

Research



Cite this article: Eikenaar C, Müller F, Leutgeb C, Hessler S, Lebus K, Taylor PD, Schmaljohann H. 2017 Corticosterone and timing of migratory departure in a songbird. *Proc. R. Soc. B* **284**: 20162300. <http://dx.doi.org/10.1098/rspb.2016.2300>

Received: 24 October 2016

Accepted: 24 November 2016

Subject Category:

Ecology

Subject Areas:

behaviour, ecology, physiology

Keywords:

Corticosterone, departure, migration, stopover, wheatear

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Electronic supplementary material is available online at <https://dx.doi.org/10.6084/m9.figshare.c.3593744>.

Corticosterone and timing of migratory departure in a songbird

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Bird migration entails replenishing fuel stores at stopover sites. There, individuals make daily decisions whether to resume migration, and must also decide their time of departure. Variation in departure timing affects the total time required to complete a migratory journey, which in turn affects fitness through arrival time at the breeding and wintering grounds. It is well established that stopover departure decisions are based on cues from innate rhythms, intrinsic factors and extrinsic factors. Yet, virtually nothing is known about the physiological mechanism(s) linking these cues to departure decisions. Here, we show for a nocturnal migratory songbird, the northern wheatear (*Oenanthe oenanthe*), that baseline corticosterone levels of birds at stopover increased both over the migratory season and with wind assistance towards the migratory destination. Corticosterone in turn predicted departure probability; individuals with high baseline corticosterone levels were more likely to resume migration on a given night. Corticosterone further predicted the departure time within the night, with high baseline levels being associated with early departures. These novel findings indicate that corticosterone may be mediating between departure cues and the timing of departure from a stopover site, which is a major step towards understanding the hormonal control of animal migration.

1. Introduction

Most migrating birds alternate bouts of travel with stopover periods that serve to rest and to replenish fuel stores [1]. At the stopover site, individuals must make daily decisions regarding when to resume migration and given a decision to depart, must also decide the time of the day to do so [2,3]. Variation in stopover departure timing is of interest since it has a large influence on the total time needed to complete migration [1,4]. This in its turn can affect fitness through arrival time at the breeding and wintering grounds [5–8]. It has been shown that departure timing depends on cues from innate circadian rhythms [9], and on cues from intrinsic and extrinsic factors, such as fuel stores and weather conditions [10–13]. Little, however, is known about the physiological mechanism linking these cues to stopover departure timing. The endocrine system is probably involved as hormones play a central role in the regulation of physiological processes and the expression of behaviour. Corticosterone, the main glucocorticoid hormone in birds, has a stimulatory effect on locomotion [14] and has often been linked to avian migration [15]. There are several observations, which together suggest that corticosterone, at baseline levels, may indeed be a critical component of the physiological link between the cues mentioned above and stopover departure timing. In migrating birds, positive correlations have been observed between corticosterone level and both fuel stores [16,17] and time of the autumn migration season [18]. This suggests that migrants' corticosterone levels reflect their motivation to depart. Corticosterone in turn may influence migrants' locomotor activity and departure timing. In red-eyed vireos (*Vireo olivaceus*) captured at a stopover site, nocturnal activity during the first hour after sunset was positively correlated with corticosterone level [19]. In northern

wheatears (*Oenanthe oenanthe*) caught and caged at stopover, corticosterone levels were positively correlated with nocturnal migratory restlessness [20], which in this species is a good proxy for individual migrants' probability of departure [21].

What is missing, however, is a more direct link between baseline corticosterone levels and accurate determination of stopover departure timing in the field. In the current study, we first investigated whether innate rhythms and intrinsic and extrinsic factors shape baseline corticosterone levels of migrants at a stopover site. We subsequently related baseline corticosterone level to departure probability, stopover duration and departure time within the day. For this purpose, we caught, blood-sampled, and radio-tagged northern wheatears (wheatear hereafter) at stopover during autumn migration. A fully automated radio-telemetry system, similar to the one described in [22], was used to determine the presence at the stopover site, and departure timing of the tagged birds. We expected that part of the variation in corticosterone levels would be explained by time within the migration season (innate rhythm), a migrant's fuel stores (intrinsic factor) and wind conditions (extrinsic factor). We furthermore expected that individuals with relatively high corticosterone levels would be more likely to depart the night after sampling, and thus to have shorter stopovers than individuals with relatively low corticosterone levels (cf. [20]). Finally, we expected that individuals with relatively high corticosterone levels would depart sooner after sunset than individuals with relatively low corticosterone levels, since an early departure maximizes the time available for a migratory flight.

2. Material and methods

(a) Study site and field procedures

Data were collected on Helgoland (54°11' N, 07°55' E), a small (1 km²) island about 50 km off the German North Sea coastline. Wheatears are small (approx. 25 g) insectivorous nocturnal trans-Saharan migrants. Wheatears commonly use Helgoland as a stopover site, but very rarely breed there [23]. In the autumn migration seasons of 2013 and 2015, wheatears were caught using mealworm-baited spring traps. All birds were caught during daylight hours, at least 1 h after sunrise and at least 1 h before sunset. Traps were monitored continuously, and when a bird was caught it was blood-sampled (approx. 70 µl) from a wing vein within 2 min from triggering the trap. The plasma was separated within 4 h of capture and frozen at -20°C until hormone assaying. Birds were ringed, and body mass was measured to the nearest 0.1 g using an electronic balance. Wing length (maximum chord) was measured to the nearest 0.5 mm [24].

In 2015, after all measurements were taken, 41 birds were fitted with a coded radio-transmitter (NTQB-1 Avian Nano Tag; weight: 0.29 g; Lotek Wireless Inc., Newmarket, Ontario, Canada). With the body mass of these birds ranging from 20.6– to 29.3 g, the relative load of the radio-transmitter was always far below the suggested upper permissible load limit of 5% of body mass [25,26]. Radio-transmitters were attached to a Rappole-type harness with the length of the leg-loops adjusted individually to birds [27]. After radio-tagging, the birds were released into the field.

(b) Recording of departure timing

Departure timing was determined using an automated telemetry system that, throughout the autumn migration season of 2015, continuously recorded signals on the used frequency (150.34 MHz). The system consisted of four telemetry towers each equipped

with a SensorGnome receiver (www.sensorgnome.org) and three 6-element Yagi antennas (Vårgårda Radio AB, Vårgårda, Sweden) constructed to match the frequency of the transmitters. The total of 12 antennas was arranged such that each one was pointing in a different direction, covering all compass directions in steps of approximately 30°. Departure events of birds obtained by this telemetry system are characterized by a rapid increase in signal strength detected from most/all antennas, because the signal strength received by the antennas is drastically increased when birds set off from the ground (barrier-free connection). This is followed by a decline in signal strength from a decreasing number of antennas until the signal is lost (electronic supplementary material, figure S1), cf. [22,28]. We determined take-off time for each bird, defined as the moment with the highest signal strength during the departure event. For subsequent analyses, we used this moment to calculate the nocturnal departure time in relation to local sunset (i.e. departure in minutes after sunset).

(c) Corticosterone assay

Corticosterone levels in the blood plasma were determined using enzyme immunoassay kits (Enzo Life Sciences, product number: ADI-901-097). Corticosterone in 15 µl of plasma (diluted in 200 µl H₂O bidest) was extracted with 4 ml dichloromethane. The dichloromethane containing the extracted sample was aspirated with a disposable Pasteur pipette and evaporated in a water bath at 48°C. The remaining corticosterone was re-dissolved in 250 µl assay buffer and analysed in duplicates following the kit manufacturer's protocol (with the only difference that we used a 6-point standard curve with a range of 20 000 to 15.63 pg ml⁻¹). An external standard was run in duplicate on each plate for calculation of intra- and inter-assay variation. To determine extraction efficiency, pooled wheatear plasma samples were spiked with corticosterone standard from the kit. Recoveries of the low (1 ng ml⁻¹), intermediate (2.5 ng ml⁻¹) and high (10 ng ml⁻¹) spikes were 87%, 93% and 70%, respectively. The intra-assay variation ranged from 0.25 to 4.35%, and the inter-assay variation was 8.3%. The lower limit of detection in our assay was determined by taking 2 s.d. above the mean of the blank wells, for which we used the total-binding wells as these only received buffer, conjugate and antibody (after [29]). This limit was 0.71 ng ml⁻¹ and was assigned to the four undetectable samples in our study.

(d) Data analysis

To achieve normality of the data, corticosterone levels were log₁₀-transformed prior to all analyses. All statistical analyses were performed in R (R Development Core Team 2014) or SPSS version 23.0 (IBM, New York). Residual analyses did not show any violation of model assumptions.

(e) Corticosterone level of wheatears at stopover

Departure probability of wheatears on Helgoland can be affected by the size of the fuel stores the birds are carrying (intrinsic factor), wind conditions (extrinsic factor) prevailing at the time of capture and time in the season (circannual rhythm and extrinsic factors) [9,30,31]. Therefore, in the analysis of corticosterone level the covariates Julian day (capture date), fuel load at capture and wind flow-assistance at capture were entered in a multiple linear regression. By adding Julian day to the model, part of the variation due to seasonality was taken into account. As most animals, including birds, show diel variation in corticosterone secretion (e.g. [32,33]), we additionally entered time of capture (which was time of blood-sampling) as a covariate. As none of the interactions between year of sampling (2013 and 2015) and the covariates was significant (all $p > 0.12$), data from both years were pooled.

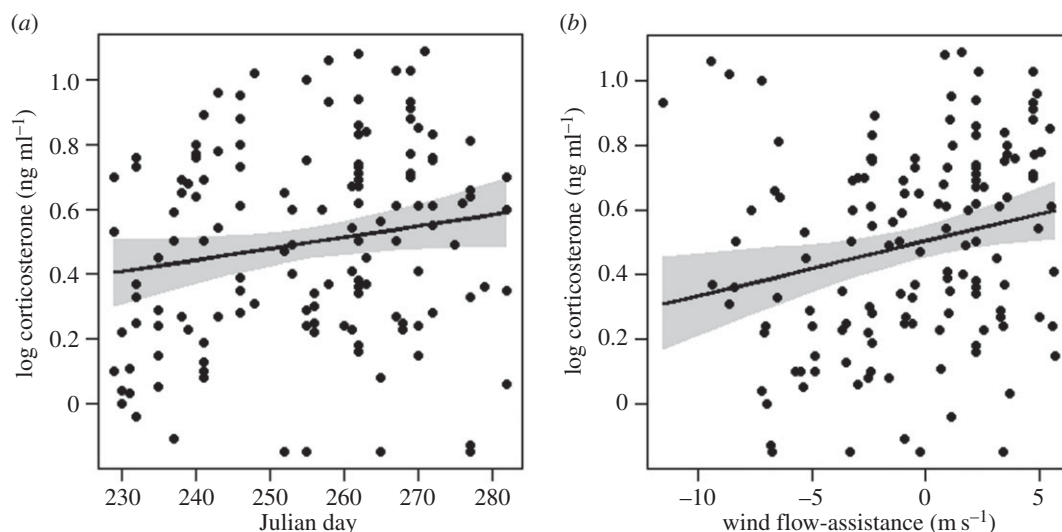


Figure 1. Baseline corticosterone level (\log_{10} -transformed) plotted against (a) Julian day (capture date) and (b) wind flow-assistance at capture in northern wheatears at stopover ($n = 143$). Given are the fitted values (black line), with the 95% confidence intervals (CIs) (grey area). The black dots represent the raw data. To show the effect of one explanatory variable on baseline corticosterone, all other variables entered into the model (table 1) were set to their mean values.

Table 1. The effects of Julian day (capture date), time of capture (equivalent to time of blood-sampling), wind flow-assistance at capture and fuel load at capture on baseline corticosterone level in northern wheatears at stopover ($n = 143$). (Parameter estimates (β) and s.e. of the linear regression model are given. $R^2 = 0.12$.)

variable	β	s.e.	t	d.f.	p -value
Julian day	0.003	0.002	2.03	1	0.044
time of capture	0.16	0.19	0.82	1	0.42
wind flow-assistance	0.017	0.006	2.71	1	0.007
fuel load	0.43	0.25	1.71	1	0.089

Wing length was used to calculate lean body mass (LBM), employing a linear regression based on 220 'lean' northern wheatears caught on Helgoland in previous years: $\text{LBM (g)} = 0.29 \text{ g mm}^{-1} \times \text{wing length (mm)} - 6.85 \text{ g}$ (linear regression: $n = 220$, $F_{1,218} = 95.07$, $\text{adj-}R^2 = 0.30$, $p < 0.0001$, after [34]). LBM was used to calculate fuel reserves: $\text{fuel load} = (\text{body mass (g)} - \text{LBM (g)}) / \text{LBM (g)}$. Each bird's wind flow-assistance experienced at the time of capture was calculated using the National Centers for Environmental Prediction (NCEP). Airspeed function of the R-Package RNCEP [35,36]. Calculations included wind components for a pressure level of 1000 mbar (close to surface), an assumed flight direction of 172° with a rho of 0.72 (which was the mean departure direction and mean resultant length (variance in direction) of the 70 radio-tagged birds in autumn 2015, F. Müller 2015, unpublished data), and an assumed airspeed of the birds of 13 m s^{-1} [37]. Resulting values of wind flow-assistance (in metres per second) describe the assisting (positive values) or impeding (negative values) effect of the prevailing winds on the bird's movement towards its migratory goal.

(f) Corticosterone and departure timing

For two radio-tagged birds, we could not reliably determine the moment of departure; one tag failed to transmit after the bird was released and of the other bird the signal strength declined without a preceding rapid increase in signal strength. Consequently, these two were excluded from the analyses of corticosterone and departure timing. The relationship between

corticosterone and the three levels of departure timing were analysed as follows. First, departure probability in the night following capture was analysed using binary logistic regression (yes/no departure). Second, minimum stopover duration, defined as the number of full nights a bird spent on Helgoland after radio-tagging, was analysed using generalized linear models with a negative binomial distribution (count data with s.d. > mean) and log link function. Third, the effect of corticosterone on nocturnal departure time was analysed using a linear regression model, and only included birds resuming migration in the night after capture. Birds continuing migration on later nights were not considered in this model, as we had no information about their corticosterone levels on the day of departure.

3. Results

(a) Corticosterone level of wheatears at stopover

There was a significant positive effect of Julian day (capture date) and wind flow-assistance at capture on baseline corticosterone levels (table 1 and figure 1). Furthermore, baseline corticosterone levels tended to increase with fuel load (table 1). Hence, corticosterone levels increased over the migratory season and with wind assistance towards the migratory goal, and tended to be higher in fat than in lean individuals. Corticosterone level was not associated with time of capture (table 1).

(b) Corticosterone and departure timing

Of the 39 radio-tagged birds, 21 departed the night after capture. Corticosterone level predicted which individuals departed and which individuals remained at the stopover site, with birds with high levels being more likely to depart than birds with low levels ($\beta \pm \text{s.e.} = 2.51 \pm 1.22$, Wald $\chi^2_1 = 4.21$, $p = 0.040$, $n = 39$; figure 2). In line with this result, there was also a near significant negative trend between corticosterone level and minimum stopover duration ($\beta \pm \text{s.e.} = -1.35 \pm 0.70$, Wald $\chi^2_1 = 3.67$, $p = 0.055$, $n = 39$; figure 3). Furthermore, for the 21 birds that departed the night after capture, corticosterone level predicted nocturnal departure time ($\beta \pm \text{s.e.} = -213.6 \pm 53.2$, $t = -4.02$, $p = 0.001$, $R^2 = 0.46$), with birds with high levels departing earlier than birds with low levels (figure 4).

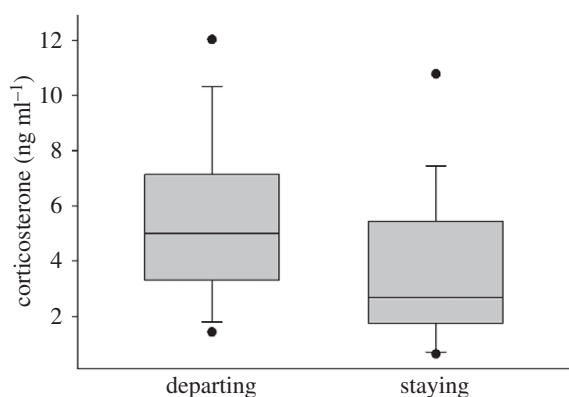


Figure 2. Boxplots of baseline corticosterone level of northern wheatears that did (departing, $n = 21$) or did not (staying, $n = 18$) depart from our stopover study site the night after being captured and sampled. Plotted are the median, 5th, 25th, 75th and 95th percentiles. Black dots indicate values beyond the 5th or 95th percentiles.

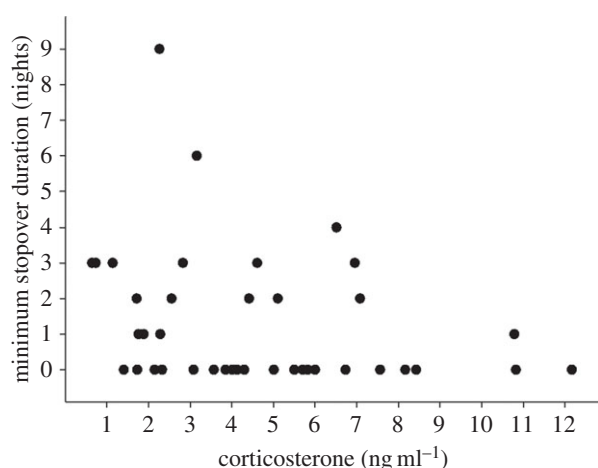


Figure 3. Baseline corticosterone level and minimum stopover duration in northern wheatears ($n = 39$). Minimum stopover duration 0 means that the bird departed the night after capture.

4. Discussion

Our study shows that part of the variation in baseline corticosterone levels of wheatears at stopover was explained by factors known to influence birds' stopover departure probability—wind conditions and time within the migration season [2,3]. This suggests that cues from extrinsic factors and innate circadian rhythms are jointly integrated by the neuro-endocrine system to shape the circulating corticosterone level of migrants at stopover. The positive association between wind flow-assistance and corticosterone level furthermore supports the suggestion that corticosterone is upregulated when migrants are close to departure [16]. However, repeated sampling of the same individuals is required to properly test this idea. Corticosterone level in turn predicted the timing of departure from our stopover study site—both on the day-to-day level as well as within the night. Individuals with relatively high corticosterone levels were more likely to depart the night after capture than individuals with relatively low corticosterone levels. Furthermore, in individuals departing the night after capture, corticosterone level predicted nocturnal departure time, with high levels being associated with early departure. Within our sample, individuals with the highest corticosterone levels

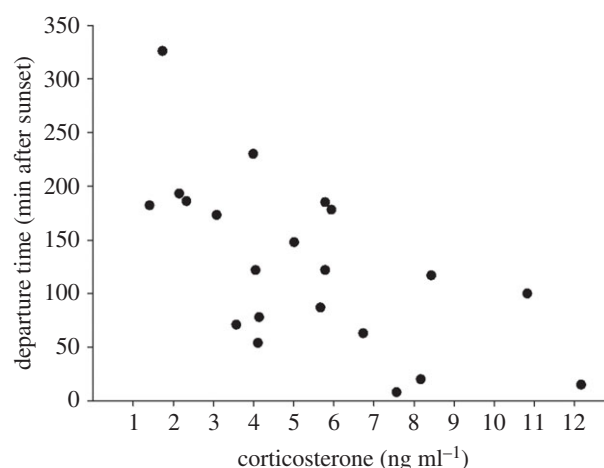


Figure 4. Baseline corticosterone level and departure time in the night after corticosterone sampling in northern wheatears at stopover ($n = 21$).

departed some 3 h earlier than individuals with the lowest levels, which in autumn on Helgoland could potentially increase the duration of a nocturnal flight of some 25%.

The transition from stopover to migratory flight (departure) involves a large increase in locomotor activity. It is well established by both correlative and experimental studies that in vertebrates corticosterone has a stimulatory effect on locomotion [14,38]. Important for the interpretation of our current results, in a previous study on migrating wheatears caught on Helgoland we showed that daytime corticosterone level predicted nocturnal locomotor activity the night after corticosterone sampling [20]. Therefore, it is very likely that in our study the associations between corticosterone and both departure likelihood and nocturnal departure time are explained by the hormone's stimulatory effect on locomotion. High corticosterone levels in departing birds may at the same time act to mobilize energy from lipid stores that is needed for migratory flight [16]. This latter function of corticosterone may help to explain why some individuals departed the night after capture despite having relatively low corticosterone levels (figure 3). Of these birds, the five individuals with the lowest corticosterone concentrations set off late in the night (figure 4). Perhaps these birds intended to make only short nocturnal flights, for example, to search for other nearby stopover areas [34,39]. Migrants intending to make short flights may not need to increase their corticosterone level as high as birds preparing for endurance flights, if short flights depend less on the mobilization of energy from lipid stores, but instead are supported more by carbohydrates, than endurance flight [40,41].

With our study, we are, to our knowledge, the first to reveal positive associations between multiple departure cues and corticosterone level of migrants at stopover. Furthermore, with the use of a fully automated radio-telemetry system we uniquely show that corticosterone predicted departure behaviour; individuals with high corticosterone levels were more likely to resume migration on a given night, and high corticosterone levels were associated with early departures. Combined, these novel observations strongly suggest that corticosterone is involved in the regulation of migratory departure. Apart from corticosterone other hormones or neuropeptides may be involved in this process [15]. Fat tissue is an active endocrine organ, releasing hormones such as adiponectin and visfatin that in migratory

birds may act as an indicator of body condition [42]. In migratory birds, fat stores have a strong positive effect on stopover departure probability [12,43,44]. In our study, however, fuel load, indicative of fat stores [17], only weakly predicted corticosterone level. This suggests that endocrine signals from the fat tissue may, in addition to corticosterone, contribute to the regulation of departure in migrants at stopover. Similarly, the pineal gland hormone melatonin too may be a player in the regulation of migratory departure from stopover sites, at least in autumn. In blackcaps (*Sylvia atricapilla*) nocturnal melatonin secretion is lower during migration than during the preceding or following periods [45]. Furthermore, an experimental increase in circulating melatonin decreases the amount of nocturnal migratory restlessness shown by migrants temporarily caged at a stopover site in autumn, but not spring [46]. Measurement of multiple endocrine signals within individual migrants is required to further investigate how multiple hormones may be involved, perhaps interlinked, in the regulation of departure from stopover sites.

Migrating birds are thought to behave optimally in that they minimize the time and/or energy required to complete migration [1,47]. Furthermore, migrants are expected to optimize arrival time at the breeding and wintering grounds as this can enhance their fitness [5–8]. Hence there should be strong selection on an accurate reaction to cues affecting the speed and/or energetic costs of migration. That migrants can indeed accurately react to such cues is supported by the observation that migrants are usually more likely to leave stopover

sites under favourable wind conditions [48,49]. Similarly, stopover departure probability increases with the progress of the spring migration season [30,50], most probably because late migrants need to speed up migration to reach the breeding grounds on time [9]. Precisely which factors link stopover departure cues to departure timing was previously completely unknown; our study now indicates that corticosterone may play a crucial part in the physiological mechanism mediating between stopover departure cues and stopover departure timing. With this novel finding, we have made a big step towards unravelling the hormonal regulation of migratory behaviour. Future manipulative studies may test the causality of the patterns observed in the current study.

Ethics. All procedures were approved by the Ministry for Agriculture, the Environment and Rural Areas, Schleswig-Holstein, Germany.

Data accessibility. The dataset supporting this article has been uploaded as the electronic supplementary material.

Authors' contributions. C.E. conceived of the study and performed laboratory analyses. C.E., F.M., C.L., K.L. and S.H. collected data. C.E., F.M. and H.S. analysed the data and wrote the manuscript. P.D.T. assisted with the set-up and running of the automated telemetry array, and provided input on the manuscript.

Competing interests. We have no competing interests.

Funding. This work was supported by two Deutsche Forschungsgemeinschaft (DFG) grants, both awarded to H.S. (SCHM 2647/1-1 and SCHM 2647/3-1).

Acknowledgements. We thank Jochen Dierschke and Klaus Müller for logistic support on Helgoland; and Oscar Vedder, Franz Bairlein, Wolfgang Goymann and two anonymous referees for useful comments on the manuscript.

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