



Baseline corticosterone levels are higher in migrating than sedentary common blackbirds in autumn, but not in spring



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ABSTRACT

Corticosterone at baseline levels is thought to be mainly involved in the regulation of uptake, storage and release of energy, processes central to avian migration. Consequently, corticosterone levels are thought to be upregulated during migration, but the temporal pattern of its secretion during migration is not well defined. For example, although it appears that corticosterone levels decrease from flight to stopover, it is unknown if levels at stopover are still elevated and it is largely unclear how these levels compare to non-migratory life-history stages. Furthermore, what role corticosterone plays in crucial migratory processes, such as refueling and departure from stopover, is far from understood. We here determined baseline corticosterone levels in migrating and resident common blackbirds (*Turdus merula*), sampled simultaneously on Helgoland, a stopover site that also supports a sedentary breeding population. In autumn, migrants had higher corticosterone levels than residents, but in spring levels did not differ between the two groups. Corticosterone levels of migrants were very similar in spring and autumn, whereas in residents levels tended to be higher in spring than autumn. Higher levels in residents in spring than autumn most likely reflect the higher daily workload faced by birds during the pre-breeding than the post-breeding period. Our study thus indicates that, relative to the levels observed in residents in autumn, in spring baseline corticosterone levels were moderately elevated in both migrants and residents and that in autumn levels were moderately elevated in migrants only. Currently, corticosterone's main function at stopover is thought to lie in the regulation of departure. Because most migrant blackbirds stay only one or two days on Helgoland, our results are in line with this idea and suggest that migrating blackbirds up-regulated their corticosterone level in anticipation of an oncoming flight bout.

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1. Introduction

Corticosterone at baseline and moderately elevated levels (i.e. not the levels observed in response to a stressor) is thought to mainly function in the regulation of food intake, locomotor activity and energy metabolism (Sapolsky et al., 2000; Landys et al., 2006). During the migration life-history (LH) stage in birds, these processes either increase or decrease from one to the next sub-stage of migration (Ramenofsky, 2010). Prior to the initial onset of migratory flight, birds engage in pre-migratory fat deposition (fueling) through over-eating (Gwinner, 1996; Berthold, 1996). This stage is followed by the actual migration consisting of migratory flight bouts, characterized by enhanced metabolism and locomotor activity, alternated with stopover periods that serve to rest and to replenish or augment fuel stores through over-eating (refueling) (Jenni and Jenni-Eiermann, 1992). Hence, corticosterone is thought

to play an important role in the regulation of avian migratory behavior (Cornelius et al., 2013). However, the temporal pattern of corticosterone secretion over the migratory sequence (pre-migratory fueling, flight bouts and stopovers) and its exact role during migration are far from understood. In captive migrants, corticosterone levels have repeatedly been observed to increase during pre-migratory fueling (Piersma et al., 2000; Landys et al., 2004a; Holberton et al., 2008). Levels seem to remain elevated above baseline to support the high energetic demands of migratory flights (Falsone et al., 2009; but see Jenni-Eiermann et al., 2009). After landing for stopover, levels appear to decrease (Landys-Cianelli et al., 2002), but if levels reach baseline and how they compare to levels in non-migratory LH stages is unknown. When migrants are ready to depart from stopover, i.e. have adequate fuel stores, levels seem to increase again (Landys-Cianelli et al., 2002; Eikenaar et al., 2013).

Although derived from species with different migratory strategies, and a mixture of laboratory and field studies, the pattern of corticosterone secretion over the migratory LH cycle suggests that

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corticosterone mainly functions in the regulation of departure on, and support of, migratory flights. In line with this idea is the observation that, similar to other LH stages (e.g. Astheimer et al., 1992; Breuner et al., 1998), corticosterone is positively associated with locomotor activity; in migrants caught and temporarily caged at stopover, corticosterone levels were positively correlated with nocturnal migratory restlessness (Eikenaar et al., 2014a). Migratory restlessness occurs when birds in migratory disposition are confined to a limited space (Berthold, 1996 and references therein), and is an accurate proxy for individual migrants' likelihood of departure (Eikenaar et al., 2014b). Correlative and experimental studies indicate that the effect of corticosterone on food intake and (re)fueling during migration is merely permissive, i.e. corticosterone does not stimulate food intake and (re)fueling (Landys et al., 2004b; Holberton et al., 2007; Eikenaar et al., 2013, 2014c).

To investigate the temporal pattern of corticosterone secretion and its role during migration, we focused on the stopover period and compared corticosterone levels between resident and migrating common blackbirds (*Turdus merula*, blackbird hereafter). Data were collected on the island of Helgoland during both the spring and autumn migration seasons. Helgoland supports a small (ca. 80 pairs) breeding population of blackbirds (Dierschke et al., 2011), and a radio-telemetry study showed that the large majority (91%) of blackbirds breeding on Helgoland are sedentary (Sacher, 2009). Birds were sampled close to, or at the start of the blackbird breeding season on Helgoland in spring, and after the breeding season and molt in autumn (Sacher, 2009; TK pers. obs.). Because both types of blackbirds were sampled during the same time period and at the same location, our dataset is the first to allow a direct and proper comparison of corticosterone levels of migratory vs. sedentary birds. Most migrating blackbirds caught on Helgoland stay only one or two days (Raiss, 1979; Ommo Hüppop, unpubl. data). Therefore, if corticosterone is up-regulated close to departure from stopover, we expected corticosterone levels to be higher in migrating than sedentary blackbirds.

2. Methods

2.1. Field 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. Blackbirds were caught from mid-March to mid-April and throughout October, periods representative of the spring and autumn blackbird migration seasons on Helgoland (Dierschke et al., 2011). Most blackbirds caught during stopover on Helgoland winter in the UK and breed in Scandinavia (Dierschke et al., 2011). Within 3 min. from capture birds were blood-sampled from the wing vein. The plasma was separated within 4 h of capture and frozen at -20°C until hormone assaying. Birds were sexed and aged (1st year or adult) on plumage (after Svensson, 1992), ringed, and fitted with a unique combination of four color-rings for later identification in the field. Fat stores were scored after Kaiser (1993) on a scale from 0 (no fat) to 8 (furcular and abdomen bulging, and breast covered with fat). All procedures were approved by the Ministry for Energy, Agriculture, the Environment and Rural Areas, Schleswig-Holstein, Germany.

Migrants were separated from residents combining two approaches. First, we made use of the ongoing, intensive ringing scheme of the Institute of Avian Research on Helgoland, during which many resident blackbirds were ringed, part as nestlings, in the breeding seasons preceding our corticosterone sampling. We assumed that birds that were ringed on Helgoland in previous breeding seasons and re-trapped by us were Helgoland residents.

This assumption is probably valid as all but one of the 22 birds that fell into this category were re-sighted on Helgoland after we color-ringed them. Second, 18 newly caught birds were considered resident because they were re-sighted more than nine days after initial trapping. We chose nine days as a cut-off point, because 95% of 1307 re-traps of supposedly migrant blackbirds on Helgoland occurred within nine days from first trapping (Ommo Hüppop, unpubl. data). Newly caught birds that were not re-sighted were considered migrants ($n = 72$). To reduce misassignment of status, eight newly caught birds that were re-sighted only within 9 days of color-ringing (range: 1–6 days) were not considered in the current study. In both seasons, searches for color-ringed birds were made almost daily from the start of trapping until at least three weeks after the last bird had been color-ringed. Given the small size of Helgoland (1 km²) and the fact that nearly all residents were re-sighted multiple times, we are confident that we re-sighted practically all resident color-ringed blackbirds.

2.2. Corticosterone assay

Corticosterone levels in plasma were determined using enzyme immunoassay kits (Enzo Life Sciences, Inc., former Assay Designs). Corticosterone in 15 μl of plasma (diluted in 200 μl H₂O bidest) 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 $^{\circ}\text{C}$. The remaining corticosterone was re-dissolved in 250 μl assay buffer and analyzed in duplicates following the kit manufacturer's protocol (with the only difference that we used a 6 point standard curve with a range of 20,000–15.63 pg/ml). An external standard was run in duplicate on each of the four plates for calculation of intra- and inter-assay variation. The intra-assay variation ranged from 1.46% to 2.33%, and the inter-assay variation was 2.62%. The lower limit of detection in our assay was 0.62 ng/ml. To determine extraction efficiency, pooled wheatear plasma samples were spiked with corticosterone standard from the kit. Recoveries of the low (1 ng/ml), intermediate (2.5 ng/ml) and high (10 ng/ml) spikes were 87%, 93% and 70%, respectively.

2.3. Data analysis

We used *T*-tests to determine whether corticosterone level differed between resident and migrant blackbirds. Because both for migrants and residents, spring and autumn represent different LH-stages, seasons were tested separately. To explore the variation in corticosterone level within migrants and within residents we employed general linear modeling. Explanatory variables were: season, sex, fat score, and the time of sampling. We used a *T*-test to determine whether age affected corticosterone levels, because only for autumn migrants there was an adequate sample of both 1st year and adult birds. Corticosterone levels were \log_{10} -transformed prior to all analyses, which resulted in a normal distribution of corticosterone data (Kolmogorov–Smirnov Test: $p = 0.2$).

3. Results

Sampling time (time from trapping until end of blood-sampling) did not affect corticosterone level in either season (spring: Spearman's $\rho = 0.17$, $p = 0.30$, $n = 41$; autumn: Spearman's $\rho = 0.17$, $p = 0.17$, $n = 71$). In spring, corticosterone levels did not differ between resident and migrating blackbirds ($t = 0.88$, $p = 0.38$, $n = 41$, Fig. 1). In autumn, corticosterone levels were higher in migrating than resident blackbirds ($t = 2.88$, $p = 0.005$, $n = 71$, Fig. 1). Excluding the extreme outlier from the

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