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Research article

Passerine stopover physiology: weather variability does not alter corticosterone dynamics after sea crossing

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Migration is an energy-intensive phase of birds' life cycle, often including the crossing of large ecological barriers during non-stop flights. Corticosterone (CORT), an adrenocortical hormone also known as the stress hormone, generally rises at the onset of migration to facilitate and sustain high-energy metabolism. Although birds can select favourable meteorological conditions at departure, weather variability en route may affect the migrants' energy reserves and their ability to cope with other stressors. This study investigated the effects of weather conditions on the physiological status of two nocturnal trans-Saharan species, the common whitethroat *Curruca communis* and the garden warbler *Sylvia borin*, upon arrival at a stopover island after crossing the Mediterranean Sea during pre-breeding migration. We assessed fuel stores and CORT variations in relation to tailwinds and air temperature experienced over the sea route. Birds that arrived at the stopover site with residual energy reserves after encountering moderate headwinds or lower temperatures had similar baseline CORT concentrations compared to those that migrated with tailwinds and higher temperatures. While both species exhibited a normal stress response to catching and handling, stress-induced CORT levels were correlated with higher temperature only in garden warblers. Our study provides novel insights into CORT dynamics, suggesting that nocturnal migratory Passerines are not largely affected by weather variability across a marine barrier during pre-breeding migration if they have sufficient energy reserves.

Keywords: bird migration, ecological barrier, energy reserves, tailwind, temperature, trans-Saharan migrants

Introduction

Migration is a predictable yet energy-demanding phase of a bird's life cycle (Berthold 2001), and environmental conditions can be decisive for its completion (Shamoun-Baranes et al. 2010). Weather conditions en route and food availability are among the core ecological factors shaping the migratory process (Covino et al. 2015). Abiotic

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conditions and the distribution and availability of resources can vary predictably or unpredictably (Newton 2008), leading to different migration strategies and corresponding physiological mechanisms regulating them (Ramenofsky and Wingfield 2007, Ramenofsky et al. 2012).

In synergy with an endogenous program (Berthold 1991, Gwinner 1996, Åkesson and Helm 2020), migratory birds exhibit a wide array of physiological and behavioural adaptations (Butler 2016, Watts et al. 2018). A key regulator of these adaptations is the hypothalamic-pituitary-adrenal (HPA) axis, which is known to modulate the endocrine response to environmental conditions by promoting the release or inhibition of circulating glucocorticoid (GC) hormones (Sapolsky et al. 2000). In migratory birds, the baseline concentration of corticosterone (CORT; the main GC in birds) rises at the onset of migration to facilitate energy metabolism and support the animal for the expected endurance flight (Jenni-Eiermann et al. 2009, Cornelius et al. 2013, Eikenaar et al. 2017, 2018, 2020, Bauer and Watts 2021). GCs have in fact a prominent role in glucose synthesis and mobilisation, a primary energy source for animals (Vágási et al. 2020). Experiencing challenging events can also activate the acute stress response within a few minutes, which involves, among others, a sudden increase in GC concentrations (Landys et al. 2006, Romero et al. 2009). This coping mechanism promotes a suite of processes aimed at minimising the effects of the stressor on the individual while facing a resource-demanding phase (Wingfield et al. 1998, Sapolsky et al. 2000, Zimmer et al. 2020). Hence, GCs not only coordinate the transition between life history stages, such as migration, but are also strategic mediators of the organism–environment interaction (Crespi et al. 2013, Romero and Wingfield 2016, Ramenofsky and Wingfield 2017).

For migratory birds, crossing a large ecological barrier on a single non-stop flight poses a significant challenge due to the need for sustained energy and favourable weather (Adamík et al. 2016, Lopez-Ricaurte et al. 2021). A study on common swifts *Apus apus* documented that to cross the Sahara individuals preferred the route with more tailwind assistance and presumably richer foraging sites (Åkesson et al. 2016). In the Afro-European flyway, many landbirds cross the Mediterranean Sea in a single flight of more than 500 km, with no opportunity to rest or refuel. Tailwinds are one of the main departure cues (Dierschke and Delingat 2001, Delingat et al. 2008, Dossman et al. 2016) and are best suited for nocturnal flights over sea barriers (Manola et al. 2020). Nocturnal migrants also tend to avoid cooler temperatures (Kemp et al. 2013, Senner et al. 2018), and adopt species-specific energy-saving strategies to minimise thermoregulation costs (Wikelski et al. 2003, Haest et al. 2020). Although birds are selective about meteorological conditions at departure before crossing an ecological barrier (Delingat et al. 2008, Morganti et al. 2011, Schmaljohann et al. 2013, Deppe et al. 2015, Sjöberg et al. 2015, 2017), less is known about the effects of weather experienced en route. Endocrine flexibility is certainly a key component in coping with both predictable and unpredictable environmental changes (Hau and Goymann 2015, Romero and Wingfield 2016, Taff et al. 2024). Given the relationship between CORT concentrations and energy reserves (Piersma et al. 2000), and its role in avian migration (Bauer and Watts 2021), the HPA axis is likely involved in adapting to environmental variability (Wingfield et al. 2017, De Bruijn and Romero 2018). Despite these insights, there is a lack of direct evidence of the physiological consequences of en route weather variability during such demanding flights over large ecological barriers.

In this study, we aimed to assess whether weather conditions within the typical range experienced while crossing the Mediterranean Sea affect CORT physiology of nocturnal long-distance migratory Passerines. We studied two trans-Saharan species (i.e. birds that spend the non-breeding season south of the Sahara Desert), the common whitethroat *Curruca communis* and the garden warbler *Sylvia borin*, upon arrival at a stopover site after the Mediterranean crossing. We hypothesised that, in birds experiencing less favourable meteorological conditions (headwinds or lower temperatures), an increase in energetic demands would be reflected by a decrease in remaining energy reserves and an increase in baseline CORT levels at stopover. However, elevated and prolonged GC concentrations can have deleterious effects on an animal's health (McEwen and Wingfield 2003). Therefore, we asked whether birds encountering less favourable weather en route and arriving with lower residual energy reserves adjust their response to acute stressors once at the stopover. Even if migrants do not experience extreme meteorological events, stress-induced CORT levels may decrease as part of an adaptive mechanism to prevent or reduce the depletion of energy reserves and the risk of proteolysis (e.g. muscle breakdown) following an exhausting and extended flight over a large sea barrier (Jenni-Eiermann et al. 2009). Hence, understanding how weather variability during the crossing of a major ecological barrier influences CORT dynamics is essential for elucidating the physiological coping mechanisms of long-distance migratory birds in a constantly changing environment.

Material and methods

Study site and experimental protocol

This study was conducted between April and May 2022 and 2023 on the island of Ponza, approximately 50 km off mainland Italy (40°55'N, 12°58'E). Situated along one of the main central Mediterranean migratory corridors in the Tyrrhenian Sea, Ponza is a stopover site for thousands of migratory birds (Maggini et al. 2020a). Since 2002, the ringing station has monitored bird migration on the island daily using mist nets checked every hour from sunrise to sunset, except on days with heavy rain or strong wind (Maggini et al. 2020a, 2020b). Nets are located on slopes with different orientation so even with moderately strong winds, a few nets are kept open, allowing researchers to sample birds even in unfavourable weather. In addition, the daily precipitation rate was low during the study period (April–May: 1.12 mm in 2022, and 0.3 mm in 2023), with rainfalls concentrated on very few days. As a result, adverse weather prevented the catching of birds on only two days in 2022 and four days in 2023, accounting for 5.6% of the total study period (Fig. 1).

To sample baseline and stress-induced CORT levels we applied the standard stress-restraint protocol (Wingfield et al. 1998, Romero and Reed 2005, Fusani et al. 2009). A selection of nets was continuously monitored from a hide and birds were extracted immediately after being caught to ensure that a blood sample was collected within three minutes to measure baseline CORT. We selected only individuals with muscle scores ≥ 1 according to EURING standards (based on ascending values from 0 to 3 for muscle score and from 0 to 8 for fat score; https://euring.org, Bairlein 1995) to reduce the risk for birds in very poor physical condition. After the first blood sampling, birds were kept in a cloth bag in the shade. Thirty minutes after capture, a second blood sample was taken to measure stress-induced CORT concentrations. The blood samples were taken by puncturing the brachial vein and collected using heparinised capillaries. The volume of each sample did not exceed 75 µl. Samples were centrifuged within 10 minutes from collection, and plasma was then immediately stored in liquid nitrogen. After being transported back to the lab, the samples were stored at −20°C until further processing (Owen 2011).

The exact time of capture and blood sampling were recorded for each bird. Almost all baseline samples were taken within two minutes, except for three whitethroats and eight garden warblers, whereby baseline blood sampling started within two minutes but ended within four minutes from the time the birds entered the net (Supporting information). We did not exclude these individuals since we accounted for the influence of sampling time on CORT concentrations in the analysis. Before release, birds were ringed and measured according to standard EURING procedures (i.e. length of the eighth primary feather and body mass; Bairlein 1995). In total, we sampled 93 garden warblers and 87 whitethroats.

Corticosterone assay

Plasma CORT concentrations were measured using a competitive enzyme-linked immunosorbent assay (ELISA) Kit (Cat. no. ADI-901-097, Enzo Life Sciences ELS) following the manufacturer's protocol and after liquid-liquid-extraction (Messina et al. 2020, Apfelbeck et al. 2024). Briefly, 200 µl of ultrapure water and 1 ml of diethyl ether were added to the samples, vortexed and put on the shaker for 30 minutes. After centrifugation, samples were freeze-decanted twice to collect the organic phase into a new glass tube, which was then dried down completely under an N_2 stream at 37°C. Samples were resuspended with 250 µl of the assay buffer provided by the manufacturer ELS and incubated overnight at 4°C before proceeding with CORT quantification.

All samples were analysed in duplicates and randomly assigned to the plates to account for inter- and intra-variance due to the time and type of sample. The intra-assay

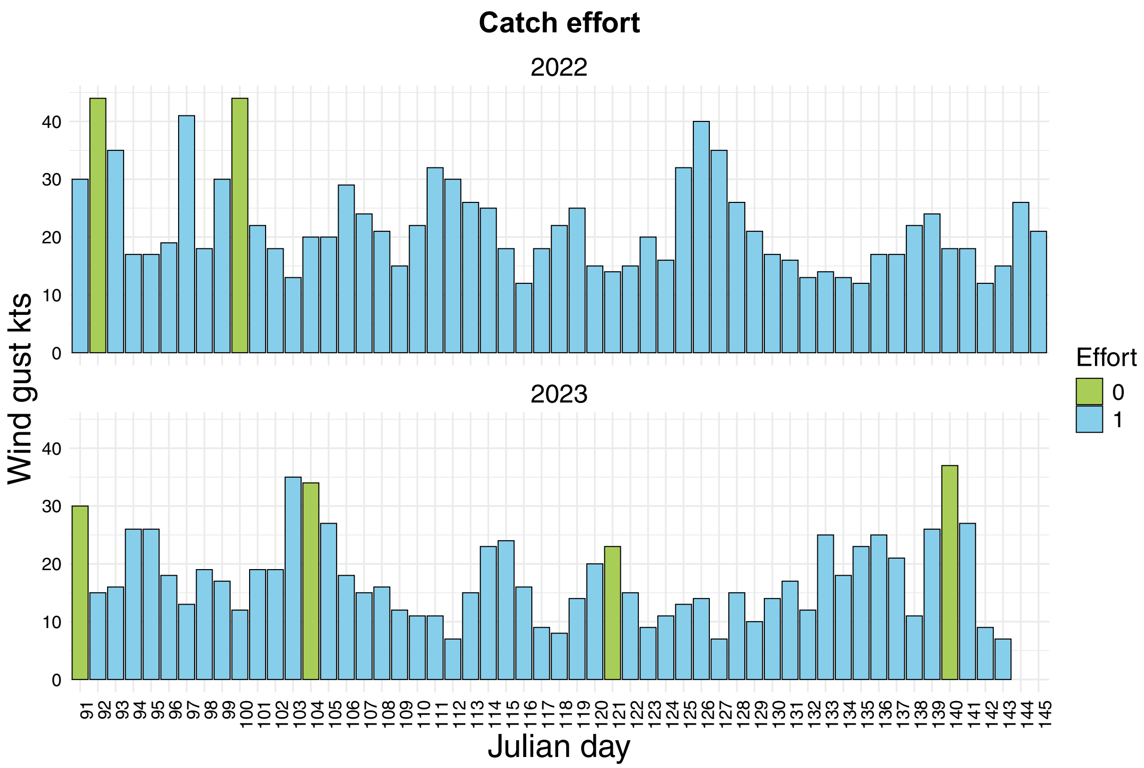

Figure 1. Catch effort of the ringing station for the study period April–May of 2022 and 2023 in relation to the daily wind gust (knots) on the island of Ponza. The green bars indicate days when all nets were closed (Effort = 0), and the blue bars indicate days where at least some or all nets were open, allowing sampling for this study (Effort = 1).

coefficient of variation was 13.1% for the garden warbler and 13.6% for the whitethroat, while the inter-assay variance was 19.6% for the garden warbler and 20.3% for the whitethroat. The detection limit of the standard curve was 27 pg ml^{-1}. We excluded samples of five whitethroats as plasma volumes were too small. We therefore statistically analysed 93 garden warblers and 82 whitethroats.

Weather data

Meteorological data were extracted from the NCEP/DOE Reanalysis II project (Kanamitsu et al. 2002) of the NOAA/OAR/ESRL PSD (Boulder, CO, USA; https://psl.noaa.gov/about), which provides free global coverage of atmospheric data at a spatial resolution of 2.5 × 2.5° and a temporal resolution of 6 hours (00, 06, 12, 18 h UTC). Using the ‘RNCEP’ package ver. 1.0.11 of R (Kemp et al. 2012), we gathered weather data from the central Mediterranean (40°0’N, 12°30’E), assuming that migrants depart from the closest North African coast (i.e. Tunisia) to arrive in Ponza (Lemke et al. 2013). We selected ‘air temperature’, ‘wind speed’ and ‘wind direction’ for the pressure levels from the sea surface (1000 mb) up to ~ 1500 m elevation (850 mb).

During migration, birds choose their flight altitude based mainly on weather conditions, season, type of migration, ecological barriers to cross and species’ ecology (Casement 1966, Liechti and Schmaljohann 2007, Schmaljohann et al. 2009, Nilsson et al. 2013). Despite these factors leading to major variability in altitude choice, migrants generally opt for altitudes between 20 and 2000 m a.s.l. when flying at night over marine ecological barriers (Bruderer et al. 2018), preferring higher elevations in the pre-breeding than in the post-breeding migration (Karlsson et al. 2012, Bradarić et al. 2024). We calculated the Pearson correlation coefficient of each weather variable along the altitudinal gradient using the ‘corrplot’ package ver. 0.95 (Wei and Simko 2024). Having found a high correlation among all variables (Supporting information), we performed separate analyses for each pressure level. Given the similarity of results at other altitudes (detailed in the Supporting information), we focused on pressure level 925 mb (~ 700 m a.s.l.) for the main results, as this is within the range of the expected flight altitudes according to the available literature (Dufour et al. 2024). Considering the shortest presumed flight route to arrive in Ponza, we estimated the animal’s direction by computing the loxodrome angle (constant compass heading on a sphere) between the assumed departure site in Tunisia (37°01’N, 11°00’E) and Ponza (direction = 21.37°). We then quantified flow assistance by calculating the tailwind component using the equation $fa_{tailwind} = y\cos\Theta$ (Kemp et al. 2012), where $fa_{tailwind}$ is tailwind flight assistance, y is the wind speed (m s^{-1}) and Θ is the angular difference between the direction of the bird's movement and the wind.

Most passerine migrants depart after dusk and fly at night (Schmaljohann et al. 2007, Packmor et al. 2020), and our studies in the neighbouring island of Ventotene showed that this is also true in garden warblers (Goymann et al. 2010). Long-distance migrants, in particular, advance their departure when they cross a large ecological barrier, probably to maximise the night-time available (Schmaljohann and Naef-Daenzer 2011, Müller et al. 2018). Consequently, we assumed that birds departing from Tunisia at sunset would be halfway through their journey; that is, at the location for which we collected weather variables, at around midnight. Thus, we examined the weather conditions over the night before the birds’ arrival on the island. Specifically, since weather data are a mean of the following six hours (i.e. 00 = mean of weather conditions measured between 00:00 and 06:00 h), we selected the weather variables at 00:00 to evaluate the conditions experienced during the nocturnal journey until the early morning. We considered examining the effects of crosswinds, but due to their strong correlation with tailwinds, we retained only tailwinds to avoid multicollinearity and ensure model parsimony.

Statistical analysis

All statistical analyses were performed separately by species using R ver. 4.2.1 (www.r-project.org).

Every day, the ringing station records peak catches in the late morning (Maggini et al. 2020b), suggesting that birds were trapped shortly after their arrival on the island. We therefore used ‘trapping time’ (the actual time of the day when birds enter the net in 24-h format) as a proxy for the arrival time of the birds on the island. Moreover, since baseline CORT concentrations exhibit circadian rhythms (Eikenaar et al. 2020), we calculated the time elapsed (in minutes) between sunrise and the exact time the bird was trapped. This variable (‘time past sunrise’) was included as a covariate in our models to account for the temporal effects on CORT levels.

We calculated the ‘scaled mass index’ (SMI), also called ‘Peig index’ (Peig and Green 2009), as a correction of body mass by body size as a proxy for the residual energy reserves of birds at arrival. The formula used was: $SMI = M_i \times (P8_0/P8_i)^{b_{SMA}}$, where M_i and P_{8i} were the body mass and the length of the eighth primary of any given individual, $P8_0$ was the average length of the eighth primaries of the species (calculated from more than 50 000 individuals for each studied species, measured in Ponza in the last 20 years; Ferretti et al. 2019, Maggini et al. 2020b), and $^{b}{}_{SMA}$ was the scaling exponent computed from the standardised major axis of the regression of body mass on the eighth primary length. Through linear regression, we verified whether and how body conditions (fat scores) were correlated with baseline and stress-induced CORT concentrations.

We performed generalized additive models (GAM) using the R package ‘mgcv’ ver. 1.9-1 (Wood 2017) to accommodate for potential non-linear relationships. The Peig index or CORT concentration (either baseline or stress-induced) was the response variable. In each model, tailwind and air temperature were the environmental predictors of interest, as our study specifically focused on the influence of weather conditions on stopover physiology. We initially included as temporal predictors the Julian day (1 January = 1), sampling time, trapping time and time past sunrise, whereas month and year were included as random effects. In the CORT models, the Peig index was additionally included as a proxy for condition. Among the temporal and condition predictors, non-significant terms were removed via backward stepwise selection based on AIC (Akaike 1973, Zuur et al. 2009). We also assessed multicollinearity through the variance inflation factor (VIF; Marquardt 1970), and excluded variables with VIF > 5. In the final model with baseline CORT as response variable, sampling time, trapping time and Julian day were retained. In the models examining stress-induced CORT and Peig index as response variables, only Julian day was retained as temporal variable. We performed diagnostic tests (collinearity, model performance, gam check, residual check) on all models using the R packages 'DHARMa' ver. 0.4.7(Hartig 2022), 'performance' ver. 0.12.4 (Lüdecke et al. 2021), 'mgcv' (Wood 2017) and 'mgcViz' ver. 0.2.0 (Fasiolo et al. 2025), and verified the homogeneity of variance by plotting residuals versus fitted values using the R package 'gratia' ver. 0.9.2 (Simpson 2024).

Results

Baseline CORT

During the pre-breeding migration at stopover, mean baseline CORT concentration was 11.68 ng ml^{-1} (95% CI: 3.10–30.77) in whitethroats and 14.03 ng ml^{-1} (95% CI: 1.84–41.62) in garden warblers. In both species, baseline CORT was not correlated with fat score (whitethroat: $\beta \pm \text{SE} = -0.071 \pm 0.609$, $t_{79} = -0.117$, $p = 0.91$; garden warbler: $\beta \pm \text{SE} = -0.759 \pm 0.920$, $t_{90} = -0.825$, $p = 0.41$; Supporting information). Baseline CORT concentration was not associated with trapping time and date (Julian day) in both species, and only in whitethroats there was a slight significant decrease of baseline CORT with the increase in sampling time (Table 1 at 925 mb and the Supporting information at both 1000 and 850 mb). In both species, baseline CORT was not significantly associated with tailwind and temperature (Table 1, Fig. 2 at 925 mb; Supporting information at 1000 and 850 mb for the whitethroat and garden warbler, respectively).

Stress-induced response

In whitethroats, the mean stress-induced CORT concentration was 27.44 ng ml^{-1} (95% CI: 8.33–70.63), whereas in garden warblers it was 29.15 ng ml^{-1} (95% CI: 5.01–71.79). In both species, stress-induced CORT was not correlated with fat score (whitethroat: $\beta \pm \text{SE} = -0.596 \pm 1.315$, $t_{79} = -0.453$, $p = 0.65$; garden warbler: $\beta \pm \text{SE} = 1.275 \pm 1.422$, $t_{90} = 0.897$, $p = 0.37$; Supporting information). In whitethroats, stress-induced CORT was not associated with weather variables (Table 1, Fig. 3a at 925 mb; Supporting information at 1000 and 850 mb). In garden warblers, stress-induced CORT significantly decreased with increasing temperatures during the crossing (Table 1, Fig. 3b at 925 mb, and Supporting information at 850 mb), and it significantly increased with higher tailwinds but only at 850 mb (around 1500 m a.s.l.), while we found a significant non-linear effect of date (Julian day) at 850 and 1000 mb (Supporting information).

Energy stores

Mean Peig index was 13.39 g (95% CI: 10.05–17.25) in whitethroats, and 16.10 g (95% CI: 12.43–20.96) in garden warblers. In both species, we found no effect of tailwind and temperature on Peig index, irrespective of the pressure level (altitude) considered (Table 1, Fig. 4; 1000 and 850 mb in the Supporting information).

The total sample of individuals captured by the ringing station in Ponza in 2022 and 2023 (5745 whitethroats and 8752 garden warblers) had median and mean fat and muscle scores of 2 and > 1.5, respectively, for both species and years (Fig. 5, Supporting information). The proportion of birds too lean to be sampled (fat = 0–1 and muscle = 0–1) was low for both species and years (< 0.2%; Supporting information). Hence, the distribution of fat and muscle scores among individuals sampled in our study was proportional to the average

Table 1. Results from general additive models (GAM) assessing the effects of tailwind, air temperature at 925 mb (~ 700 m), included in all models, and outcome-specific temporal predictors on baseline and stress-induced CORT concentrations, and Peig index in whitethroats and garden warblers. Significant p-values refer to the smooth term significance and are highlighted in bold. 'Mean effect' reflects the average predicted response on the link scale for each focal predictor, with all other predictors held at their mean. Confidence interval (CI) width represents the average 95% confidence interval span. VIF values indicate the degree of multicollinearity among predictor variables.

		Whitethroat (n = 82)				Garden warbler (n = 93)			
Response variable	Metrics predictors	p-value	Mean effect	95% CI width	VIF	p-value	Mean effect	95% CI width	VIF
Baseline	Tailwind	0.381	0.093	0.048	1.01	0.548	0.083	0.062	1.01
	Temperature	0.101	0.098	0.057	1.01	0.562	0.087	0.069	1.01
	Julian days	0.392	0.101	0.065	1.04	0.374	0.092	0.075	1.22
	Trapping time	0.076	0.079	0.052	1.84	0.169	0.064	0.051	4.83
	Sampling time	0.052	0.092	0.046	1.06	0.431	0.074	0.056	1.28
Stress induced	Tailwind	0.473	0.036	0.014	1.1	0.133	0.038	0.017	1.01
	Temperature	0.456	0.037	0.016	1.1	**0.036**	0.037	0.018	1.01
	Julian days	0.275	0.037	0.015	1.05	**0.013**	0.035	0.019	1.14
Peig index	Tailwind	0.08	0.079	0.011	1.1	0.0774	0.065	0.007	1.01
	Temperature	0.924	0.075	0.015	1.1	0.619	0.064	0.008	1.01
	Julian days	0.234	0.085	0.03	1.09	0.674	0.062	0.01	1

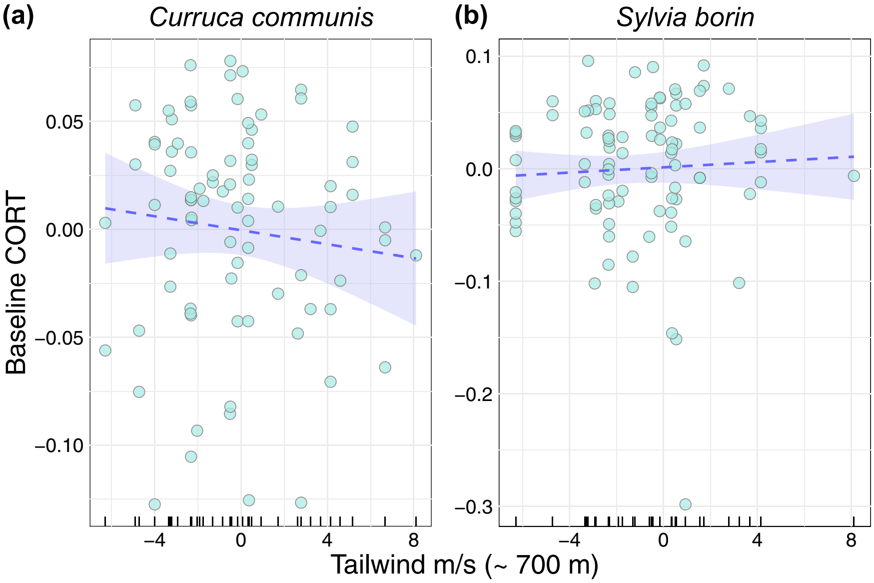

Figure 2. Baseline CORT concentrations (partial residuals) of (a) whitethroats and (b) garden warblers as a function of the average tailwind measured along the Mediterranean route to Ponza during the night before the bird's arrival (00:00–06:00 h). Each circle represents one individual. The purple dashed line shows the fitted values with the 95% confidence intervals (violet area).

energy conditions observed on all individuals that arrived at the stopover site.

Discussion

This study shows that within the range of weather conditions that migratory Passerines experience while crossing the sea during the pre-breeding migration, temperature and tailwind do not correlate with the baseline concentration of CORT, nor with the residual energy reserves of birds captured on a stopover island. Both study species were able to show a full stress response irrespective of weather conditions, but the extent of the response was significantly correlated with temperature at sea only in garden warblers. These findings confirm that long non-stop flights over the sea are not inherently stressful for nocturnal long-distance migratory Passerines.

We need to consider that our study has two limitations. First, we conducted sampling on days with good to moderately unfavourable weather, as ringing operations were

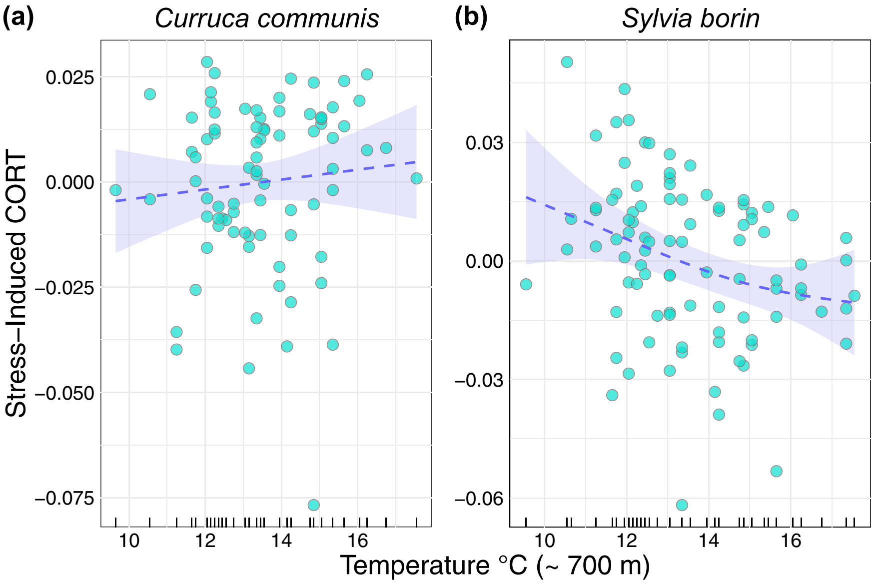

Figure 3. Stress-induced CORT concentrations (partial residuals) in (a) whitethroats and (b) garden warblers as a function of air temperature measured along the Mediterranean route to Ponza during the night before the bird's arrival (00:00–06:00 h). Every circle represents an individual. The purple dashed line shows the fitted values with the 95% confidence intervals (violet area).

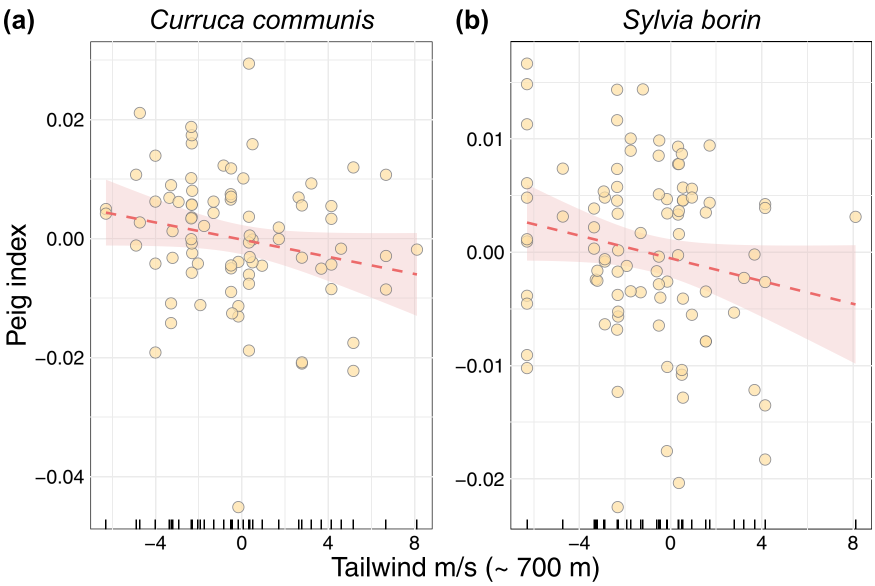

Figure 4. Peig index (partial residuals) of (a) whitethroats and (b) garden warblers as a function of the tailwind component measured along the Mediterranean route to Ponza during the night before the bird's arrival (00:00–06:00 h). Each circle represents one individual. The red dashed line shows the fitted values with the 95% confidence intervals (reddish area).

suspended with strong winds and heavy rain (5.6% of the study period; Fig. 1). Previous studies indicated that small Passerine birds do not depart for long migratory routes if conditions at departure are not favourable (Schmaljohann and Naef-Daenzer 2011, Schmaljohann et al. 2013, Haest et al. 2020). Second, we collected blood samples only from birds that were above a physiological threshold (muscle score ≥ 1) as we wanted to avoid possible serious consequences for the health of the birds. Nevertheless, as the fat and muscle scores of birds caught at the ringing station during the study period show that most individuals arriving to Ponza were in good condition (0.2% of birds were too lean; Fig. 5, Supporting information), the birds sampled in our study reflect quite well the heterogeneity of physiological conditions observed

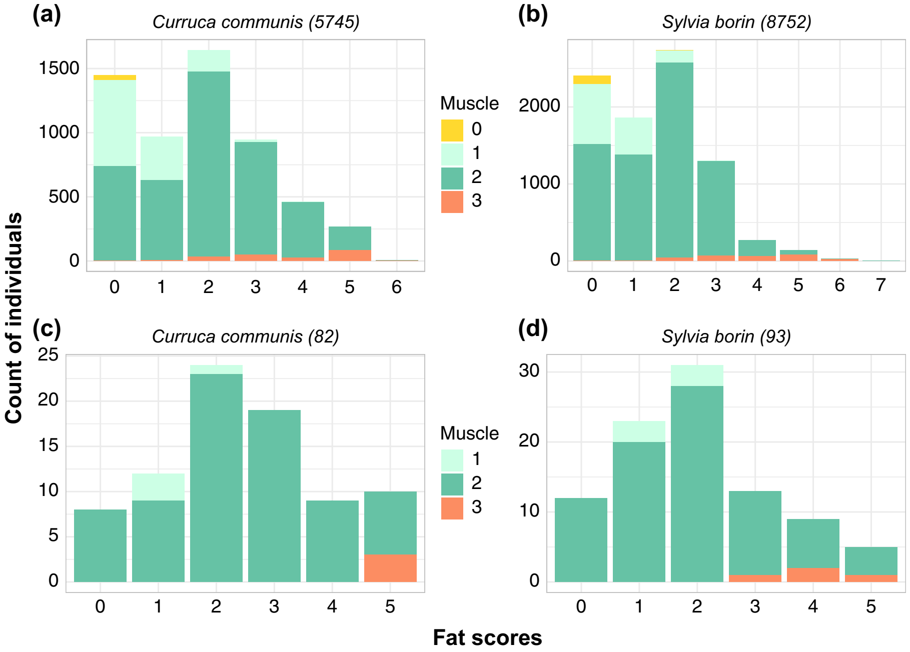

Figure 5. Distribution of fat and muscle scores (following EURING guidelines with ascending values from 0 to 8 and from 0 to 3, respectively) among the total sample of individuals caught by the ringing station in 2022 and 2023 – (a) 5745 whitethroats, and (b) 8752 garden warblers – and among the individuals sampled in this study in 2022 and 2023 – (c) 82 whitethroats and (d) 93 garden warblers.

on arrival at the stopover site, validating our results as representative of natural migratory scenarios.

Weather effects on CORT dynamics

Wind and temperature conditions did not influence baseline CORT levels. This result is in line with another study where baseline CORT concentrations did not change after long-endurance flights (Jenni-Eiermann et al. 2009). Besides, the baseline CORT concentrations observed in our study aligned with the seasonal pattern (Tsvey et al. 2019, Huber et al. 2020) and followed natural daily rhythms in both species (Supporting information; Romero and Remage-Healey 2000), underlying the role of CORT in sustaining predictable energy-consuming phases of the life cycle (Romero et al. 1997, Romero 2002, Landys et al. 2006).

Both species mounted a full stress response as indicated by acute, stress-induced CORT concentrations after capture and handling. This finding supports a prior study conducted at the same location and time of the year showing that the HPA axis is fully responsive to novel stressors (Huber et al. 2020). Furthermore, the range of stress-induced CORT concentrations observed was similar to that reported by Tsvey et al. (2019) during pre-breeding migration on the Courish Spit in the Baltic Sea. Contrary to our expectations, however, we found no indication that unfavourable weather influenced the stress-induced response in both species. Birds facing moderate headwinds or lower temperatures still arrived with residual energy reserves and displayed similar stress-induced CORT levels as those migrating with tailwinds. Only in garden warblers did stress-induced CORT levels decrease significantly with increasing temperature, and independently, there was a significant variation in stress-induced CORT levels as the season advanced (Supporting information). This tendency may reflect reduced thermoregulatory costs due to higher air temperature towards the end of the season (Ruuskanen et al. 2021). CORT levels are indeed affected by ambient temperature, albeit the underlying mechanisms remain unclear as numerous studies have reported contextual and species-specific differences in the response of GCs to temperature changes (Jessop et al. 2016, Xie et al. 2017, De Bruijn and Romero 2018).

Altogether, we did not find support for the hypothesis that less favourable weather conditions affect CORT physiology. Endocrine adjustments to predictable events during specific life-history stages may optimise physiological and behavioural output by modifying baseline hormone levels, maximising CORT responses or even altering receptor sensitivity (Sapolsky et al. 2000, Bauer and Watts 2021). We cannot therefore support the hypothesis that increased energy demands related to less favourable weather conditions influence CORT dynamics in migratory Passerines when they embark on a large barrier crossing such as the Mediterranean Sea during pre-breeding migration.

Weather effects on energy reserves

Experiencing headwinds or low temperatures along the Mediterranean route did not influence the birds' energy reserves upon arrival at the stopover site. Our result aligns with a radar study where Alerstam et al. (2011) documented that nocturnal passerine migrants were less selective about wind conditions, flying even with little or no tailwind. In general, migrants rely on supportive winds to reduce flight time while minimising the costs of travel (Alerstam and Lindström 1990, Bruderer et al. 1995, Åkesson and Bianco 2021). Surprisingly, we found that the residual energy reserves showed a marginal negative trend with tailwinds in both species. Although this result was not statistically significant, it raises the possibility that, regardless of direction, stronger winds might subtly impose higher energetic costs on individuals carrying larger fat loads, owing to increased effort to maintain stability or control flight speed during prolonged journeys (Alerstam and Lindström 1990, Bowlin and Wikelski 2008). Another plausible explanation is that waiting for optimal winds may even be costlier than flying with a slight or moderate headwind (Fransson 1998, Karlsson et al. 2011). Migration speed is generally higher during pre-breeding migrations than during post-breeding migrations, as early arrival at the breeding grounds confers a reproductive advantage (Yohannes et al. 2009, Karlsson et al. 2012, Nilsson et al. 2013, Jacobsen et al. 2017, Schmaljohann 2018, Costa et al. 2021). Birds arriving on Ponza may therefore prioritise speed over wind assistance when crossing the sea to reach their breeding grounds faster. Alternatively, other environmental factors may be more crucial for safely completing the sea crossing. For instance, a recent study by Cooper et al. (2023) found that independently of species, season or location, the presence of high atmospheric pressure was more important than tailwinds in determining departure at both pre-breeding and post-breeding stopover sites. Despite these considerations, our findings suggest that birds could handle a broad range of weather variability and still reach the stopover in good body conditions, regardless of wind or temperature differences while crossing the sea.

Effects of body condition

We did not observe a stronger acute stress response with lower fat scores in both species. This may be due to the fact that we did not examine birds in emaciated conditions where stress-induced CORT may increase to promote protein breakdown as an alternative source of energy (Jenni et al. 2000, Falsone et al. 2009). Even if it was nearly significant, only in garden warblers did baseline CORT decrease with an increase in fat scores. This result partially aligns with those of DeSimone et al. (2020), where baseline CORT showed a negative association with energy reserves in gray catbirds *Dumetella carolinensis* during the pre-breeding stopover after crossing the Gulf of Mexico.

The role of GCs in regulating energy metabolism during stressful events has been largely explored across vertebrates. However, in birds, the interplay between CORT variations and energy reserves is not well outlined. On one side, several studies examining CORT variation during migration observed a negative correlation between circulating CORT and fat stores, either with baseline (Falsone et al. 2009) or stress-induced concentrations (Snell et al. 2022). Similar results were found in a study on several migratory species in another Mediterranean stopover island (Jenni et al. 2000), as well as during the breeding season of a non-migratory species (Mentesana et al. 2024). On the other side, other studies found a positive correlation between CORT concentrations and metabolic rate (Landys et al. 2005, Jimeno et al. 2018, Jimeno and Verhulst 2023), and between CORT and fat score, but not between circulating CORT and fuel deposition (Eikenaar et al. 2013). Altogether these findings suggest that the link between CORT and energy reserves depends on different internal and external factors, such as the individual's life history stage and environmental context (Patterson et al. 2014). Species-specific ecology and different environmental conditions experienced before migration may likely lead to the adoption of distinct tactics to complete the extended journey towards the breeding areas successfully.

Conclusions

To our knowledge, this is the first study to investigate hormonal mechanisms and energy conditions of birds at stopover in relation to weather conditions encountered over the Mediterranean Sea route during pre-breeding migration. Overall, our findings confirm the idea that migratory birds are physiologically equipped to cope with weather variability, at least within the range of meteorological conditions recorded at sea before experimental birds arrived at the stopover site. Once in Ponza, birds were able to display an induced acute stress response. We are aware that our sampled birds represent only those birds that successfully crossed the ecological barrier. However, we should keep in mind that the range of conditions experienced by our study individuals prior to reaching the island is related to the departure choice, which these individuals made before embarking on the crossing. Therefore, our study does not allow us to draw conclusions on the potential effects of more extreme weather conditions.

In the last decades, unpredictable meteorological perturbations have increased at a high rate in the Mediterranean region (Insua-Costa et al. 2022). Unfavourable atmospheric conditions along the way may increase the risk of depleting fuel reserves and alter the ability of individuals to deal with stressors (e.g. predation) once they reach their stopover sites. It remains unclear how birds strategically adjust their physiological responses to inclement weather over the Mediterranean Sea. Bearing in mind that species' ecology and context can shape GC physiology (Romero and Beattie 2022), future studies that integrate physiology and hormone analyses with weather data should aim to elucidate how migrants respond to unpredictable meteorological perturbations in a larger range of species and with more extreme weather conditions. Though this may present logistical challenges, these data would contribute greatly to understanding how severe weather events, associated with environmental and climatic change, impact on bird migration.

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Data availability statement

Data are available from the Phaidra Digital Repository: https://phaidra.vetmeduni.ac.at/o:4201 (Calabretta et al. 2025).

Supporting information

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

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