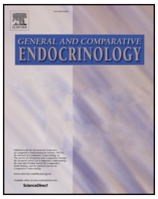
General and Comparative Endocrinology 276 (2019) 45–51

Contents lists available at ScienceDirect

General and Comparative Endocrinology

journal homepage: www.elsevier.com/locate/ygcen



Post-natal corticosterone exposure affects ornaments in adult male house sparrows (*Passer domesticus*)

Sophie M. Dupont[a,*], Jacquelyn K. Grace[b], François Brischoux[a], Frédéric Angelier[a]

[a] *Centre d'Etudes Biologiques de Chizé, CNRS-ULR, UMR 7372, 79360 Villiers en Bois, France*
[b] *Dept. of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843, USA*

ARTICLE INFO

Keywords:
Early-life stress
Glucocorticoid
Ornament
House sparrow

ABSTRACT

In vertebrates, the ontogeny of several crucial organismal systems is known to occur early in life. Developmental conditions can ultimately have important consequences on adult fitness by affecting individual phenotype. These developmental effects are thought to be primarily mediated by endocrine systems, and especially by glucocorticoids. In this study, we tested how post-natal exposure to corticosterone (the primary avian glucocorticoid) may subsequently affect the expression of ornaments in adult male house sparrows (*Passer domesticus*). Specifically, we investigated the long-term consequences of this manipulation on the size and color of several visual signals: badge, wing bar, tarsus and beak. Post-natal corticosterone exposure had a strong negative impact on the size, but not the color, of some male ornaments (badge and wing bar surface area). Because wing bar and badge surface area are used as sexual and/or hierarchical signals in house sparrow, we showed that early life stress can affect some aspect of attractiveness and social status in this species with potentially important fitness consequences (e.g. sexual selection and reproductive performance).

Future studies need now to explore the costs and benefits of this developmental plasticity for individuals (i.e. fitness).

1. Introduction

Early life is considered a critical step of the life-history cycle because the ontogeny of crucial organismal systems occurs during that specific period (Lindström, 1999). Accordingly, developmental conditions are well known to influence growth, perinatal survival, adult phenotype and ultimately individual fitness (Mousseau and Fox, 1998). For some species, poor developmental conditions, such as nutritional constraints, infections, or high parasite loads, appear to have a detrimental effect on adult fitness (i.e., "the silver spoon effect", Metcalfe and Monaghan, 2001). Alternatively, several studies have also suggested that developmental conditions could prime the organism to match the phenotype to the environmental conditions which are likely to be encountered during adulthood (i.e., "the environmental matching hypothesis"; Monaghan, 2008). Under the latter hypothesis, poorer developmental conditions can be associated with better adult performances when adults live in a harsh environment (Monaghan, 2008; Crino and Breuner, 2015; Nettle and Bateson, 2015).

The endocrine system is one mechanism that mediates the influence of developmental conditions on adult phenotype and performance (Lessells, 2008; McGlothlin and Ketterson, 2008). More precisely the hypothalamic-pituitary-adrenals (HPA) axis and associated exposure to glucocorticoids is one of the primary mechanisms vertebrates use to sense stressors in their environment and alter their phenotype in response (Spencer et al., 2009; Romero, 2004; Harris and Seckl, 2011; Levine, 2002). Glucocorticoids are often classified as the main "stress" hormones in vertebrates because they are secreted in response to stressors or energetic challenges (Sapolsky et al., 2000; Romero, 2004). In this way, they are involved in allostasic processes, which mediate behavioral and physiological adjustments to environmental changes (McEwen and Wingfield, 2003; Romero et al., 2009; Angelier and Wingfield, 2013). Developing organisms can be exposed to glucocorticoids either through maternal transfer (e.g. glucocorticoid yolk deposition in oviparous species or maternal glucocorticoid secretion in viviparous species) or through the stimulation of the HPA axis of the developing organism itself (Groothuis and Schwabl, 2008; Meylan et al., 2012). Developmental exposure to glucocorticoids is known to affect the ontogeny of several organismal systems in vertebrates, and therefore, to be an important driver of phenotypic plasticity (Dufty et al., 2002; Wada, 2008; Schoech et al., 2011). Therefore, understanding how developmental exposure to glucocorticoids may subsequently affect adult phenotype and fitness is crucial to assess the impact

---

* Corresponding author.
E-mail address: sophie.dupont@cebc.cnrs.fr (S.M. Dupont).

https://doi.org/10.1016/j.ygcen.2019.02.021
Received 7 September 2018; Received in revised form 4 February 2019

of early life stressors on wild vertebrates (Crino and Breuner, 2015).

Several studies have shown that developmental conditions and glucocorticoid exposure can have both short-term and long-lasting effects on morphology, physiology and behavior (reviewed in Schoech et al., 2011; Crino and Breuner, 2015). For instance, experimental post-natal glucocorticoid exposure can affect growth (Kriengwatana et al., 2013; Grace et al. 2017a) with long-term effects on adult body size (Kriengwatana et al., 2013). Post-natal glucocorticoid exposure also affects metabolism (Spencer and Verhulst, 2008; Careau et al., 2014; Schmidt et al., 2012), cognition (Crino et al., 2014a), neophobic and antipredator behavior (Spencer and Verhulst, 2007; Grace et al., 2017b).

A few studies have examined the direct impact of developmental conditions on fitness and reproductive performance of wild vertebrate species (Van De Pol et al., 2006; Stamps, 2006; Descamps et al., 2008; Bouwhuis et al., 2015; Marshall et al., 2017). For example, zebra finch males that were developmentally stressed (i.e., post-natal corticosterone (CORT) exposure) had a reduced adult life expectancy compared to controls (Monaghan et al., 2012). In this same species, Crino et al. (2014b) also reported that post-natal corticosterone treatment resulted in subsequent higher reproductive success, suggesting that early life glucocorticoid exposure can be beneficial later in life, at least under some circumstances. The difficulty of following wild individuals throughout their lifetime (Stamps, 2006; Clutton-Brock and Sheldon, 2010; Cam and Aubry, 2011) has led many researchers to rely on secondary sexual signals as a proxy for adult reproductive success (Spencer et al., 2003, 2005; Buchanan et al., 2003, 2004; Schmidt et al., 2013). However, most of these studies have focused on acoustic signals (reviewed in Peters et al., 2014) while neglecting visual signals (but see Crino et al., 2014b). In addition, several studies have examined whether nutritional developmental conditions can affect the expression of secondary sexual visual signals during adulthood (e.g., Hill, 2000; Naguib and Nemitz, 2007; Hubbard et al., 2015; Honarmand et al., 2017; Naguib et al., 2008; Noguera et al., 2017). But, to our knowledge, only a single study has experimentally tested whether developmental glucocorticoid exposure could affect such signals and they did not find any relationship between bill coloration and developmental CORT exposure (Crino et al., 2014b).

Here, we tested the influence of a post-natal exposure to CORT, the primary avian glucocorticoid, on the expression of potential secondary sexual signals in adult male house sparrows (*Passer domesticus*). This species is especially relevant to test this hypothesis because ornaments have been extensively studied in this species (Laucht and Dale, 2012; Møller, 1987a,b; Buchanan et al., 2001; Laucht et al., 2011). Although the role of house sparrow badge (size and coloration) in sexual selection is debated (reviewed in Nakagawa et al., 2007), this ornament has been linked to male physiological condition (Buchanan et al., 2001; Gonzalez et al., 2001; Laucht et al., 2011, 2010), hierarchical status (Møller, 1987a,b; Bókony et al., 2006), body condition (Poston et al., 2005), age (Veiga, 1993; Nakagawa et al., 2007; Morrison et al., 2008) and sexual motivation (Møller, 1990). In addition, wing bar is also affected by age and condition (Laucht and Dale, 2012) and it has been identified as a visual ornament which is used by females for sexual selection (Moreno-Rueda and Hoi, 2012). Recently, beak and tarsus colorations have also been suggested as potential secondary sexual signals (Laucht et al., 2010; Laucht and Dale, 2012). Overall, these multiple ornaments have the potential to signal an individual status (condition, age, fighting ability; Bókony et al., 2006; Nakagawa et al., 2007; Laucht and Dale, 2012) and sexual attractiveness (at least for wing bar: Moreno-Rueda and Hoi, 2012). In this study, we specifically tested whether post-natal CORT exposure affected the expression of all these visual signals in adult male house sparrows. Post-natal CORT exposure could mimic poor developmental conditions or increase early-life energy expenditure, leading to poor quality adult males who would therefore display smaller or less colorful visual signals (i.e., the "silver-spoon hypothesis", Lindström, 1999). Alternatively, post-natal CORT exposure may shape the phenotype of the sparrows to increase their ability to cope with a stressful environment (i.e., the "environmental matching hypothesis"; Monaghan, 2008). Under that scenario, post-natal CORT treatment could affect life-history strategy and reproductive investment (Crino and Breuner, 2015). Because post-natal CORT exposure is associated with reduced lifespan in house sparrows (Grace et al., 2017a), we would expect that post-natal CORT exposure will lead to increased investment in visual sexual signals. Therefore, we predict that post-natal CORT exposure may specifically affect the ornaments, which are involved in sexual selection (e.g. wing bar, Moreno-Rueda and Hoi, 2012). Finally, post-natal CORT treatment may also have no effect on these signals, as previously reported in a domestic bird species (Crino et al., 2014b).

2. Material and methods

2.1. Study species and post-natal CORT treatment

This study focused on seventeen wild-origin first-breeding male house sparrows that were held in captivity under standardized conditions. These sparrows were used previously to investigate the impact of post-natal glucocorticoid exposure on development and adult behavior, physiology and morphology (see Grace et al., 2017a,b). In brief, wild nestlings in their nests were given corticosterone (CORT) non-invasively by injecting live mealworms with 20 µl of 0.6 mg mL^{-1} CORT (days 8 and 9 post-hatching) or 0.9 mg mL^{-1} CORT (day 11 post-hatching) suspended in dimethyl sulfoxide (DMSO). Treatment occurred in the morning on days 8 and 9 post-hatching and both morning and evening on day 11 post-hatching, when half of the chicks in the study were given CORT-injected mealworms (CORT-fed group) while the other half were given DMSO-only mealworms (Control group). This technique resulted in a temporary and acute increase in circulating CORT levels (see Grace et al., 2017a for further details). At fledging, all individuals were transferred to captivity and were held under standardized conditions. They were fed *ad libitum* with commercial seed mixture and water, were supplied with salt/mineral blocks and millet on the stalk, and kept on a natural daylight schedule. At the beginning of the breeding season (May 2016), when birds were approximately one year-old, the sexual ornaments of 17 surviving males were measured (10 CORT-fed sparrows, 7 controls).

2.2. Badge and wing bar surface area

Following the methods of previous studies, we determined maximal badge length and width on live birds using a ruler to the nearest 0.1 cm (Møller, 1987a). These two measurements correspond respectively 1) to the highest vertical distance between the base of the beak and the black feather tips of the badge; 2) to the highest horizontal distance between black feathers composing the badge. We determined the badge surface area using the regression equation previously established and validated by Møller (1987a) and Gonzalez et al. (2001) for house sparrows: badge size $(\mathrm{mm}^2) = 166.7 + 0.45 \times$ badge length $(\mathrm{mm}) \times$ badge width (mm).

One photograph of the left wing of each individual was taken with a Canon EOS D500 ($N = 16$ because one photograph was of low quality and could not be used). Birds were placed at the same distance from the camera and with the back oriented towards the camera. The wing was opened and was positioned flat on a board. Then, the white wing bar surface area was determined with Gimp (version 2.8.22). Specifically, the contours of the wing bar were delimited with the free selection tool of the software and the number of pixels calculated. Pixel number was then converted into mm^2 using a reference of known surface area.

2.3. Badge, beak, tarsus and wing bar color

Birds were photographed always at the same distance in front of a gray background including one colored standard reference. They were held successively in four standardized positions (see Laucht and Dale, 2012 for more details) in order to take pictures with the best viewing angle of the badge, the beak, the tarsus and the wing bar respectively. For each individual, the contours of the black badge and the white wing bar were delimited using the free selection tool of Gimp. For the beak and the tarsus, a specific part of the ornament was selected: a triangle ($0.26\,cm^2$) and a rectangle ($0.35\,cm^2$) were respectively drawn at the base of the lower mandible and on the upper half of the tarsus. For each selected surface, the proportions of Red (R), Blue (B) and Green (G) were extracted by using Gimp. These values were then converted into hue (H), saturation (S) and brightness (B). Hue is expressed in degree and corresponds to the specific tone of a color. Saturation is expressed in percentage and corresponds to the color intensity. Brightness is expressed in percentage and corresponds to the relative darkness of a color (0% and 100% respectively indicate a black and a white surface). By applying the same methodology, we also determined the HSB values for the colored-standard reference that was present in all photographs. This reference was used to obtain standardized and comparable HSB values for each individual (see Laucht and Dale, 2012 for further details). Note that the pictures of the badge were only used for color determination and they could not be used to determine badge size because part of the badge was not visible in some pictures.

2.4. Body size and body condition

For each individual, wing length was measured with a ruler to the nearest 0.1 cm, and beak and tarsus length were measured with a caliper to the nearest 0.1 mm. Birds were weighed with an electronic scale to the nearest 0.1 g. Body condition was calculated using the scaled mass index (SMI) following Peig and Green, 2009. Tarsus length was highly correlated with body mass (tarsus: $r = 0.626$; $F_{1,15} = 9.65$; $p = 0.007$) and was therefore used to calculate the SMI of house sparrows ($SMI_i = M_i x (\frac{L_0}{L_i})^b$). The terms M_i and L_i respectively correspond to the body mass and the tarsus length of the individual i. The term L_0 is the arithmetic mean value of tarsus length for the whole study population ($L_0 = 18.94\,mm$, $n = 17$ individuals). The exponent b corresponds to the slope estimate of a standardized major axis regression of log-transformed body mass on log-transformed tarsus length ($b = 1.03$).

2.5. Statistical analysis

We used linear models (LM) with a normal error distribution to test the influence of the post-natal CORT treatment on (1) badge surface area and coloration, (2) wing bar surface area and coloration, (3) beak length and coloration, (4) tarsus length and coloration. For each model, post-natal CORT treatment and SMI were included as explanatory variables. Regarding the coloration of ornaments, we also included the size of the studied ornament as an explanatory variable in the models. Interactions were not included because of the limited sample sizes ($N = 17$ for badge, tarsus and beak; $N = 16$ for wing). All statistical analyses were performed with R.3.1.1 (R core Team, 2015).

3. Results

3.1. Ornament size

Badge surface area was significantly smaller in CORT-fed males compared to controls ($F_{1,14} = 14.26$, $p = 0.002$; Fig. 1A), and there was no significant effect of SMI on badge surface area ($F_{1,14} = 1.98$, $p = 0.18$). CORT-fed males also had smaller wing bars than controls ($F_{1,13} = 12.06$, $p = 0.004$; Fig. 1B) and wing bar surface area was negatively correlated with SMI ($F_{1,13} = 6.65$, $p = 0.023$).

Beak length was significantly and positively correlated with SMI ($F_{1,14} = 7.21$, $p = 0.018$). However, there was no significant effect of post-natal CORT treatment on beak length ($F_{1,14} = 0.251$, $p = 0.624$, Fig. 1C). Tarsus length was not affected by the post-natal CORT treatment or SMI ($F_{1,14} = 0.005$, $p = 0.945$; $F_{1,14} < 0.001$, $p = 0.991$ respectively, Fig. 1D).

3.2. Ornamental coloration

For all ornaments, no color variables (hue, saturation, brightness) were explained by post-natal CORT treatment or by SMI or by ornament size (Table 1).

4. Discussion

In this study, we showed that developmental CORT exposure negatively affected the size of plumage-based, but not structural ornaments in a wild bird species. Specifically, we found that male house sparrows that had received CORT treatment as nestlings had smaller badges and wing bars as adults. However, we did not find any impact of post-natal CORT exposure on beak and tarsus length or on the coloration of any of these ornaments (badge, wing bar, beak and tarsus). Because wing bar size is an important determinant of mate selection in this species (Laucht and Dale, 2012; Moreno-Rueda and Hoi, 2012; Laucht et al., 2011), our study suggests that early-life exposure to corticosterone reduces some aspects of sexual attractiveness in male house sparrows. In addition, we also found that post-natal CORT exposure had a negative impact on badge size, which has previously been associated with physiological status, condition, and fighting abilities (Buchanan et al., 2001; Gonzalez et al., 2001; Laucht et al., 2011, 2010; Møller, 1987a,b; Bókony et al., 2006; Poston et al., 2005). Previous work in this species has also found reduced survival due to post-natal CORT exposure (Grace et al., 2017a). Together with our result, this provides support for the “silver spoon hypothesis”: early-life CORT exposure leads to poor quality adult males, probably by mimicking poor developmental conditions or increasing early-life energy expenditure.

4.1. Post-natal CORT treatment, badge and wing bar size

We found that post-natal CORT exposure was associated with smaller plumage-based visual signals later in life (badge and wing bar size). Although numerous studies have examined the impact of developmental CORT exposure on adult acoustic signals (i.e. song) in birds (Spencer et al., 2003, 2005; Buchanan et al., 2004; Schmidt et al., 2013), only a single study has focused on adult visual sexual ornaments. Similar to our results for color of ornaments, Crino et al. (2014b) found no relationship between developmental CORT treatment and the color of sexual ornaments in zebra finches. To our knowledge, our study is therefore the first to show that developmental CORT exposure can affect the expression (i.e., size) of sexual (wing bar, Moreno-Rueda and Hoi, 2012) and hierarchical (badge, Nakagawa et al., 2007) ornaments.

Although the effect of glucocorticoids, specifically, on avian sexual ornamentation is relatively understudied, several studies have reported a negative effect of poor developmental conditions on the size or the color of sexual plumage ornaments in birds (Butler and McGraw, 2010; Ohlsson et al., 2002; Walker et al., 2013; Naguib and Nemitz, 2007; Hubbard et al., 2015; Honarmand et al., 2017). Because we found that developmental CORT exposure can also negatively affect the size of wing bars, our study suggests that CORT may mediate the influence of poor developmental conditions on the expression of sexual ornaments later in life.

In vertebrates, glucocorticoid secretion classically increases in response to energetic challenges (Sapolsky et al., 2000; Romero, 2004). Increased CORT levels trigger multiple behavioral and physiological changes that may help nestlings survive such challenges (Wingfield et al., 1998; Angelier and Wingfield, 2013). These changes are often associated with a reallocation of resources from growth or other life-history traits to immediate survival (Wingfield and Sapolsky, 2003;

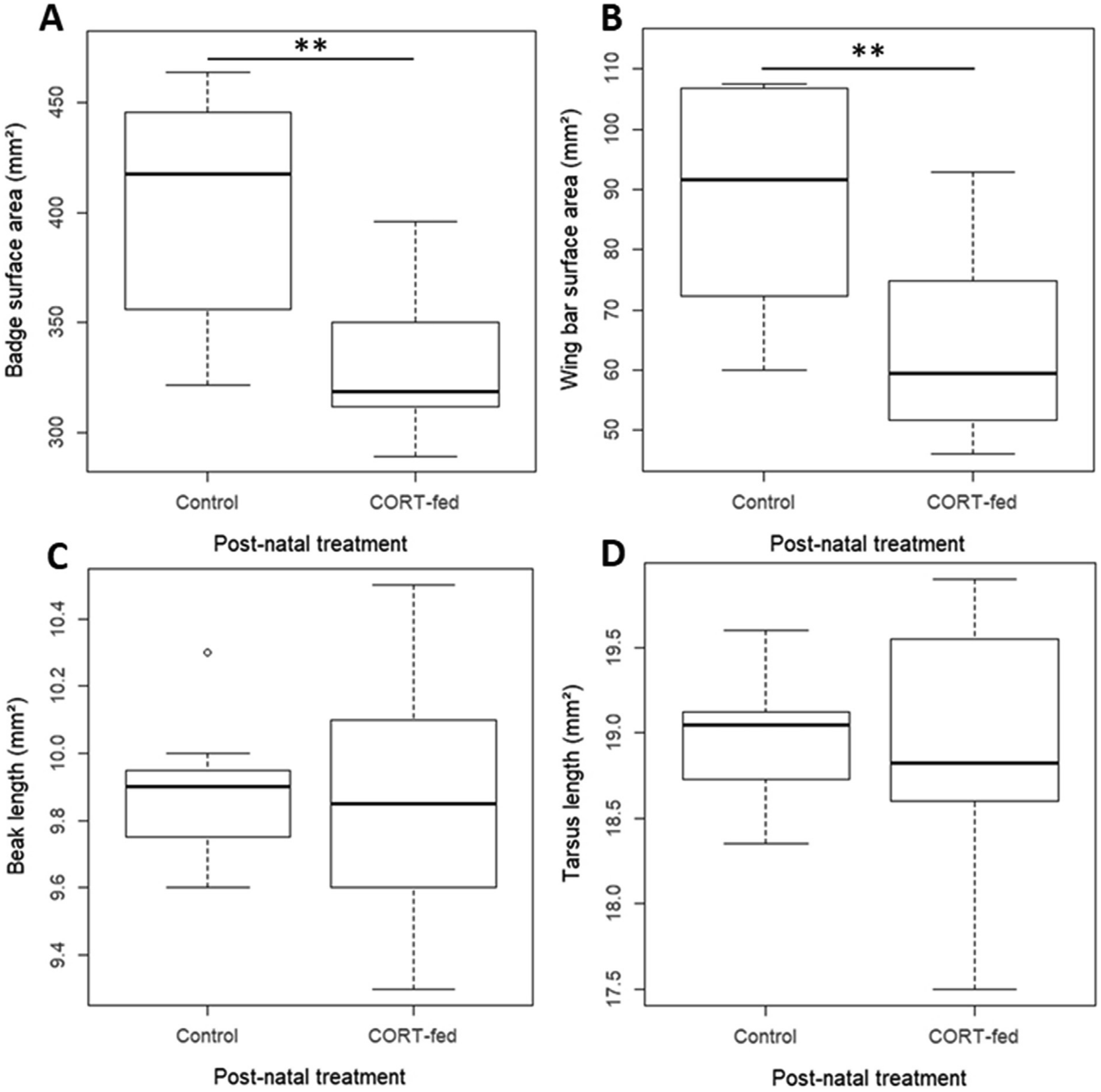


Fig. 1. Post-natal treatment effect on badge surface area (A), wing bar surface area (B), beak length (C) and tarsus length (D). Box-and-whisker plots represent the data: the top and bottom of the boxes represent the first and last quartiles, respectively; the line across the box represents the median. The whiskers represent the fifth and ninety-fifth percentiles, and the circles represent outliers.

Angelier and Wingfield, 2013). For example, elevated CORT levels in chicks can be associated with depletion of energy reserves (i.e. protein catabolism; Sapolsky et al., 2000; Landys et al., 2006), delayed growth (Hull et al., 2007; Wada and Breuner, 2008; Grace et al., 2017a), poor body condition (Davison et al., 1983; Kitaysky et al., 2003; Schoech et al., 2011), and immuno-depression (Loiseau et al., 2008; Stier et al., 2009). All of these changes may have long-term consequences on physiological determinants of sexual signals later in life and on life-history strategy (i.e., reproductive investment: Taborsky, 2006; Schoech et al., 2011; Crino and Breuner, 2015). For instance, poor developmental nutritional conditions and CORT exposure have important long-term effects on the functioning of the HPA axis (Hull et al., 2007; Crino et al., 2014b; Haussmann et al., 2012; Love and Williams, 2008; Marasco et al., 2012; Spencer et al., 2009; Pakkala et al., 2016), which interacts with the hypothalamic-pituitary-gonadal (HPG) axis to regulate sexual hormone secretion (e.g., testosterone) in vertebrates (Wingfield and Sapolsky, 2003). Therefore, long-term modifications of the HPA axis could affect adult badge and wing bar sizes, which are under control of testosterone levels in house sparrows (Evans et al., 2000; Gonzalez et al., 2001; Buchanan et al., 2001; Laucht et al., 2011; Laucht and Dale 2012), as are many other vertebrate sexual and hierarchical ornaments (Hau, 2007).

Similarly, CORT is known to affect the growth and structure of feathers, and the color and quality of the plumage (DesRochers et al., 2009; Jenni-Eiermann et al., 2015). For example, CORT-implanted barn owl nestlings (*Tyto alba*) produced feathers with less phaeomelanic coloration relative to control nestlings (Roulin et al., 2008). Therefore, a long-term modification of the HPA axis could explain why plumage ornaments are overall smaller in CORT-treated birds relative to control ones. Further studies are necessary to assess how post-natal CORT exposure may mechanistically affect badge and wing bar sizes in house sparrows.

4.2. Post-natal CORT treatment, body size and color of ornaments

We did not find any effect of post-natal CORT exposure on the other

Table 1
The effects of post-natal CORT treatment, SMI and ornament size on color variables (i.e., hue, saturation and brightness) of sexual ornaments (i.e., badge, wing bar, beak and tarsus). Main effects were tested using a linear model with a normal error distribution.

Ornament	Color variable	Explanatory variable	df	F-value	p-value
Badge	Hue	post-natal CORT treatment	1,13	3.577	0.081
		SMI	1,13	0.001	0.979
		Badge surface	1,13	3.480	0.085
	Saturation	post-natal CORT treatment	1,13	0.722	0.411
		SMI	1,13	1.803	0.202
		Badge surface	1,13	0.215	0.651
	Brightness	post-natal CORT treatment	1,13	0.386	0.545
		SMI	1,13	0.239	0.633
		Badge surface	1,13	0.061	0.809
Wing bar	Hue	post-natal CORT treatment	1,12	1.622	0.227
		SMI	1,12	0.063	0.805
		Wing bar surface area	1,12	0.909	0.359
	Saturation	post-natal CORT treatment	1,12	1.797	0.205
		SMI	1,12	0.393	0.542
		Wing bar surface area	1,12	0.663	0.432
	Brightness	post-natal CORT treatment	1,12	2.097	0.173
		SMI	1,12	0.809	0.386
		Wing bar surface area	1,12	2.452	0.143
Beak	Hue	post-natal CORT treatment	1,13	0.008	0.930
		SMI	1,13	0.051	0.825
		Beak length	1,13	4.32	0.058
	Saturation	post-natal CORT treatment	1,13	0.031	0.863
		SMI	1,13	0.737	0.406
		Beak length	1,13	0.157	0.698
	Brightness	post-natal CORT treatment	1,13	0.051	0.825
		SMI	1,13	0.371	0.553
		Beak length	1,13	0.137	0.717
Tarsus	Hue	post-natal CORT treatment	1,13	0.049	0.828
		SMI	1,13	0.162	0.694
		Tarsus length	1,13	0.052	0.823
	Saturation	post-natal CORT treatment	1,13	0.016	0.902
		SMI	1,13	0.245	0.629
		Tarsus length	1,13	1.14	0.306
	Brightness	post-natal CORT treatment	1,13	0.094	0.764
		SMI	1,13	0.007	0.937
		Tarsus length	1,13	0.116	0.739

visual attributes we examined, such as tarsus and beak lengths or the color of all our variables of interest (i.e., tarsus, beak, badge, wing bar). Although there is little literature examining the effect of post-natal CORT on ornaments in birds, we can again look to studies investigating developmental nutritional constraints, which typically increase circulating CORT (Kitaysky et al., 1999; Pravosudov and Kitaysky, 2006). There, we see that although developmental nutritional constraints are often associated with low quality ornaments in birds, this is not always the case (e.g., Blount et al., 2003; Naguib et al., 2008; Krause and Naguib, 2015; Honarmand et al., 2017). Together with our results, this suggests that specific ornaments and/or the characteristics of specific ornaments may be more sensitive to poor developmental conditions and post-natal CORT exposure than others in some species. Several studies have shown that individuals are able to compensate for a bad start in life (Lindstrom et al., 2005) and accordingly we did not find any effect of postnatal CORT on the color of ornaments, or on adult body size (tarsus and beak), consistent with previous research in this system (Grace et al., 2017a) Experimental birds were able to catch-up with control birds despite the well-known acute negative effect of CORT exposure on early-life growth in birds (e.g. Davison et al., 1983; Kitaysky et al., 2003; Schoech et al., 2011) including the house sparrow (Loiseau et al., 2008; Grace et al., 2017a). Our study demonstrates that CORT exposure does not always have long-lasting consequences on structural body size (see also Grace et al., 2017a) or the color of some ornaments (beak, tarsus, badge and wing bar), at least when individuals are maintained in optimal captive conditions (i.e. food *ad libitum*).

It remains unclear why the coloration of ornaments is not affected by post-natal CORT exposure (see also Crino et al., 2014b). The expression of some ornaments may not be determined by physiological systems that are affected by developmental CORT exposure. For example, a few studies did not find any evidence that CORT levels are related to melanin-based plumage color in birds (Jenkins et al., 2013; Fairhurst et al., 2015; Angelier et al., 2018) and this could explain why the color of ornaments were not affected by developmental CORT exposure in our study.

4.3. Conclusion

In this study, we demonstrated that developmental CORT exposure can affect the expression of male ornaments, which are used as sexual and/or hierarchical signals (badge and wing bar size) in house sparrows (Laucht and Dale, 2012; Møller, 1987a,b; Nakagawa et al., 2007; Laucht et al., 2011). It shows that early life stress can affect attractiveness and social status in this species with potentially important fitness consequences (e.g. sexual selection and reproductive performance). We only studied individuals one year after CORT exposure and future studies should now examine whether these effects of developmental CORT exposure on ornaments persist through the entire lifetime of individuals (average life span for house sparrows: 5–6 years old, Anderson, 2006). Finally, CORT may also affect reproductive strategies and CORT-fed individuals may invest their resources towards parental care at the expense of the expression of specific ornaments (see Crino et al., 2014b for an example). Therefore, future studies should also examine the consequences of developmental CORT exposure on mate choice and reproductive performance to fully assess the impact of early-life stress on individual fitness.

Acknowledgements

We thank L. Froud, L. Martin-Gousset, J. Pavie and D. Ménard for field work and caring for captive birds.

This material is based upon work supported under a Fondation Fyssen Postdoctoral Fellowship to J. Grace. This work was supported by the Centre National de la Recherche Scientifique, the Centre d'Etudes Biologiques de Chizé, the CPER ECONAT, and the Agence Nationale de la Recherche (ANR project URBASTRESS ANR-16-CE02-0004-01 to F. Angelier). S. Dupont was supported by a grant from the Conseil Général des Deux-Sèvres and the Région Nouvelle-Aquitaine.

References

Anderson, T.R., 2006. Biology of the Ubiquitous House Sparrow: From Genes to Populations. Oxford University Press, New York.

Angelier, F., Parenteau, C., Trouvé, C., Angelier, N., 2018. The behavioural and physiological stress responses are linked to plumage coloration in the rock pigeon (*Columbia livia*). Physiol. Behav. 184, 261–267. https://doi.org/10.1016/j.physbeh.2017.12.012.

Angelier, F., Wingfield, J.C., 2013. Importance of the glucocorticoid stress response in a changing world: theory, hypotheses and perspectives. Gen. Comp. Endocrinol. 190, 118–128. https://doi.org/10.1016/j.ygcen.2013.05.022.

Blount, J.D., Metcalfe, N.B., Birkhead, T.R., Surai, P.F., 2003. Carotenoid modulation of immune function nd sexual attractiveness in zebra finches. Science 300, 125–127. https://doi.org/10.1126/science-1082142.

Bókony, V., Lendvai, Á.Z., Liker, A., 2006. Multiple cues in status signalling: the role of wingbars in aggressive interactions of male House Sparrows. Ethology 112, 947–954.

https://doi.org/10.1111/j.1439-0310.2006.01246.x.

Bouwhuis, S., Vedder, O., Becker, P.H., 2015. Sex-specific pathways of parental age effects on offspring lifetime reproductive success in a long-lived seabird. Evolution 69, 1760–1771. https://doi.org/10.1111/evo.12692.

Buchanan, K.L., Evans, M.R., Goldsmith, A.R., Bryant, D.M., Rowe, L.V., 2001. Testosterone influences basal metabolic rate in male house sparrows: a new cost of dominance signalling? Proc. R. Soc. Lond. B Biol. Sci. 268, 1337–1344.

Buchanan, K.L., Leitner, S., Spencer, K.A., Goldsmith, A.R., Catchpole, C.K., 2004. Developmental stress selectively affects the song control nucleus HVC in the zebra finch. Proc. R. Soc. B Biol. Sci. 271, 2381–2386. https://doi.org/10.1098/rspb.2004.2874.

Buchanan, K.L., Spencer, K.A., Goldsmith, A.R., Catchpole, C.K., 2003. Song as an honest signal of past developmental stress in the European starling (*Sturnus vulgaris*). Proc. R. Soc. Lond. B Biol. Sci. 270, 1149–1156.

Butler, M.W., McGraw, K.J., 2010. Past or present? Relative contributions of developmental and adult conditions to adult immune function and coloration in mallard ducks (*Anas platyrhynchos*). J. Comp. Physiol. B. https://doi.org/10.1007/s00360-010-0529-z.

Cam, E., Aubry, L., 2011. Early development, recruitment and life history trajectory in long-lived birds. J. Ornithol. 152, 187–201.

Careau, V., Buttemer, W.A., Buchanan, K.L., 2014. Early-developmental stress, repeatability, and canalization in a suite of physiological and behavioral traits in female zebra finches. Integr. Comp. Biol. 54, 539–554. https://doi.org/10.1093/icb/icu095.

Clutton-Brock, T., Sheldon, B.C., 2010. Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. Trends Ecol. Evol. 25, 562–573. https://doi.org/10.1016/j.tree.2010.08.002.

R Core Team, 2015. A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna https://www.R-project.org.

Crino, O.L., Breuner, C.W., 2015. Developmental stress: evidence for positive phenotypic and fitness effects in birds. J. Ornithol. 156, 389–398. https://doi.org/10.1007/s10336-015-1236-z.

Crino, O.L., Driscoll, S.C., Ton, R., Breuner, C.W., 2014a. Corticosterone exposure during development improves performance on a novel foraging task in zebra finches. Anim. Behav. 91, 27–32. https://doi.org/10.1016/j.anbehav.2014.02.017.

Crino, O.L., Prather, C.T., Driscoll, S.C., Good, J.M., Breuner, C.W., 2014b. Developmental stress increases reproductive success in male zebra finches. 20141266-20141266. Proc. R. Soc. B Biol. Sci. 281. https://doi.org/10.1098/rspb.2014.1266.

Davison, T.F., Rea, J., Rowell, J.G., 1983. Effects of dietary corticosterone on the growth and metabolism of immature Gallus domestlcus. Gen. Comp. Endocrinol. 50, 463–468.

Descamps, S., Boutin, S., Berteaux, D., Gaillard, J.-M., 2008. Age-specific variation in survival, reproductive success and offspring quality in red squirrels: evidence of senescence. Oikos 117, 1406–1416.

DesRochers, D.W., Reed, J.M., Awerman, J., Kluge, J.A., Wilkinson, J., van Griethuijsen, L.I., Aman, J., Romero, L.M., 2009. Exogenous and endogenous corticosterone alter feather quality. Comp. Biochem. Physiol. A. Mol. Integr. Physiol. 152, 46–52. https://doi.org/10.1016/j.cbpa.2008.08.034.

Dufty, A.M., Clobert, J., Møller, A.P., 2002. Hormones, developmental plasticity and adaptation. Trends Ecol. Evol. 17, 190–196.

Evans, M.R., Goldsmith, A.R., Norris, S.R.A., 2000. The effects of testosterone on antibody production and plumage coloration in male house sparrows (Passer domesticus). Behav. Ecol. Sociobiol. 47, 156–163.

Fairhurst, G.D., Bond, A.L., Hobson, K.A., Ronconi, R.A., 2015. Feather-based measures of stable isotopes and corticosterone reveal a relationship between trophic position and physiology in a pelagic seabird over a 153-year period. Ibis 157, 273–283. https://doi.org/10.1111/ibi.12232.

Gonzalez, G., Sorci, G., Smith, L.C., Lope, F., 2001. Testosterone and sexual signalling in male house sparrows (Passer domesticus). Behav. Ecol. Sociobiol. 50, 557–562.

Grace, J.K., Froud, L., Meillère, A., Angelier, F., 2017a. House sparrows mitigate growth effects of post-natal glucocorticoid exposure at the expense of longevity. Gen. Comp. Endocrinol. 253, 1–12. https://doi.org/10.1016/j.ygcen.2017.08.011.

Grace, J.K., Martin-Gousset, L., Angelier, F., 2017b. Delayed effect of early-life corticosterone treatment on adult anti-predator behavior in a common passerine. Physiol. Behav. 177, 82–90. https://doi.org/10.1016/j.physbeh.2017.04.018.

Groothuis, T.G., Schwabl, H., 2008. Hormone-mediated maternal effects in birds: mechanisms matter but what do we know of them? Philos. Trans. R. Soc. B Biol. Sci. 363, 1647–1661. https://doi.org/10.1098/rstb.2007.0007.

Harris, A., Seckl, J., 2011. Glucocorticoids, prenatal stress and the programming of disease. Horm. Behav. 59, 279–289. https://doi.org/10.1016/j.yhbeh.2010.06.007.

Hau, M., 2007. Regulation of male traits by testosterone: implications for the evolution of vertebrate life histories. BioEssays 29, 133–144. https://doi.org/10.1002/bies.20524.

Haussmann, M.F., Longenecker, A.S., Marchetto, N.M., Juliano, S.A., Bowden, R.M., 2012. Embryonic exposure to corticosterone modifies the juvenile stress response, oxidative stress and telomere length. Proc. R. Soc. B Biol. Sci. 279, 1447–1456. https://doi.org/10.1098/rspb.2011.1913.

Hill, G.E., 2000. Energetic constraints on expression of carotenoid-based plumage coloration. J. Avian Biol. 31 559–566. https://doi.org/559-566 10.1034/j.1600-048X.2000.310415.x.

Honarmand, M., Krause, E.T., Naguib, M., 2017. Implications of nutritional stress as nestling or fledgling on subsequent attractiveness and fecundity in zebra finches (*Taeniopygia guttata*). PeerJ 5, e3628. https://doi.org/10.7717/peerj.3628.

Hubbard, J.K., Jenkins, B.R., Safran, R.J., 2015. Quantitative genetics of plumage color: lifetime effects of early nest environment on a colorful sexual signal. Ecol. Evol. 5, 3436–3449. https://doi.org/10.1002/ece3.1602.

Hull, K.L., Cockrem, J.F., Bridges, J.P., Candy, E.J., Davidson, C.M., 2007. Effects of corticosterone treatment on growth, development, and the corticosterone response to handling in young Japanese quail (*Coturnix coturnix japonica*). Comp. Biochem. Physiol. A. Mol. Integr. Physiol. 148, 531–543. https://doi.org/10.1016/j.cbpa.2007.06.423.

Jenkins, B.R., Vitousek, M.N., Safran, R.J., 2013. Signaling stress? An analysis of phaeomelanin-based plumage color and individual corticosterone levels at two temporal scales in North American barn swallows, *Hirundo rustica erythrogaster*. Horm. Behav. 64, 665–672. https://doi.org/10.1016/j.yhbeh.2013.08.006.

Jenni-Eiermann, S., Helfenstein, F., Vallat, A., Glauser, G., Jenni, L., 2015. Corticosterone: effects on feather quality and deposition into feathers. Meth. Ecol. Evol. 6, 237–246. https://doi.org/10.1111/2041-210X.12314.

Kitaysky, A.S., Kitaiskaia, E.V., Piatt, J.F., Wingfield, J.C., 2003. Benefits and costs of increased levels of corticosterone in seabird chicks. Horm. Behav. 43, 140–149. https://doi.org/10.1016/S0018-506X(02)00030-2.

Kitaysky, A.S., Piatt, J.F., Wingfield, J.C., Romano, M., 1999. The adrenocortical stress-response of Black-legged Kittiwake chicks in relation to dietary restrictions. J. Comp. Physiol. B 169, 303–310. https://doi.org/10.1007/s003600050225.

Krause, E.T., Naguib, M., 2015. Zebra finch males compensate in plumage ornaments at sexual maturation for a bad strat in life. Front. Zool. 12.

Kriengwatana, B., Wada, H., Macmillan, A., MacDougall-Shackleton, S.A., 2013. Juvenile nutritional stress affects growth rate, adult organ mass, and innate immune function in zebra finches (*Taeniopygia guttata*). Physiol. Biochem. Zool. 86, 769–781. https://doi.org/10.1086/673260.

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. https://doi.org/10.1016/j.ygcen.2006.02.013.

Laucht, S., Dale, J., 2012. Correlations of condition, testosterone, and age with multiple ornaments in male house sparrows: patterns and implications. Condor 114, 865–873. https://doi.org/10.1525/cond.2012.110194.

Laucht, S., Dale, J., Mutzel, A., Kempenaers, B., 2011. Individual variation in plasma testosterone levels and its relation to badge size in House Sparrows Passer domesticus: it's a night-and-day difference. Gen. Comp. Endocrinol. 170, 501–508. https://doi.org/10.1016/j.ygcen.2010.11.007.

Laucht, S., Kempenaers, B., Dale, J., 2010. Bill color, not badge size, indicates testosterone-related information in house sparrows. Behav. Ecol. Sociobiol. 64, 1461–1471. https://doi.org/10.1007/s00265-010-0961-9.

Lessells, C.M., 2008. Neuroendocrine control of life histories: what do we need to know to understand the evolution of phenotypic plasticity? Philos. Trans. R. Soc. B Biol. Sci. 363, 1589–1598. https://doi.org/10.1098/rstb.2007.0008.

Levine, S., 2002. Regulation of the hypothalamic-pituitary-adrenal axis in the neonatal rat: the role of maternal behavior. Neurotox. Res. 4, 557–564. https://doi.org/10.1080/10298420290030569.

Lindström, J., 1999. Early development and fitness in birds and mammals. TREE 14, 343–348.

Lindstrom, J., Metcalfe, N.B., Royle, N.J., 2005. How are animals with ornaments predicted to compensate for a bad start in life? A dynamic optimization model approach. Funct. Ecol. 19, 421–428. https://doi.org/10.1111/j.1365-2435.2005.00974.x.

Loiseau, C., Sorci, G., Dano, S., Chastel, O., 2008. Effects of experimental increase of corticosterone levels on begging behavior, immunity and parental provisioning rate in house sparrows. Gen. Comp. Endocrinol. 155, 101–108. https://doi.org/10.1016/j.ygcen.2007.03.004.

Love, O., Williams, T., 2008. Plasticity in the adrenocortical response of a free-living vertebrate: the role of pre- and post-natal developmental stress. Horm. Behav. 54, 496–505. https://doi.org/10.1016/j.yhbeh.2008.01.006.

Marasco, V., Robinson, J., Herzyk, P., Spencer, K.A., 2012. Pre- and post-natal stress in context: effects on the stress physiology in a precocial bird. J. Exp. Biol. 215, 3955–3964. https://doi.org/10.1242/jeb.071423.

Marshall, H.H., Vitikainen, E.I.K., Mwanguhya, F., Businge, R., Kyabulima, S., Hares, M.C., Inzani, E., Kalema-Zikusoka, G., Mwesige, K., Nichols, H.J., Sanderson, J.L., Thompson, F.J., Cant, M.A., 2017. Lifetime fitness consequences of early-life ecological hardship in a wild mammal population. Ecol. Evol. 7, 1712–1724. https://doi.org/10.1002/ece3.2747.

McEwen, B.S., Wingfield, J.C., 2003. The concept of allostasis in biology and biomedicine. Horm. Behav. 43, 2–15. https://doi.org/10.1016/S0018-506X(02)00024-7.

McGlothlin, J.W., Ketterson, E.D., 2008. Hormone-mediated suites as adaptations and evolutionary constraints. Philos. Trans. R. Soc. B Biol. Sci. 363, 1611–1620. https://doi.org/10.1098/rstb.2007.0002.

Metcalfe, N.B., Monaghan, P., 2001. Compensation for a bad start: grow now, pay later? Trends Ecol. Evol. 16, 254–260.

Meylan, S., Miles, D.B., Clobert, J., 2012. Hormonally mediated maternal effects, individual strategy and global change. Philos. Trans. R. Soc. B Biol. Sci. 367, 1647–1664. https://doi.org/10.1098/rstb.2012.0020.

Møller, A.P., 1990. Sexual behavior is related to badge size in the house sparrow *Passer domesticus*. Behav. Ecol. Sociobiol. 27, 23–29.

Møller, A.P., 1987a. Social control of deception among status signalling house sparrows *Passer domesticus*. Behav. Ecol. Sociobiol. 20, 307–311.

Møller, A.P., 1987b. Variation in badge size in male house sparrows *Passer domesticus*: evidence for status signalling. Anim. Behav. 35, 1637–1644.

Monaghan, P., 2008. Early growth conditions, phenotypic development and environmental change. Philos. Trans. R. Soc. B Biol. Sci. 363, 1635–1645. https://doi.org/10.1098/rstb.2007.0011.

Monaghan, P., Heidinger, B.J., D'Alba, L., Evans, N.P., Spencer, K.A., 2012. For better or worse: reduced adult lifespan following early-life stress is transmitted to breeding partners. Proc. R. Soc. B Biol. Sci. 279, 709–714. https://doi.org/10.1098/rspb.2011.

1291.

Moreno-Rueda, G., Hoi, H., 2012. Female house sparrows prefer big males with a large white wing bar and fewer feather holes caused by chewing lice. Behav. Ecol. 23, 271–277. https://doi.org/10.1093/beheco/arr182.

Morrison, E.B., Kinnard, T.B., Stewart, I.R.K., Poston, J.P., Hatch, M.I., Westneat, D.F., 2008. The links between plumage variation and nest site occupancy in male house sparrows. Condor 110, 345–353.

Mousseau, T.A., Fox, C.W., 1998. The adaptative significance of maternal effects. Trends Ecol. Evol. 13, 403–407.

Naguib, M., Heim, C., Gil, D., 2008. Early developmental conditions and male attractiveness in zebra finches. Ethology 114, 255–261. https://doi.org/10.1111/j.1439-0310.2007.01466.x.

Naguib, M., Nemitz, A., 2007. Living with the past: nutritional stress in juvenile males has immediate effects on their plumage ornaments and on adult attractiveness in zebra finches. PLoS One 2, e901. https://doi.org/10.1371/journal.pone.0000901.

Nakagawa, S., Ockendon, N., Gillespie, D.O.S., Hatchwell, B.J., Burke, T., 2007. Assessing the function of house sparrows' bib size using a flexible meta-analysis method. Behav. Ecol. 18, 831–840. https://doi.org/10.1093/beheco/arm050.

Nettle, D., Bateson, M., 2015. Adaptive developmental plasticity: what is it, how can we recognize it and when can it evolve? Proc. R. Soc. B Biol. Sci. 282, 20151005. https://doi.org/10.1098/rspb.2015.1005.

Noguera, J.C., Metcalfe, N.B., Monaghan, P., 2017. Postnatal nutrition influences male attractiveness and promotes plasticity in male mating preferences. Sci. Nat. 104. https://doi.org/10.1007/s00114-017-1524-y.

Ohlsson, T., Smith, H.G., Raberg, L., Hasselquist, D., 2002. Pheasant sexual ornaments reflect nutritional conditions during early growth. Proc. R. Soc. Lond. B Biol. Sci. 269, 21–27.

Pakkala, J.J., Norris, D.R., Sedinger, J.S., Newman, A.E.M., 2016. Experimental effects of early-life corticosterone on the hypothalamic-pituitary-adrenal axis and pre-migratory behavior in a wild songbird. Funct. Ecol. 30, 1149–1160. https://doi.org/10.1111/1365-2435.12603.

Peig, J., Green, A.J., 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. Oikos 118, 1883–1891. https://doi.org/10.1111/j.1600-0706.2009.17643.x.

Peters, S., Searcy, W.A., Nowicki, S., 2014. Developmental stress, song-learning, and cognition. Integr. Comp. Biol. 54, 555–567. https://doi.org/10.1093/icb/icu020.

Poston, J.P., Hasselquist, D., Stewart, I.R.K., Westneat, D.F., 2005. Dietary amino acids influence plumage traits and immune responses of male house sparrows, *Passer domesticus*, but not as expected. Anim. Behav. 70, 1171–1181. https://doi.org/10.1016/j.anbehav.2005.02.015.

Pravosudov, V.V., Kitaysky, A.S., 2006. Effects of nutritional restrictions during post-hatching development on adrenocortical function in western scrub-jays (Aphelocoma californica). Gen. Comp. Endocrinol. 145, 25–31. https://doi.org/10.1016/j.ygcen.2005. 06.011.

Romero, L.M., 2004. Physiological stress in ecology: lessons from biomedical research. Trends Ecol. Evol. 19, 249–255. https://doi.org/10.1016/j.tree.2004.03.008.

Romero, L.M., Dickens, M.J., Cyr, N.E., 2009. The reactive scope model — a new model integrating homeostasis, allostasis, and stress. Horm. Behav. 55, 375–389. https://doi.org/10.1016/j.yhbeh.2008.12.009.

Roulin, A., Almasi, B., Rossi-Pedruzzi, A., Ducrest, A.-L., Wakamatsu, K., Miksik, I., Blount, J.D., Jenni-Eiermann, S., Jenni, L., 2008. Corticosterone mediates the condition-dependent component of melanin-based coloration. Anim. Behav. 75, 1351–1358. https://doi.org/10.1016/j.anbehav.2007.09.007.

Sapolsky, R.M., Romero, L.M., Munck, A.U., 2000. How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. Endocr. Rev. 21, 55–89.

Schmidt, K.L., MacDougall-Shackleton, E.A., MacDougall-Shackleton, S.A., 2012. Developmental stress has sex-specific effects on nestling growth and adult metabolic rates but no effect on adult body size or body composition in song sparrows. J. Exp. Biol. 215, 3207–3217. https://doi.org/10.1242/jeb.068965.

Schmidt, K.L., Moore, S.D., MacDougall-Shackleton, E.A., MacDougall-Shackleton, S.A., 2013. Early-life stress affects song complexity, song learning and volume of the brain nucleus RA in adult male song sparrows. Anim. Behav. 86, 25–35. https://doi.org/10.1016/j.anbehav.2013.03.036.

Schoech, S.J., Rensel, M.A., Heiss, R.S., 2011. Short- and long-term effects of developmental corticosterone exposure on avian physiology, behavioral phenotype, cognition, and fitness: a review. Curr. Zool. 57, 514–530. https://doi.org/10.1093/czoolo/57.4.514.

Spencer, K., Buchanan, K., Goldsmith, A., Catchpole, C., 2003. Song as an honest signal of developmental stress in the zebra finch (*Taeniopygia guttata*). Horm. Behav. 44, 132–139. https://doi.org/10.1016/S0018-506X(03)00124-7.

Spencer, K.A., Evans, N.P., Monaghan, P., 2009. Postnatal stress in birds: a novel model of glucocorticoid programming of the hypothalamic-pituitary-adrenal axis. Endocrinology 150, 1931–1934. https://doi.org/10.1210/en.2008-1471.

Spencer, K.A., Verhulst, S., 2008. Post-natal exposure to corticosterone affects standard metabolic rate in the zebra finch (*Taeniopygia guttata*). Gen. Comp. Endocrinol. 159, 250–256. https://doi.org/10.1016/j.ygcen.2008.09.007.

Spencer, K.A., Verhulst, S., 2007. Delayed behavioral effects of postnatal exposure to corticosterone in the zebra finch (*Taeniopygia guttata*). Horm. Behav. 51, 273–280. https://doi.org/10.1016/j.yhbeh.2006.11.001.

Spencer, K.A., Wimpenny, J.H., Buchanan, K.L., Lovell, P.G., Goldsmith, A.R., Catchpole, C.K., 2005. Developmental stress affects the attractiveness of male song and female choice in the zebra finch (*Taeniopygia guttata*). Behav. Ecol. Sociobiol. 58, 423–428. https://doi.org/10.1007/s00265-005-0927-5.

Stamps, J.A., 2006. The silver spoon effect and habitat selection by natal dispersers. Ecol. Lett. 9, 1179–1185. https://doi.org/10.1111/j.1461-0248.2006.00972.x.

Stier, K.S., Almasi, B., Gasparini, J., Piault, R., Roulin, A., Jenni, L., 2009. Effects of corticosterone on innate and humoral immune functions and oxidative stress in barn owl nestlings. J. Exp. Biol. 212, 2085–2091. https://doi.org/10.1242/jeb.024406.

Taborsky, B., 2006. Mothers determine offspring size in response to own juvenile growth conditions. Biol. Lett. 2, 225–228. https://doi.org/10.1098/rsbl.2005.0422.

Van De Pol, M., Bruinzeel, L.W., Heg, D., Van Der Jeugd, H.P., Verhulst, S., 2006. A silver spoon for a golden future: long-term effects of natal origin on fitness prospects of oystercatchers (*Haematopus ostralegus*): fitness consequences of early conditions. J. Anim. Ecol. 75, 616–626. https://doi.org/10.1111/j.1365-2656.2006.01079.x.

Veiga, J.P., 1993. Badge size, phenotypic quality, and reproductive success in the House sparrow: a study on honest advertisement. Evolution 47, 1161–1170.

Wada, H., 2008. Glucocorticoids: mediators of vertebrate ontogenetic transitions. Gen. Comp. Endocrinol. 156, 441–453. https://doi.org/10.1016/j.ygcen.2008.02.004.

Wada, H., Breuner, C.W., 2008. Transient elevation of corticosterone alters begging behavior and growth of white-crowned sparrow nestlings. J. Exp. Biol. 211, 1696–1703. https://doi.org/10.1242/jeb.009191.

Walker, L.K., Stevens, M., Karadas, F., Kilner, R.M., Ewen, J.G., 2013. A window on the past: male ornamental plumage reveals the quality of their early-life environment. 20122852-20122852. Proc. R. Soc. B Biol. Sci. 280. https://doi.org/10.1098/rspb.2012.2852.

Wingfield, J.C., Maney, D.L., Breuner, C.W., Jacobs, J.D., Lynn, S., Ramenofsky, M., Richardson, R.D., 1998. Ecological bases of hormone—behavior interactions: the "emergency life history stage". Am. Zool. 38, 191–206.

Wingfield, J.C., Sapolsky, R.M., 2003. Reproduction and resistance to stress: when and how. J. Neuroendocrinol. 15, 711–724.