



Endocrine regulation of migratory departure from stopover: Evidence from a longitudinal migratory restlessness study on northern wheatears

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ARTICLE INFO

Keywords:

Corticosterone
Fuel
Mediator
Migration
Restlessness
Stopover

ABSTRACT

Most migrating birds make stopovers to replenish fuel stores. The decision to resume migration from stopover to a large extent shapes the temporal organization of migration. This decision is known to be shaped by a suite of intrinsic and extrinsic factors such as the bird's fuel stores and current weather conditions. However, how departures from stopover are physiologically regulated is largely unknown. We here present data that strongly indicate that corticosterone, a hormone with a stimulatory effect on locomotion, acts as a mediator between fuel stores and departure from stopover. In migrating northern wheatears (*Oenanthe oenanthe*) temporarily caged at stopover, we observed a positive relationship between the change in fuel stores and the concurrent change in glucocorticoid metabolite (GCM) levels measured in the birds' droppings. We also found a positive relationship between the change in GCM levels and the change in the intensity of nocturnal migratory restlessness. As in northern wheatears nocturnal migratory restlessness is an accurate proxy for stopover departure likelihood, our results indicate that corticosterone mediates between fuel stores and the decision to resume migration. Our unique longitudinal study represents a considerable advance in our understanding of the endocrine regulation of avian migration.

1. Introduction

Most songbird migrants travel between their breeding and wintering grounds following a stop-and-go strategy with alternating cycles of migratory movement (flight) and fuel accumulation (migratory fueling) during stopover. Stopover departure decisions, i.e. decisions when to leave a stopover site and resume migration, to a large extent determine the speed of migration and thereby arrival time at the breeding and wintering grounds (Schmaljohann and Both, 2017). Stopover departure decisions are known to be shaped by cues from innate rhythms (time within the migration season), intrinsic factors (e.g. fuel stores), and extrinsic factors (e.g. wind conditions) (Chernetsov, 2012; Jenni and Schaub, 2003), but how these cues are translated into actual departure is not very well known. Corticosterone, the main glucocorticoid hormone in birds, is thought to serve metabolic functions and to be involved in the uptake, storage and release of energy, and is known to have a stimulatory effect on locomotor activity (Landys et al., 2006, and references therein). Comparative and experimental work has indicated that circulating levels of corticosterone reflect an animal's energetic needs, both immediate, unforeseen demands and predictable demands occurring on a larger temporal scale, i.e. on a seasonal basis (e.g. Hau

et al., 2010; Jimeno et al., 2017; Romero, 2002). Avian migration is a life-history stage characterized by predictable high energy demands and extreme locomotor activity, rendering corticosterone a promising candidate for the regulation of migratory behavior. Löhms et al. (2006) found that exogenous corticosterone increased the frequency of visits to the food bowl in migrants temporarily caged at a stopover site, however, it was unknown if food intake increased or whether this observation was attributable to corticosterone stimulating locomotor activity. Currently, it seems that corticosterone's role in migratory fueling is merely permissive (Holberton et al., 2007; Landys et al., 2004), and that it does not stimulate fueling (Eikenaar, 2017). Rather, corticosterone may play a role in the regulation of departure behavior, and could even act as a mediator between departure cues and actual departure; corticosterone, at baseline or moderately elevated levels, has been linked to both the strength of intrinsic departure cues and to (proxies for) stopover departure likelihood. First, positive associations have been found between corticosterone level and migrants' fuel stores (e.g. Landys-Cianelli et al., 2002; Piersma et al., 2000) and time within the migration season (Falsone et al., 2009). Second, in passerine migrants, caught and temporarily caged at stopover, corticosterone levels were positively correlated with nocturnal locomotor activity (Eikenaar

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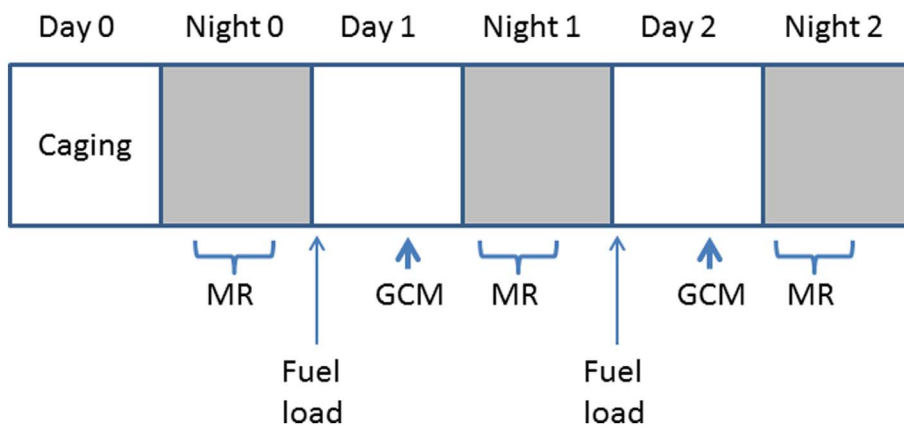


Fig. 1. Schematic representation of the experiment. Within-individual changes in the parameters of interest were calculated by subtracting the values measured on day 1 or night 1 from the values measured on day 2 or night 2. GCM: glucocorticoid metabolite sampling; MR: migratory restlessness measurements.

et al., 2014a; Löhmus et al., 2003), which may be indicative of stopover departure. Recently, a study on northern wheatears (*Oenanthe oenanthe*, wheatear hereafter), a long-distance migrant, integrated these fragmented observations. Eikenaar et al. (2017) showed that in wheatears caught at stopover during autumn, corticosterone levels increase with stronger departure cues, i.e. with the progress of the migration season, with more wind support, and tend to increase with larger fuel stores. Corticosterone in its turn appears to stimulate departure, as individuals with relatively high corticosterone levels had both higher departure likelihood and departed earlier within the night than individuals with relatively low corticosterone levels (Eikenaar et al., 2017). The mediating role of corticosterone may be ubiquitous among migrating birds; the patterns described for wheatears in Eikenaar et al. (2017) are virtually identical in common blackbirds (*Turdus merula*), a species with a migration strategy very different from that of wheatears (Eikenaar et al., under review). High corticosterone in migrants ready to depart is thought to have at least two functions: it probably regulates the release of the large amount of energy that the birds will soon need when they are flying (Landys-Cianelli et al., 2002; Piersma et al., 2000), and it likely has a direct effect on departure through corticosterone's stimulatory effect on locomotion (Landys et al., 2006, and references therein). The fact that corticosterone levels explain almost half of the variation in migrating wheatears' nocturnal departure time (Eikenaar et al., 2017) provides (circumstantial) evidence for the second function; energy requirements per time unit of flight unlikely differ between birds departing early or late in the night, hence, corticosterone does more than facilitating the release of energy from the fuel stores.

In most avian species, migrants travel individually, i.e. each bird makes its own decision when to depart from a stopover site to resume migration. Hence, when studying the physiological mechanism(s) regulating migratory decision making, longitudinal data are far more informative than cross-sectional data. It also means that if corticosterone indeed mediates between departure cues and departure behavior, then also *within an individual* migrant, corticosterone level should increase with stronger departure cues, and this increase should subsequently increase the individual's motivation to depart. In the current study we investigated this by measuring within individual changes in fuel stores (an intrinsic departure cue), corticosterone metabolite levels, and departure likelihood. To be able to collect these data, we temporarily caged migrating wheatears caught at a stopover site in spring. To avoid repeated blood-sampling within a short time period and to be able to measure several individuals simultaneously, we measured glucocorticoid metabolite (GCM) levels in the birds' excreta, a method which we have validated for wheatears and successfully used before (Eikenaar et al., 2014a, 2014b). We measured the birds' intensity of nocturnal migratory restlessness, which in wheatears is a good proxy for an individual's departure likelihood in the field (Eikenaar et al., 2014c). We expected that within-individual changes in fuel stores are predictive of changes in GCM levels, and that changes in GCM levels are predictive of

changes in the intensity of migratory restlessness.

2. Methods

2.1. Experimental procedures

The study was conducted on Helgoland (54°11' N, 07°55' E), a small island ca. 50 km off the German North Sea coastline. From 10 to 25 April 2016, migrating wheatears were caught using mealworm-baited spring traps. Upon trapping, birds were ringed, sexed on plumage following Svensson (1992), and wing length (maximum chord) was measured to the nearest 0.5 mm. Wing length was used to calculate lean body mass (LBM), employing a linear regression based on 220 'lean' wheatears caught on Helgoland in earlier studies: $LBM [g] = 0.29 \text{ g mm}^{-1} \times \text{wing length [mm]} - 6.85 \text{ g}$ (linear regression: $n = 220$, $F_{1,218} = 95.07$, $adj-R^2 = 0.30$, $p < 0.0001$, after Schmaljohann and Naef-Daenzer (2011)). Approx. 1–3 h after trapping, 26 birds (14 males and 12 females) were put in individual cages (40 × 40 × 30 cm) set up in two indoor rooms with artificial lighting. Upon caging, each bird received a food tray with 40 g of mealworms (*Tenebrio monitor*). Birds were held in captivity for three nights (Fig. 1), after which they were released. The lights in the rooms were switched on at local sunrise and again switched off at local sunset. The temperature in the rooms was held constant at approx. 20 °C, and birds had ad libitum access to water. Each morning, immediately after lights on, each bird was weighed to the nearest 0.1 g. The morning body mass was, together with LBM, used to calculate the bird's fuel stores at that moment: $\text{fuel load} = (\text{body mass [g]} - LBM [g]) / LBM [g]$. Fuel load thus represents the amount of fuel a bird carries relative to its lean body mass. Recent measurements of birds' fat stores by quantitative magnetic resonance indicated that wheatears temporarily caged on Helgoland can deposit significant amounts of fat (> 1 g at a LBM of approx. 22 g) within a single day (T. Klinner, unpublished data). This shows that the changes in fuel load that we report in the current study reflect changes in fat stores (and not water gain/loss). Immediately after being weighed each bird received a food tray with 40 g of mealworms. Food was removed 1 h before lights off and weighed to determine daily food intake.

For the measurement of GCM levels, in the first and second full day in captivity, birds' droppings were collected on paper sheets placed on the cage bottom. Droppings were collected during a 30 min period starting 8 h after lights on. As 30 min lies well below wheatears' gut passage time (Franz Bairlein, unpublished data, Eikenaar et al., 2014b), any stress resulting from the placing of the paper sheets could not have been detectable in our samples. For each bird, all droppings collected during a 30 min period were put in a sealable 2 ml eppendorf tube, weighed and homogenized, and frozen at –20 °C until later processing (see below).

Nocturnal migratory restlessness was recorded automatically with motion-sensitive microphones, attached to the right wall of each cage.

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