



Early developmental conditions affect stress response in juvenile but not in adult house sparrows (*Passer domesticus*)

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ABSTRACT

The short- and long-term consequences of developmental conditions on fitness have received growing attention because the environmental conditions during early life may influence growth, condition at independence, recruitment, reproductive success or survival. We tested here, in a natural house sparrow population, if early conditions during nestling stage affected the stress response of the birds (i) shortly after fledging and (ii) next year, during their first breeding. We experimentally manipulated brood size to mimic different rearing conditions, creating reduced (−2 chicks) and enlarged broods (+2 chicks), while in a third group brood size was not manipulated. Nestling nutrition state decreased with post-manipulation brood sizes as indicated by lower body mass. Fledglings with higher body mass at the age of ten days showed lower stress response than birds that were leaner at the same age. Fledglings reared in large broods showed a higher response to stress protocol than chicks from small broods, and this effect was in significant interaction with the age of fledglings at capture. This interaction indicates that the effects of the brood size became gradually smaller as the fledglings grew older and were further from their nestling period. The effects of early conditions vanished by the next year: the stress response of adult first time breeders was unrelated to the brood size they fledged from. These results suggest that stress response may reflect the actual state of an individual, rather than its developmental history.

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1. Introduction

Environmental conditions during early stages of life can influence the development of an organism and may result in permanent changes in adult behaviour and physiology (Magrath, 1991; Sedinger et al., 1995; Lindström, 1999; Netcalfe and Monaghan, 2001; Cam et al., 2003). For example, in altricial birds, where the nestling period is critical since nestlings are entirely dependent on their parents to feed them from hatching to fledging, several studies have shown that conditions during early development can influence key fitness components, such as growth and condition at independence (Burness et al., 2000; Dijkstra et al., 1990), recruitment (Green and Cockburn, 2001; Alonso-Alvarez et al., 2006), reproductive success (Haywood and Perrins, 1992) and finally survival (Sedinger et al., 1995; Magrath, 1991).

Although various studies have shown consequences of early development on reproductive success and survival, physiological mechanisms underlying these effects have been rarely investigated (but see Verhulst et al., 2006; Alonso-Alvarez et al., 2006).

Among fitness-related physiological mechanisms, the capacity to adequately respond to stressful events may be one crucial component. In response to environmental stressors, such as decrease in food availability or harsh weather, the hypothalamus–pituitary–adrenal axis triggers a rapid secretion of glucocorticoids, and in particular the corticosterone hormone. Elevation of corticosterone in bloodstream allows individuals to cope with stressful events by regulating homeostasis and by stimulating various context-dependent mechanisms that may enhance the immediate survival, such as foraging and locomotor activities (Wingfield et al., 1990; Breuner et al., 1998), increased food intake (Astheimer et al., 1992; Wingfield and Silverin, 1986; Koch et al., 2002), enhanced plasma glucose levels via gluconeogenesis (Norris, 1997; Ramage-Healey and Romero, 2001), and decreased triglyceride concentration in the blood (Ramage-Healey and Romero, 2001). All of these responses allow the organism to cope with the stressful period and therefore the stress response is thought to be adaptive (Wingfield, 2005). Despite its significance, still little is known about how early developmental conditions affect the stress response in free-living animals.

In this study, we investigated in a natural house sparrow population, whether early conditions during nestling stage may affect

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the stress hormone levels, as a physiological mechanism underlying life-history decisions (Sinervo and Svensson, 1998). We manipulated the brood size, (increasing or decreasing the number of nestlings) to mimic different conditions of nestling stage because both experimental and correlational evidence supports the idea that brood size has long-term consequences on body condition (DeKogel, 1997), basal metabolic rate (Verhulst et al., 2006), plumage coloration (Jacot and Kempnaers, 2007), brain development (Nowicki et al., 2002; Spencer et al., 2003) and immune response (Saino et al., 1997; Horak et al., 1999; Dubiec et al., 2006; Alonso-Alvarez et al., 2006). We used the capture and restraint protocol (Wingfield, 1994) to measure initial and stress-induced response of individuals (i) shortly after fledging and (ii) the following year, during the first breeding of the birds. Although conditions during early development (e.g. exposure to elevated levels of stress hormones) has been shown to modify the physiological response to experimentally induced stress in adulthood in mice and rats, (Anisman et al., 1998; Penke et al., 2001; Parfitt et al., 2004), little is known about these mechanisms in natural populations.

We predicted that stress response after fledging reflects the conditions of early development in the nest, with individuals from enlarged broods responding to the stress protocol more strongly than individuals from reduced broods.

2. Methods

The study was carried out during two breeding seasons (2005–2006) in a population of house sparrows breeding in nest boxes at the Centre d'Etudes Biologiques de Chizé, France (46°09'N, 0°24'W, Chastel et al., 2003; Lendvai et al., 2007). In 2005, all nest boxes were checked every third day to determine the date of clutch initiation and clutch size. Starting nine days after the clutch completion, nest boxes were checked at least once every day to determine the exact date of hatching (day 0). At day 5, nestlings were ringed with a numbered metal ring. Nestling body mass (± 0.1 g) and tarsus length (± 0.1 mm) were measured on day 10. House sparrow nestlings fledged approximately on day 14 (Anderson 2006).

2.1. Brood size manipulation

Brood size was manipulated in 24 pairs of synchronous nests (maximum difference in hatching date was one day). On day 2, two nestlings were exchanged between nests, creating reduced (-2 chicks) and enlarged broods ($+2$ chicks). Pre-manipulation brood-sizes ranged from two to seven chicks. Broods with two or three chicks were only to be enlarged; broods with six or seven chicks were only to be reduced. Broods with four or five chicks (modal brood sizes) were randomly allocated to the treatments (Lendvai et al., 2007). If for a given nest no other synchronous brood was available, it was not manipulated. Post-manipulation brood sizes were in the natural brood size range.

2.2. Measuring stress response

In 2005, 20 fledglings (mean age: 34.45 days, range: 24–70 days) were captured with mist nets. Immediately upon capture, the birds were removed from the net and a blood sample (50–100 μ l) was collected from the brachial vein. The time required to collect the sample was recorded. Birds were then placed in an opaque cloth bag, and a second blood sample was collected 30 min later. Body mass (± 0.1 g) and tarsus length (± 0.1 mm) were measured. Blood samples were centrifuged, plasma fraction was separated and stored at -20°C until hormone assays.

From the chicks ringed in 2005, we captured 47 individuals as breeding adults in 2006. Adults were captured in their nest box using a wire trap, when rearing 7–9 days old chicks. We used the

same capture–handling–restraint protocol as for the fledglings in 2005. The time required to collect the sample was also recorded for all but one adult.

2.3. Corticosterone assay

Total corticosterone levels (i.e. corticosterone either bound or unbound to binding proteins) were measured from plasma samples by radioimmunoassay at the Centre d'Etudes Biologiques de Chizé following the methods detailed in Lormée et al. (2003). Corticosterone was extracted from a 50 μ l plasma sample and determined in duplicates. Hormone concentrations were run in one assay (coefficient of intra-assay variation was 6.7%, $n=6$ duplicates). Minimal detectable corticosterone level was 0.4 ng/ml (lowest measurement: 1.16 ng/ml).

2.4. Statistical analyses

All data processing and statistical analyses were performed in the **R** computing environment (R Development Core Team 2006). Since unmanipulated brood sizes (from two to six chicks) overlapped largely with both reduced and enlarged brood sizes, we analysed the effects of brood sizes by using brood size at day 10 as a covariate in the models after controlling for the treatment using a three level factor (enlarged, reduced, unmanipulated).

The effect of brood size on chick body mass was analysed by linear mixed-effects model (lme function in **R**), using treatment groups as fixed factor, brood size at day 10 as covariate and brood identity as random factor. Initial and stress-induced corticosterone levels were analysed by fitting hierarchical general linear models (lm function in **R**). The magnitude of stress response was expressed as the stress-induced corticosterone levels. We also calculated the rate of increase from initial to stress-induced corticosterone levels per minute (ng/ml/min; Silverin et al. 1997; Lindström et al. 2005). The latter measure of stress response was highly correlated with the stress-induced corticosterone levels ($r=0.920$, $P=0.0001$), and the statistical analyses of these variables gave nearly identical results, hence we report only the results for stress-induced corticosterone levels to facilitate the comparison with other published results.

The probability that a chick became a breeding adult in 2006 (i.e. recruitment) was analysed by binary logistic regression (glm function in **R**, with binomial family and logit link). The effects of the terms in the model were investigated by likelihood ratio tests between a null model and a model containing the given term.

Assumptions and fit of the models were checked by graphical diagnostic methods using plot.lm function in **R** (Faraway, 2006). Model selection was undertaken in a stepwise forward manner. Initial models always contained treatment groups and brood size regardless of their significance, since these were part of the study design. We added factors, covariates and all two-way interaction terms to the model one-by-one. If the addition of a given term significantly increased the model fit, it was retained in the model, and the addition of further main effects and interactions were tested again until the model fit could not be increased by additional terms (the final model). For the rejected terms, we report statistics obtained at the moment of rejection. Interaction terms were non-significant unless otherwise indicated. Backward model selection yielded the same significant predictors, although it was less practical, since due to the small sample sizes initial models containing all main effects and interactions had very low or zero residual degrees of freedom.

To account for seasonal variation in the corticosterone levels, we used the date of female capture as covariate in the models. Daily maximum temperatures were obtained from a meteorological station situated 2 km from the study site. We report two-tailed probabilities and means \pm SE throughout the paper.

3. Results

3.1. The effects of manipulation and stress response of fledglings

Body mass of the nestlings measured at day 10 was strongly and negatively related to the brood size (treatment groups: $F_{2,64} = 0.232, p = 0.793$, brood size: $F_{1,64} = 7.618, p = 0.007$; $N = 279$ chicks in 68 broods). The time needed for the first blood sampling ($3.94 \text{ min} \pm 0.34$) influenced the initial corticosterone levels ($F_{1,18} = 9.250, p = 0.007$). After controlling for this effect, the age of the birds predicted their initial corticosterone levels: younger birds had higher levels of circulating corticosterone than older ones (Table 1, panel A). Brood size, body mass measured in the nest at day 10 and the maximum daily ambient temperature was unrelated to the initial corticosterone levels (Table 1, panel A).

The daily maximum ambient temperature and the body mass measured in the nest influenced stress-induced corticosterone (Table 1, panel B). Both the temperature and the body mass had a significant negative effect on the stress-induced corticosterone levels. Fledglings from large broods responded more to the capture stress than fledglings from small broods, but this brood size effect was in significant interaction with the age of the birds, showing that the effects of brood size changed in opposite direction with age, i.e. the age effect was positive in small broods, whereas it was negative in large broods (Table 1, panel B; Fig. 1).

3.2. Stress response of adults

In 2006, we captured 47 breeding birds that we ringed as chicks in 2005. The probability of acquiring a nest box (i.e. becoming a breeding adult) was influenced by the brood size from which the birds fledged as nestlings: chicks from enlarged broods had significantly lower chance of recruitment than chicks from unmanipulated or reduced broods (binary logistic regression, treatment groups: $\chi^2 = 6.679, p = 0.035$, brood size = $3.921, p = 0.047$; $N = 47 + 238$ chicks that respectively were and were not recorded as breeders in 2006).

Table 1

General linear model of initial (panel A) and stress-induced (panel B) corticosterone levels of fledgling house sparrows in 2005 ($N = 20$). Statistics are shown for terms in the final model and for terms at the moment of rejection during the forward model selection procedure. Interaction terms were non-significant, unless otherwise indicated.

Predictor variables	df	F	P
<i>Panel A</i>			
<i>Terms in the final model^a</i>			
Handling time	1,13	11.43	0.005
Treatment groups	2,13	0.65	0.535
Brood size as nestling	1,13	2.01	0.180
Age at capture (days)	1,13	6.45	0.025
<i>Rejected terms</i>			
Maximum daily temperature	1,13	0.29	0.598
Body mass as nestling	1,13	0.85	0.372
<i>Panel B</i>			
<i>Terms in the final model^b</i>			
Treatment groups	2,9	3.89	0.060
Brood size as nestling	1,9	12.30	0.006
Maximum daily temperature	1,9	11.41	0.008
Body mass as nestling	1,9	5.65	0.041
Age at capture (days)	1,9	1.07	0.326
Brood size as nestling × Age at capture	1,9	6.41	0.032

^a Initial model contained handling time, treatment groups and brood size as nestling.

^b Initial model contained treatment groups and brood size as nestling.

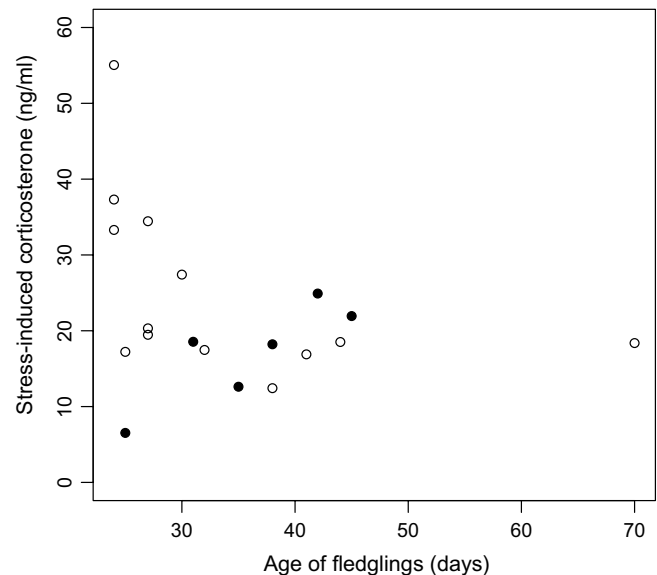


Fig. 1. The relationship between stress-induced corticosterone levels, the age and brood size of house sparrow fledglings. In small broods (2–4 chicks, filled circles) the stress-induced corticosterone levels increased with age, whereas in large broods (5–7 chicks, open circles) they decreased with age, resulting in a significant brood size \times age interaction.

We excluded from the following analyses the data of 7 females, whose mate was removed as part of an experimental manipulation (Lendvai and Chastel, 2008). Therefore, we used the data of 19 females and 21 males. Though the mean time needed for the collection of the first blood sample was $2.83 \pm 0.1 \text{ min}$, initial corticosterone levels were related to the handling time ($F_{1,37} = 15.208, p < 0.001$), therefore we controlled for this effect in the further models of initial corticosterone levels.

The daily maximum temperature was negatively related to the initial corticosterone levels (Table 2, panel A). The capture date, sex, and the brood size of the birds' current brood did not predict the initial corticosterone levels (Table 2, panel A). Conditions of early development in the previous year did not influence the initial corticosterone levels of birds as adults: neither natal brood size, nor the body mass at 10 days of age was related to the initial corticosterone levels (Table 2, panel A).

Stress-induced corticosterone levels were not related to capture date and the current brood size of the individuals (Table 2, panel B). Stress-induced corticosterone levels differed between sexes (Table 2, panel B, Fig. 2), with an interaction between sex and daily maximum temperature, showing that stress response was negatively related to the temperature in males ($B = -1.03, p = 0.012$) but not in females ($B = 0.44, p = 0.251$). Finally, conditions of early development did not influence the stress-induced corticosterone levels: natal brood size was not related to the adults' stress-induced corticosterone levels (Table 2, panel B, Fig. 3).

4. Discussion

In this study we manipulated brood size to investigate the effects of rearing conditions on the stress response of individuals in two distinct life stages. On one hand, we found that early conditions had a significant effect on the stress response of juveniles shortly after fledging: birds reared in large broods showed a higher response to stress protocol than birds reared in small broods. Interestingly however, this relationship were in significant interaction with the age of the fledglings, indicating that the effects of the

Table 2

General linear model of initial (panel A) and stress-induced (panel B) corticosterone levels of breeding house sparrows in 2006 (N=40). Statistics are shown for terms in the final model and for terms at the moment of rejection during the forward model selection procedure. Interaction terms were non-significant, unless otherwise indicated.

Predictor variables	df	F	P
<i>Panel A</i>			
<i>Terms in the final model^a</i>			
Treatment groups	2,33	1.15	0.327
Brood size as nestling	1,33	<0.001	0.995
Maximum daily temperature	1,33	6.58	0.015
<i>Rejected terms</i>			
Capture date	1,33	0.16	0.695
Sex	1,33	1.65	0.208
Actual brood size	1,33	1.24	0.274
Body mass as nestling	1,33	1.21	0.280
<i>Panel B</i>			
<i>Terms in the final model^b</i>			
Treatment groups	2,32	0.002	0.997
Brood size as nestling	1,32	0.06	0.815
Sex	1,32	6.32	0.017
Maximum daily temperature	1,32	1.06	0.310
Sex × maximum daily temperature	1,32	7.46	0.010
<i>Rejected terms</i>			
Capture date	1,32	0.06	0.811
Actual brood size	1,32	0.53	0.472
Body mass as nestling	1,32	1.51	0.228

^a Initial model contained handling time, treatment groups and brood size as nestling.

^b Initial model contained treatment groups and brood size as nestling.

brood size on the stress response became gradually smaller as the juveniles grew older and were further from the nestling period. In addition, we found that body mass measured at day 10 just before fledging, had an effect on the stress response with lower stress-induced corticosterone levels in heavier nestlings. On the other hand, we found that the rearing conditions had no significant effect on the stress response of the adults. Taken together, these results suggest that early environmental conditions influence the stress response shortly after fledging but may have either little or no persistent consequences for the adult stress responses in this species, or stabilising selection may act on the stress susceptibility, eliminating individuals with very weak or strong corticosterone responses.

The stress response during the juvenile life stage may be alone a crucial component of fitness. A recent study tested whether individual variation in the stress response early in life has long-term consequences to survival and recruitment in the European white stork (*Ciconia ciconia*; Blas et al., 2007). Blas et al. found a negative relationship between a nestling's stress-induced corticosterone levels and the probability of survival. Moreover, for a given level of corticosterone, the survival probability was higher when the bird was in good condition (Blas et al., 2007). In our study, the heavier juveniles were before fledging, the weaker was their stress response. We suggest that individuals should adjust their stress response according to their current state to meet the energetic requirements induced by the stressor: therefore to gain the same survival probability, individuals in low condition are expected to respond more strongly to the same stressor than individuals in good condition.

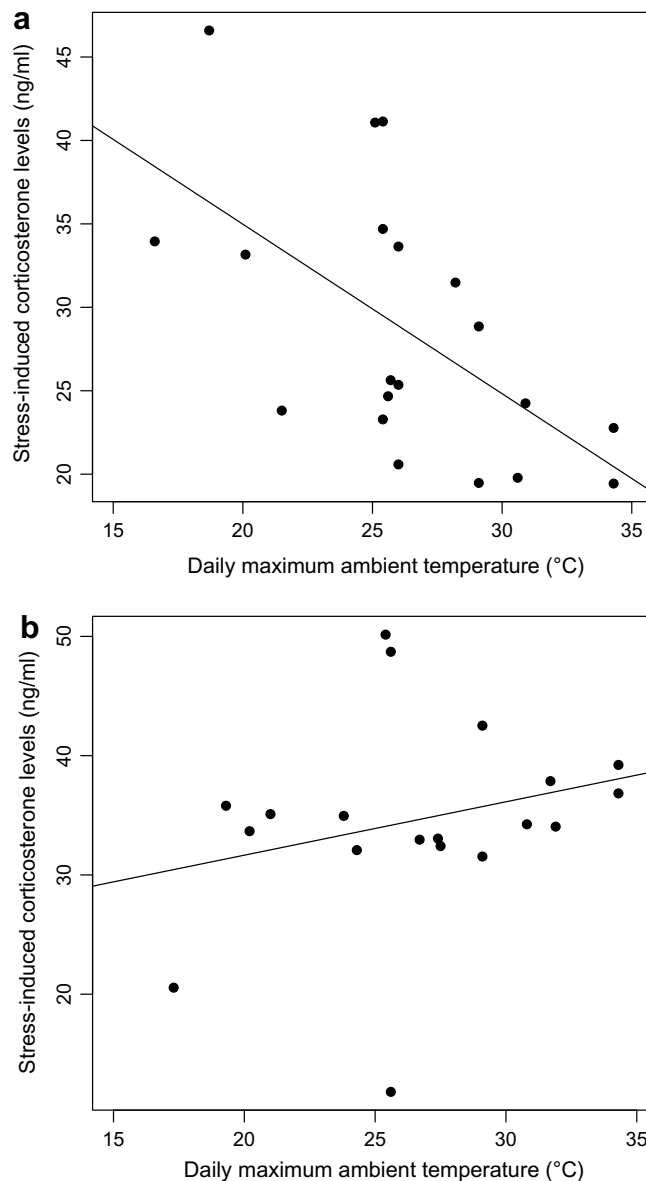


Fig. 2. The effects of ambient temperature on the stress response of adult male (a) and female (b) house sparrows.

Another line of evidence is also consistent with this scenario. We found that the daily temperature was negatively related to the fledglings' stress response. The period shortly after fledging is supposed to be energetically costly (indicated also by elevated baseline corticosterone levels shortly after fledging, which decreased as the juveniles were older; see also Heath, 1997; Romero et al., 2006; Stowe et al., 2008), when the juveniles receive less food from their parents, but their feathers are still growing (Anderson, 2006). In inclement weather it may be more demanding to properly cope with a stressor than in mild weather, therefore one may expect higher stress responses in low daily temperatures. This idea is corroborated by a previous study that found such relationships in three passerine species (Romero et al. 2000).

Brood size manipulation had a significant effect on the recruitment: chicks reared in enlarged broods had lower probability to become a breeding adult next year compared with chicks from unmanipulated or reduced broods. By manipulating brood size, we indirectly manipulated the nestling competition for resources and thus nutritional status of the nestlings (DeKogel, 1997; Chastel and Kersten, 2002). Consequently, production of corticosterone could

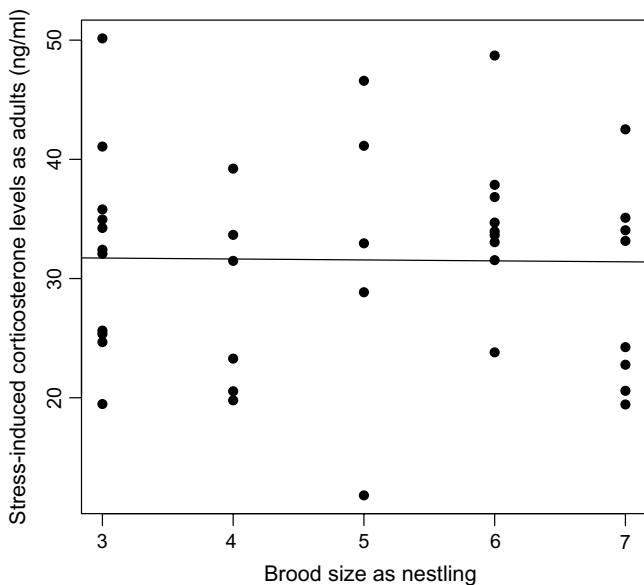


Fig. 3. The effects of early developmental conditions on the stress response of adult house sparrows. The x axis shows the size of the brood at day 10 from which the birds fledged. The y axis shows the maximum levels of corticosterone of the birds in the next year, when they were captured as breeding adults.

increase in enlarged-brood nestlings, which suffered of reduced availability of resources, compared with nestlings from reduced-broods, as demonstrated by Saino et al. (2003). Similarly, experimental brood reduction resulted in lower baseline corticosterone levels in the collared dove (*Streptopelia decaocto*) (Eraud et al., 2008), and in the spotless starling (*Sturnus unicolor*) (Gil et al., 2008; although the latter relationship disappeared once handling time was taken into account). Some other studies found no effect on baseline corticosterone levels (Romero et al., 2006) while one study in the white stork found that baseline corticosterone was the highest in broods with a single nestling, although the latter result may be due to low feeding efficiency of poor-quality parents which may explain increased nestling mortality and elevated corticosterone in the surviving chick (Blas et al., 2005). Taken together, the potential production of corticosterone, during early development, may affect different physiological parameters such as immunity (Apanius, 1998) or antioxidant defences (Lin et al., 2004a; Lin et al., 2004b) that have importance later in life (Robles et al., 2001; Blount et al., 2003; Alonso-Alvarez et al., 2006). However, by the next year, early conditions in the nest did not have any impact on the adults. We propose two alternative explanations for this result.

First, our results may show that stabilising selection acts on the stress response. If the early developmental conditions have long lasting effects on the birds' physiology, individuals with different stress responsiveness may have different survival probability, as demonstrated by Blas et al. (2007) and Suorsa et al. (2003). As a consequence, very low- and high-responders to stress may be selected against and therefore the initial conditions may have little consequences in the surviving adults. This result corresponds well to our finding that in the fledglings, the effects of brood size on the stress response progressively disappeared with age. Early developmental conditions affect the adult stress response in laboratory mammals (see introduction) and a similar, but rather weak effect was found in western scrub-jays (*Aphelocoma californica*) (Pravosudov and Kitaysky, 2006), where one year old scrub jays that experienced nutritional deficits during post-hatching development showed a marginally significant trend to have stronger adrenocortical stress response.

An alternative explanation for our results may be that the physiological changes due to brood size manipulation were not per-

manent and diminished quickly after the nestling period being replaced by actual environmental effects, such as the ambient temperature. This may also explain the disappearing effects of brood size on the fledglings' stress response, which may result in opposite trends in chicks from large and small broods reflecting the relative stressfulness of the nestling vs. the fledgling period. Early conditions may have therefore rather short-term consequences on the stress response, and the individual variability in the adult stress responses reflects the birds' current breeding conditions rather than their developmental history. Indeed, house sparrow parents were found to modulate their stress response in function of the current level of reproductive effort (Lendvai et al., 2007). In this study, the quickly changing meteorological conditions (measured by the maximal daily temperature) predicted more strongly the stress response of adult females than their developmental conditions.

Moreover, we found an effect of sex on stress response, with males presenting a lower stress response than females. This result is in agreement with those reported by Lindstrom et al. (2005) who demonstrated that male house sparrows, in function of their dominant status, show modulation of the stress response. Indeed, social status maintenance can be costly because the competitive interactions with other members of the group can induce social stress (Abbott et al., 2003; Goymann and Wingfield, 2004) and the social stress may mask the effects of early developmental conditions. However, this finding is in contradiction with others studies (Lendvai et al., 2007; Romero, 2006) that did not find differences between males and females. We explain this discrepancy by the fact that contrary to the above studies, we only tested one year-old first-time breeders, and that this difference may disappear with time and breeding experience.

Therefore, our results show that early conditions have weak effects on the capacity to respond to a stress in this species. We have to underline that adults seem to have a rather good control on their stress response (Lendvai et al., 2007; Lendvai and Chastel, 2008), that may not be constrained by the early conditions in the nest.

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