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Research paper

Cues, corticosterone and departure decisions in a partial migrant

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ABSTRACT

Most migrating birds make multiple stopovers to fuel and/or rest. The decision to resume migration from stopover is based on various cues, such as time within the season and wind conditions. There are hints that the strength of these departure cues shapes corticosterone level, which in its turn appears to regulate the timing of departure. We here provide results that very strongly indicate that indeed departure cues jointly shape corticosterone level of migrants at stopover. We compared corticosterone level between migrating and sedentary common blackbirds (*Turdus merula*) sampled simultaneously at the same location during autumn migration. As expected, in migrating individuals corticosterone level was positively associated with time within the season and with current wind conditions. The latter was only apparent in adult birds and not in 1st year migrants, thus matching the observation that 1st year autumnal migrants are less wind selective than adults. In contrast to the migrants, in sedentary blackbirds these "cues" did not explain variation in corticosterone level. Furthermore, stopover departure seemed more likely and to occur earlier in the night in migrants with high corticosterone level. Our unique comparative study thus supports the newly developed concept that corticosterone mediates between departure cues and stopover departure timing in avian migrants.

1. Introduction

All over the globe, throughout the year, billions of birds migrate between their breeding areas and wintering grounds. Billions of other birds follow a contrasting strategy by staying in the area where they bred. Migratory individuals generally differ from sedentary individuals in that their body is adapted to travelling (Leisler and Winkler, 2003). Some adaptations are structural, for example, migrants typically have longer and pointier wings increasing air speed and decreasing drag than residents whose rounder wings produce higher maneuverability (e.g. Marchetti et al., 1995; Fiedler, 2005). Other adaptations are physical and only apparent during the migration life-history stage, for example, migrants' ability to rapidly accumulate large subcutaneously fat stores that serve as fuel for endurance flights (Lindström, 2003). Additionally, migrants have to adapt behaviorally by making several decisions during their travels which sedentary individuals obviously do not face. The most important set of behavioral decisions is related with the temporal organization of migration, i.e. the decision when to start migrating, when to land for resting and fueling at stopover sites, and when to again resume migration. At the seasonal scale, the temporal organization of migration, including the change in physiology and motivation to migrate, is mainly regulated by innate circannual rhythms (Berthold, 1996; Gwinner, 1996; Maggini and Bairlein, 2010, 2012). At the smaller temporal scale, daily departure decisions at stopover and in flight are based on a mix of cues from innate circadian rhythms (Coppack et al., 2008; Eikenaar et al., 2016), extrinsic departure cues such as wind conditions (Liechti, 2006) and intrinsic departure cues such as the size and rate of accumulation of the fuel stores (Schmaljohann and Eikenaar, 2017).

Temporary physical adaptations require changes in the birds' physiology. For example, for the rapid synthesis of fat as fuel during the migration seasons birds upregulate the activity of the enzyme complex fatty acid synthase (Ramenofsky, 1990). Behavioral decisions too depend on underlying physiological mechanisms, but how pivotal decisions, such as departure from stopover, are physiologically regulated remains uncertain. Currently, it appears that several hormones, possibly in concert, are involved in these decisions. For example, in garden warblers (*Sylvia borin*) temporarily caged at stopover in autumn, exogenous melatonin decreased migratory restlessness (Fusani et al., 2013), which probably reflects a decrease in the motivation to depart (Eikenaar

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et al., 2014a). Parts of the physiological regulation of stopover departure decisions were recently detailed for the northern wheatear (*Oenanthe oenanthe*), a long-distance songbird migrant. In this study, Eikenaar et al. (2017a) found that baseline corticosterone (corticosterone hereafter) level of migrants at stopover appeared to be shaped by multiple departure cues, and that corticosterone level in turn explained variation in departure timing, both at the day-to-day level and within the night. This is so far the best candidate model demonstrating endocrine mediation between departure cues and departure timing, but further research is required to test its validity. For example, if the idea that factors functioning as departure cues shape corticosterone level in migratory birds is correct, then in sedentary birds that do not make departure decisions these same factors should not shape corticosterone level. Also, the positive association between corticosterone and departure timing should be shown for more migrant species.

To further our understanding of corticosterone's role in the physiological regulation of migration, we studied the common blackbird (*Turdus merula*, blackbird hereafter), a partial migrant in which some individuals are migratory and others sedentary. In this species, the initial decision whether or not to migrate appears to be linked to corticosterone; Fudickar et al. (2013) found that in the pre-migratory period, individuals that eventually migrated tended to have higher baseline corticosterone levels than individuals that stayed at the breeding grounds. Studying a partial migrant allowed us to a) link corticosterone to extrinsic and intrinsic cues in both migrating and sedentary wild individuals sampled simultaneously at a single site, and b) link corticosterone level to departure timing in this short-distance migrant. We expected that, similar to northern wheatears, also in migrating blackbirds corticosterone acts as a mediator between departure cues and stopover departure timing. Specifically, based on the results of Eikenaar et al. (2017a), we expected that part of the variation in corticosterone level in migrating blackbirds would be jointly explained by the time within the migration season (innate rhythm), the prevailing wind conditions (extrinsic departure cue), and the birds' fuel stores (intrinsic departure cue). Furthermore, as 1st year migrants were found to be less wind selective than adults (Mitchell et al., 2012, 2015), we expected an interaction between wind conditions and age, with wind affecting corticosterone level in adults more strongly than in 1st year birds. In contrast to their migrating conspecifics, we expected corticosterone levels of sedentary blackbirds to be independent of the factors that act as departure cues in migratory birds. Finally, we expected that migrants with relatively high corticosterone levels would be more likely to depart the night after sampling, and to depart sooner after sunset than migrants with relatively low corticosterone levels.

2. Methods

2.1. Trapping 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. Helgoland holds a small sedentary breeding population of blackbirds (currently ca. 60 breeding pairs, Jochen Dierschke, unpublished data) and is used by thousands of blackbirds as a stopover site during their migration between the Scandinavian breeding areas and wintering grounds in the UK and western Central Europe (Dierschke et al., 2011). Blackbirds, both residents and migrants, were caught throughout October 2014 and from early October to mid-November 2016, periods during which many blackbirds make a stopover on Helgoland during their autumn migration (Dierschke et al., 2011). All birds were caught between 7 am and 6 pm (local time). Within 3 min. from capture birds were blood-sampled from the wing vein, meaning that corticosterone levels determined from these samples are within baseline levels for this species (Eikenaar et al., 2015). Correspondingly, in the current dataset, corticosterone level was not related to handling time (Spearman's rho = 0.038, p = 0.59, and n = 206). The plasma was separated within 1 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 (furcula and abdomen bulging, and breast covered with fat). In 2016, after all measurements were taken, 71 birds sampled for corticosterone were fitted each with a coded radio-transmitter (NTQB-1 Avian Nano Tag; weight: 0.29 g; Lotek Wireless Inc., Newmarket, ON, Canada). Radio-transmitters were attached to a Rappole-type harness with the length of the leg-loops adjusted individually to birds' body size (Naef-Daenzer, 2007). As the tagged birds weighed at least 80 g, the relative load of the radio-transmitter including the harness (total weight: 0.4 g) was at maximum 0.5% and thus always far below the suggested upper permissible load limit of 5% of body mass (Cochran, 1980). After radio-tagging the birds were released into the field. All procedures were approved by the Ministry for Agriculture, the Environment and Rural Areas, Schleswig-Holstein, Germany.

2.2. Assignment of migratory status

In both years, weather permitting, daily searches for color-ringed birds were made from the start of trapping until one month after the last blackbird was color-ringed in that year. Helgoland is small (1 km^2) and birds are easily re-sighted, if they stay on the island. Sedentary individuals were separated from migrants combining two approaches (Eikenaar et al., 2015, 2017b; Eikenaar and Hegemann, 2016). First, we assumed that 18 blackbirds ringed (with a metal ring only) on Helgoland in previous breeding seasons and re-trapped and color-ringed by us in one of the autumn seasons were Helgoland residents (12 in 2014 and 6 in 2016). This assumption rests on a radio-telemetry study showing that most (91%) blackbirds hatched on Helgoland are sedentary (Sacher, 2009) and the fact that migratory birds seldom return to Helgoland during a later migration period (Dierschke, 2002). The assumption seems valid also for the 18 blackbirds previously ringed on Helgoland, because 15 of these were re-sighted on Helgoland, usually several weeks after color-ringing indicating that they were sedentary and not migratory individuals. Second, 23 first captures were considered sedentary, because they were re-sighted more than 19 days after initial capture. We chose 19 days as a cut-off point, because our radio-telemetry data revealed that the longest stopover made by migrating blackbirds was 19 days (median stopover duration was four days, n = 54). These 23 blackbirds were re-sighted rapidly and multiple times after color-ringing at capture (median number of days until first re-sighting was 4 days (range: 0–36 days), and the median number of their re-sightings during the year of study was 4 observations (range: 1–18 observations)). Moreover, as 21 of the 41 individuals (51%) being assigned as residents were re-sighted ad libitum on Helgoland in the winter following our autumnal fieldwork, we are confident that our approach to identify sedentary blackbirds was reliable. First captures that were never re-sighted (n = 111) or from which we radio-tracked their departure events (see below, n = 54) were considered as migrants (n = 165). 21 first captures that were not radio-tagged and that were re-sighted only within 19 days of initial capture (range: 1–15 days) most likely were migrants, but could also have been residents that died during the fieldwork period. Therefore, to reduce the possibility of a misassignment in migratory-/sedentary-status and to have conservative assignments, these

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