Stress hormone dynamics: an adaptation to migration?

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The hormone corticosterone (CORT) is an important component of a bird’s response to environmental stress, but it can also have negative effects. Therefore, birds on migration are hypothesized to have repressed stress responses (migration-modulation hypothesis). In contrast to earlier studies on long-distance migrants, we evaluate this hypothesis in a population containing both migratory and resident individuals. We use a population of partially migratory blue tits (Cyanistes caeruleus) in southern Sweden as a model species. Migrants had higher CORT levels at the time of capture than residents, indicating migratory preparations, adaptation to stressors, higher allostatic load or possibly low social status. Migrants and residents had the same stress response, thus contradicting the migration-modulation hypothesis. We suggest that migrants travelling short distances are more benefited than harmed by retaining the ability to respond to stress.

Keywords: stress; corticosterone; partial migration

1. INTRODUCTION

In life, there are both predictable and unpredictable circumstances requiring mobilization of defence mechanisms. Life-history stages, such as breeding and migration, are predictable events. Birds leaving on migration can prepare for the migratory journey by adjusting their physiology and leave under favourable conditions. Predator attacks and sudden weather changes are unexpected and occur unpredictably.

An animal’s physiological response to environmental changes involves shifts in circulating levels of hormones. Glucocorticoids are steroids involved in the regulation of feeding behaviour, activity and metabolism but are also an important component of the response to environmental stressors (Renerkens et al. 2002; Landys et al. 2004). The most important glucocorticoid in birds is corticosterone (CORT). Predictable events are met by long-term changes in the circulating levels of CORT. Unpredictable events result in stress-induced physiological responses by rapidly increasing the circulating levels of CORT (hereafter referred to as the stress-related response) (Landys et al. 2006).

In general, birds have low circulating CORT levels with occasional peaks during stress-related responses. When birds prepare for migration, CORT levels become elevated (Holberton 1996), which is suggested to mobilize energy reserves to meet increased demands (Landys et al. 2006). Glucocorticoids are also active in other processes such as the release of fatty acids from adipose tissues and lipogenesis. Some of these processes might actively mobilize resources away from muscles, i.e. degrade muscle tissue (Holmes & Phillips 1976). Therefore, a reduced stress-related response has been proposed to be part of an adaptive process protecting muscle tissue during migration, the migration-modulation hypothesis (Holberton et al. 1996). However, the inability to respond to stressors might have survival consequences, as predator attacks might be more frequent on migration routes and in new environments, knowledge of the nearest cover will be rudimentary.

Partially migratory populations consist of both migratory and resident individuals (Terrill & Able 1988). Depending on external factors, such as population density, winter food sources (Nilsson et al. 2006b) and individual disposition (Pulido et al. 1996), individuals can change from being migrants to becoming residents (Able & Belthoff 1998; Nilsson et al. 2008). In this study, we evaluate the migration-modulation hypothesis by analysing CORT levels at the time of capture and the stress-related responses in a partially migratory blue tit (Cyanistes caeruleus) population in southern Sweden. Apart from the northern breeding range, i.e. Scandinavia, the blue tit is mainly resident. The CORT levels in this study originate from faecal samples and represent the integration of CORT over a period of time.
8 h starting at the time of the ACTH challenge and also once at 08.00 the next morning (23 h after challenge).

(b) Extraction and hydrolysis of faecal samples
The dry-weight of droppings was measured to quantify the amount of hormones. Corticosterone metabolites were extracted in 1 ml ethanol at room temperature for 3 h. Samples were vortexed for 90 min and centrifuged at 1100 \(g\) for 6 min. Four hundred micro litres of the ethanol supernatant was transferred to 12 /C2 75 glass test tubes and dried under a stream of nitrogen gas in a water bath at 40°C. Two hundred micro litres sodium acetate buffer with \(\beta\)-glucuronidase/arylsulfatase, 1:100 was added and the samples were incubated for 16–18 h at 39°C. After incubation, samples were vortexed and transferred to new tubes.

(c) CORT assay
CORT was analysed in a direct CORT radio-immuno assay (with tritium-labelled CORT; Perkin Elmer Life Sciences NET399 and CORT antibody from Esoterix Endocrinology B3-163). Each sample was run in duplicates (50 \(\mu\)l of hydrolysed extract mixed with 50 \(\mu\)l phosphate buffered gelatine saline in each) and mean values were compared with a standard curve (1.95–500 pg per sample) and expressed as nanogram or milligram dry faeces with a detection limit of 10 ng mg \(^{-1}\). All samples including the validation experiment were analysed in a single assay (intra-assay variation was 4.4%).

(d) Statistics
The observed hormone concentrations were slightly skewed and therefore square-root transformed before analyses. CORT concentrations were analysed with \(t\)-tests and repeated mixed model ANOVA on transformed values using SAS v. 9.1. Body mass, capture date and time of sampling were included in the model as covariates but since none of these variables was significant (\(p > 0.1\)), they were removed from the model.

3. RESULTS
The blue tits in the validation experiment responded with an increase in CORT 60 min after the ACTH-challenge. This peak lasted during the first 2 h (figure 1) and then returned to pre-injection levels the next morning.

Migratory birds had significantly higher concentrations of CORT at the time of capture than residents (\(t\)-test, \(t = 2.27, d.f. = 46, p = 0.027\), figure 2). The birds responded to capture by an increase in CORT levels (repeated mixed model, effect of time \(F_{1,43.7} = 15.54, p < 0.001\), figure 2). Migrants had overall higher CORT concentrations (repeated mixed model, \(F_{1,43.6} = 87.88, p = 0.007\)). However, the rate of increase in CORT in the stress-related response was similar for migrants and residents, as indicated by the non-significant interaction between migratory status and the two measures of CORT levels (at the time of capture and stress-related response, table 1) with significantly higher CORT levels in migrants during the stress-related response (\(t\)-test, \(t = 2.10, d.f. = 46, p = 0.003\)). Body mass and the date of capture had no effect on CORT levels. A full model with all tested variables retained is shown in table 1.

4. DISCUSSION
We found higher CORT levels at the time of capture in migratory blue tits compared with residents. As migration is a predictable life-history event, it could be anticipated by increased CORT levels enhancing metabolism of lipid stores for migration (Landys et al. 2004). This has also been observed in other partial migrants, such as European blackbirds Turdus merula, (Schwabl et al. 1984) and willow tits Parus montanus (Silverin et al. 1989), as well as in long-distance migrants such as white-crowned sparrows Zonotrichia leucophylla gambelii and bar-tailed godwits Limosa lapponica (Romero et al. 1997; Landys-Ciannelli et al. 2002).

There are also other non-exclusive explanations for the higher CORT levels at the time of capture in migrants. If migrants forage less, gut passage time might be longer, and each dropping would contain...
more CORT, besides any possible dietary differences that might affect passage time. Differences in CORT have also been suggested to result from seasonal physiological changes (Romero et al. 1997). Besides, extended stress might result in higher CORT levels as an adaptation to the stressor (Romero 2004). Higher energy demands owing to migration are unlikely, as migrants have lower basal metabolic rates than residents (A. L. K. Nilsson, J.-Å. Nilsson & T. Alerstam 2002, unpublished data). Social dominance hierarchies are often used to explain partial migration (Gauthreaux 1978). Subdominance can result in elevated CORT levels at the time of capture (Silverin 1997). In direct comparisons, dominance was context-dependent (A. L. K. Nilsson, J.-Å. Nilsson & T. Alerstam 2003, unpublished data); under favourable migratory conditions, migrants selected for different personalities: daily rhythm and the response to social stress. Also in the dark-eyed junco (Junco hyemalis) there is evidence for input that greatly improved the paper. This is Report no. 249 from the Falsterbo Bird Observatory.

The work has been carried out in accordance with Swedish law and legal requirements relating to conservation and animal welfare. Our work has also been carried out along ‘Guidelines for the treatment of animals in behavioural research and teaching’ (Anon. 2006).

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Table 1. The listed effect of all investigated variables on CORT levels analysed in a mixed model ANOVA. d.f., degrees of freedom; $F$, $F$-tests; $p$, significance level.

<table>
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<td>0.01</td>
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Figure 2. CORT concentration (ng mg–1) at time of capture and 30–60 min after capture.

In conclusion, we suggest that the migration-modulation hypothesis is not valid for partial migrants travelling short distances, as these migrants are better benefited by the higher survival value offered by a retained stress-related response. Increased CORT levels at the time of capture in partial migrants could be part of an adaptive mechanism preparing migrants, or a consequence of social dominance hierarchies between migrants and residents in a population.


