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Biol. Lett. 2009 **5**, 480-483 first published online 8 May 2009
doi: 10.1098/rsbl.2009.0193

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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. Glucocorticosteroids are steroids involved in the regulation of feeding behaviour, activity and metabolism but are also an important component of the response to environmental stressors (Reneerkens *et al.* 2002; Landys *et al.* 2004). The most important glucocorticosteroid 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). Glucocorticosteroids 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.

2. MATERIAL AND METHODS

The study was conducted during 2004 using 48 juvenile females: 20 migrants and 28 residents. At both capturing sites, birds were sexed and aged according to Svensson (1992). Migratory blue tits were captured at Falsterbo (55°23' N, 12°49' E), a migratory passage site at a peninsula in southwestern Sweden where migratory blue tits from southernmost Scandinavia concentrate. Few blue tits have migrated more than 150 km before arriving there and apart from two locally breeding pairs, the blue tits captured there are on migration (Nilsson *et al.* 2006a, 2008). Approximately 4000 blue tits are ringed annually at the bird observatory. Residents were captured at an inland site (55°42' N, 13°28' E), 53 km northeast of Falsterbo. In this area, a nest box project annually rings a large number of nestlings, which later are recaptured in autumn as residents. Unringed individuals, mainly of local origin, were also included in the study (six local recoveries). Based on recapture rates of ringed and unringed individuals prior to and during the migratory period, the contribution of potential migrants to the category residents is estimated to be 30 per cent, i.e. 6.6 individuals (A. L. K. Nilsson, J.-Å. Nilsson, T. Alerstam & M. Stjernman 2005, unpublished data). Hence, residents might contain a small proportion of migrants, but this will only increase variation and make the analyses more conservative.

Birds were mistnetted and put in individual cages, 0.45 × 0.30 × 0.48 m, with at least three perches and access to water and meal worms *Tenebrio* sp., for collection of faecal droppings. The bottom of each cage was covered with a paper sheet with a plastic surface and faecal droppings were collected with plastic pipettes. Droppings were collected in tubes once within 30 min of capture for CORT levels at the time of capture and once after 30–60 min for stress-related response to capture and handling, reflecting CORT levels after stress (Carere *et al.* 2003). Samples were frozen.

(a) Validation of corticosterone assay

To ensure that the CORT assay used in this study was able to measure CORT metabolites in faeces, we performed a validation test with an adrenocorticotrophic hormone (ACTH) challenge on three captive blue tits. The birds were captured at Falsterbo and kept in individual cages. They received water and food ad libitum. The birds were injected with ACTH (100 IU kg⁻¹ body mass, i.e. 1.5 IU per 50 µl PBS) in the pectoral muscle at 09.00 in the morning after capture. Faecal samples were collected once every 60 min for

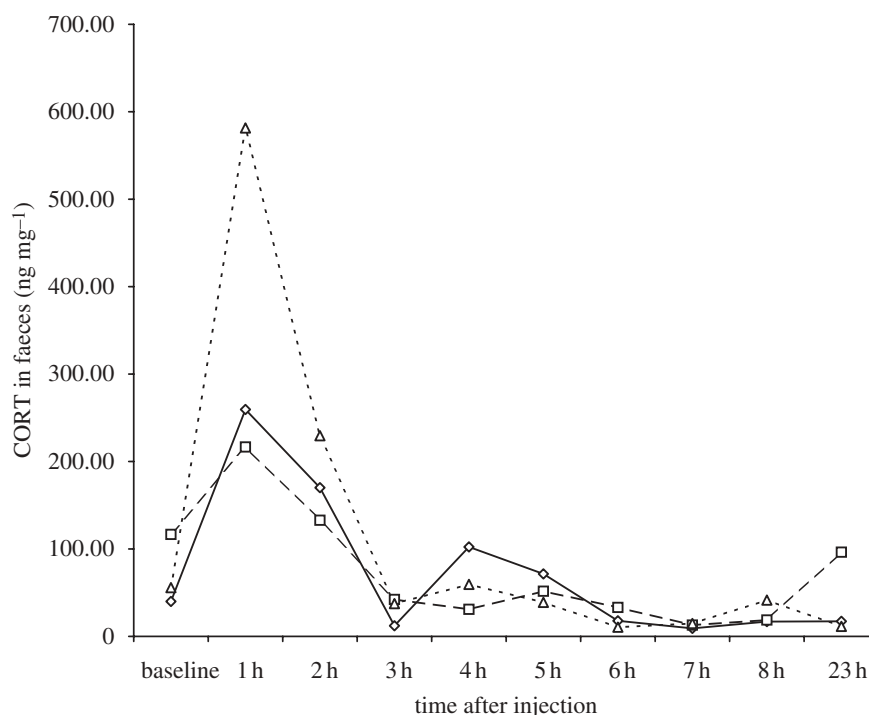


Figure 1. CORT concentrations in three blue tits injected with ACTH at time=0. The challenged birds are: diamonds and solid line, CA09447; squares and dashed line, CB46655; triangles and dotted line, CD45872.

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 1100g for 6 min. Four hundred micro litres of the ethanol supernatant was transferred to 12 × 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 β -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 μ l of hydrolysed extract mixed with 50 μ 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 leucophrys 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

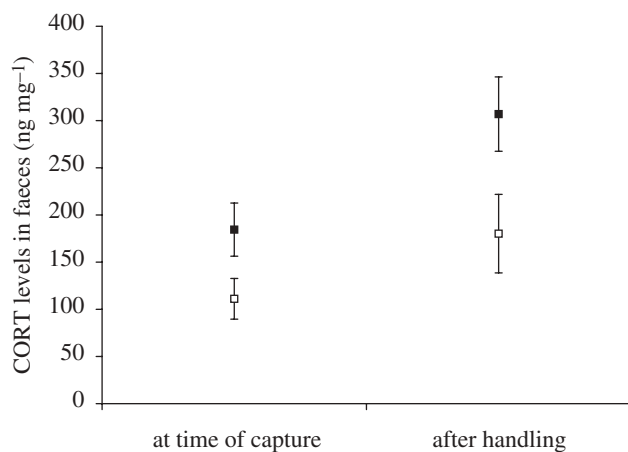


Figure 2. CORT concentration (ng mg^{-1}) in migrant (filled boxes) and resident blue tits (open boxes) at the time of capture and 30–60 min after capture.

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.

parameters	d.f.	F	p
status	1, 42.4	7.55	0.0108
sampling event	1, 42.7	16.24	0.0002
status \times sampling event	1, 42.6	1.03	0.31
mass	1, 41.3	0.45	0.50
date	1, 43.4	0.01	0.93

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 were dominant. Presumably, residents are dominant over migrants, except under favourable conditions, potentially explaining the higher CORT levels at the time of capture among migrants.

In contrast to the migration-modulation hypothesis, both migratory and resident blue tits showed a clear stress-related response. Also in the dark-eyed junco *Junco hyemalis* displaying differential migration by different sex and age classes, birds did retain a stress response (Ramenofsky *et al.* 1999). Hence, there seems to be a difference in stress-related responses between long-distance migrants and partial migrants (Silverin 1997 and this study).

Optimal physiological adaptations may differ between long-distance and partial migrants. Blue tit

migration is short and slow, awaiting the safest possible weather conditions before crossing barriers (Nilsson *et al.* 2006a). If repressing stress-related responses is an adaptation for long-distance migration, migrants travelling short distances might be benefited by retaining them. They would enable short-distance migrants facing less predictable weather conditions to survive. The value of retaining responses on migration must be higher for partial migrants than the potential risk of tissue loss.

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.

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).

We are grateful to the Falsterbo Bird Observatory and to Marina Dimitrova, Håkan Karlsson and Sara Henningson. We would also like to thank the three anonymous reviewers for input that greatly improved the paper. This is Report no. 249 from the Falsterbo Bird Observatory.

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