Short-term dehydration influences baseline but not stress-induced corticosterone levels in the house sparrow (*Passer domesticus*)

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ABSTRACT

Future environmental variations linked to climate change are expected to influence precipitation regimes and thus drinking water availability. Dehydration can be a particularly challenging physiological state for most organisms, yet no study has examined the effect of dehydration on the functioning of the hypothalamic–pituitary–adrenal axis in wild endothermic animals, despite its central role in maintaining homeostasis. In this study, we experimentally imposed a temporary water shortage (~20 h) on captive house sparrows in order to investigate the consequences of short-term dehydration on baseline and stress-induced corticosterone levels. As expected, water-deprived birds displayed higher plasma osmolality and haematocrit. Additionally, water-deprived birds had lower defecation rates, suggesting that the mechanisms allowing caecal water absorption may be triggered very rapidly during water deprivation. Baseline but not stress-induced corticosterone levels were higher in water-deprived birds. Taken together, these results suggest that water restriction may have critical consequences on several corticosterone-related traits such as energy budget (protein catabolism and possibly feeding reduction), enhanced mobility (to promote water acquisition) and potential responses to predators (thirst threshold overriding the acute stress response). Owing to the possible fitness consequences of such components of the day-to-day life of birds, further studies should aim at investigating the influence of future changes in precipitation regimes and drinking water availability on bird populations.

INTRODUCTION

Organisms respond to environmental variations with behavioural and/or physiological adjustments (Zera et al., 2007), and most of these responses are mediated by endocrine systems (Angelier and Wingfield, 2013; Taff and Vitousek, 2016). Regulation of such systems [e.g. the hypothalamic–pituitary–adrenal (HPA) axis] usually results in important modifications in the circulating concentrations of mediators (e.g. corticosteroid) in the blood (Wingfield et al., 1998). In turn, such modifications in circulating hormone levels activate or inhibit specific physiological and/or behavioural mechanisms which allow an individual to cope with challenging situations (Zera and Harshman, 2001; Wingfield and Sapolsky, 2003; McEwen and Wingfield, 2003; Romero et al.,

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2009). Seminal examples of such responses have been documented for a wide array of environmental disturbances such as resource availability, predation pressure, habitat modification and anthropogenic disturbance (Wingfield, 2013; Wingfield et al., 2017).

Among these disturbances, current or indeed future environmental variations linked to climate change have been of central interest for ecologists (Hoffmann and Sgro, 2011; McNamara et al., 2011). However, to our knowledge, most studies have only focused on the thermal consequences of climate change for wild animals (e.g. Saino et al., 2010; Burger et al., 2012). Climate change is also expected to influence precipitation regimes and thus water availability, with potential consequences for populations (Pearce-Higgins et al., 2015; Dupoué et al., 2017; Santini et al., 2018). Drinking water is among the most vital resources, and water acquisition and maintenance of water balance are critical components of the day-to-day life of most organisms (e.g. Perez et al., 2017). As a consequence, dehydration can be a particularly challenging physiological state for most organisms (reviewed in Rymer et al., 2016). Accordingly, dehydration is known to trigger behavioural and physiological adjustments that restore water balance and/or to reduce water loss (Gutiérrez et al., 2011, 2015; Peña-Vilalabos et al., 2013; Sabat et al., 2017). So far, most studies have examined the consequences of disruption of the water balance on metabolism (e.g. Gutiérrez et al., 2015), oxidative status (e.g. Sabat et al., 2017), body condition (Gutiérrez et al., 2011) and immunity (Gutiérrez et al., 2013; Sabat et al., 2019). Interestingly, corticosterone has been suggested as a central mediator of these physiological traits (reviewed in Sapolsky et al., 2000; Romero, 2004; Landys et al., 2006). Increased circulating corticosterone levels are often related to increased metabolic rate (Jimeno et al., 2017), depressed body condition (Lynn et al., 2010; Angelier et al., 2015), reduced immunity (e.g. Martin et al., 2005; Gao and Deviche, 2019) and increased oxidative stress (reviewed in Costantini et al., 2011). Despite the robust links between corticosterone and these physiological mechanisms, no study has to our knowledge examined the effect of dehydration on corticosterone secretion in wild endothermic animals.

However, glucocorticoids (well-studied mediators of organismal allostasis; McEwen and Wingfield, 2003; Romero et al., 2009) and especially corticosterone should theoretically respond to dehydration for two main reasons. First, corticosteroids are important mediators of osmoregulation and they are involved in the control of salt and water balance in most vertebrates (reviewed in McCormick and Bradshaw, 2006; see also Landys et al., 2006). Corticosterone, as a mineralocorticoid, has been shown to play a role in both ion and water transport after an osmotic challenge in vertebrates (McCormick and Bradshaw, 2006). Specifically, corticosterone is involved in mechanisms regulating salt retention and Na reabsorption (McCormick and Bradshaw, 2006). Given the tight relationship between salt and water balance, corticosterone is likely to respond to dehydration and osmotic stress (Dupoué et al., 2014, 2016).

In addition, it is also important for countercurrent concentrating mechanisms, in order to maintain plasma volume (Landys et al., 2006). Corticosterone secretion, as a 'stress hormone', is also known to increase when organisms undergo some form of physiological stress, such as osmotic stress (Allen et al., 1975; Gutiérrez, 2014).

Taken together, these elements strongly suggest that corticosterone levels should respond to short-term dehydration in order to promote behavioural and physiological adjustments to restore water balance and/or to reduce water loss. In addition to increasing circulating baseline corticosterone levels, dehydration may also functionally affect the release of this hormone in response to stress (Angelier and Wingfield, 2013). Specifically, dehydrated individuals may reach very high corticosterone levels because of the putative cumulative effect of dehydration and stress (McEwen and Wingfield, 2003; Romero et al., 2009; Wada and Heidinger, 2019).

In this study, we tested these hypotheses in the house sparrow (*Passer domesticus*). This species is particularly well suited to investigations of the physiological responses to short-term dehydration for several reasons (Goldstein and Zahedi, 1990; Gerson and Guglielmo, 2011). First, it inhabits a wide variety of habitats ranging from rural places to highly urbanized areas, and a wide variety of climates ranging from subarctic areas to desert regions, all of which display contrasting water availability. Second, even in places where water availability is relatively high, house sparrows may face temporal water shortage depending on climatic conditions (e.g. during summer droughts or winter cold spells when availability of free water is highly reduced). Finally, this species is easy to maintain in captivity in order to experimentally test the consequences of short-term water restriction. We experimentally imposed a temporary water shortage (~20 h) to captive house sparrows in order to investigate the consequences of short-term dehydration on (1) baseline corticosterone levels and (2) stress-induced corticosterone levels (i.e. the corticosterone levels reached after a 30 min restraint stress; Wingfield et al., 1992). Concomitantly, we examined how this short-term dehydration affects body mass, osmolality, haematocrit and defecation rate, four variables that should be affected by dehydration. Specifically, we logically predicted that water shortage will be associated with (1) body mass loss because of dehydration (respiratory and trans-cutaneous water loss); (2) higher haematocrit and osmolality (proxies of hydration state); (3) lower defecation rate (number of faeces produced per unit of time) as longer retention time of faeces should improve caecal capacity for water absorption in order to decrease water loss; (4) higher baseline corticosterone levels because of the stress of being dehydrated but also because of the involvement of corticosterone in osmoregulation; and (5) higher stress-induced corticosterone levels if dehydration and restraint stress have cumulative effects on individual stress.

MATERIALS AND METHODS
Captive housing
Study individuals were part of a captive colony of house sparrows, *Passer domesticus* (Linnaeus 1758), maintained at the Centre d'Etudes Biologiques de Chizé (CEBC) in outdoor aviaries. On 15 November 2017 (10 days before the onset of the experiment), all experimental birds ($N=21$ adult females and $N=10$ adult males, all 2 years old) were moved into two indoor aviaries (housing respectively 15 and 16 birds), where they were individually placed in wire bird cages (Vision S01, 45.5×35.5×51 cm) allowing visual and acoustic contact between individuals. Birds were supplied with mixed seeds *ad libitum*, salt/mineral blocks,

water (changed daily) and millet on the stalk. Grit was supplied 3 times per week and cages were equipped with perches of varying height. Birds were kept on a 10 h:14 h light:dark cycle (light from 08:00 h to 18:00 h), and the rooms were maintained at 20°C.

Experimental procedures
The evening before measurements were taken (shortly before the onset of the night phase at ~18:00 h), we removed water bowls from the cages of water-deprived birds (controls retained access to water) in order to minimize disturbances the day after (birds typically cease feeding and drinking at night); food remained in the cages and birds were weighed.

On the measurement day at ~14:00 h (i.e. 20 h after water removal including the night period, ~6 h effective water-shortage duration under daylight conditions), birds were captured and a small blood sample was collected within ~3 min (mean±s.e.m. 2.49± 0.77 min, maximum 4 min). Birds were weighed and maintained in cloth bags for 30 min (mean±s.e.m. 31.88±1.63 min, maximum 36.83 min) before a second blood sample was collected.

Birds were then returned to their cages without food (seeds, salt/mineral blocks and millet were all removed) but with *ad libitum* access to water for 30 min. After this post-handling rehydration phase, birds were weighed again (total time of 1 h since the previous body mass measurement) in order to quantify mass gain linked solely to drinking. Because we aimed to measure the influence of short-term dehydration on both baseline and stress-induced corticosterone levels and because we could only confidently obtain baseline blood samples on a limited number of birds (baseline sampling has to occur within 3 min of capture), we only treated 2 birds per room and per day. Each treatment (water deprivation versus control) was evenly distributed between rooms. In order to avoid any influence of captivity time on our experiment, half of the birds were first subjected to the water-restricted condition and half of the birds were in the control condition. The birds experienced the other treatment during the second part of our experiment. As a consequence, all individuals experienced both treatments (water deprivation and control). All experimental procedures were finished in mid-December when all birds were returned to their outdoor aviaries.

All experimental procedures were approved by French authorities (authorization CE84-2019-9540 issued by the Comité d'Ethique Poitou-Charentes to F.B. and F.A.).

Physiological measurements
Blood samples (100 μl) were obtained via brachial venipuncture with 27-gauge needles and heparinized microcapillary tubes. Haematocrit (volume % of red blood cells) was measured on 10 μl aliquots (Hirschmann minicaps microcapillary tubes) with a haematocrit centrifuge (Compur M 1101, Bayer). The remaining blood was centrifuged at 2000 g for 7 min, and plasma was separated and kept at −20°C for 1 month in sealed tubes until assays were conducted. All laboratory analyses were performed at the CEBC.

Plasma corticosterone was determined by radioimmunoassay, as described in Lormée et al. (2003). The minimum detectable corticosterone concentration was 0.28 ng ml^{-1}, and the intra- and inter-assay coefficients of variation were 8.05% and 9.05%, respectively (samples were assayed in duplicate, in three assays). Baseline and stress-induced samples from the same individuals within treatment were always run in the same assays, while treatments were randomly distributed between assays.

Plasma osmolality (mOsm kg^{-1}) was measured from 2 μl aliquots on a Vapro2 osmometer (Elitech group).

Finally, because birds can retain faeces in their digestive tract in order to increase the caecal capacity for water absorption and thus to decrease water loss, we counted faeces produced by the birds for the duration of the experiment (i.e. 20 h) and computed a defecation rate index (total number of faeces produced per hour). The same procedure was repeated during the rehydration phase of the experiment (when birds had access to water *ad libitum*), for which we also computed a defecation rate index.

Statistical analyses

Body mass changes were investigated using repeated-measures designs with treatment (water deprived versus control) as the factor and the three body mass measurements as the repeated variables. Osmolality, haematocrit, defecation rate, and baseline and stress-induced corticosterone levels were investigated using generalized linear mixed models with treatment (water deprived versus control) as the factor. Relationships between corticosterone and other variables were investigated with generalized linear mixed models. Because all individuals experienced both treatments, individual identity was included as a random factor in all analyses. The sex of the bird never influenced our results and this parameter was not retained in our final analyses. Results are displayed as means±s.e.m. All analyses were performed with Statistica 12.

RESULTS

Body mass changes

We found a significant effect of time ($F_{2,60}$=513.60, P<0.0001; Fig. 1) and of the interaction between time and treatment ($F_{2,60}$=75.12, P<0.0001; Fig. 1). Initial body mass was similar between treatments (Fisher's LSD, P=0.23; Fig. 1). During the treatment, all birds lost mass, but water-deprived individuals lost more mass than control birds (Fisher's LSD, P<0.0001; Fig. 1). During the post-handling restraint rehydration phase, water-deprived individuals gained mass (Fisher's LSD, P=0.001; Fig. 1), while control individuals lost mass (Fisher's LSD, P<0.0001; Fig. 1). Final body mass remained lower in water-deprived individuals (Fisher's LSD, P=0.001; Fig. 1).
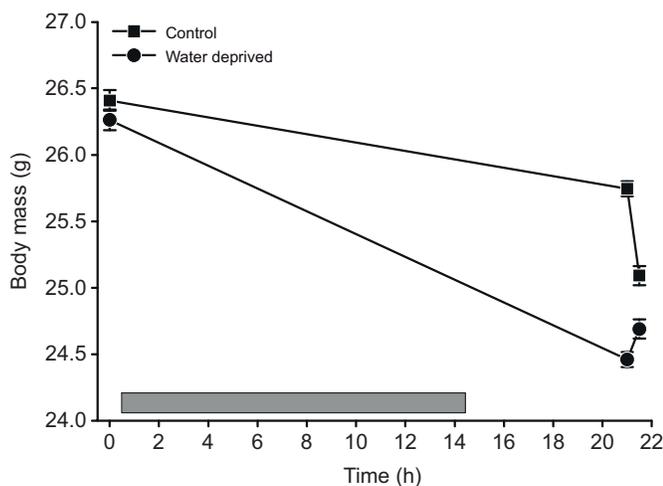
Indices of dehydration

Osmolality was significantly higher in water-deprived individuals ($F_{1,30}$=4.62, P=0.03; Fig. 2). Across treatment, osmolality was negatively related to body mass loss during the experiment ($F_{1,30}$=4.42, P=0.04). Similarly, haematocrit was significantly higher in water-deprived individuals ($F_{1,30}$=21.38, P<0.0001; Fig. 2). Across treatment, haematocrit was negatively related to body mass loss during experiment ($F_{1,30}$=16.55, P<0.0001).

Defecation rate

The number of faeces produced was significantly lower in water-deprived individuals ($F_{1,30}$=14.40, P=0.0007; Fig. 3). During the post-handling restraint rehydration phase, the number of faeces produced was similar between treatments ($F_{1,30}$=0.02, P=0.88).

Corticosterone levels

Baseline corticosterone was significantly higher in water-deprived individuals ($F_{1,30}$=13.077, P=0.001; Fig. 4). Across treatment, baseline corticosterone was negatively related to body mass loss during the experiment ($F_{1,30}$=9.55, P=0.004), but was not related to either haematocrit (P=0.2) or osmolality (P=0.87). Stress-induced

Fig. 1. Variation in body mass of control and water-deprived house sparrows during the experiment. Time is displayed on the *x*-axis, and 0 indicates the onset of the experiment (~18 h, see Materials and Methods for details). The grey bar indicates the night period. Values are represented as means±s.e.m. *N*=31 birds in each group. See Results for details on statistical differences.
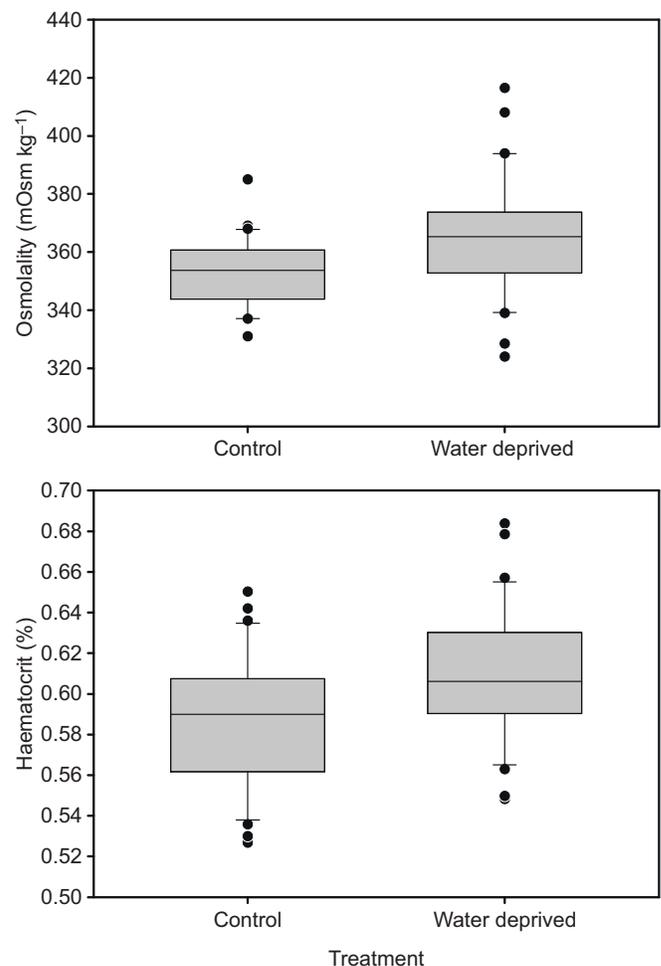

Fig. 2. Osmolality (top) and haematocrit (bottom) in control and water-deprived house sparrows. The top and bottom of the boxes represent the first and last quartiles, the line across the box represents the median, the whiskers represent the fifth and ninety-fifth percentiles, and the circles represent outliers. *N*=31 birds in each group. See Results for details on statistical differences.
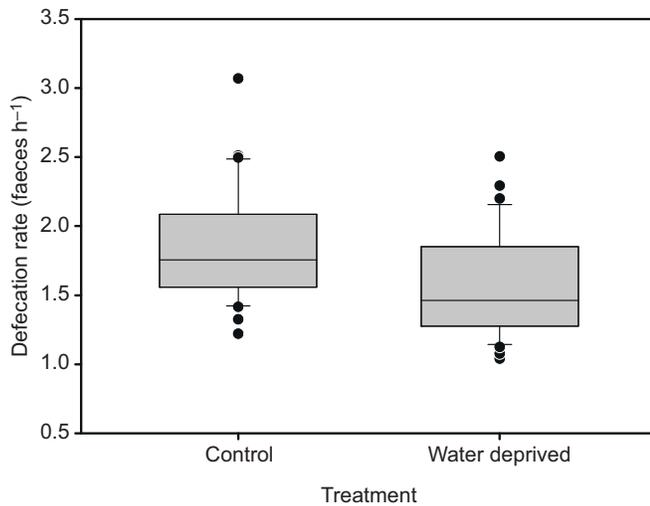
Fig. 3. Defecation rate of control and water-deprived house sparrows. The top and bottom of the boxes represent the first and last quartiles, the line across the box represents the median, the whiskers represent the fifth and ninety-fifth percentiles, and the circles represent outliers. N=31 birds in each group. See Results for details on statistical differences.

corticosterone was similar between water-deprived and control birds ($F_{1,30}$=0.13, P=0.72; Fig. 4).

DISCUSSION

In this study, we experimentally tested for the first time the influence of short-term dehydration on both baseline and stress-induced corticosterone levels in house sparrows. Corticosterone levels were expected to increase during short-term dehydration in order to promote behavioural and physiological adjustments that should restore water balance and/or reduce water loss. In addition, as a proxy of stress levels, corticosterone levels were also expected to increase in water-restricted birds if dehydration is perceived as a stressor.

Dehydration in water-deprived sparrows

Although the duration of water restriction was modest (i.e. 20 h including the night period, ∼6 h effective water-shortage duration under daylight conditions as birds typically cease feeding and drinking at night), all the proxies we used to assess dehydration responded as predicted. Water-deprived birds displayed higher plasma osmolality and haematocrit levels than control birds, suggesting a loss of body fluids (see also Goldstein and Zahedi, 1990; Gerson and Guglielmo, 2011). Both respiratory and transcutaneous water loss could be responsible for such a loss of body fluids. Similarly, water-deprived birds lost more mass than controls, strengthening the fact that water-deprived birds lost body fluids during the experimental treatment. Importantly, such a loss of body mass may also be linked to a reduction of food intake during water deprivation (MacMillen, 1962). We did not assess food consumption in our study, and thus we cannot tease apart the respective contribution of water loss versus feeding reduction on the body mass loss we detected (Moldenhauer and Wiens, 1970). Yet, complementary results on defecation rates (see below), and especially those rates during the post-handling restraint rehydration phase suggest that feeding reduction may not have occurred during our experiment, or at least that feeding reduction and water loss occur concomitantly (Moldenhauer and Wiens, 1970). Nonetheless, future studies should usefully test for the
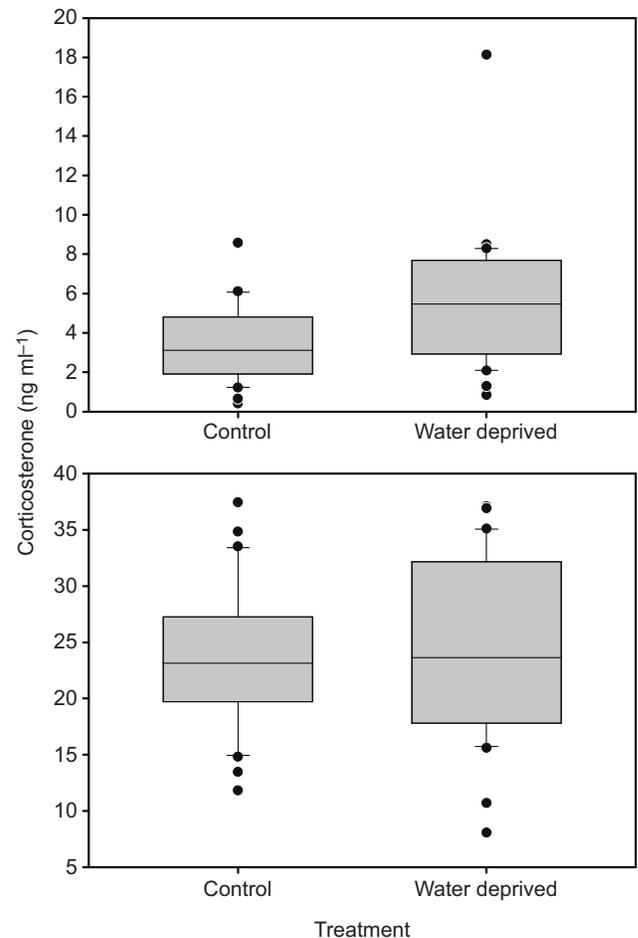

Fig. 4. Baseline (top) and stress-induced (bottom) corticosterone levels in control and water-deprived house sparrows. The top and bottom of the boxes represent the first and last quartiles, the line across the box represents the median, the whiskers represent the fifth and ninety-fifth percentiles, and the circles represent outliers. N=31 birds in each group. See Results for details on statistical differences.

influence of short-term water deprivation on foraging behaviour in order to assess whether such a temporary reduction of access to water may negatively affect the overall energy budget of small passerine birds. In the same vein, future studies are required in order to assess how stages of dehydration (i.e. minor versus severe) would influence the magnitude of such a reduction in feeding. Finally, our experimental design did not test for possible influences of water restriction on the activity levels of birds, and future studies should investigate the behavioural consequences of water restriction in birds.

A longer retention time of faeces in the digestive tract is known to improve caecal capacity for water absorption in birds (Gasaway et al., 1976; Chaplin, 1989; Goldstein, 1989; Skadhauge, 2012). Accordingly, we found that water-deprived birds had lower defecation rates than controls, suggesting that the mechanisms allowing caecal water absorption may be triggered very rapidly (within a few hours) during water deprivation. Such a lower defecation rate may also be linked to the putative feeding reduction discussed above (MacMillen, 1962; Moldenhauer and Wiens, 1970). We cannot entirely rule out this alternative hypothesis, or indeed separate the respective contribution of increased retention time of faeces versus feeding reduction. Yet, the fact that water-

deprived birds had similar defecation rates to control birds during the post-handling restraint rehydration phase (during which access to food was precluded) strongly suggests that the lower defecation rates we detected during water deprivation are linked to mechanisms that aim to reduce additional water loss (Moldenhauer and Wiens, 1970), rather than a preceding reduction of feeding. Future studies should investigate not only faeces number but also their size, mass and water content (i.e. water-restricted birds could have produced smaller and drier faeces than control birds).

Influence of water deprivation on baseline corticosterone levels

According to our prediction, we found that baseline corticosterone levels were higher in water-deprived birds. Indeed, corticosterone is a pleiotropic mediator, and such a result was expected for several reasons. First, corticosterone is presumed to act as a mineralocorticoid, and thus to play a role in the maintenance of osmotic balance (reviewed in McCormick and Bradshaw, 2006; see also Landys et al., 2006). Because our experimental treatment affected water balance (increased osmolality and haematocrit), the increase in baseline corticosterone level we found may reflect the role of this hormone in the control of osmotic balance (Allen et al., 1975; Bradshaw, 1975). Second, house sparrows and other bird species have been shown to increase protein catabolism in response to water restriction, as a metabolic strategy to compensate for water loss and to produce water to maintain osmotic balance (Goldstein and Zahedi, 1990; Gerson and Guglielmo, 2011). In this respect, increased corticosterone levels could reflect such a metabolic strategy. In turn, the possible loss of condition in water-restricted individuals (body mass loss, possible protein catabolism) could also induce elevated baseline corticosterone levels. This interpretation is supported by the absence of a correlation between osmolality and baseline corticosterone levels across treatment, while both variables were negatively correlated to body mass loss. Body mass loss, and more specifically protein catabolism, has been shown to be associated with increased baseline corticosterone levels in numerous bird species (Cherel et al., 1988; Lynn et al., 2003, 2010; Angelier et al., 2015). Actually, both mechanisms are plausible and may even interact with each other. Future studies are required to disentangle the role of corticosterone on protein catabolism, or the role of loss of condition on corticosterone, or indeed the interactions between these mechanisms.

Finally, the dehydration produced by our treatment may have triggered a state of osmotic stress, a form of physiological stress that may activate the HPA axis, which in turn would result in increased levels of circulating corticosterone (Wingfield et al., 1998; Wingfield, 2013; Sapolsky et al., 2000). Clearly, future studies are needed to disentangle these hypotheses. In this respect, concomitant measurements of other endocrine regulators of water balance and osmotic homoeostasis in non-mammalian vertebrates (i.e. arginine vasotocin, aldosterone, prolactin) would be helpful (Arad and Skadhauge, 1984). Overall, all of these physiological responses to water restriction would produce increased baseline corticosterone levels, which in turn may enhance mobility (Breuner et al., 1998; Lynn et al., 2003; Angelier et al., 2007; Krause et al., 2017) and thus allow dehydrated individuals to disperse to alternative localities in order to promote water acquisition. It is noteworthy that the longer retention time of faeces to improve caecal capacity for water absorption may be mediated by increased corticosterone levels (Grubb and Bentley, 1992). Finally, higher baseline corticosterone concentrations may also result from the decreased plasma volume due to water restriction. It is noteworthy to highlight that corticosterone has an important role for

countercurrent concentrating mechanisms in order to maintain plasma volume (Landys et al., 2006). Clearly, future studies should aim to assess the response of plasma volume to water restriction as well as its consequences for circulating hormonal mediators.

Influence of water deprivation on stress-induced corticosterone levels

Interestingly, stress-induced corticosterone levels were similar between treatments, indicating that maximal stress-induced corticosterone levels may be independent of dehydration state. Such contrasted dynamics of the corticosterone stress response may have important consequences on the speed at which behavioural and physiological components change in response to an additional stress (Angelier and Wingfield, 2013). These stress-related behavioural and physiological effects are mediated by the binding of corticosterone to low-affinity receptors, which occurs only when the high-affinity receptors are saturated with corticosterone (Romero, 2004; Landys et al., 2006), and such binding is likely to occur earlier in water-restricted birds because of their higher baseline corticosterone levels. In that respect, it would be interesting to measure the kinetics of the corticosterone stress response by measuring corticosterone levels after 15 min of restraint, for example. In addition, it would be interesting to measure the speed at which birds return to baseline corticosterone levels after release from handling restraint, in order to determine whether the water-restricted birds return to normal corticosterone levels faster.

Although stress-induced corticosterone levels were similar between treatments, behavioural and physiological responses to stress appeared to be very different. During the post-handling restraint rehydration phase (when individuals had access to water), control birds showed a rapid mass loss, suggesting that the restraint protocol was associated with increased body mass loss in that group (through increased metabolism and the use of body reserves) and reduced drinking behaviour. Conversely, water-restricted individuals increased body mass during this rehydration phase, demonstrating that they drank significant amounts of water during the 30 min following the restraint protocol. This suggests not only that they drank water to restore their osmotic balance but also that the necessity to drink and to restore their osmotic balance (and thus the thirst threshold) overrode the behavioural/physiological impacts of restraint stress, which were found in control birds.

Conclusion

Elevated baseline corticosterone levels induced by water restriction may have critical consequences for several major life-history traits such as energy budget (protein catabolism and possibly feeding reduction), enhanced mobility (to promote water acquisition) and potential responses to predators (thirst threshold overriding the acute stress response). Owing to the possible fitness consequences of such components of the day-to-day life of birds, further studies should aim to investigate the influence of future changes in precipitation and free water availability on bird populations.

C.P., F.A.; Supervision: F.B., F.A.; Project administration: F.B., F.A.; Funding acquisition: F.B., F.A.

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