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No evidence for an effect of traffic noise on the development of the corticosterone stress response in an urban exploiter

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ABSTRACT

Anthropogenic noise can have important physiological and behavioral effects on wild animals. For example, urban noise could lead to a state of chronic stress and could alter the development of the hypothalamus–pituitary–adrenal (HPA) axis. Supporting this hypothesis, several studies have found that human disturbance is associated with increased circulating corticosterone (CORT) levels. However, it remains unclear whether increased CORT levels are the result of anthropogenic noise or other anthropogenic factors. Here, we experimentally tested the impact of urban noise on the CORT stress response in an urban exploiter (the house sparrow, *Passer domesticus*) by exposing chicks to a traffic noise ('disturbed chicks') or not ('control chicks'). If noise exposure has a negative impact on developing chicks, we predicted that (1) disturbed chicks will grow slower, will be in poorer condition, and will have a lower fledging probability than controls; (2) disturbed chicks will have higher baseline CORT levels than control; (3) the CORT stress response will be affected by this noise exposure. Contrary to these predictions, we found no effect of our experiment on growth, body condition, and fledging success, suggesting that house sparrow chicks were not negatively affected by this noise exposure. Moreover, we did not find any effect of noise exposure on either baseline CORT levels or the CORT stress response of chicks. This suggests not only that house sparrow chicks did not perceive this noise as stressful, but also that the development of the HPA axis was not affected by such noise exposure. Our study suggests that, contrary to urban avoiders, urban exploiters might be relatively insensitive to urban noise during their development. Further comparative studies are now needed to understand whether such insensitivity to anthropogenic noise is a consistent phenomenon in urban exploiters and whether this is a major requirement of an urban way of life.

1. Introduction

Urbanization imposes drastic environmental changes to wild vertebrates and animal communities strongly differ between urban and non-urban environments (Marzluff, 2001; Clergeau et al., 2006; McKinney, 2006; Chace and Walsh, 2006). Interestingly, some species seem to rely on the urban environment ("urban exploiters") and individuals from these species can be found almost exclusively in urban areas. On the other hand, some species seem unable to live in an urban environment ("urban avoiders") while others can live in the urban environment without necessarily relying exclusively on it ("urban adapters", Blair, 1996; Shochat et al., 2006; Croci et al., 2008). In the context of urban sprawl, it appears crucial to understand the proximate causes of these differences between species because it will help assessing the ability or inability of species to adjust to urban-related environmental changes (Shochat et al., 2006; McDonnell and Hahs, 2013; Partecke, 2013).

Urbanization is characterized by multiple environmental modifications that may constrain or benefit to wild vertebrates (e.g. food availability, temperature, pollution, noise, Marzluff, 2001; Grimm et al., 2008; Barber et al., 2010). In that context, a major challenge is to disentangle the relative effect of each of these modifications on individual performances. Among all these modifications, anthropogenic noise is often perceived as a major constraint for wild urban vertebrates because it can impair behavioral and physiological functions that are essential to daily and seasonal routines (Barber et al., 2010; Kight and Swaddle, 2011; Francis and Barber, 2013). For instance, urban noise can alter acoustic communication and may preclude individuals to reproduce properly (Slabbekoorn and den Boer-Visser, 2006; Patricelli and Blickley, 2006; Warren et al., 2006; Halfwerk et al., 2011; Schroeder et al., 2012; Potvin and MacDougall-Shackleton, 2015).

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Moreover, such noise can also impede individuals to perceive crucial auditory stimuli, such as predatory threats (Barber et al., 2010; Halfwerk and Slabbekoorn, 2013; Meillère et al., 2015a). In addition to all these auditory constraints, repeated exposure to urban noise may also be perceived as a succession of stressors, and individuals may not have evolved to deal with such a stressful environment (Tennessen et al., 2014). Therefore, this noisy urban environment could lead to a state of chronic stress (or allostatic overload) with important fitness costs (McEwen and Wingfield, 2003; Bonier et al., 2009; Bonier, 2012). Moreover, this repeated exposure to urban noise could also alter the stress sensibility of individuals (Bonier, 2012; Crino et al., 2013), and therefore, reduce their ability to cope with other stressors (Angelier and Wingfield, 2013). In vertebrates, the faculty of individuals to cope with stress is primarily driven by the hypothalamus–pituitary–adrenal (HPA) axis (McEwen and Wingfield, 2003; Romero, 2004; Romero et al., 2009). In response to a stressor, this endocrine axis is activated and this results in the secretion of glucocorticoids (corticosterone (CORT) in birds, Wingfield et al., 1998; Sapolsky et al., 2000). In turn, increased circulating glucocorticoids levels mediate physiological and behavioral changes through permissive, inhibitory and stimulatory actions (Sapolsky et al., 2000; Romero, 2004; Landys et al., 2006). Overall, this glucocorticoid stress response aims to restore homeostasis by redirecting available resources from activities that are not essential to immediate survival towards self-maintenance processes (Wingfield et al., 1998; Wingfield and Sapolsky, 2003).

In the field, endocrinologists usually study this endocrine axis by monitoring baseline glucocorticoid levels (i.e. glucocorticoid levels that are independent of the stress of capture), which are a proxy for individual allostatic load and energetic constraints (Landys et al., 2006; Romero et al., 2009). Indeed, elevated baseline glucocorticoid levels can be seen as a proxy for nutritional deficit or chronic stress (Kitaysky et al., 2007; Busch and Hayward, 2009; Lynn et al., 2010a; Angelier et al., 2015) and are often associated with poor performances (Bonier et al., 2009). Most studies have shown that loud human-related activities are indeed associated with increased baseline glucocorticoid levels in adults and little is known about the impact of anthropogenic noise on circulating glucocorticoid levels of developing vertebrates (Creel et al., 2002; Thiel et al., 2008; Hayward et al., 2011; Blickley et al., 2012; Tennessen et al., 2014; but see Owen et al., 2014). Several studies have found that anthropogenic disturbance is associated with increased glucocorticoid levels and poor reproductive performances in developing vertebrates (Müllner et al., 2004; Walker et al., 2005; Crino et al., 2011; Strasser and Heath, 2013; Potvin and MacDougall-Shackleton, 2015), but it remains unclear whether this was the result of anthropogenic noise or other anthropogenic factors. To our knowledge, a single study has experimentally tested the impact of anthropogenic noise on baseline glucocorticoid levels of developing wild vertebrates. Surprisingly and contradictorily to correlative studies (Crino et al., 2011; Strasser and Heath, 2013), it did not report any change in baseline glucocorticoid levels in response to noise exposure (Crino et al., 2013). Therefore, additional experimental studies in other wild vertebrate species appear necessary to better assess the impact of noise exposure on baseline glucocorticoid levels. In addition, endocrinologists also monitor stress-induced glucocorticoid levels (i.e. maximal glucocorticoids levels reached in response to a standardized stressor) because they help understand how individuals would physiologically react to an additional stressor if it occurs (i.e. stress sensibility, Wingfield et al., 1998; Angelier and Wingfield, 2013). Indeed, this response is crucial to consider because it appears to be involved in life-history trade-offs (Ricklefs and Wikelski, 2002; Wingfield and Sapolsky, 2003). Moreover, the magnitude of this stress response is linked to survival under some circumstances (Romero and Wikelski, 2001; Blas et al., 2007; Breuner et al., 2008; Angelier et al., 2009). Several studies have investigated the causes of inter-individual variation in the glucocorticoid stress response and they have demonstrated that developmental conditions and early-life stressors can affect the development of this stress response with potential long-lasting effects (Love and Williams, 2008; Wada et al., 2009; Lynn et al., 2010b; Whitman et al., 2011; Zimmer et al., 2013). Repeated noise exposure may be perceived as a stressor by developing offspring and, therefore, it may affect the development of the HPA axis and the glucocorticoid stress response with potential fitness consequences. Here again, we lack experimental data on the impact of anthropogenic noise on the development of the glucocorticoid stress response and so far, a single study has found an effect of noise exposure on the stress response (Crino et al., 2013).

In this study, we aimed to experimentally test the impact of urban noise on the glucocorticoid stress response of nestlings in the house sparrow (*Passer domesticus*), an urban exploiter. To do so, we measured baseline and stress-induced CORT levels (CORT being the main glucocorticoid in birds) of chicks that were experimentally exposed to a traffic noise ('disturbed chicks') or not ('control chicks'). Because the HPA axis can be related to the energetic status (e.g. Kitaysky et al., 1999) and the developmental stage (Wada et al., 2009), we concomitantly monitored the body size and the body condition of these chicks to understand whether a potential modification of the HPA axis was related to energetic constraints or delayed growth in disturbed chicks. Because noise exposure may alter parental investment, impose energetic constraints to the developing offspring and/or be perceived as a stressor, we predicted that disturbed chicks (1) will grow slower and be in poorer condition than control chicks (prediction 1); (2) will have higher baseline CORT levels than controls (prediction 2); and (3) will have a lower fledging probability than controls (prediction 3). Finally, we also predicted that this noise exposure will affect the CORT stress response (prediction 4). Because the CORT stress response is often dampened when chicks suffer from high stress level (Love and Williams, 2008; Zimmer et al., 2013) or even noise exposure (Crino et al., 2013), we predicted that the CORT stress response of disturbed chicks will be dampened relative to controls if exposure to chronic noise is associated with energetic constraints and/or is perceived as a stressor by house sparrow chicks.

2. Material and methods

2.1. Study site and experimental procedure

This study was carried out during the breeding season at the Centre d'Etudes Biologiques de Chizé (CEBC) in France (46°09′N, 0°24′) where a free-living population of house sparrows has been studied for almost twenty years (Leloutre et al., 2014). All nest boxes ($n = 67$) were checked every two days to determine laying date. When an egg was found in a nest, clutch size was determined by checking the nest box 7 days later. Hatching date and brood size were then determined by checking regularly the number of chicks and eggs in each nest box.

To investigate the impact of urban noise on the development of house sparrow chicks, we used an experimental protocol previously detailed and validated (see Meillère et al. (2015a) for detailed methodology). At this rural site, we experimentally exposed some nest boxes to a traffic noise from April to July ("disturbed" nest boxes, $n = 21$) while others remained undisturbed and exposed solely to the rural background noise ("control" nest boxes, $n = 46$). Traffic noise was obtained through recording the sounds produced by a 4 lane highway close to Paris during 2 min. Traffic noise was broadcast by an iPod shuffle (Apple Inc., Cupertino,

CA) connected to Logitech LS11 stereo speakers (Logitech, Fremont, CA; frequency response 70–20,000 Hz). This recording was broadcast in a loop 6 h a day (from 9 to 12 AM and from 2 to 5 PM). The speakers were hidden approximately 3–4 m from the nest boxes and the volume was adjusted to the noise level that was measured at different time of day in multiple urban sites where house sparrows breed (~61 dBA). The traffic noise exposure produced low frequency noise (see Meillère et al. (2015a) for spectrograms and power spectra of background noise at a disturbed and a control nest). The rural background noise was also measured at the CEBC in multiple occasions and averaged 43 dBA (see Meillère et al., 2015a for further details). All the noise measurements were conducted using a Voltcraft SL-200 digital sound meter (Voltcraft, Hirschau, Germany).

2.2. Body size, body condition and fledging success

The growth of each chick of the brood was monitored by measuring body mass, and tarsus, bill, and wing lengths when the chicks were three days old ($n = 132$) and nine days old ($n = 78$). Body mass was measured with a precision scale (±0.1 g, Scaltec, SBA53). Tarsus and bill lengths were measured using a caliper (±0.1 mm) and wing length was measured using a ruler (±0.5 mm). Each chick of a given nest was individually identified with a color ring when they were three days old. They were then ringed with an aluminum ring when they were nine days old.

For each chick, body condition was calculated when the chick was 3 days old ($n = 132$) and, then, 9 days old ($n = 78$) by using scaled mass indices (Peig and Green 2009, 2010). The scaled mass index adjusts the mass of all individuals to that expected if they had the same body size, and was computed for each individual as detailed in Peig and Green (2009). Scaled mass indices were computed by using wing length because this body size variable correlates the best with body mass. However, all the results remain unchanged if scaled mass indices were computed by using another morphometric measurement (tarsus length or bill length).

The fledging success of each chick was also monitored by checking their presence at the nest at the end of the developmental period. Thus, successful fledging was assumed if they reach 17 days old.

2.3. CORT stress response and hematocrit

For all 9 days old chicks ($n = 78$), we collected blood samples according to the standardized stress protocol established by Wingfield et al. (1992). Briefly, an initial blood sample was collected immediately after capture from the brachial vein into heparinized microcapillary tubes (~75 µl). The handling time was minimal after initial disturbance and all the chicks of a given nest were sampled quickly after initial disturbance of the brood (2 min 24 ± 42 s, Mean ± SE, max: 4 min 05 s). There was no effect of handling time on CORT levels, and therefore, these initial samples were considered to reflect baseline CORT levels (Romero and Reed, 2005; Angelier et al., 2010). After collection of the initial blood samples, chicks were placed into cloth bags, and subsequent blood samples were collected 30 min later (~75 µl, when CORT levels have been shown to peak in some nestling passerines (e.g. Wada et al. (2007)) to monitor stress-induced CORT levels. Hematocrit was also determined by centrifuging the first 10 µl of collected blood in a microcapillary tube (11,000 rpm, 3 min): the volume of red blood cells was expressed as a percentage of the total blood volume. All chicks were released at their nest after the procedure. Baseline CORT levels, stress-induced CORT levels and hematocrit could not be assessed for a few birds (final sample size, baseline: $n = 71$, stress-induced: $n = 77$, hematocrit: $n = 73$).

2.4. Molecular sexing and CORT assay

Blood samples were centrifuged and plasma was decanted and both plasma and red cells were stored at −20 °C until analyzed at the lab. The sex was determined by polymerase chain reaction (PCR) amplification of part of two highly conserved genes (CHD) genes present on the sex chromosomes at the CEBC, as detailed in Leloutre et al. (2014). Plasma concentrations of CORT were determined by radioimmunoassay at the CEBC, as described previously (Angelier et al., 2007). The minimum detectable CORT level was 0.83 ng mL^{-1}, and the intra- and inter-assay coefficients of variation were 7.07% and 9.99% respectively.

2.5. Statistical analyses

All analyses were performed with SAS statistical software (ver. 9.4; SAS Institute). First, we used generalized linear mixed models (GLMM, normal distribution, identity link function) to test whether disturbed and control chicks differed in body condition (dependent variable: scaled mass index, independent factors: sex, brood size, disturbance and their interactions) with nest as a random factor. Second, we used GLMM (normal distribution, identity link function) to test whether disturbed and control chicks differed in body size (dependent variable: tarsus, bill or wing lengths, independent factors: sex, brood size, disturbance and their interaction) with nest as a random factor. All these analyses were conducted for 3 days old and 9 days old chicks. Sex could only be included in these analyses for 9 days old chicks since molecular sexing was conducted for 9 days old chicks only (see below). Third, we used GLMM (normal distribution, identity link function) to test whether disturbed and control chicks differed in baseline, stress-induced CORT levels and hematocrit (dependent variable: baseline or stress-induced CORT levels or hematocrit, independent factors: sex, disturbance, scaled mass index, brood size at day 9, and their interactions) with nest as a random factor. We included scaled mass index and brood size as independent variables for these analyses (CORT and hematocrit) because body condition and brood size are known to be related to these physiological variables under some circumstances. Fourth, we used GLMM (binomial distribution, logit link function) to test whether disturbed and control chicks differed in fledging success (dependent variable: fledging success, dependent variables: brood size at hatching, disturbance, and their interaction) with nest as a random factor. This analysis included all hatched chicks but sex could not be included in this analysis because molecular sexing was conducted when the chicks were 9 days old. Finally, we used GLMM (binomial distribution, logit link function) to test whether disturbed and control 9 days old chicks differed in fledging success (dependent variable: fledging success, dependent variables: brood size at day 9, disturbance, scaled mass index, physiological measure, and their interaction). Because baseline CORT levels, stress-induced CORT levels and hematocrit levels were not available for all chicks, all these variables could not be included in the same model. Therefore, we ran three different models with baseline CORT levels, stress-induced CORT levels or hematocrit as the physiological dependent variable.

3. Results

3.1. Effect of chronic noise exposure on body size and body condition

When the chicks were 3 days old, there was no significant effect of brood size ($F_{1,49} = 0.45$, $p = 0.506$), disturbance ($F_{1,49} = 1.13$, $p = 0.293$; Fig. 1A) and their interaction ($F_{1,49} = 1.35$, $p = 0.251$) on scaled mass index. Similarly, there was no significant effect of

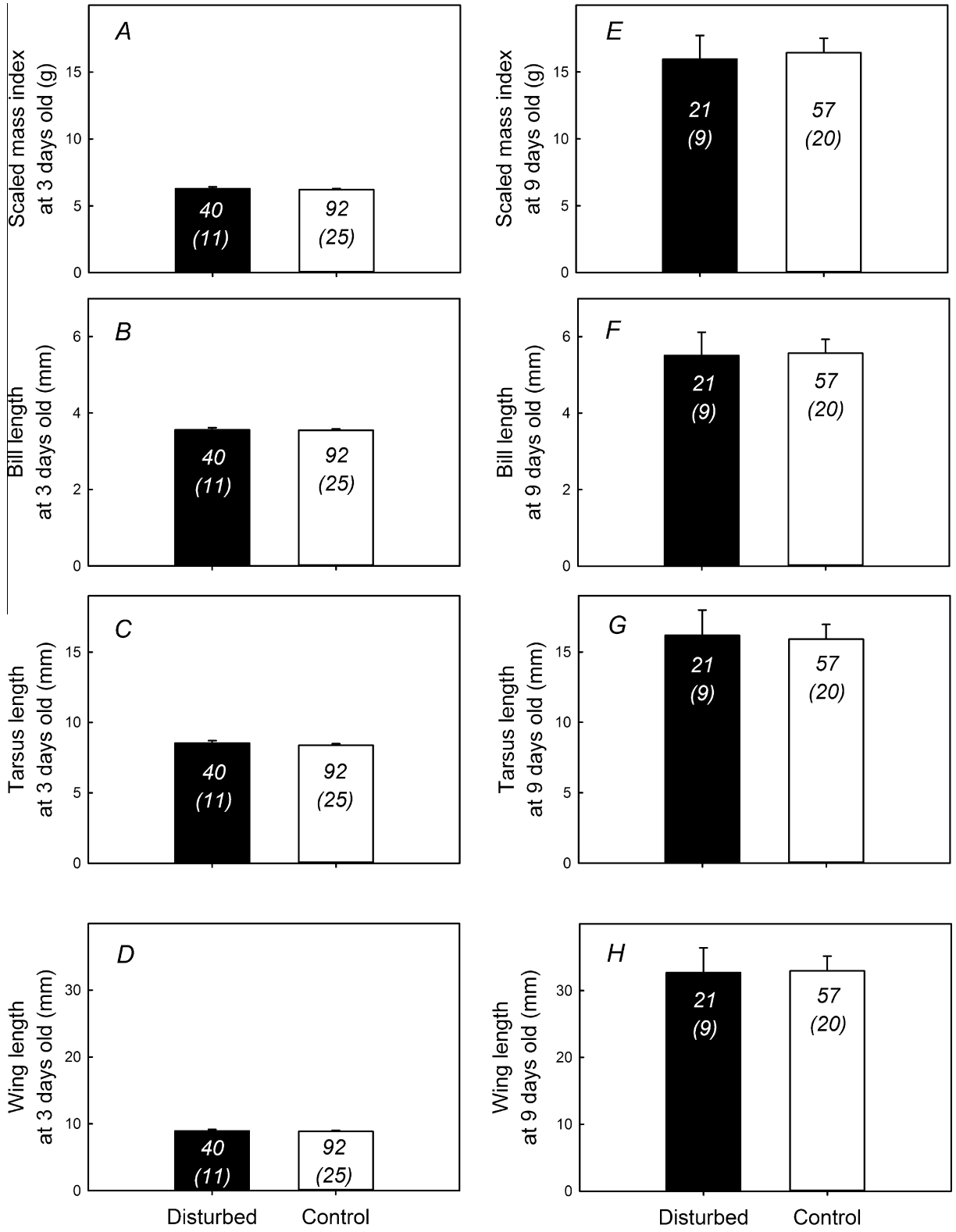

Fig. 1. Influence of an experimental noise exposure on body condition (A, E), bill length (B, F), tarsus length (C, G), and wing length (D, H) of house sparrow chicks. These analyses were conducted for 3-days old (A, B, C, D) and 9-days old chicks (E, F, G, H). Body condition was estimated by using scaled mass indices (Peig and Green, 2009). Data are expressed as Means ± SE. Numbers and numbers in parentheses respectively denote the number of chicks and the number of nests used for these analyses.

brood size (bill: $F_{1,49} = 2.03$, $p = 0.161$; tarsus: $F_{1,49} = 1.21$, $p = 0.277$; wing: $F_{1,49} = 1.97$, $p = 0.167$), disturbance (bill: $F_{1,49} = 0.14$, $p = 0.711$; tarsus: $F_{1,49} = 0.76$, $p = 0.387$; wing: $F_{1,49} = 0.92$, $p = 0.342$; Fig. 1B–D) and their interaction (bill: $F_{1,49} = 0.20$, $p = 0.655$; tarsus: $F_{1,49} = 0.71$, $p = 0.404$; wing: $F_{1,49} = 0.88$, $p = 0.352$) on body size.

When the chicks were 9 days old, there was no significant effect of brood size ($F_{1,49} = 1.38$, $p = 0.246$), disturbance ($F_{1,49} = 0.01$,

$p = 0.943$; Fig. 1E), sex ($F_{1,49} = 3.56$, $p = 0.066$) and their interactions (all p-values > 0.200) on scaled mass index. Similarly, there was no significant effect of brood size (bill: $F_{1,49} = 0.60$, $p = 0.442$; tarsus: $F_{1,49} = 0.05$, $p = 0.827$; wing: $F_{1,49} = 0.59$, $p = 0.446$), disturbance (bill: $F_{1,49} = 1.13$, $p = 0.293$; tarsus: $F_{1,49} = 2.03$, $p = 0.161$; wing: $F_{1,49} = 2.79$, $p = 0.102$; Fig. 1F–H), sex (bill: $F_{1,49} = 0.01$, $p = 0.922$; tarsus: $F_{1,49} = 0.02$, $p = 0.898$; wing: $F_{1,49} = 0.14$, $p = 0.706$), and their interactions (bill: all interactions, $p > 0.350$; tarsus: all interactions, $p > 0.150$; wing: all interactions, $p > 0.130$) on body size.

3.2. Effect of chronic noise exposure on the CORT stress response and hematocrit

There was no significant effect of brood size ($F_{1,36} = 1.36$, $p = 0.252$), disturbance ($F_{1,36} = 2.33$, $p = 0.135$; Fig. 2A), sex ($F_{1,36} = 0.24$, $p = 0.629$), scaled mass index ($F_{1,36} = 1.80$, $p = 0.188$) and their interactions (all interactions, $p > 0.100$) on baseline CORT levels of 9 days old chicks. Similarly, there was no significant effect of brood size ($F_{1,42} = 0.16$, $p = 0.688$), disturbance ($F_{1,42} = 0.01$, $p = 0.915$; Fig. 2B), sex ($F_{1,42} = 0.23$, $p = 0.635$), scaled mass index ($F_{1,42} = 0.01$, $p = 0.909$) and their interactions (all interactions, $p > 0.140$) on stress-induced CORT levels of 9 days old chicks. Finally, there was no significant effect of brood size ($F_{1,38} = 0.84$, $p = 0.366$), disturbance ($F_{1,38} = 1.85$, $p = 0.182$; Fig. 2C), sex ($F_{1,38} = 0.49$, $p = 0.486$), scaled mass index ($F_{1,38} = 0.94$, $p = 0.340$) and their interactions (all interactions, $p > 0.150$) on hematocrit levels of 9 days old chicks.

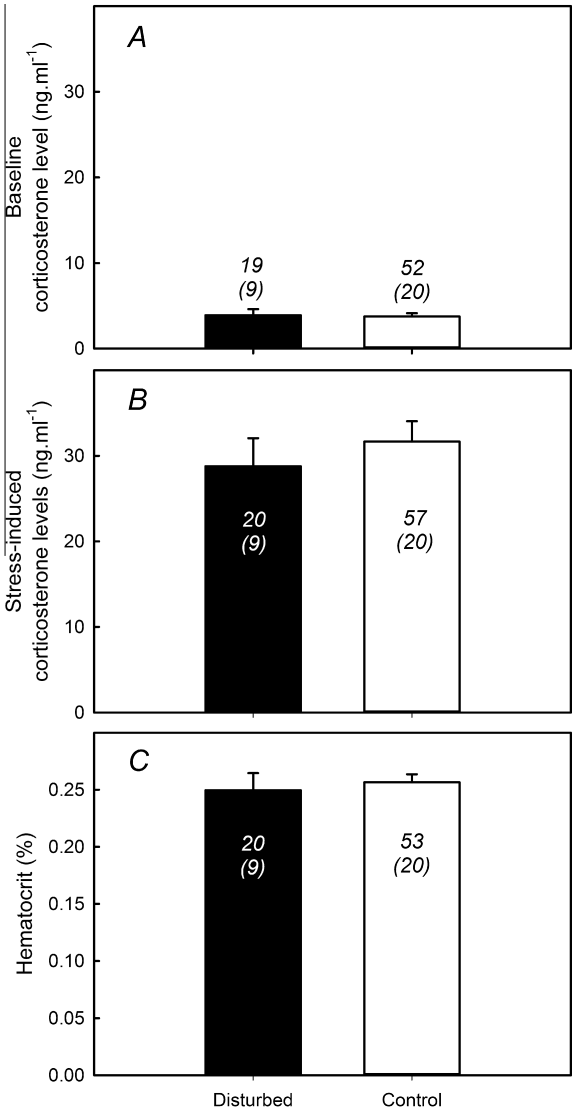

Fig. 2. Influence of an experimental noise exposure on baseline CORT levels (A), stress-induced CORT levels (B), and hematocrit (C) of 9 days-old house sparrow chicks. Data are expressed as Means ± SE. Numbers and numbers in parentheses respectively denote the number of chicks and the number of nests used for these analyses.

3.3. Effect of chronic noise exposure on fledging success

When focusing on all hatched chicks, there was no significant effect of brood size ($F_{1,122} = 0.07$, $p = 0.786$), disturbance ($F_{1,122} = 0.30$, $p = 0.585$; Fig. 3) or their interaction ($F_{1,122} = 0.02$, $p = 0.883$) on fledging success. When focusing on the chicks that reached 9 days, there was no significant effect of brood size ($F_{1,43} = 0.13$, $p = 0.717$), sex ($F_{1,43} < 0.01$, $p = 0.959$), disturbance ($F_{1,43} = 0.06$, $p = 0.805$), scaled mass index ($F_{1,43} < 0.01$, $p = 0.988$), and their interactions (all interactions, $p > 0.150$) on fledging success. Moreover, fledging success was not significantly related to baseline CORT levels ($F_{1,36} < 0.01$, $p = 0.986$), stress-induced CORT levels ($F_{1,42} = 0.26$, $p = 0.614$), hematocrit levels ($F_{1,38} = 1.02$, $p = 0.318$) and any interaction between these variables and sex or disturbance (all interactions, $p > 0.350$).

4. Discussion

In this study, we did not find any evidence for an effect of exposure to traffic noise on the CORT stress response in nestling House sparrows. Contrary to our prediction, baseline CORT levels did not differ between disturbed and control chicks, suggesting that disturbed chicks were not constrained by this experimental noise exposure. Moreover, we did not find any effect of our experimental treatment on the CORT stress response of 9 days old house sparrow chicks, demonstrating that noise exposure does not have a large impact on CORT regulation in this species. Although habituation to our sound treatment may explain the lack of difference between groups, we found this simple explanation unlikely as the same treatment produced strong behavioral shifts in sparrow parents (Meillère et al., 2015a). All together, these results suggest that urban exploiters do not response to urban noise with elevated HPA axis activity during their development, which could potentially explain their ability to live in highly urbanized area.

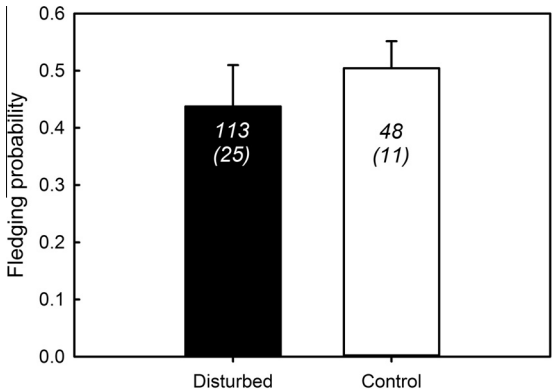

Fig. 3. Influence of an experimental noise exposure on fledging probability of 9 days-old house sparrow chicks. Data are expressed as Means ± SE. Numbers and numbers in parentheses respectively denote the number of chicks and the number of nests used for these analyses.

4.1. Is urban noise stressful for developing sparrows?

Exposure to traffic noise may have a direct effect on baseline CORT levels if such a noise is perceived as stressful by the developing chicks. Indeed, several studies have demonstrated that anthropogenic disturbance is associated with increased baseline CORT levels in wild birds (e.g. Walker et al., 2005; Thiel et al., 2008; Hayward et al., 2011). For instance, Blickley et al. (2012) found that an experimental exposure to anthropogenic noise is associated with elevated fecal CORT levels in greater sage grouses (*Centrocercus urophasianus*). Interestingly, such effect is also apparent in chicks in some bird species (Müllner et al., 2004; Walker et al., 2005; Crino et al., 2011; Strasser and Heath, 2013), suggesting that developing offspring perceive anthropogenic disturbances such as noise as stressors. However and contrary to our prediction, we did not find any influence of traffic noise exposure on baseline CORT levels in house sparrow chicks, suggesting that they may not perceive this urban-related noise as a stressor. Supporting this interpretation, a recent study did not find any significant influence of urbanization on CORT levels in juvenile and adult house sparrows (Meillère et al., 2015b).

On the other hand, noise exposure may have been perceived as stressful by the house sparrow chicks without affecting their circulating CORT levels measured when they were 9 days old. Indeed, chronic stress does not always translate into elevated CORT levels in birds (Busch and Hayward, 2009; Dickens and Romero, 2013). For instance, chronic stress is associated with reduced or unchanged baseline CORT levels in European starlings (*Sturnus vulgaris*, Rich and Romero, 2005; Cyr and Romero, 2007, 2008; Kostelanetz et al., 2009). In vertebrates, chronic stress has a complex influence on the HPA axis and chronic stress often translates into modifications of a single or several features of CORT regulation (Dickens and Romero, 2013). In this study, we did not report any difference in either baseline or stress-induced CORT levels between disturbed chicks and controls. Moreover, we did not find any evidence that disturbed chicks suffer from chronic stress (growth, condition, hematocrit, fledging success, but see Meillère et al. (2015c) regarding telomere length), supporting therefore the idea that exposure to traffic noise did not trigger a state of chronic stress in our study.

Importantly, disturbed chicks may also have habituated to noise exposure (Cyr and Romero, 2009) and, therefore, they may have not perceived this noise as a stressful event when they were sampled after nine days of noise exposure. The experimental treatment may have had short-term effects on circulating CORT levels of house sparrow chicks that became attenuated as chicks habituated to the traffic noise treatment. Because we only sampled chicks after 9 days of exposure to our experimental treatment, our study could not disentangle habituation from insensibility of house sparrow chicks to noise. Habituation is considered as a major but overlooked process in studies focusing on chronic stress (Cyr and Romero, 2009; Dickens and Romero, 2013; Angelier and Wingfield, 2013) and future studies would definitely benefit from testing the ability of developing offspring to habituate to noise. Importantly and contrary to other species, the stress physiology of house sparrow chicks appears to not be sensitive to anthropogenic noise whatever the proximate causes of this relative insensitivity are.

4.2. Does urban noise impose energetic constraints for developing sparrows?

In addition to a direct effect on CORT levels, chronic noise could indirectly affect baseline CORT levels of developing offspring by imposing energetic constraints to the chicks. Indeed, CORT is involved in catabolic activities (Landys et al., 2006) and CORT secretion increases when individuals fast (Lynn et al., 2003, 2010; Angelier et al., 2015) and reach a poor body condition (Kitaysky et al., 2001; Müller et al., 2010). Chronic noise could indeed affect parental behavior and reduce parental nest attendance and brood provisioning (Schroeder et al., 2012). Such a modification of parental behavior could translate into important energetic constraints for the brood, and therefore, into elevated circulating CORT levels. Although we previously reported that parental antipredator behavior was increased by this chronic noise exposure (Meillère et al., 2015a), we did not report any effect of our experimental treatment on the body condition, the hematocrit, the growth or the fledging success of house sparrow chicks. This suggests that disturbed parents were as able as controls to fulfill their brood energy requirements although future studies should specifically examine the influence of traffic noise exposure on brood provisioning rate to confirm this.

On the other hand, the influence of anthropogenic noise exposure on the HPA axis may depend on the intensity of the acoustic disturbance. Thus, another study reported that chronic noise exposure was associated with a reduced brood provisioning and a lower breeding success in the house sparrows (Schroeder et al., 2012). In this latter study, noise intensity was higher (Mean: 68.0 dB, Schroeder et al., 2012) than in our experiment (Mean: 63.32 dBA). Together, these two studies suggest that the influence of anthropogenic noise on CORT levels may follow a non-linear relationship with detrimental effects beginning to appear when sound intensity reaches an upper threshold value. This discrepancy between our results and those from Schroeder et al. (2012) may also depend on other characteristics of the sound that was broadcast (e.g. frequency, time of the day) and on the hearing range of sparrows. Finally, inter-population differences in noise sensitivity could also play a role since these two studies were conducted in different location (Scandinavia: Schroeder et al., 2012; Western Europe: this study). Supporting this possibility, previous studies have reported inter-population variations in morphological (e.g. Murphy, 1985) and physiological measurements (e.g. Martin et al., 2004) in this species although not in direct relation with traffic noise. Future studies are now required to better assess the detailed relationship that links noise characteristics (intensity, frequency, duration) to population responses to this disturbance.

4.3. Exposure to urban noise and the ontogeny of the CORT stress response

In vertebrates, glucocorticoids are important mediators of the development processes (Wada, 2008) and the development of the HPA axis results in an increasing ability of individuals to activate the glucocorticoid stress response through development (Sims and Holberton, 2000; Wada et al., 2007; Rensel et al., 2010a). Importantly, there is a large inter-individual variability in the CORT stress response of developed chicks, suggesting that genetic and environmental factors affect the ontogeny of this stress reactivity (Wada et al., 2009). Indeed, early life conditions and stressors can have a huge impact on stress physiology and the HPA axis (Marasco et al., 2012; Zimmer and Spencer, 2014; Crino et al., 2014) and it has been suggested that this plasticity of the HPA axis could shape the physiological phenotype of individuals to make it match the environmental conditions the individual is likely to encounter during its life (Monaghan, 2008; Zimmer et al., 2013; Angelier and Wingfield, 2013). For example, early life stress can induce a hyper-activation of the HPA axis that results therefore in elevated stress-induced CORT levels later in life (Pravosudov and Kitaysky, 2006; Rensel et al., 2010b; Banerjee et al., 2012; Marasco et al., 2012; Crino et al., 2014). On the other hand, early life stress can also induce a dampened stress response in offspring and this modification can persist during adulthood (Love and

Williams, 2008; Crino et al., 2013; Zimmer et al., 2013). However, we did not find any effect of noise exposure on stress-induced CORT levels of house sparrow chicks, suggesting that our experimental procedure did not affect the ontogeny of the HPA axis although noise exposure may have affected other stress physiology parameters such as corticosterone binding globulin (CBG), or glucocorticoid receptors regulation (Wada et al., 2007; Zimmer and Spencer, 2014; Schmidt et al., 2014). In addition, noise exposure did not affect body size, body condition, hematocrit, and fledging success of house sparrow chicks. This suggests that noise exposure may not have been perceived as a stressor by house sparrow chicks as evidenced by the similar stress responses of disturbed and control chicks.

Although we did not find any evidence that noise exposure affects stress physiology in house sparrow chicks, a recent study reported that a similar experimental exposure to traffic noise was associated with a dampened stress response in white-crowned sparrows (Crino et al., 2013). Interestingly, this suggests that all species may not be able to equally cope with urban noise, with urban exploiters being not affected to large extent by urban noise exposure. Supporting this possibility, the impact of urbanization on the stress response of wild vertebrates appears relatively inconsistent (Bonier, 2012; Grunst et al., 2014; Foltz et al., 2015) with for example no clear difference in the CORT stress response between urban and rural house sparrows (Fokidis et al., 2009; Bókony et al., 2012; Meillère et al., 2015b). So far, the impact of anthropogenic noise on circulating glucocorticoid levels has mainly been investigated in "urban avoiders" and "urban adapters" and very little is known on the potential impact of anthropogenic noise on "urban exploiters". Although limited to a single species, our study provides one of the first evidence that urban exploiters may be relatively insensitive to urban noise during their development. This physiological insensitivity to novel stressors during development combined with a high behavioral flexibility during adulthood (Meillère et al., 2015a) might also explain why this species has been successful in colonizing numerous parts of the world. Further comparative studies are now required to understand whether insensitivity to anthropogenic noise is a consistent phenomenon in urban exploiters and whether this is a major requirement of an urban way of life.

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