-assistance and implications for movement research. – J. Theor. Biol. 308: 56–67.

Kemp, M. U., Shamoun-Baranes, J., Dokter, A. M., Van Loon, E. and Bouten, W. 2013. The influence of weather on the flight altitude of nocturnal migrants in mid-latitudes. – Ibis 155: 734–749.

Klasing, K. C. 1998. Nutritional modulation of resistance to infectious diseases. – Poult. Sci. 77: 1119–1125.

Klasing, K. C. 2004. The costs of immunity. – Acta Zool. Sin. 50: 961–969.

Kokko, H. 1999. Competition for early arrival in migratory birds. – J. Anim. Ecol. 68: 940–950.

Lagerveld, S., Janssen, R., Manshanden, J., Haarsma, A.-J., De Vries, S., Brabant, R. and Scholl, M. 2017. Telemetry for migratory bats: a feasibility study. – Wageningen Marine Research report no. C011/17, pp. 1–58.

Lameris, T. K., Van Der Jeugd, H. P., Eichhorn, G., Dokter, A. M., Bouten, W., Boom, M. P., Litvin, K. E., Ens, B. J. and Nolet, B. A. 2018. Arctic geese tune migration to a warming climate but still suffer from a phenological mismatch. – Curr. Biol. 28: 2467–2473.e4.

Larcombe, S. D., Coffey, J. S., Bann, D., Alexander, L. and Arnold, K. E. 2010. Impacts of dietary antioxidants and flight training on post-exercise oxidative damage in adult parrots. – Comp. Biochem. Physiol. B 155: 49–53.

Lee, K. A. 2006. Linking immune defenses and life history at the levels of the individual and the species. – Integr. Comp. Biol. 46: 1000–1015.

Lensink, R., van Gasteren, H., Hustings, F., Buurma, L. S., van Duin, G., Linnartz, L., Vogelzang, F. and Witkamp, C. 2002. Vogeltrek over Nederland, 1976–1993. – Schuyt & Co.

Leung, T. L. F. and Koprivnikar, J. 2016. Nematode parasite diversity in birds: the role of host ecology, life history and migration. – J. Anim. Ecol. 85: 1471–1480.

Linek, N., Brzęk, P., Gienapp, P., O'Mara, M. T., Pokrovsky, I., Schmidt, A., Shipley, J. R., Taylor, J. R. E., Tiainen, J., Volkmer, T., Wikelski, M. and Partecke, J. 2021. A partial migrant relies upon a range-wide cue set but uses population-specific weighting for migratory timing. – Movem. Ecol. 9: 63.

Linscott, J. A. and Senner, N. R. 2021. Beyond refueling: investigating the diversity of functions of migratory stopover events. – Ornith. Appl. 123: duaa074.

Loonstra, A. H. J., Verhoeven, M. A., Senner, N. R., Both, C. and Piersma, T. 2019. Adverse wind conditions during northward Sahara crossings increase the in-flight mortality of black-tailed godwits. – Ecol. Lett. 22: 2060–2066.

Matson, K. D., Ricklefs, R. E. and Klasing, K. C. 2005. A hemolysis–hemagglutination assay for characterizing constitutive innate humoral immunity in wild and domestic birds. – Dev. Comp. Immunol. 29: 275–286.

Matson, K. D., Tieleman, B. I. and Klasing, K. C. 2006. Capture stress and the bactericidal competence of blood and plasma in five species of tropical birds. – Physiol. Biochem. Zool. 79: 556–564.

Matson, K. D., Horrocks, N. P. C., Tieleman, B. I. and Haase, E. 2012a. Intense flight and endotoxin injection elicit similar effects on leukocyte distributions but dissimilar effects on plasma-based immunological indices in pigeons. – J. Exp. Biol. 215: 3734–3741.

Matson, K. D., Horrocks, N. P. C., Versteegh, M. A. and Tieleman, B. I. 2012b. Baseline haptoglobin concentrations are repeatable and predictive of certain aspects of a subsequent experimentally-induced inflammatory response. – Comp. Biochem. Physiol. A 162: 7–15.

McWilliams, S., Carter, W., Cooper-Mullin, C., DeMoranville, K., Frawley, A., Pierce, B. and Skrip, M. 2021. How birds during migration maintain (oxidative) balance. – Front. Ecol. Evol. 9: 742642.

Millet, S., Bennett, J., Lee, K. A., Hau, M. and Klasing, K. C. 2007. Quantifying and comparing constitutive immunity across avian species. – Dev. Comp. Immunol. 31: 188–201.

Møller, A. P. and Erritzøe, J. 1998. Host immune defence and migration in birds. – Evol. Ecol. 12: 945–953.

Mouritsen, H. and Larsen, O. N. 2001. Migrating songbirds tested in computer-controlled Emlen funnels use stellar cues for a time-independent compass. – J. Exp. Biol. 204: 3855–3865.

Nebel, S., Bauchinger, U., Buehler, D. M., Langlois, L. A., Boyles, M., Gerson, A. R., Price, E. R., McWilliams, S. R. and Guglielmo, C. G. 2012. Constitutive immune function in European starlings, *Sturnus vulgaris*, is decreased immediately after an endurance flight in a wind tunnel. – J. Exp. Biol. 215: 272–278.

Nebel, S., Buehler, D. M., MacMillan, A. and Guglielmo, C. G. 2013. Flight performance of western sandpipers *Calidris mauri* remains uncompromised when mounting an acute phase immune response. – J. Exp. Biol. 216: 2752–2759.

Nilsson, C., Klaassen, R. H. G. and Alerstam, T. 2013. Differences in speed and duration of bird migration between spring and autumn. – Am. Nat. 181: 837–845.

Nilsson, C., Bäckman, J. and Alerstam, T. 2014. Seasonal modulation of flight speed among nocturnal passerine migrants: differences between short- and long-distance migrants. – Behav. Ecol. Sociobiol. 68: 1799–1807.

Norris, K. and Evans, M. R. 2000. Ecological immunology: life history trade-offs and immune defense in birds. – Behav. Ecol. 11: 19–26.

Norte, A. C., Costantini, D., Araújo, P. M., Eens, M., Ramos, J. A. and Heylen, D. 2018. Experimental infection by microparasites affects the oxidative balance in their avian reservoir host the blackbird *Turdus merula*. – Ticks Tick Borne Dis. 9: 720–729.

Owen, J. C. 2011. Collecting, processing, and storing avian blood: a review: avian blood collection techniques. – J. Field Ornithol. 82: 339–354.

Owen, J. C. and Moore, F. R. 2006. Seasonal differences in immunological condition of three species of thrushes. – Condor 108: 389–398.

Owen, J. C. and Moore, F. R. 2008. Relationship between energetic condition and indicators of immune function in thrushes during spring migration. – Can. J. Zool. 86: 638–647.

Owen, J., Moore, F., Panella, N., Edwards, E., Bru, R., Hughes, M. and Komar, N. 2006. Migrating birds as dispersal vehicles for West Nile virus. – EcoHealth 3: 79–85.

Packmor, F., Klinner, T., Woodworth, B. K., Eikenaar, C. and Schmaljohann, H. 2020. Stopover departure decisions in songbirds: do long-distance migrants depart earlier and more independently of weather conditions than medium-distance migrants? – Movem. Ecol. 8: 6.

Peig, J. and Green, A. J. 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. – Oikos 118: 1883–1891.

Quaye, I. K. 2008. Haptoglobin, inflammation and disease. – Trans. R. Soc. Trop. Med. Hyg. 102: 735–742.

Råberg, L., Grahn, M., Hasselquist, D. and Svensson, E. 1998. On the adaptive significance of stress-induced immunosuppression. – Proc. R. Soc. B 265: 1637–1641.

Rüppel, G., Hüppop, O., Lagerveld, S., Schmaljohann, H. and Brust, V. 2023. Departure, routing and landing decisions of long-distance migratory songbirds in relation to weather. – R. Soc. Open Sci. 10: 221420.

Salewski, V. and Schaub, M. 2007. Stopover duration of palearctic passerine migrants in the western Sahara – independent of fat stores? – Ibis 149: 223–236.

Schaub, M., Liechti, F. and Jenni, L. 2004. Departure of migrating European robins, *Erithacus rubecula*, from a stopover site in relation to wind and rain. – Anim. Behav. 67: 229–237.

Schmaljohann, H. and Both, C. 2017. The limits of modifying migration speed to adjust to climate change. – Nat. Clim. Change 7: 573–576.

Schmaljohann, H. and Eikenaar, C. 2017. How do energy stores and changes in these affect departure decisions by migratory birds? A critical view on stopover ecology studies and some future perspectives. – J. Comp. Physiol. A 203: 411–429.

Schmaljohann, H., Fox, J. W. and Bairlein, F. 2012. Phenotypic response to environmental cues, orientation and migration costs in songbirds flying halfway around the world. – Anim. Behav. 84: 623–640.

Schmaljohann, H., Eikenaar, C. and Sapir, N. 2022. Understanding the ecological and evolutionary function of stopover in migrating birds. – Biol. Rev. 97: 1231–1252.

Scope, A., Filip, T., Gabler, C. and Resch, F. 2002. The influence of stress from transport and handling on hematologic and clinical chemistry blood parameters of racing pigeons (*Columba livia domestica*). – Avian Dis. 46: 224–229.

Shamoun-Baranes, J. and van Gasteren, H. 2011. Atmospheric conditions facilitate mass migration events across the North Sea. – Anim. Behav. 81: 691–704.

Sheldon, B. C. and Verhulst, S. 1996. Ecological immunology: costly parasite defences and trade-offs in evolutionary ecology. – Trends Ecol. Evol. 11: 317–321.

Sjöberg, S., Alerstam, T., Åkesson, S., Schulz, A., Weidauer, A., Coppack, T. and Muheim, R. 2015. Weather and fuel reserves determine departure and flight decisions in passerines migrating across the Baltic Sea. – Anim. Behav. 104: 59–68.

Skrip, M. M., Bauchinger, U., Goymann, W., Fusani, L., Cardinale, M., Alan, R. R. and McWilliams, S. R. 2015. Migrating songbirds on stopover prepare for, and recover from, oxidative challenges posed by long-distance flight. – Ecol. Evol. 5: 3198–3209.

Smith, R. J. and Moore, F. R. 2005. Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. – Behav. Ecol. Sociobiol. 57: 231–239.

Spina, F., Baillie, S. R., Bairlein, F., Fiedler, W. and Thorup, K. 2022. The Eurasian African bird migration atlas. – https://migrationatlas.org.

Svensson, L. 1992. Identification guide to European passerines. – British Trust for Ornithology.

Taylor, P. D. et al. 2017. The Motus Wildlife Tracking System: a collaborative research network to enhance the understanding of wildlife movement. – Avian Conserv. Ecol. 12: 1–11.

Therneau, T. M. 2024a. survival: a package for survival analysis in R. – https://cran.r-project.org/web/packages/survival/index.html.

Therneau, T. M. 2024b. coxme: mixed effects Cox models. – https://cran.r-project.org/web/packages/coxme/index.html.

Therneau, T. M. and Grambsch, P. M. 2013. Modeling survival data: extending the Cox model. – Springer.

Tidball, J. G. 2005. Inflammatory processes in muscle injury and repair. – Am. J. Physiol. Regul. Integr. Comp. Physiol. 288: R345–R353.

Tomotani, B. M., Gienapp, P., De La Hera, I., Terpstra, M., Pulido, F. and Visser, M. E. 2021. Integrating causal and evolutionary analysis of life-history evolution: arrival date in a long-distant migrant. – Front. Ecol. Evol. 9: 630823.

Tseng, C. F., Lin, C. C., Huang, H. Y., Liu, H. C. and Mao, S. J. T. 2004. Antioxidant role of human haptoglobin. – Proteomics 4: 2221–2228.

Tsvey, A., Bulyuk, V. N. and Kosarev, V. 2007. Influence of body condition and weather on departures of first-year European robins, *Erithacus rubecula*, from an autumn migratory stopover site. – Behav. Ecol. Sociobiol. 61: 1665–1674.

van de Crommenacker, J., Horrocks, N. P. C., Versteegh, M. A., Komdeur, J., Tieleman, B. I. and Matson, K. D. 2010. Effects of immune supplementation and immune challenge on oxidative status and physiology in a model bird: implications for ecologists. – J. Exp. Biol. 213: 3527–3535.

van de Crommenacker, J., Richardson, D. S., Koltz, A. M., Hutchings, K. and Komdeur, J. 2012. Parasitic infection and oxidative status are associated and vary with breeding activity in the Seychelles warbler. – Proc. R. Soc. B 279: 1466–1476.

van Dijk, J. G. B. and Matson, K. D. 2016. Ecological immunology through the lens of exercise immunology: new perspective on the links between physical activity and immune function and disease susceptibility in wild animals. – Integr. Comp. Biol. 56: 290–303.

van Mastrigt, T., Matson, K. D., Lagerveld, S., Huang, X. S., de Boer, W. F. and van der Jeugd, H. P. 2024. Data from: Effects of immune status on stopover departure decisions are subordinate to those of condition, cloud cover and tailwind in autumn-migrating common blackbirds *Turdus merula*. – Dryad Digital Repository, https://doi.org/10.5061/dryad.ffbg79d3q.

van Vliet, J., Musters, C. J. M. and ter Keurs, W. J. 2009. Changes in migration behaviour of blackbirds *Turdus merula* from the Netherlands. – Bird Study 56: 276–281.

Weber, T. P. and Hedenström, A. 2000. Optimal stopover decisions under wind influence: the effects of correlated winds. – J. Theor. Biol. 205: 95–104.

Wikelski, M., Tarlow, E. M., Raim, A., Diehl, R. H., Larkin, R. P. and Visser, G. H. 2003. Avian metabolism: costs of migration in free-flying songbirds. – Nature 423: 704–704.

Xu, Y., Laine, V. N., Meramo, K., Santangeli, A., Poosakkannu, A., Suominen, K. M., Gaultier, S., Keller, V., Brotons, L., Pulliainen, A. T., Lilley, T. M. and Lehikoinen, A. 2024. Slow-lived birds and bats carry higher pathogen loads. – One Earth 7: 1–12.

Zehnder, S. and Karlsson, L. 2001. Do ringing numbers reflect true migratory activity of nocturnal migrants? – J. Ornithol. 142: 173–183.

Zylberberg, M. 2015. Common measures of immune function vary with time of day and sampling protocol in five passerine species. – J. Exp. Biol. 218: 757–766.