



Regular article

Corticosterone predicts nocturnal restlessness in a long-distance migrant

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ABSTRACT

The decision made by migrating birds to stop refueling and to depart from stopover depends on cues from innate rhythms, intrinsic factors such as fuel reserves, and extrinsic factors such as weather conditions. The physiological mechanism behind this decision, however, is largely unexplored. The transition from refueling to flight involves an increase in both locomotion and energetic demands. Because, at baseline levels, corticosterone stimulates locomotion and is involved in the mobilization of energy, this hormone could encourage departure of migrants. We collected field data on baseline corticosterone, migratory restlessness, and actual departure in northern wheatears at stopover. Additionally, in refueling long-term captive conspecifics, we measured migratory restlessness while simultaneously collecting droppings to determine glucocorticoid metabolite (GCM) levels. We found that migratory restlessness at stopover was positively correlated with corticosterone level. Similarly, in refueling long-term captive birds, migratory restlessness was positively correlated with concurrently measured GCM levels in droppings. To our best knowledge, our study is the first to simultaneously measure a hormonal signal and migratory restlessness. In conclusion, our results are consistent with the hypothesis that, by increasing locomotor activity, baseline corticosterone is involved in the regulation of departure of migrants at stopover. Future studies could reveal how corticosterone is up-regulated in migrants that are ready to depart.

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Introduction

To support migratory flight, birds accumulate large amounts of fuel in the form of fat. Fuel accumulation occurs before departure from the breeding and wintering grounds (pre-migratory fueling) as well as during stopovers between flight bouts (refueling). Because the time spent refueling at stopover sites by far exceeds the time in actual flight (e.g. Green et al., 2002; Schmaljohann et al., 2012), the time required to complete migration is mainly determined by the duration of stopovers. Consequently, many studies, both empirical and theoretical, have investigated which factors influence departure decisions of migrants at stopover sites and hence stopover duration (reviewed in Chernetsov, 2012; Jenni and Schaub, 2003). It is well established that departure decisions depend on cues from innate rhythms, intrinsic factors such as fuel reserves, and extrinsic factors such as weather conditions (Chernetsov, 2012; Jenni and Schaub, 2003). In contrast, our understanding, and even identification, of the physiological mechanism(s) involved in the regulation of departure is very limited (reviewed in Cornelius et al., 2013). The transition from stopover refueling to active flight involves an increase in both locomotion and energetic demands. Corticosterone, at baseline and moderately elevated levels (i.e. not the levels observed in response to a stressor), is involved in the mobilization of energy during the predictable life-history cycle, and has a stimulatory effect

on locomotion (reviewed in Landys et al., 2006). Therefore, at baseline levels, corticosterone perhaps stimulates departure of migrating birds. Observations from several studies are in line with this idea. In migratory active captive garden warblers (*Sylvia borin*), a nocturnal migrant, autumn baseline corticosterone levels were higher at night than during the day (Schwabl et al., 1991). Observations on captive pre-migratory fueling red knots (*Calidris canutus*) and wild refueling bar-tailed godwits (*Limosa lapponica*) suggest that baseline corticosterone levels are low in the early stages of (re)fueling but rise in preparation for flight (Landys-Cianelli et al., 2002; Piersma et al., 2000). In captive white-crowned sparrows (*Zonotrichia leucophrys gambelii*) and captive dark-eyed juncos (*Junco hyemalis*) photo-stimulated into migratory condition, the expression of migratory restlessness is accompanied by an increase in baseline corticosterone level (Holberton et al., 2008; Landys et al., 2004). Migratory restlessness occurs when birds in migratory disposition are confined to a limited space, i.e. caged, and mainly consists of wing fluttering while perched (Berthold et al., 2000; Biebach et al., 1985). Importantly, it was recently shown that migratory restlessness measured in birds at stopover is an accurate proxy for a bird's likelihood to depart; birds that showed little restlessness were less likely to depart from stopover than birds that showed much restlessness (Eikenaar et al., 2014a). In red-eyed vireos (*Vireo olivaceus*) captured and caged at a stopover site, nocturnal activity in the first hour after sunset was positively correlated with corticosterone level (Löhmus et al., 2003). Unfortunately, as birds were not blood-sampled immediately after capture, corticosterone levels in this study may

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have reflected handling stress (Löhmus et al., 2003). Finally, fecal glucocorticoid metabolite levels in wild blue tits (*Cyanistes caeruleus*) were higher in migratory than in resident individuals (Nilsson and Sandell, 2011).

The aim of the current study was to further characterize the relationship between baseline corticosterone and departure in migrant birds at stopover. For this purpose we took a dual approach by combining a study on wild birds at stopover with a study on captive birds. We used the northern wheatear (*Oenanthe oenanthe*), a nocturnal long-distance migrant, as a model species. In the field birds were caught, immediately blood-sampled for baseline plasma corticosterone, and subsequently caged to measure nocturnal migratory restlessness. Additionally, at release part of these birds was equipped with a radio-transmitter in order to determine their departure latency. Using long-term captive birds, in a fasting–refueling experiment we measured migratory restlessness and simultaneously collected their droppings to determine baseline glucocorticoid metabolite (GCM) level. Our study is the first to link baseline corticosterone level to actual stopover departure, and to simultaneously measure a hormonal signal (GCMs) and migratory restlessness. We expected positive relationships between migratory restlessness and both baseline corticosterone level and GCM level. Furthermore, we expected birds with high baseline corticosterone levels to depart earlier from stopover than birds with low levels.

Methods

Field study

The study was conducted on Helgoland (54°11'N, 07°55'E), a small island ca. 50 km off the German North Sea coastline. Northern wheatears rarely breed on Helgoland (Dierschke et al., 2011). In the 2013 spring (May) and autumn (August and September) migration seasons, northern wheatears were caught using mealworm-baited spring traps ($n = 39$ in spring and $n = 83$ in autumn). Most (56) individuals trapped in autumn were first-year birds. All birds were trapped between 8 am and 7 pm, well after sunrise and well before sunset. Corticosterone level was not correlated with time of capture (Spearman's $\rho = -0.05$, $p = 0.55$, $n = 122$). Traps were monitored continuously and when a bird was caught it was taken from the trap and blood-sampled (ca. 80 μ l) immediately from the wing vein. All samples were taken within 2 min from closing of the trap and thus represent true baseline levels (Eikenaar et al., 2013). The plasma was separated within 2 h of blood-sampling and frozen at -20 °C until assaying. After blood-sampling, birds were ringed, wing length (maximum chord) was measured to the nearest 0.5 mm, and body mass to the nearest 0.1 g. 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: $LBM [g] = 0.29 \text{ g mm}^{-1} \times \text{wing length [mm]} - 6.85 \text{ g}$ (linear regression: $n = 220$, $F_{1,218} = 95.07$, $adj-R^2 = 0.30$, $p < 0.0001$, after Schmaljohann and Naef-Daenzer, 2011). LBM was used to calculate fuel reserves: fuel load = (body mass [g] – LBM [g]) / LBM [g]. Fuel load thus represents the amount of fuel a bird carries relative to its lean body mass. Approx. 1 h after trapping, birds were put in individual cages (40 × 40 × 30 cm) set up in a single indoor room with artificial lighting. Throughout the experiment the lights in the room were switched on at 7 am and off at 9 pm CET, the temperature was held constant at approx. 20 °C, and birds had ad libitum access to water. Each morning, immediately after lights were switched on, each bird was weighed to the nearest 0.1 g, after which it received a food tray with 30 g of mealworms. Food trays were removed immediately before lights-off. Birds were released after the third night in captivity. Migratory restlessness was recorded automatically with motion-sensitive microphones (Piezo-Scheibe 27 mm, Conrad Electronics SE, Hirschau, Germany), that detect vibrations caused by sound or movement. Microphones were attached to the right wall of the cages, which were acoustically separated from

each other by placing them on polystyrene. Each movement of a bird generated an impulse that was transmitted to a recording device. To avoid the recording of occasional non-migratory activity, we set a threshold of three impulses per second before it was recorded as an activity count. Another device created a CSV file summarizing the activity counts over 15 min periods. Individual tracking of radio-tagged birds revealed that northern wheatears leave Helgoland exclusively at night, between 1 and 5.5 h after sunset (Schmaljohann et al., 2013). Therefore, migratory restlessness was defined as the number of 15 min periods between 1 and 5.5 h after lights-off, during which a bird showed at least five activity counts (after Eikenaar et al., 2014a).

On the afternoon of 21 August, 16 birds, caught over the previous four days, were taken from their cages, fitted with a 0.42 g Holohil BD-2N radio-transmitter and released between 3 and 4 pm. Using a Yaesu FT-290RII receiver and a Yagi hand-held antenna we searched for all tagged birds from 16 fixed points distributed to cover the whole island. Daily searches, starting the day after release, lasted from approx. 10 to 12 am. To exclude temporary misses, each bird was searched for at least two days after the radio-signal had been received for the last time. No tag-losses occurred while the birds were on Helgoland. All procedures were approved by the Ministry for Agriculture, the Environment and Rural Areas, Schleswig-Holstein, Germany.

Fasting–refueling experiment

From August 2013 onwards, 24 adult northern wheatears, hatched in captivity, were housed indoors in individual cages of 40 × 40 × 50 cm in three separate rooms. They all had ad libitum access to food and water, and the temperature in the rooms was maintained at approx. 20 °C. To promote migratory fueling, on 1 September (when all birds had completed molt) the photo-period in the bird rooms was changed from long days (14 L:10 D) to short days (12 L:12 D). Starting 22 October, when all birds had accumulated large fuel stores (mean and SD fuel load = 0.67 ± 0.19), the birds were subjected to a fasting–re-feeding trial to simulate stopover refueling (water was provided ad libitum at all times). Birds were fasted by reducing the daily amount of food to 2 g until they were a few grams above their individual LBM. At that point, they were allowed to refuel by increasing the daily amount of food to 20 g. On the 11th night of refueling, when the birds had replenished a considerable part of their fuel stores (mean and SD fuel load = 0.55 ± 0.18), excreta were collected on paper sheets placed on the cage bottom. Sheet were placed in the cages 5 min prior to lights-off and again removed the next morning at lights-on. For each bird, all excreta collected in the entire night were put in a 2 ml Eppendorf tube, weighed and homogenized, and frozen at -20 °C until later processing (see below). Each day of the trial, birds were weighed to the nearest 0.1 g immediately after lights had turned on. Migratory restlessness was recorded as described above, but was defined as the number of 15 min periods in the entire night during which a bird showed at least five activity counts. The reason for using the full night is that, unlike on Helgoland, we do not know the 'time window of departure' for long-term captive northern wheatears. The experiment was conducted at the Institute of Avian Research, Wilhelmshaven, Germany. All procedures were approved by the Lower Saxony State Office for Consumer Protection and Food Safety, Germany.

Corticosterone assay

Corticosterone levels in plasma were determined using enzyme immunoassay kits (Enzo Life Sciences, Inc., former Assay Designs). Corticosterone in 15 μ l of plasma (diluted in 200 μ l double-distilled water) was extracted with 4 ml dichloromethane. The dichloromethane containing the extracted corticosterone was aspirated with a disposable Pasteur pipette and evaporated in a water bath at 48 °C. The remaining corticosterone was re-dissolved in 250 μ l assay buffer and analyzed in duplicates following the kit manufacturer's protocol (with the only difference

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