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Research paper

An exception to the rule: Captivity does not stress wild migrating northern wheatears

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ABSTRACT

Wild animals typically suffer from stress when brought into captivity. This stress is characterized by elevated circulating glucocorticoid levels and weight loss. We here describe for the first time a case where a wild animal, the long-distance migrating northern wheatear, does not show signs of stress when caged. We captured these birds on a stopover site during their spring migration and caged them individually with ad libitum access to food and water. The birds were divided into four groups and were blood-sampled immediately in the field, a few hours after caging, one day after caging, or three days after caging, respectively. From these blood-samples we determined circulating corticosterone level. Food intake and body mass were also monitored. We found that, with very few exceptions, corticosterone levels were low and did not differ among the groups. Accordingly, almost all birds consumed huge quantities of food and substantially increased their body mass. Together these results clearly show that caging does not result in indications of stress in wild migrating northern wheatears. Confinement-specific conditions such as restricted movement normally stress animals. We suggest migratory birds may not perceive such conditions as stressors due to their hyperphagic state, a notion that requires further testing.

1. Introduction

Wild animals may be brought into captivity for conservation and/or scientific purposes. Confinement typically stresses wild animals, which physiologically is characterized by an increased release of glucocorticoid hormones (corticosterone or cortisol) (e.g. Wingfield et al., 1982; Mathies et al., 2001; Portz et al., 2006; Titon et al., 2017; Fischer et al., 2018). An increase in circulating glucocorticoids shifts metabolism towards energy mobilization and stimulates locomotion, allowing the animal to escape from the adverse conditions that brought about the hormonal surge (Wingfield et al., 1998; Sapolsky et al., 2000). Caged wild animals, however, have nowhere to escape to, and the behavioural and physiological changes adaptive under natural conditions may be deleterious under caged conditions (Morgan and Tromborg, 2007); whereas in free-living animals feed-back mechanisms ascertain glucocorticoids return to baseline levels after the cessation of the stressor, in caged wild animals glucocorticoid levels usually remain elevated for days or sometimes even weeks (e.g. Marra et al., 1995; Dickens et al., 2009; Kuhlman and Martin, 2010; Adams et al., 2011; Fokidis et al., 2011; de Assis et al., 2015; Lattin et al., 2017; Love et al., 2017; Titon et al., 2017; Fischer et al., 2018). These persistent high glucocorticoid levels possibly are causative of the loss of body mass often occurring in the early stages of captivity (e.g. Dickens et al., 2009; Angelier et al., 2016; Lattin et al., 2017; Love et al., 2017; Titon et al., 2017; Fischer et al., 2018). Body mass loss may result from elevated locomotor activity and/or reduced food intake; loss of appetite is one of the effects of elevated glucocorticoid levels (Sapolsky et al., 2000). Surprisingly little, however, is known about food intake by temporarily caged animals.

Many of the studies measuring the effect of temporary confinement on glucocorticoid levels have been conducted on sedentary (non-migratory) bird species (Dickens et al., 2009; Kuhlman and Martin, 2010; Fokidis et al., 2011; Angelier et al., 2016; Lattin et al., 2017; Love et al., 2017; Fischer et al., 2018). Sedentary birds differ from migratory birds in many aspects, but one remarkable adaptation to migration that may be relevant to how wild birds react to being caged is that during the migration period birds become hyperphagic. When making a stopover in between endurance flights, birds spent a large part of their time foraging in order to replenish their fuel stores (Ilyina and Grachova, 1990; Dierschke et al., 2003). Hyperphagia results in substantial body mass increases over short time periods (Bairlein, 1985; Bairlein and Gwinner, 1994; Lindström, 2003). Interestingly, extreme food intake and rapid body mass increase by migratory birds do not only occur in the field, but have also been observed in migrants caught at stopover sites and temporarily caged with ad libitum access to food. For

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example, northern wheatears (*Oenanthe oenanthe*) can eat (mealworms) up to the equivalent of their body mass in a single day, and, by that, rapidly increase their body mass and fuel stores (Corman et al., 2014; Eikenaar et al., 2015). These observations strongly contrast with the general pattern of body mass loss in caged sedentary birds and suggest that migratory birds exhibiting hyperphagia do not experience temporary confinement as a stressor. Perhaps, therefore, migrating birds upon caging may not, or only briefly, upregulate their corticosterone levels. Some potential support for this idea comes from a study by Wingfield et al. (1982) on Gambel's white-crowned sparrows (*Zonotrichia leucophrys gambelli*), a migratory bird. Wild individuals were captured from wintering flocks (October-January) and caged in environmental chambers with a photoperiod mimicking autumn day length. Subsequent sampling revealed that one day after caging corticosterone levels were increased and body mass decreased as compared to measurements taken immediately after capture in the field, but that these differences had disappeared after four days in captivity (Wingfield et al., 1982). This suggests that somewhere in between one and four days of caging, the birds had acclimatized to being in captivity and started eating. Unfortunately, food intake was not measured and it was unclear whether the birds were in a migratory state.

Here we investigated how wild hyperphagic migrants react to captivity. For this, we caught and temporarily caged wild northern wheatears (wheatears hereafter) at a stopover site during their spring migration. Wheatears are small (ca. 25 g) nocturnal long-distance migrants, and we have previously suggested that caging does not stress these birds (Eikenaar et al., 2018a), a suggestion based on the observation that most individuals consume large amounts of food while in captivity. In the current study we determined how long after caging the birds' started to feed and monitored their changes in body mass. Blood samples to determine corticosterone levels were taken on the day of caging, and on the first and third full days of captivity. Each bird was sampled only once. To obtain a reference corticosterone level, other wheatears were sampled immediately after capture in the field. All samples were taken in the second half of the afternoon to minimize any possible effect that time of day may have on corticosterone level. Migrants' corticosterone levels have been found to increase over the migration season, at least in autumn (Falsone et al., 2009; Eikenaar et al., 2017, 2018b). To exclude a potential seasonal effect, captures of the individuals assigned to each of the four blood-sampling groups were spread equally over the study period.

We hypothesized that being in captivity does not stress wheatears. We therefore expected that the birds start to feed when corticosterone levels have returned to baseline after handling at transfer into the cages, which in (long-term captive) wheatears occurs somewhere between 30 min and 1 h after handling (C. Eikenaar, unpubl. data). Furthermore, we expected that corticosterone levels do not differ between free-flying individuals and individuals sampled while in captivity, with the possible exception of birds sampled on the third day in captivity. The reason for this exception is that in migrating birds corticosterone, at baseline levels, appears to mediate between cues that signal the birds when to depart from a stopover site, such as the size of the fuel stores and weather conditions, and actual departure (Eikenaar et al., 2017, 2018a,b). Refueling by temporarily caged wheatears results in a stronger departure cue from the fuel stores, which in its turn could lead to increased corticosterone levels.

2. Methods

2.1. Field 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. Northern wheatears are common migrants on Helgoland, but rarely breed there (Dierschke et al., 2011). In April and May 2018, 68 northern wheatears were caught using mealworm-baited spring traps. The traps were monitored continuously and upon capture 17 birds used to obtain reference corticosterone levels were blood-sampled (ca. 70 µl) from the wing vein. All samples were taken within 2 min from closing of the trap and thus represent true baseline levels (Eikenaar et al., 2013). The plasma was separated within 1 h of blood-sampling and frozen at −20 °C until assaying. After blood-sampling, birds were ringed, wing length (maximum chord after Svensson (1992)) was measured to the nearest 0.5 mm, and body mass to the nearest 0.1 g. When these measurements were taken the birds were released. The birds used to obtain reference corticosterone levels were trapped from 16:00 to 17:00 CET. Birds of which corticosterone level was to be determined while in captivity (see below) were not blood-sampled in the field, but otherwise handled as above. Wing length was used to calculate lean body mass (after Schmaljohann and Naef-Daenzer, 2011).

2.2. Caging and sampling

Birds to be caged were trapped from 9:00 to 12:00 CET. Approx. 1 h after trapping, birds were put in individual cages (40x40x30 cm) set up in three indoor rooms with artificial lighting. Throughout the study the lights in the room were switched on at 7:00 and off at 21:00 CET (following Eikenaar and Schläfke, 2013; Eikenaar et al., 2014). The temperature in the rooms was held constant at approx. 20 °C, and birds had ad libitum access to water. Upon caging and each following morning immediately after lights were switched on, a food tray with 40 g of mealworms was placed in each cage. The birds were divided into three groups of 17 birds each, spread equally over the rooms. The birds in the three groups were blood-sampled either on the day of caging, or on the first or third full days of captivity, respectively. One bird was accidentally blood-sampled on the second full day in captivity, and is included here as if blood-sampled on the third full day in captivity. All blood-samples were taken close to 17:00 CET, within 2 min from entering the room. Immediately after blood-sampling, body mass was measured to the nearest 0.1 g, and the amount of food eaten that day was determined by subtracting grams of food left-over from the 40 g. After these measurements were taken the bird was released. When a bird was caged for a full day, daily food intake was determined by subtracting grams of food left-over at lights off from the 40 g. The birds blood-sampled on the day of caging were filmed to determine the time it took them to start feeding. All procedures were approved by the Ministry for Agriculture, the Environment and Rural Areas, Schleswig-Holstein, Germany.

2.3. Corticosterone assay

Corticosterone levels in the blood plasma were determined using enzyme immunoassay kits (Enzo Life Sciences, product number: ADI-901-097). Corticosterone in 15 µl of plasma (diluted in 200 µl H_2Obidest) was extracted with 4 ml dichloromethane. The dichloromethane containing the extracted sample was aspirated with a disposable Pasteur pipette and evaporated in a water bath at 48 °C. The remaining corticosterone was re-dissolved in 250 µl assay buffer and analyzed in duplicates following the kit manufacturer's protocol (with the only difference that we used a 6 point standard curve with a range of 20,000 to 15.63 pg/ml). An external standard was run in duplicate on each plate for calculation of intra-and inter-assay variation. To determine extraction efficiency, pooled wheatear plasma samples were spiked with corticosterone standard from the kit. Recoveries of the low (1 ng/ml), intermediate (2.5 ng/ml) and high (10 ng/ml) spikes were 87%, 93% and 70%, respectively. The intra-assay variation ranged from 1.48% to 3.94%, and the inter-assay variation was 6.2%. The lower limit of detection in our assay was determined by taking two standard deviations below the mean of the blank wells, for which we used the total-binding wells as these only received buffer, conjugate and antibody. This limit was 0.67 ng/ml and was assigned to the four undetectable samples in our study (two were birds sampled in the field

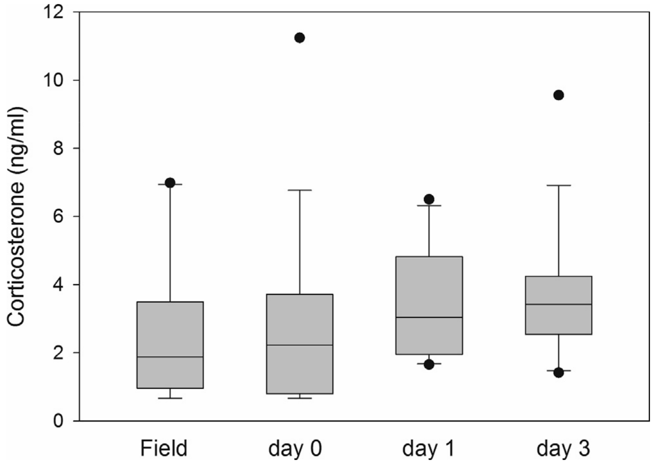

Fig. 1. Boxplots of corticosterone level of northern wheatears at a spring stopover site sampled in the field (Field), on the day of caging (day 0), on the first full day in captivity (day 1), or on the third full day in captivity (day 3). All birds were sampled between 16:00 and 17:00 CET. Plotted are the median, first and third quantiles, 10th and 90th percentiles, and values beyond these percentiles. N = 17 for each group, however, for graphical purposes two birds with extremely high corticosterone levels were not plotted in the graph (28.02 ng/ml, sampled on the day of caging, and 19.52 ng/ml, sampled on the third full day in captivity).

and two were birds sampled on the day of caging).

2.4. Data analysis

Corticosterone data were not normally distributed; however, log-transforming corticosterone level to achieve normality resulted in unequal variances among the four blood-sampling groups. Therefore, we performed a (non-parametric) Kruskal-Wallis H test to test whether (untransformed) corticosterone levels differed among the groups. The test statistic was based on mean ranks. Descriptive results are presented as mean ± SD. All analyses were done using SPSS 24.0 (IBM, New York).

3. Results

The corticosterone levels of the free-flying wheatears were comparable to baseline levels previously observed in migrating wheatears (Eikenaar et al., 2013, 2014, 2017), and were not different from those observed in any of the groups sampled while in captivity (Kruskal-Wallis H (3) = 7.48, p = 0.058, n = 68, Fig. 1). Two individuals showed very high corticosterone levels, indicative of stress. One, sampled on the day of caging had a corticosterone level of 28.02 ng/ml. Another bird, sampled on the third full day in captivity had a corticosterone level of 19.52 ng/ml. Excluding these two individuals from the analysis did not change the results (Kruskal-Wallis H (3) = 7.66, p = 0.054, n = 66).

The birds sampled on the day of caging all consumed food between caging and blood-sampling some 4–7 h later, with the exception of the individual with very high corticosterone level. Most individuals ate some 8–12 g of mealworms, which is about half a wheatear's lean body mass (which was 23.1 ± 1.1 g for the wheatears used in this study). Feeding latency, the time between caging and start of feeding, was 50 ± 36 min (n = 16), with quite a few individuals already feeding in the first half hour of being in the cage (Fig. 2). Corticosterone level was not related with feeding latency (Spearman's rho = −0.26, p = 0.34, n = 16), nor with the rate of food intake (g mealworms/h) once the birds had started to eat (Spearman's rho = −0.04, p = 0.88, n = 16).

For the 17 birds sampled on the third full day in captivity we could calculate daily food intake, which was very high: 26.9 ± 7.9 g and 28.1 ± 8.2 g in the 1st and 2nd full day in captivity, respectively. In these birds, the change in body mass from capture until sampling three days later was 8.3 ± 5.1 g. The bird with very high corticosterone level on the third day (19.52 ng/ml) did eat, but much less than the other birds, and consequently lost body mass (a reduction of 3.7 g). When excluding this bird, daily food intake was 28.1 ± 6.4 g and 29.1 ± 7.3 g in the 1st and 2nd full day in captivity, and the hange in body mass from capture to sampling was 9.0 ± 4.1 g.

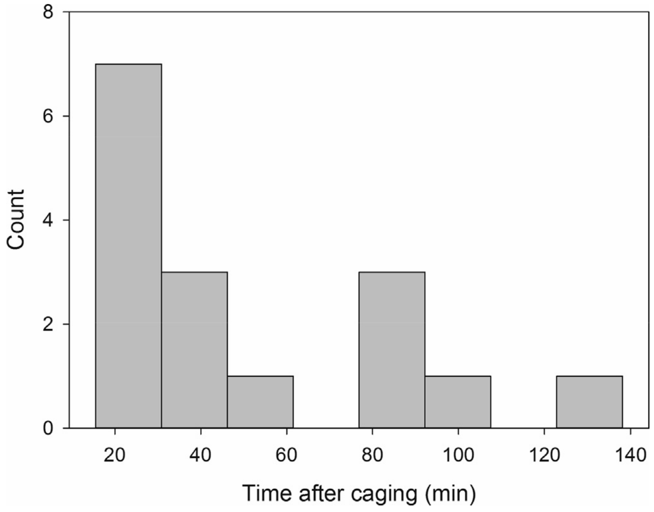

Fig. 2. Histogram of the time between caging and the start of feeding by northern wheatears caught at a spring stopover site (n = 16).

4. Discussion

Our study is, to our best knowledge, the first deviation from the norm that animals when brought into captivity suffer from stress (e.g. Mathies et al., 2001; Portz et al., 2006; Dickens et al., 2009; de Assis et al., 2015; Angelier et al., 2016; Lattin et al., 2017; Love et al., 2017; Titon et al., 2017; Fischer et al., 2018). We caged wild migrating wheatears at a stopover site and found that most individuals start to feed soon after being caged, often within 30 min. Food intake was generally very high with food intake over a full day typically exceeding the birds' own lean body mass. This hyperphagia led to substantial increases in body mass. Furthermore, corticosterone levels were not different between birds sampled in the field and birds sampled while caged, and were comparable to those previously observed in free-flying migrating wheatears (Eikenaar et al., 2013, 2014, 2017). Even those birds sampled only a few (4–7) hours after having been caged had low corticosterone levels. Two individuals were exceptional in that they had very high corticosterone levels and ate very poorly. These individuals show that migratory wheatears are capable of mounting a stress response, which confirms earlier observations on this species both under field and laboratory conditions (C. Eikenaar, unpubl. data). Finally, although not significantly different among the groups, corticosterone levels did appear to increase when birds were refueling. This matches the idea that corticosterone is involved in the regulation of departure from stopover (see hypotheses).

Our observation that migrating wheatears generally do not show signs of stress when caged may well represent a broader phenomenon. Despite the absence of data on corticosterone levels in other migrant species caged at stopover, data on food intake collected on Helgoland on other species suggests that migratory birds generally adapt well to caging. Blackcaps (*Sylvia atricapilla*), Dunnocks (*Prunella modularis*), European robins (*Erithacus rubecula*), garden warblers (*Sylvia borin*) and common redstarts (*Phoenicurus phoenicurus*) when caged at stopover can all consume large amounts of food (Thomas Klinner, in prep.). If these birds were stressed by the caging, we would expect that, because of the loss of appetite typical of elevated glucocorticoid levels (Sapolsky et al., 2000), they would not eat very well, as likely happened in the current study with the two wheatears with very high corticosterone levels. Also, the very short time it took the wheatears to start eating after being caged has been observed in other passerine migrants. In garden warblers and common whitethroats (*Sylvia communis*) caged at a spring stopover site, part (approx. 20%) of the birds already consumed food within 30 min of caging (Schwilch et al., 2001).

The reason that migrating wheatears and perhaps other migrating birds too, show no indications of stress when caged can only be speculated on. Perhaps, migrants' hyperphagic state in combination with ad libitum access to food dampens the physiological stress response normally observed when wild (non-migratory) birds are caged. Confinement-specific stressors, such as restricted movement and reduced foraging time due to overabundant and/or more energy-condensed food may cause stress in caged animals (Morgan and Tromborg, 2007). Migratory birds caged at stopover, however, may not perceive these circumstances as stressors. Stopover departure decisions to a large extent are governed by the availability of food, with migrants being more likely to stay when food is plentiful than when food is scarce (e.g. Bibby and Green, 1981; Ottich and Dierschke, 2003; Dierschke et al., 2005). In other words, if a migrant finds itself at a good stopover site, that is, high food availability, it should want to stay at that stopover site to consume as much food as it can metabolize. Experiments on long-term captive migrants have indeed found that migratory restlessness, a good proxy for departure likelihood (Eikenaar et al., 2014), is very low during simulated stopover refueling (feeding on ad libitum food after a fast) (e.g Biebach, 1985; Fusani and Gwinner, 2004). Hence, after handling stress has subsided, migrants caged at stopover with ab libitum food may not want to leave the restricted area, i.e. the cage, and their hyperphagic condition may assure that they spend much of their time feeding. Some support for this idea comes from our finding that quite a few individuals started to feed very soon after being caged, most likely even before corticosterone had returned to baseline level after the handling stress at caging. More conclusive support for this potential explanation for why in migrating wheatears caging does not result in signs of stress may come from an experiment in which wheatears are caged both during and outside of the migration period, either with ad libitum food or with limited food. Measurements of their corticosterone levels at various times could then reveal how wheatears cope with temporary captivity in different contexts (different life-history periods), and whether food availability has an effect on this.

Irrespective of the reason for why caged migrating wheatears do not show indications of stress, it brings the advantage that behavioural and physiological parameters measured in focal individuals are not affected by (chronically) elevated corticosterone levels. This is important because some behaviours are much easier to measure in temporarily caged birds than in wild birds. For example, stopovers are dynamic periods, during which migrants may not only replenish their fuel stores, but have also been suggested to recover physiologically from endurance flight (e.g. Schwilch et al., 2002; Owen and Moore, 2008; Skrip et al., 2015). Studying dynamic processes requires collecting longitudinal data (repeated measurements of individual birds), which is much easier in caged than in free-flying individuals. The possibility to cage wild migrants without stressing them will much facilitate collecting such data. When doing so, we do urge to measure food intake as this appears to be a good indicator of the occurrence of stress. We suggest migrants that eat poorly to be released as this will both benefit the bird as well as reduce noise in the data.

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