



Baseline and stress-induced corticosterone levels are higher during spring than autumn migration in European robins

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ABSTRACT

During spring and autumn migrations, birds undergo a suite of physiological and behavioral adaptations known as migratory disposition. The position of migratory seasons within the annual cycle and specifics of environmental conditions in each season could lead to formation of specific regulatory mechanisms of spring and autumn migratory disposition. However, this topic remains largely unstudied. Here we compared corticosterone (CORT) concentration (baseline and stress-induced) in European robins (*Erithacus rubecula*) captured during seven consecutive migratory seasons on the Courish Spit in the Baltic Sea; > 650 plasma samples were analyzed in total. We found that baseline and stress-induced CORT concentrations in free-living robins during spring migration were nearly twice as high comparing to autumn passage. Moreover, the strength of relationship between these two parameters differed between the seasons. In autumn, individuals with elevated baseline CORT level invariably expressed high stress response; in spring, the stress response was more variable. These facts are in line with the hypothesis that spring and autumn migrations are separate life history stages characterized by similar physiological and behavioral adaptations but somewhat different regulatory mechanisms. Further work is needed to understand effects of seasonal differences in CORT concentrations in regulation of migratory disposition in birds.

1. Introduction

Spring and autumn migrations are separate life history stages in most passerine species breeding at temperate and high latitudes (Jacobs and Wingfield, 2000; Wingfield, 2005). During both migratory seasons, birds cover large distances and often follow the same routes and expend similar amounts of energy each way (Newton, 2008, 2012). As a result, a similar suite of morphological, physiological, and behavioral adaptations, known as migratory disposition, develops in spring and in autumn (Berthold, 1975; Dolnik, 1975). Migratory disposition is characterized by hyperphagia and fattening, changes in daily activity rhythm, seasonally appropriate orientation of migratory activity, muscle hypertrophy, and changes in muscle enzymatic activities and hematocrit (reviewed in: Ramenofsky and Wingfield, 2007, 2006). These adaptations allow migratory birds to cover distances between breeding and wintering grounds. However, an overall speed of spring migration is often higher, and its total duration is shorter than in autumn (Nilsson et al., 2013). Environmental factors, such as temperature, wind conditions, and food abundance, also differ significantly between autumn and spring (Ramenofsky et al., 2008). Migratory

disposition in spring is stimulated by increasing photoperiod, which also stimulates development of the reproductive system and increases level of sex hormones (Dawson et al., 2001; Ramenofsky and Wingfield, 2006; Wingfield et al., 1990). During autumn migration, the reproductive system is inactive and the level of sex hormones is low. The position of migratory seasons within the annual cycle and seasonal difference in actions of environmental factors could potentially lead to development of poorly understood specific regulatory mechanisms of spring and autumn migratory disposition (Cornelius et al., 2013; Wingfield, 2005).

The leading role in regulation of birds' behavior and physiology belongs to the endocrine system (Norris and Carr, 2013). Corticosterone (CORT), the main glucocorticoid hormone in birds, seems to be involved in regulation of migratory behavior and physiology (Cornelius et al., 2013; Jenni et al., 2000; Ramenofsky et al., 2012). It is assumed that the baseline concentration of this hormone has a permissive effect on hyperphagia and fattening (Eikenaar, 2017), might increase the level of migratory activity (Breuner et al., 1998; Dolnik and Blyumental, 1967), and even impact the migratory orientation (Löhmus et al., 2003); all of these factors are the main components of migratory

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Table 1
Sample dates and sample size for baseline and stress-induced CORT concentrations in different years/seasons.

	2013		2014		2015		2016	
	Autumn	Spring	Autumn	Spring	Autumn	Spring	Autumn	
	9.10–23.10	7.04–30.04	11.09–29.10	10.04–14.05	10.09–19.10	17.04–12.05	6.09–19.10	
Baseline	18	62	84	23	78	16	76	
Stress-induced	9	50	63	23	74	16	75	

disposition. Moreover, it was also shown that CORT at baseline and moderately elevated levels (i.e., not the levels observed in stress response) mobilizes energy reserves and regulates metabolism and fuel types used during migratory flight (Jenni et al., 2000; Sapolsky et al., 2000). Recently, it was proposed that CORT level may serve as a readiness cue for a migratory departure from stopover sites (Eikenaar et al., 2017).

Apart from these functions, CORT is released in response to the numerous stressful stimuli, which in turn triggers physiological and behavioral changes that help an organism to deal with effects of the stressful event (Romero and Wingfield, 2015; Sapolsky et al., 2000; Wingfield and Romero, 2001). There is increasing evidence that CORT binds to different types of receptors (Sapolsky et al., 2000; Romero, 2004). Baseline (low) CORT concentrations bind to mineralocorticoid receptors, while (high) concentrations released during stress response bind to glucocorticoid receptors. For the house sparrow, (*Passer domesticus*), it was reported that these two receptor types were differently expressed at different times of the year (Lattin and Romero, 2013). Activation of each receptor type can have distinct physiological and behavioral effects (Sapolsky et al., 2000; Romero, 2004). Consequently, seasonal differences in baseline CORT concentrations probably have different physiological and behavioral consequences, in contrast with seasonal differences in stress-induced CORT concentrations. It is currently unclear whether CORT release during stress leads to any specific changes in behavior and physiology during migrations, but without doubt, an adequate stress response is essential during migration when birds permanently face unpredictable weather conditions, social interactions, food availability, and predators (Ramenofsky et al., 2012).

To date, there is only a limited number of studies directly addressing and comparing CORT concentrations between migratory seasons, and the available data are quite equivocal (e.g., Eikenaar et al., 2015; Romero et al., 1997). In passerines, it was reported that both baseline and stress-induced CORT concentrations were higher in spring than in autumn (Romero et al., 1997), or there was a lack of seasonal difference in baseline CORT concentrations (Eikenaar et al., 2015). In available publications, comparisons were established on the basis of only one pair of migratory seasons, and no information was provided regarding reproducibility of the observed pattern in subsequent seasons. Moreover, as CORT concentration varies depending on environmental conditions (Romero and Wingfield, 2015), the observed patterns may be related to conditions of a particular pair of seasons without reflecting the actual season-related difference. Our preliminary data based on the restricted subsample from two autumn and two spring migratory seasons (Loshchagina et al., 2017) had indicated that both baseline and stress-induced CORT concentrations are higher in spring than in autumn; however, the sample size was too narrow to draw a reliable conclusion.

Here we compared CORT concentrations (baseline and stress-induced) in European robins (*Erithacus rubecula*) captured in seven consecutive migratory seasons on the Courish Spit in the Baltic Sea. We tested two opposite predictions. According to the first one, the position of migratory seasons within the annual cycle and seasonal differences in environmental conditions enable specific regulatory mechanisms of migratory disposition and produce different baseline CORT concentrations in spring and autumn. Alternatively, considering the similarity of components of migratory disposition between the seasons, one can

expect that baseline CORT levels are not different in autumn and spring. Because baseline and stress-induced CORT concentrations are likely to represent partly independent hormonal systems (Romero, 2004), the stress-induced concentration may show a distinct pattern from baseline level. Assuming that the appropriate stress response is essential for survival (Romero and Wingfield, 2015), we expected that European robins respond to stress with a marked elevation of CORT concentrations in both migratory seasons. Owing to the correlative nature of our data, we aimed to provide the reliable estimates of CORT concentrations in spring and autumn migratory seasons and did not intend to infer causal relationships between plasma CORT and physiological or behavioral parameters.

2. Methods

2.1. Study site and model species

The study was performed at the Biological Station Rybachy of the Zoological Institute RAS on the Courish Spit in the Baltic Sea in seven consecutive migratory seasons (autumn 2013 – autumn 2016, Table 1). The European robin is a small songbird that migrates within Europe. Only a few pairs breed on the Courish Spit (because of the prevalence of dry pine forest and sand dunes as the main habitat types), as shown by very few captures of this species during the breeding season (Tsvey, 2008). However, the Courish Spit is intensively used by European robins during seasonal migrations: it is the most common species of nocturnal migrants captured here during both spring and autumn (Tsvey, 2008). Trapping of birds was conducted at two field sites located 11 km apart. At Rybachy field site (55°09'N, 20°51'E), birds were captured in mist nets; at Fringilla field site (55°05'N, 20°44'E), birds were captured in Rybachy-type funnel traps and mist nets. The funnel traps are located in the open area at the border between the forest the sand dunes. European robins are captured in these traps mostly in the early morning hours with just occasional captures during the daytime (Tsvey, 2008). Telemetry data revealed that the area in close proximity to the traps was very rarely used for refueling (Tsvey et al., unpubl.). Visual observations have shown that the sand dunes around the traps attract robins and different species of thrushes while they cease their nocturnal flight (Bolshakov K.V., pers.comm.). As robins were captured in funnel traps during the morning twilight, we assume that most of these birds represented newly landed migrants. In mist nets, birds were captured during the entire day; these captures represent individuals at different stages of stopover (from newly landed birds to those ready for a new migratory flight). Trapping and animal handling comply with the animal care laws of the Russian Federation and were approved by the Zoological Institute RAS ethical committee (permit #2013-01-03).

2.2. Blood sampling

We followed standard stress-restraint protocol to measure baseline and stress-induced CORT concentrations (Wingfield and Romero, 2001). We used a stopwatch to measure the time between the bird colliding with the net or when it crossed the entrance of the funnel trap and the end of the first blood sampling. This time varied between 50 s and 5 min 52 s (2 min 44 s, on average). After the first sampling, the

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