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# Corticosterone and the departure likelihood of migrants from stopover

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# Corticosterone and the departure likelihood of migrants from stopover

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## *Abstract*

During migration birds have to decide when to leave stopover sites. This decision depends on extrinsic factors such as weather conditions but also on intrinsic factors such as fuel reserves. However, the physiological mechanism which underlies this decision is at this time unknown. Birds which are ready to depart need high amounts of fuel reserves to have the availability of energy during flight and also an increase of locomotion. Corticosterone, the main glucocorticoid hormone in birds, at baseline level is involved in the mobilization of energy and in stimulation of locomotion. In this study we collected field data of baseline corticosterone, migratory restlessness and actual departure of northern wheatears at stopover. Migratory restlessness was positively correlated with baseline corticosterone-level. Also, a trend was found that birds with higher baseline corticosterone-levels left the stopover earlier. This is, to our knowledge, the first study that combined a hormonal signal and migratory restlessness. Our results consistently support the idea that corticosterone is involved in departure likelihood of migrants during stopover. Future studies should ascertain how corticosterone is up regulated in migrants that are ready to depart from stopover.

## *Keywords*

Migration, Corticosterone, Departure, Stopover, Radio-telemetry, Wheatear, *Oenanthe*

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## *Zusammenfassung*

Während des Zuges müssen Vögel entscheiden wann die Rastgebiete wieder verlassen werden. Diese Entscheidung hängt von extrinsischen Faktoren wie zum Beispiel von verschiedenen Wetterbedingungen, aber auch von intrinsischen Faktoren wie Energiereserven ab. Die physiologischen Mechanismen, die hinter dieser Entscheidung stecken, sind jedoch zum jetzigen Zeitpunkt noch unverstanden. Vögel, die bereit sind den Rastplatz zu verlassen, benötigen Fettreserven, die während des Fliegens in Energie umgewandelt werden können sowie eine erhöhte Locomotion. Corticosteron, das Haupt-Glucocorticoid Hormon bei Vögeln, auf einem Grundniveau steht im Zusammenhang mit der Mobilisation von Energie und führt weiterhin zu einer Stimulierung des Bewegungsapparates. In dieser Studie sammelten wir Felddaten von Corticosteron auf einem Grundniveau, Zugunruhe und den tatsächlichen Abzug von Steinschmättern an einem Rastplatz. Zugunruhe korrelierte positiv mit dem Corticosteron-Level auf Grundniveau. Desweiteren zeigte sich ein Trend, dass Vögel mit höheren Corticosteron Grundniveauwerten eher den Rastplatz verließen als Vögel mit geringeren Corticosteronwerten. Auf unserem Wissensstand basierend ist das die erste Untersuchung, die ein hormonelles Signal mit Zugunruhe in Verbindung bringt. Unsere Ergebnisse unterstützen die Hypothese, dass Corticosteron involviert ist in die Abzugswahrscheinlichkeit von migrierenden Vogelarten an einem Rastplatz. Nachfolgende Studien sollten untersuchen wie Corticosteron bei Zugvögeln hochreguliert wird, wenn sie bereit sind den Rastplatz zu verlassen.

## *Schlagwörter*

Vogelzug, Corticosteron, Abzug, Rastplatz, Radio-Telemetrie, Steinschmätzer, *Oenanthe*

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# *Introduction*

Throughout the year, long distance migrants may spend up to a quarter of the year in migratory mode. These birds are known to house many physiological and behavioral adaptations (e.g. hyperphagia, nocturnal activity, change in muscle enzyme activities) to cover such a challenge (Bairlein 1985; Lundgren and Kiessling 1985; Gwinner 1996). Also, when flying for long periods most birds have to make one or more breaks (so called stopovers) to rest and/or to refuel their fat and protein loads to overcome the next flight bout. These stopovers are such an important stage during migration that birds spend far more time in storing fuel at stopover sites than they do flying. As it is known that birds are expected to be time minimizers (Lindström, Å. and Alerstam, T. 1992), the decision to depart from a stopover site is fundamental for migrants to make sure to arrive in time at further stopover sites, wintering or breeding grounds so that survival and reproductive output are maximized (Farmer and Wiens 1999). Environmental factors such as food availability (Schaub and Jenni, 2000), weather conditions (Schmaljohann and Naef-Daenzer 2011) and predation pressure (Schmaljohann and Dierschke 2005) are known to affect the decision to depart. Also intrinsic factors such as fuel reserves are important for the likelihood of departure (Jenni and Schaub 2003; Newton 2008; Dierschke and Delinghardt 2001). For example, Eikenaar and Schälffe (2013) found that northern wheatears (*Oenanthe oenanthe*) with high fuel reserves showed more (nocturnal) migratory restlessness (so called Zugunruhe) than birds with small fuel reserves. This can be interpreted as birds with higher Zugunruhe being more motivated to continue migration because they have enough energy reserves to cover the next flight bout. The phenomenon of Zugunruhe is typically most developed in migrating bird species. In captivity, birds in migratory disposition show periods of wing-whirring, together with increased hopping, body-turning and other activities (Berthold 1996). Because cages are usually too small to fly these activities may reflect migrating behavior similar to their free-living conspecifics (Berthold 1996; Gwinner 1996) and indeed, recently Eikenaar et al.

(2014) could show in northern wheatears that Zugunruhe is a good proxy for departure likelihood; birds with higher Zugunruhe left the stopover site earlier than birds with lower Zugunruhe. However, although good knowledge about factors affecting departure likelihoods, we almost know nothing about the physiological mechanism that signals a bird to depart from stopover.

Corticosterone, the main glucocorticoid hormone in birds, is most frequently linked with the stress response: corticosterone levels increase steeply when birds are confronted with emergency situations such as bad weather conditions or predation events (Wingfield, 1994). In contrast, at baseline and moderately elevated levels, corticosterone plays an important role to regulate the intake, storage and mobilization of energy during predictable life-history stages, such as migration (Landys et al. 2006). Indeed, elevated baseline levels of corticosterone were found in a variety of avian species during spring migration (e.g. Holberton et al. 1996; Holberton 1999). In captive red knots (*Calidris canutus*) the plasma baseline corticosterone concentrations more than doubled when energy storage for migration was complete and dropped to a very low level when they started their voluntary fasts after unsuccessful breeding seasons (Piersma et al. 2000). Also, bar-tailed godwits (*Limosa lapponica*) refueling at a stopover site, showed highest corticosterone levels immediately prior to departure (Landys-Cianelli et al. 2002). When energy storage is complete, corticosterone may function to mobilize stored energy that is needed for the oncoming flight bout, for example through elevation of plasma free fatty acids (Landys-Cianelli et al. 2002; Landys et al. 2006).

There is evidence that corticosterone directly stimulates locomotive activity (Belthof and Dufty 1998; Breuner et al. 1998) but these studies measured activity in birds that were not in a migratory disposition. However, in captive white-crowned sparrows (*Zonotrichia leucophrys gambelli*) at spring migration, corticosterone levels showed an increase during the early-night period when Zugunruhe is at its maximum (Landys et al. 2004). Also Löhmus et al. (2002) showed in red eyed vireos (*Vireo olivaceus*), that birds with corticosterone levels higher than the average presented more activity in

orientation cages than those with lower corticosterone-levels (but see Holberton et al. 2007). However, as these birds were sampled after having spent hours in cages, corticosterone levels might reflect capture stress instead of true baseline corticosterone levels. In the study of Eikenaar et al. (2013) on the role of corticosterone as a promoter of refueling in northern wheatears, they found results that are in line with the idea that corticosterone may function as a departure cue. For that, two subspecies of northern wheatears were studied during their simultaneous stopovers on Helgoland, a small German offshore island. Wheatears belonging to the *oenanthe* subspecies are known to make shorter stopovers on Helgoland than *leucorhoa* wheatears (Dierschke and Delingat 2001; Dierschke et al. 2005). Consequently, *oenanthe* wheatears are more likely to depart the night after trapping than *leucorhoa* wheatears (Dierschke and Delingat 2001; Dierschke et al. 2005). Eikenaar et al. (2013) found higher corticosterone levels in *oenanthe* wheatears than *leucorhoa* wheatears, which indirectly supports the idea that corticosterone signals migratory readiness.

To test the idea that corticosterone functions as a departure cue we caught northern wheatears (*Oenanthe oenanthe*) during their fall stopover on Helgoland. We determined their baseline corticosterone levels and linked this to the amount of Zugunruhe in the first night after capture. Furthermore, 16 of these birds were fitted with radio-transmitters to precisely determine their stopover duration. All 16 birds were released the same day to avoid different weather conditions.

If corticosterone indeed is involved in departure likelihood we hypothesize: (1) a positive correlation between baseline corticosterone-levels and Zugunruhe: birds with higher baseline corticosterone-levels are expected to show more Zugunruhe during the first night after capture compared to birds with low baseline corticosterone-levels, and (2) birds with higher baseline corticosterone-levels are expected to depart earlier than birds with lower baseline corticosterone-levels.

# *Methods*

## *Study site and field methods*

Data were collected on the small island Helgoland (54°11'N, 07°55'E), ca. 50km off the German coastline. In 2013, at the peak of autumn migration (mid-August until the end of September) northern wheatears were caught between 7 am and 7 pm and all birds were caged for three days. Because wheatears are small insectivores (ca. 25g), spring traps were baited with mealworms. In northern wheatears, corticosterone increases dramatically due to stress after two minutes from capture (Eikenaar *et al.* 2013). To get baseline-levels of corticosterone, traps were observed continuously and a blood sample (ca. 100 µl) was taken from the brachial vein within two minutes from capture (time was recorded). The plasma was separated with a centrifuge no longer than 5h after capture and frozen at -20°C until hormone assaying. All birds were ringed, aged (first year birds show a yellow inner mandible) according to Svensson (1992) and sexed via molecular sexing in the lab. Wing lengths were measured according to Svensson (1992) for fuel load calculation (see below) and subspecies determination. Birds were weighed to the nearest 0.1g using an electronic scale. Fat stores were scored according to Kaiser (1993) ranging from 0 (no fat) to 8 (furcula and abdomen overlapped with fat) and muscle stores according to Bairlein (1994) ranging from 0 (sternum sharp, muscle depressed) to 3 (breast muscle overlaps sternum). Within an hour after capture, birds were placed into individual cages (40x40x30cm) with a maximum of 20 birds in a single indoor room. During the study, the temperature was held constant at approx. 20°C and lights (artificial light source) went on every morning at 7 a.m. and off at 9 p.m.. All birds had *ad libitum* access to water and each morning after lights were switched on, all birds were weighted to nearest 0.1g. Every morning when light switched on each bird got a food tray with 30g of mealworms per day and when the light switched off food trays were removed. During the autumn season we caught 83 wheatears. 51 birds of these 83 were

females and 32 were males. Out of the 83 trapped birds 48 birds belonged to the *leucorhoa* subspecies and 28 birds belonged to the *oenanthe* subspecies. 11 birds did not allow a determination of the subspecies because wing lengths were in the overlapping area of the two subspecies. In total we caught 65 juveniles and 28 adult wheatears.

Zugunruhe was recorded automatically following Eikenaar and Schläfke (2013) with motion-sensitive microphones (developed by R. Nagel, Wilhelmshaven, Germany) attached to right wall of the cages. Each time a bird moved, an impulse was sent to a recording device (developed by S.F. Fischer, Bremen, Germany). To avoid the recording of occasional non-migratory activity, we set a threshold of 3 impulses per second before it was recorded as an activity count. Another device (developed by S.F. Fischer, Bremen, Germany) constructed a CSV file summarizing all activity counts over 15 minute periods. We then expressed Zugunruhe following Maggini and Bairlein (2013) as the number of 15 min intervals in which a bird showed at least five activity counts in a period of time between 1-5.5h after lights off. We used this time frame because Schmaljohann et al. (2013) could show that northern wheatears leave Helgoland only at night between 1-5.5h after sunset. We also calculated the intensity of Zugunruhe by summing up the total number of activity counts in a period of time between 1-5.5h after lights went off.

Within the first 4 days of the season we caught 16 birds. In all birds we measured Zugunruhe in each night of the 4 days of captivity. All 16 birds were fitted with a 0.42g Holohil BD-2N radio-transmitter. To avoid weather affecting departure decisions, all birds were released on the same day between 3-4 PM. Using a Yaesu FT-290RII receiver and a Yagi hand-held antenna we searched for all tagged birds from 16 fixed locations to cover the whole island every day and every night until we did not receive a signal on three consecutive days. A bird was considered to have departed when we had no signal three days in row. All approaches were carried out under license of the Ministry for Agriculture, the Environment and rural Areas, Schleswig-Holstein, Germany.



### *Corticosterone assay*

To determine corticosterone plasma levels we used enzyme immunoassay kits (Enzo Life Sciences, Inc., former Assay Designs) following Eikenaar et al. (2013). We diluted 15 µl of Plasma in 200µl double distilled water. To extract corticosterone from plasma we added 4 µl of dichloromethane. The dichloromethane containing the extracted corticosterone was aspirated with a disposable Pasteur pipette and evaporated in a water bath at 48°C. We re-dissolved the remaining corticosterone in 250µl assay buffer and analyzed corticosterone in duplicates following the kit manufacturer's protocol (with the only difference that we used a six point standard curve with a range of 20,000–15.63pg/ml). We ran an external standard in duplicate on each plate for calculation of intra-and inter-assay variation. Furthermore, pooled wheatear plasma samples were spiked with corticosterone standard from the kit, to determine extraction efficiency. Recoveries of the low (1ng/ml), intermediate (2.5ng/ml) and high (10ng/ml) spikes were 87%, 93% and 71%, respectively (Eikenaar et al. 2013). The intra variation ranged from 0.25% to 4.35%, and the inter-assay variation was 10.98 %. The lowest detectable limit in our assay was 0.54 ng/ml and two samples were set to this threshold of detection because these sample were under the threshold.

### *Variables and statistics*

We performed all analysis using the statistical software package R 2.13.1 (R Development Core Team 2011). We analyzed the effect of several independent variables on Zugunruhe and Zugunruhe intensity (as defined above). In the model fuel load was included due to Eikenaar and Schläpke (2013) found in wheatears a positive correlation with Zugunruhe at spring migration. For this fuel load was calculated for each bird as: Fuel load= (Body mass (g) - Lean body mass (g))/ Lean body mass (g), where Lean body mass was estimated after Schmaljohann and Naef- Daenzer (2011). Following Schmaljohann and Naef- Daenzer (2011), we calculated lean body mass from

wing length using a linear regression based on 220 'lean' wheatears: lean body mass (g) =  $0.29\text{mm}^{-1} \times \text{wing length (mm)} - 6.85\text{g}$  (linear regression:  $n= 220$ ,  $F_{1,218}= 95.07$ ,  $\text{adj-}R^2 = 0.30$ ,  $P<0.001$ ). Because of a strong positive correlation between the calculated fuel load and the visual scores of fat (spearman's  $\rho = 0.5$ ,  $p<0.001$ ,  $n=92$ ) and due to the more objective estimate of fuel load, we used Fuel load for all analyses. Date of capture was also included in the model due to the fact that the progress in the season is influencing migration activity, as that birds later in the season could be in hurry to reach wintering/or breeding areas (Aebischer et al. 1996, Lozano et al. 1996, Currie et al. 2000). Zugunruhe data were not normally distributed with a high amount of zero counts where 52% of all bird we caught showed no Zugunruhe. We therefore performed generalized linear models (GLM) with a negative binomial distribution and log-link function to examine relationships between Zugunruhe/Zugunruhe intensity, corticosterone level, fuel load and date of capture with the full data set including all zero counts. GLM's with negative binomial distributions are used for count data with a high amount of zeros and where the observed variance is higher than the estimated variance of a model, so called over-dispersion. For the transmitter experiment we also ran a GLM with negative binomial distribution and log-link function. The number of nights stayed on Helgoland after release was set as the dependent variable, and corticosterone level and change in fuel load from capture to release were entered as independent variables. We used change of fuel load instead of fuel load of capture due to fact that these birds we held in captivity for a varying number of days. To normalize corticosterone data, we  $\log_{10}$ -transformed corticosterone levels prior to all analyses.

# Results

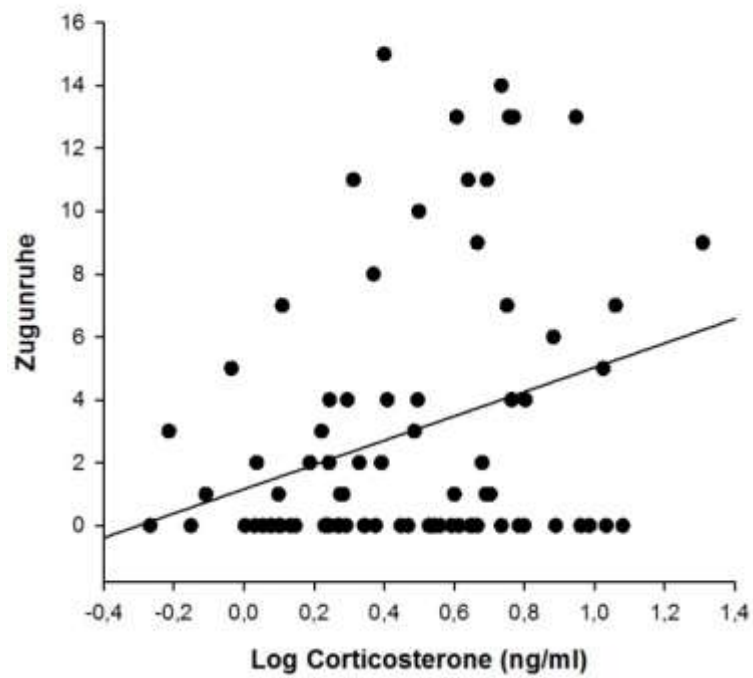
## *Corticosterone and Zugunruhe*

As shown in table 1, a strong positive relationship was found between corticosterone level and Zugunruhe (negative binomial GLM:  $n=83$ ,  $\beta \pm SE = 1.66 \pm 0.44$ ,  $z\text{-value} = 2.73$ ,  $P < 0.006$ , figure 1a). Birds that had higher corticosterone levels showed more Zugunruhe in the first night after capture than birds with low corticosterone levels. We found no relationship between Zugunruhe and fuel load (negative binomial GLM:  $n=83$ ,  $\beta \pm SE = 0.15 \pm 1.97$ ,  $z\text{-value} = 0.08$ ,  $P = 0.94$ ) and neither between Zugunruhe and date of capture (negative binomial GLM:  $n=83$ ,  $\beta \pm SE = 0.03 \pm 0.018$ ,  $z\text{-value} = 2.73$ ,  $P = 0.10$ ). Results were very similar when Zugunruhe intensity was expressed as the total number of activity within one night. Zugunruhe intensity positive correlates with corticosterone (negative binomial GLM:  $n=83$ ,  $\beta \pm SE = 2.04 \pm 0.78$ ,  $z\text{-value} = 2.62$ ,  $P < 0.009$ , figure 1b) but no relationship was found with fuel load (negative binomial GLM:  $n=83$ ,  $\beta \pm SE = 2.23 \pm 2.60$ ,  $z\text{-value} = 0.86$ ,  $P = 0.39$ ) and date of capture (negative binomial GLM:  $n=83$ ,  $\beta \pm SE = -0.04 \pm 0.02$ ,  $z\text{-value} = -1.85$ ,  $P = 0.06$ ).

Table1. GLM with corticosterone, date of capture and fuel load as independent variables and Zugunruhe as the dependent variable. Note that estimates for corticosterone should be interpreted in terms of  $\log_{10}$ -transformed corticosterone levels.

	Estimate	Std. Error	z value	Pr(> z )
Intercept	0.72	0.44	1.60	0.103
Corticosterone	1.66	0.61	2.73	<b>0.006</b>
Date of capture	0.03	0.018	-1.64	0.100
Fuel load	0.15	1.97	0.08	0.938

a)



b)

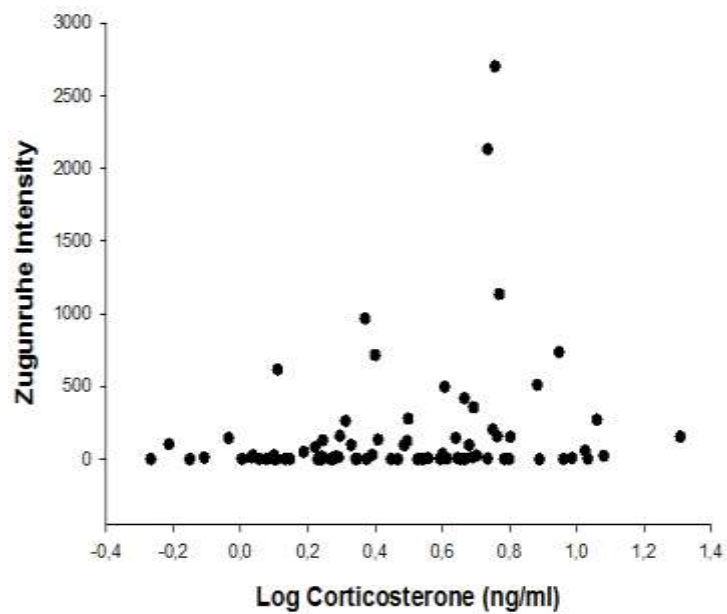


Figure 1. Relationship between baseline corticosterone-level and Zugunruhe in the night after capture as a) the number of 15 min periods in which a bird showed at least five activity counts in a period of time between 1-5.5h after lights off, and b) the total number of activity counts in a period of time between 1-5.5h after lights off. (n =83).

### *Corticosterone and departure latency*

Baseline corticosterone level at capture was negatively correlated with the number of nights stayed on Helgoland after release (negative binomial GLM:  $n=16$ ,  $\beta \pm \text{SE} = -5.72 \pm 2.72$ ,  $z\text{-value} = -2.1$ ,  $P = 0.036$ , Figure 2). Birds with higher corticosterone levels departed earlier than those birds with lower levels of corticosterone. The change in fuel load from capture to release showed a negative trend on the number of nights stayed on Helgoland (negative binomial GLM:  $n=16$ ,  $\beta \pm \text{SE} = -31.09 \pm 17.85$ ,  $P = 0.082$ ). Birds which gained more fuel during confinement departed earlier from stopover site than birds which gained less fuel.

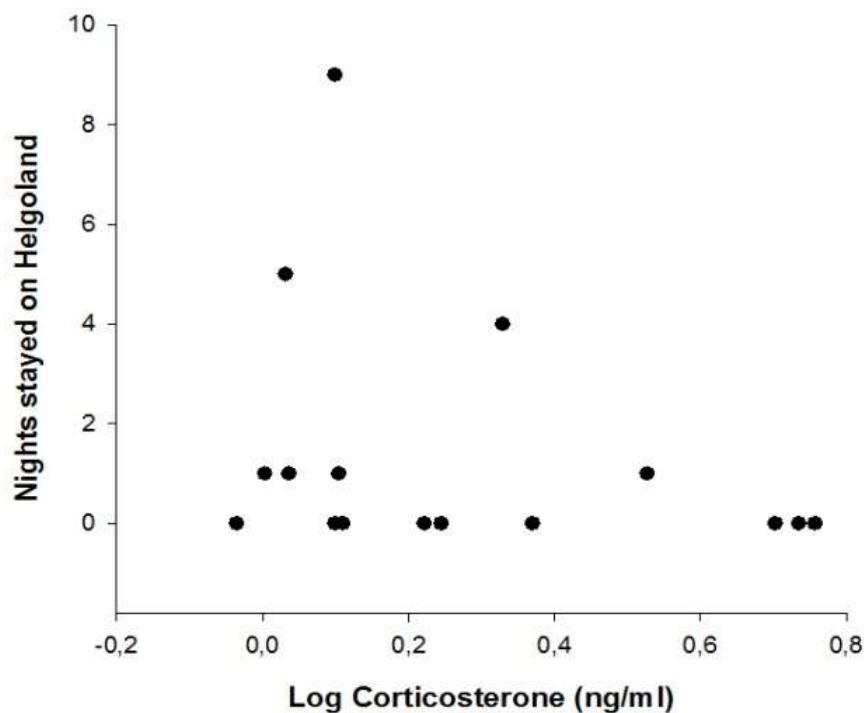


Figure 2. Relationship between corticosterone level at capture and the number of nights northern wheatears stayed on Helgoland after release from temporary captivity ( $n=16$ ).

## Discussion

In this study we show that corticosterone might be involved in the regulation of departure from stopover in a long-distance migrant. Birds with higher corticosterone levels showed higher Zugunruhe (migratory restlessness) than birds with lower corticosterone levels. Furthermore, we found a trend that the likelihood to depart from a stopover-site, determined by radio-telemetry, increased when birds had higher baseline corticosterone levels. In a variety of migrating bird species, studies found increased adrenal activity and elevated plasma corticosterone-levels (Naik and George 1963; Holberton et al. 1996; Romero et al. 1997; Piersma and Ramenofsky 1998; Holberton 1999; Piersma et al. 2000). Our results are also in line with previous studies which showed that corticosterone might be a direct stimulus for locomotion and migratory restlessness (Belthof and Dufty 1998; Breuner et al. 1998; Landys et al. 2002, Löhmus et al. 2003 2004). Possibly, when energy storage is complete, corticosterone might be up regulated and signals a bird to depart. We can only speculate how this physiological mechanism acts. In adult Japanese quail (*Coturnix coturnix japonica*) the hormone ghrelin inhibits food intake (Shousha et al. 2002). On the other Hand we know that increasing ghrelin leads to stimulation of corticosterone release (see review Kaiya et al. 2013). So, if a bird is ready to depart he should have accumulated enough energy to cover the next flight bout. The energy storage is complete and ghrelin could then act as signal for satiety that tells the individual to stop accumulating more energy. When ghrelin increases corticosterone starts to release and this increasing of baseline corticosterone level could then lead to an actual stimulation of the locomotion activity that is required for departure from stopover. Additionally, corticosterone may function to mobilize stored energy that is needed for the oncoming flight bout, for example through elevation of plasma free fatty acids (Landys-Cianelli et al. 2002, Landys et al. 2006).

In contrast to northern wheatears that were studied in spring migration

(Marginni and Bairlein 2013, Eikenaar et al. 2013), we found no relationship between fuel load and Zugunruhe in autumn migration. Possibly, in autumn, birds are not in a hurry to reach wintering sites, as they are in spring to reach their breeding grounds. The early arrival in spring migration houses some advantages, for example higher reproductive success: Being one of the first back in the breeding grounds allows occupying the best territories and thus mating with the most attractive partner (Aebischer et al. 1996, Lozano et al. 1996, Currie et al. 2000). Arriving earlier in the wintering grounds may have no, or only a small, fitness gain for individuals and therefore birds at autumn migration might take more stops. The pressure on high fuel loads seems, for that, to be low. Furthermore, to continue migration from Helgoland in autumn, crossing the North Sea in order to reach the mainland takes only 50 km. For wheatears, covering these 50 km might be not a high challenge, so also lean birds should cover this stretch easily. Especially if we consider that most of the birds we trapped belonged to the *leucorhoa* subspecies which are able to fly thousands of kilometers over the open sea. Whereas in spring, birds on Helgoland have to travel longer distances on their way to the breeding grounds to cross the open water. To bridge this ecological barrier it might be necessary to have a higher fuel load then in autumn.

In this study more than half of the birds showed no migratory restlessness in the first night of captivity. In contrast to earlier studies (Maginni and Bairlein 2013; Eikenaar et al. 2013), this is an unexpectedly large proportion of birds. Caging could have stressed part of the birds (Wingfield 1982) and stress could lead to a motionless behavior. However, corticosterone levels in temporarily confined wheatears are only moderately elevated and still at a baseline level (unpublished data) and for this, stress reactions to the caging event of individuals of our study seems an unlikely explanation. There is a lack of knowledge what birds do after they arrive on stopover sites. A few observations could find that birds after landing need to sleep (Schwilch et al. 2001). In long distant migrants flying non-stop over big ecological barriers, the urge to sleep may take

precedence over other activities (Schwilch et al. 2001).

In our study, the individuals that showed no Zugunruhe during the first night of captivity perhaps compensated for sleep deprivation. In autumn, wheatears of the *leucorhoa* subspecies may fly non-stop over the ocean from the Faroe Islands or the Shetlands to Helgoland. *Oenanthe* wheatears do not make such barrier crossings (Dierschke and Delingat 2001). Interestingly, the proportion of birds without Zugunruhe was higher in the *leucorhoa* than in the *oenanthe* subspecies. Of the 48 *leucorhoa* wheatears, 28 (54%) showed no Zugunruhe in the first night of capture whereas out of 28 *oenanthe* wheatears only 9 (34%) showed no Zugunruhe ( $\chi^2=3.44$ ,  $df=1$ ,  $P=0.064$ ). Sleep compensation thus seems a plausible explanation for the motionless behavior in the first night of captivity, at least in the *leucorhoa* subspecies.

In conclusion, our results consistently support the idea that corticosterone is involved in the regulation of departure from stopover. To infer causality between corticosterone and departure from stopover, in future studies corticosterone levels need to be experimentally manipulated. Furthermore, future studies should ascertain how corticosterone is up regulated in migrants that are ready to depart from stopover.



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## References

- Aebischer, A., Perrin, N., Krieg, M., Studer, J., Meyer, D.R. 1996. The role of territory choice, mate choice and arrival date on breeding success in the Savi's Warbler *Locustellalus cinioides*. *Journal of Avian Biology*, 27, 134–152.
- Bairlein, F. 1985. Body weight and fat deposition of Palaearctic passerine migrants in the central Sahara. *Oecologia* 66, 141–146.
- Bairlein, F. 1994. *Manual of Field Methods. European-African Songbird Migration*. Institut für Vogelforschung, Wilhelmshaven, Germany.
- Belthof, J.R., Dufty Jr., A.M. 1998. Corticosterone, body condition and locomotor activity: a model for dispersal in screech owls. *Anim. Behav.* 55, 405–415.
- Berthold P. 1996. *Control of bird migration*. Berlin, Germany: Springer.
- Breuner, C.W., Greenberg, A.L., Wingfield, J.C. 1998. Noninvasive corticosterone treatment rapidly increases activity in Gambel's white-crowned sparrows (*Zonotrichia leucophrys gambelii*). *Gen.Comp.Endocrinol.* 111, 386–394.
- Currie, D., Thompson, D.B.A., Burke, T. 2000. Patterns of territory settlement and consequences for breeding success in the Wheatear *Oenanthe oenanthe*. *Ibis*, 142, 389–398.
- Dierschke, V., Delingat, J. 2001. Stopover behaviour and departure decision of northern wheatears, *Oenanthe oenanthe*, facing different onward non-stop flight distances. *Behavioural Ecology and Sociobiology*, 50, 535–545.
- Dierschke, V., Mendel, B., Schmaljohann, H. 2005. Differential timing of spring migration in northern wheatears *Oenanthe oenanthe*: hurried males or weak females? *Behavioural Ecology and Sociobiology*, 57, 470–480.

- Eikenaar, C., Schläpke, J.L. 2013. Size and accumulation of fuel reserves predict nocturnal restlessness in a migratory bird. Biol. Lett. <http://dx.doi.org/10.1098/rsbl.2013.0712>.
- Eikenaar, C., Fritsch, A., Bairlein, F. 2013. Corticosterone and migratory fueling in Northern wheatears facing different barrier crossings. Gen. Comp. Endocrinol. 186, 181–186.
- Eikenaar, C., Kliner, T., Szostek, K.L., Bairlein, F. 2014. Migratory restlessness in captive individuals predicts actual departure in the wild. Biol. Lett. <http://dx.doi.org/10.1098/rsbl.2014.0154>.
- Farmer, A. H., Wiens, J. A. 1999. Models and reality: time-energy trade-offs in pectoral sandpiper (*Calidris melanotos*) migration. Ecology 80: 2566–2580.
- Gwinner, E. 1996. Circadian and circannual programmes in avian migration. J. Exp. Biol. 199: 39–48
- Holberton R. L., Parrish J.D., Wingfield J.C. 1996. Modulation of the adrenocortical stress responses in neotropical migrants during autumn migration. Auk 113:558–564
- Holberton, R.L. 1999. Changes in patterns of corticosterone secretion concurrent with migratory fattening in a neotropical migratory bird. Gen. Comp. Endocrinol. 116, 49–58.
- Holberton, R.L., Wilson, C.M., Hunter, M.J., Cash, W.B., Sims, C.G. 2007. The role of corticosterone in supporting migratory lipogenesis in the dark-eyed junco, *Junco hyemalis*: a model for central and peripheral regulation. Physiol. Biochem. Zool. 80, 125–137.
- Jenni, L., Schaub, M. 2003. Behavioural and physiological reactions to environmental variation in bird migration: a review. In: Berthold, P.,

- Gwinner, E., Sonnenschein, E. (Eds.), Avian Migration. Springer, Berlin-Heidelberg, pp. 155–171.
- Kaiser, A. 1993. A new multi-category classification of subcutaneous fat deposits of song birds. *J. Field. Ornithol.* 64, 246–255.
- Kaiya, H., Kangawa, K., Miyazato, M. 2013. Update on ghrelin biology in birds. *General and comparative endocrinology*, 190, 170-175.
- Landys, M.M., Ramenofsky, M., Guglielmo, C.G., Wingfield, J.C. 2004. The low- affinity glucocorticoid receptor regulates feeding and lipid breakdown in the migratory Gambel's white-crowned sparrow *Zonotrichia leucophrys gambelii* . *J. Exp. Biol.* 207, 143–154.
- Landys, M.M., Ramenofsky, M., Wingfield, J.C. 2006. Actions of glucocorticoids at a seasonal baseline as compared to stress-related levels in the regulation of periodic life processes. *Gen. Comp. Endocrinol.* 148, 132–149.
- Landys-Cianelli, M.M., Ramenofsky, M., Piersma, T., Jukema, J., Castricum Ringing Group, Wingfield, J.C. 2002. Baseline and stress-induced plasma corticosterone during long-distance migration in the bar-tailed godwit, *Limosa lapponica* . *Physiol. Biochem. Zool.* 75, 101–110.
- Lindström, Å., Alerstam, T. 1992. Optimal fat loads in migrating birds: a test of the time-minimization hypothesis. *American Naturalist*, 140, 477–491.
- Lozano, G.A., Perreault, S., Lemon, R.E. 1996. Age, arrival date and reproductive success of male American Redstarts *Setophaga ruticilla*. *Journal of Avian Biology*, 27, 164–170.
- Löhmus, M., Sandberg, R., Holberton, R.L., Moore, F.R. 2003. Corticosterone levels in relation to migratory readiness in red-eyed vireos (*Vireo olivaceus*). *Behav. Ecol. Sociobiol.* 54, 233–239.

- Lõhmus, M., Sundström, L.F., Moore, F.R. 2006. Non-invasive corticosterone treatment changes foraging intensity in red-eyed vireos *Vireo olivaceus*. J. Avian Biol. 37, 523–526.
- Lundgren, B. O., Kiessling, K.-H. 1985. Seasonal variation in catabolic enzyme activities in breast muscle of some migratory birds. Oecologia 66, 468–471.
- Maggini I, Bairlein F. 2012. Innate Sex Differences in the Timing of Spring Migration in a Songbird. PLoS ONE 7(2): e31271. doi:10.1371/journal.pone.0031271
- Naik, D. V., George, J. C. 1963. Histochemical demonstration of increased corticoid level in the adrenal of *Sturnus roseus* (Linnaeus) towards the migratory phase. *Pavo*, 1, 103–105.
- Piersma T., Ramenofsky M. 1998. Long-term decreases of corticosterone in captive migrant shorebirds that maintain seasonal mass and moult cycles. J Avian Biol 29:97–104.
- Piersma, T., Reneerkens, J., Ramenofsky, M. 2000. Baseline corticosterone peaks in shorebirds with maximal energy stores for migration: a general preparatory mechanism for rapid behavioural and metabolic transitions? Gen. Comp. Endocrinol. 120, 118–126
- Romero L.M., Ramenofsky M., Wingfield J.C. 1997. Season and migration alters the corticosterone response to capture and handling in an Arctic migrant, the White-crowned sparrow (*Zonotrichia leucophrys gambelii*). Comp Biochem Physiol 116C:171–177
- Schaub, M., Jenni.L. 2000. Fuel deposition of three passerine bird species along the migration route. Oecologia 122:306–317

- Schmaljohann, H., Dierschke, V. 2005. Optimal bird migration and predation risk: a field experiment with northern wheatears *Oenanthe oenanthe*. *J. Anim. Ecol.* 74, 131–138.
- Schmaljohann, H., Naef-Daenzer, B. 2011. Body condition and wind support initiate the shift of migratory direction and timing of nocturnal departure in a songbird. *J. Anim. Ecol.* 80, 1115–1122.
- Schmaljohann H., Rautenberg T., Muheim R., Naef-Daenzer B., Bairlein F. 2013 Response of a free-flying songbird to an experimental shift of the light polarization pattern around sunset. *J Exp Biol* 216: 1381-1387
- Schwilch, R., Piersma, T., Holmgren, N., Jenni, L. 2002. Do migratory birds need a nap after a long non-stop flight?. *Ardea*, 90(1), 149-154.
- Svensson, L. 1992. Identification Guide to European Passerines, fourth ed. Stockholm
- Wingfield, J. C. 1994. Modulation of the adrenocortical response to stress in birds. *In* K. G. Davey, R. E. Peter, and S. S. Tobe (eds.), *Perspectives in comparative endocrinology*, pp. 520-528. National Research Council Canada, Ottawa.