



Natural variation in stress response is related to post-stress parental effort in male house sparrows

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ABSTRACT

The central life-history trade-off between current and future reproductive effort seems to be mediated by corticosterone in birds. However, still little is known about how naturally occurring corticosterone levels during an acute stress may influence subsequent parental behavior. In this study we observed the parental behavior of free-living male house sparrows (*Passer domesticus*) both before and after they were subjected to a standard capture–handling stress. We investigated the relationships between corticosterone levels, pre- and post-stress parental behavior, while we statistically controlled for a number of other variables using a multivariate regression method, the path analysis. We found that males' baseline feeding rate predicted the body mass of the nestlings, indicating that male parental care is directly linked to fitness. Corticosterone levels were not explained by baseline feeding rate, but both baseline and stress-induced corticosterone levels had a negative influence on the males' post-stress feeding behavior. Moreover, males with large bib size had a stronger stress response and lower post-stress feeding rate than small bibbed males. These results indicate that naturally occurring variation in baseline and stress-induced corticosterone levels may influence subsequent parental decisions: individuals mounting a robust stress response are likely to reduce their parental commitment. Parental effort may be regulated in a complex manner, with corticosterone mediating the life-history trade-off between current reproduction and survival. However, different resolutions of this trade-off were apparent only following the stress, therefore the ability to modulate the stress response and maintain parental care in stressful situations may be important in life-history evolution.

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Introduction

Iteroparous organisms are faced with the problem of resource allocation between successive reproductive events. The concept of parental investment postulates that parents in a given reproductive event may increase the survival of their offspring by providing care at the expense of future breeding (Williams, 1966; Trivers, 1972; Stearns, 1992). This allocation dilemma between current and future reproduction is a central tenet in life-history theory (Stearns, 1992). Hormones play a crucial role in mediating life-history trade-offs, and studying these physiological mechanisms is essential to understanding life-history evolution (Sinervo and Svensson, 1998; Ketterson and Nolan, 1999). For example, it is well documented that increased levels of circulating testosterone enhance mating efforts at the expense of parental activities. For instance, subcutaneous implants of testosterone increased the frequency of singing while it decreased the contribution to incubation and feeding rate in blue-headed vireo (*Vireo solitarius*) (Van Roo, 2004). Similar results have been obtained

in a number of bird species (e.g. Silverin, 1980; Hegner and Wingfield, 1987; Dittami et al., 1991; Ketterson et al., 1992).

Similarly, it has been repeatedly suggested that corticosterone mediates the trade-off between survival and reproduction, because high corticosterone levels are hypothesized to reduce reproductive behavior (Wingfield et al., 1995, 1998; reviews by Wingfield and Sapolsky (2003), Romero (2004) and Breuner et al. (2008)). However, surprisingly few studies have investigated the fine scale relationship between the stress response and its consequences on parental behavior (but for a recent study, see Miller et al. (2009)). The inhibiting effects of corticosterone on reproduction in birds are mainly based on studies that showed that an experimental increase in corticosterone levels resulted in a sharp decrease or abandonment of reproductive activity. For instance, Silverin (1986) found that corticosterone-implanted pied flycatchers (*Ficedula hypoleuca*) either abandoned or reduced their feeding rates and produced fewer fledglings than control ones, although the implants caused a chronic elevation of hormone concentrations significantly in excess of natural baseline levels. In the black-legged kittiwake (*Rissa tridactyla*), Kitaysky et al. (2001) found that corticosterone-implanted parents spent more time away from the nest and less time brooding/guarding chicks than sham-implanted controls. A number of other studies have

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shown that a simulated chronic stress induced the cessation or considerable decrease of reproductive behavior (Angelier et al., 2007, 2009; Almasi et al., 2008). To better understand how hormones mediate trade-offs, it is crucial to investigate both natural variation in the hormone concentrations and behavior (Sinervo, 1999; McGlothlin et al., 2007; Williams, 2008).

In this study, we aimed at investigating the relationship between the naturally occurring variation in response to a momentary acute stress and the parental behavior. To do so, we observed the parental behavior of male house sparrows both before and after they were subjected to an experimental stress protocol. Male house sparrows are ideal models for such a study because (i) the males' feeding effort is highly variable between individuals (Schwagmeyer and Mock, 2003; Nakagawa et al., 2007a) and (ii) the development and fledging success of the nestlings is strongly determined by the amount of male feeding effort, therefore, the variable male feeding effort is directly related to a fitness component (Hoi et al., 2003).

Here, our main interest was to test whether the magnitude of stress response is related to the parental behavior in the period following the stress. To do so, we carried out our analyses in three steps. First, we investigated the factors that may influence pre-stress (i.e. baseline) male feeding behavior and we tested whether male parental effort influenced the body size and condition of the chicks. Second, we investigated whether hormone levels (baseline and stress-induced corticosterone) were affected by pre-stress male feeding effort. Finally, we asked whether corticosterone levels (measures of stress response) predicted males' post-stress investment.

Methods

Study species and population

The study was carried out between March and July 2006, on a free-living population of house sparrows that breed in nest boxes in Chizé (46°08'50" N, 0°25'29" W), France. A large proportion of the adults used in this study were first captured either in previous years or during the pre-breeding period using mist nets and marked with a unique metal ring and color combination. Nest boxes were monitored daily to determine laying dates, clutch sizes, hatching dates, and the number of hatchlings. The authors attest to possess the legal authorized use of wild animals 'Certificat d'autorisation d'expérimenter sur animaux vivants N°79-2' delivered to O. Chastel by 'Services Vétérinaires des Deux Sèvres'.

Protocol

The study consisted of three parts (Fig. 1). First, we measured pre-stress (i.e. baseline) parental effort of male parents, then we captured

them and measured their response to a standardized stressor, finally we measured their post-stress parental effort again. To standardize breeding stage between the birds, male parents were captured in their nest on day 7 after hatching (day 0). To measure the stress response, we used a standard capture–handling–restraint protocol (Wingfield, 1994). Immediately after capture, we collected a small amount of blood (approximately 100 µl) from the brachial vein and recorded the time required to collect the sample. After collection of the initial blood samples, birds were placed in cloth bags, and the chicks were weighed (to the nearest 0.5 g). Body mass of the chicks is a good indicator of parental fitness, because it strongly predicts fledging success and recruitment rate of the nestlings (Schwagmeyer and Mock, 2008). We collected a second blood sample from the males 30 min following the first bleeding, when corticosterone levels are known to be at their maximum in this species (Breuner and Orchinik, 2001; Lindström et al., 2005; Romero et al., 2006). Blood samples were kept on ice and centrifuged (5000 rpm, 6 min) as soon as possible. Plasma was separated and stored at –20 °C until hormone assays. After the second blood sample was collected, we measured the males' wing length, the length and width of the bib (to the nearest mm) and the body mass (to the nearest 0.5 g) before releasing them. Twenty-three males were randomly selected and were taken into captivity, because these birds were subjects of a mate-removal experiment in the same population (Lendvai and Chastel, 2008). Therefore, post-stress feeding effort data are not available for these birds.

To measure parental effort, we carried out behavioral observations for 1–2 h at each nest for both the baseline and the post-stress period (Fig. 1). We aimed at collecting two observations before capturing the male (baseline: days 6 and 7), and two observations after the capture (post-stress: days 8 and 9). Observations lasted for 1 h, and whenever it was possible, they were carried out early in the morning and mid-day, with alternating the two time periods on consecutive days. The daily scheduling of samples was based on the recommendations of Schwagmeyer and Mock (1997): the combination of these observation hours was the best to predict the within-nest change of daily delivery rate, and also accounted for more than 98% of the between-nest variation in feeding rate. Observations were carried out using a spotting scope from a car parked 25–60 m from the focal nest. To ensure that we observe the birds' natural behavior, we recorded if the behavior of the birds was apparently disturbed, e.g. because of some continuous human activity near the nestbox. The time during which the disturbance occurred was discarded from the observation time. In a few cases when the disturbance was continuous, the observation was cancelled and repeated later. During the observations we recorded the number of food deliveries made by each parent. Feeding rates were defined as the number of food deliveries per hour per chick (i.e. per capita feeding rate). Mean feeding rates were calculated and square-root transformed for the baseline and for the post-stress periods.

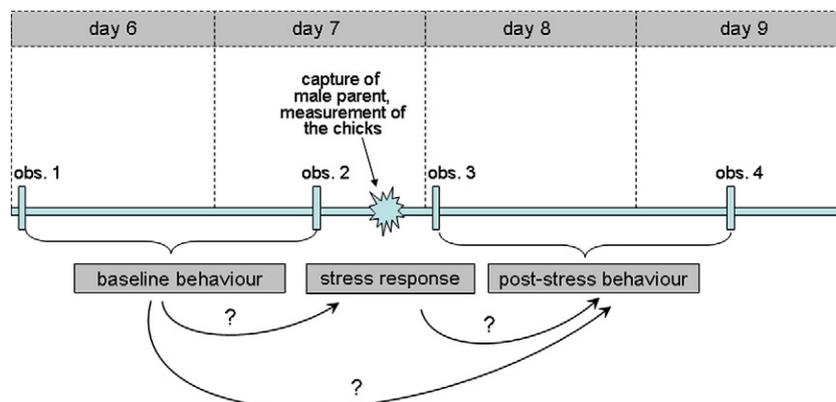


Fig. 1. Schematic diagram of the study protocol during four consecutive days in a given focal nest, where day 0 stands for the hatching date. Obs. 1–4 denote subsequent 1-h behavioral observations. Question marks show the main relationships analyzed in this study.

Corticosterone assay

Corticosterone levels were determined by radioimmunoassay at the Centre d'Etudes Biologiques de Chizé. Total plasma corticosterone was measured in samples (50 μ L) after ethyl ether extraction by radioimmunoassays using a commercial antiserum, raised in rabbits against corticosterone-3-(Ocarboxy-methyl) oxime bovine serum albumin conjugate (Biogenesis, UK). Cross-reaction was 9% with 1-desoxycorticosterone and less than 0.1% with other plasma steroids. Duplicate aliquots (100 μ L) of the extracts were incubated overnight at 4 °C with 8000 cpm of 3 H-Corticosterone (Amersham Pharmacia Biotech-France) and antiserum. The bound and free corticosterone were separated by adding dextran-coated charcoal. After centrifugation, the bound fraction was counted in a liquid scintillation counter. Minimal detectable corticosterone levels were 0.4 ng ml (lowest measurement: 1.26 ng ml). Hormone concentrations were run in one assay (coefficient of intra-assay variation was 6.7%, $N=6$ duplicates).

Data processing and statistical analysis

We collected baseline behavior from 56 males. Corticosterone data were available for 48 males, because in 8 nests, only the behavior was recorded, but the parents were not captured (Lendvai et al., 2009a). After the blood sampling, some males were removed from the nest and taken into captivity, as part of another experiment (see earlier), therefore post-stress behavior was observed for 24 males that were released after the capture. Brood sizes ranged from two to six chicks.

All data processing and statistical analyses were performed in the R computing environment (R Development Core Team, 2006). We used path analysis to investigate how corticosterone levels were related to post-stress behavior while taking into account the effect of other variables that may have influenced the corticosterone levels, the post-stress behavior or both. Path analysis is a multivariate multiple regression method that is used to test expected causal relationships, especially when there are multiple correlations between variables of interest, and when both direct and indirect effects should be considered (Li, 1975; Sinervo, 1999; Szentirmai et al., 2007; Hatch and Westneat, 2007; Miller et al., 2009). Causality in our model design is mainly inferred by temporal constraints: e.g. bib size is formed during the molt well before our observations; therefore we expected a directional relationship between bib size and feeding rate. Similarly, since the observations of baseline behavior preceded the capture–handling stress, we expected that baseline behavior could influence the stress response, but not *vice versa*. However, since hormone–behavior interactions are often considered as bidirectional, despite these time constraints, we also tested a model with bidirectional paths (i.e. a covariance structure) between corticosterone levels and feeding rate. In our path model, we used a set of candidate variables that described external conditions, the brood or the focal individual (Table 1). External conditions included the date (of capture), daily maximum temperature, and handling time for the baseline corticosterone levels. Since most birds were captured in the afternoon hours (mean capture time being 16:41 \pm 31 min SE), circadian variation in corticosterone levels is unlikely to influence our results. This

Table 1
Variables used in the path model.

External variables	Brood variables	Focal bird's attributes
Date of capture	Brood size	Bib size
Daily maximum temperature	Body mass of chicks (mean per brood)	Baseline feeding rate
Handling time		Post-stress feeding rate
		Baseline corticosterone
		Stress-induced corticosterone

assumption was corroborated by preliminary analyses showing no effect of time of capture on either baseline or stress-induced corticosterone levels ($p>0.3$, $p>0.2$, respectively). Therefore time of capture was not included in the path models. Variables that described the brood included brood size and mean body mass of the chicks per brood. The focal individual's attributes included bib size (calculated as in Møller (1987)), baseline feeding rate, corticosterone levels and post-stress feeding rate. We define stress response as the stress-induced corticosterone levels, while in the path model, we control for the variation in baseline corticosterone levels. A similar approach was used by Bókony et al. (2009).

Path analysis was carried out in R using the 'sem' package. To test the fit of the model to the data we used a χ^2 test with root mean square error of approximation (RMSEA) that corrects the χ^2 for model parsimony and small sample size. RMSEA index shows good fit when it is close to zero (and the p value is not significant). We also give a BIC (Bayesian information criterion) which adjusts the likelihood-ratio χ^2 statistic for the number of parameters in the model, the number of observed variables and the sample size. The smaller the BIC value, the better is the model fit. To show the relationships between variables of interest, we provide standardized coefficients (i.e. partial regression parameters varying between -1 and 1). Our initial path model was constructed *a priori* based on the knowledge from previous studies. For the path analysis, we used all available data (i.e. pairwise complete observations), but preliminary analyses showed that our results were not affected by lower sample sizes for post-stress behavioral samples.

Results

Our initial path model with bidirectional paths between corticosterone and parental behavior did not fit the data ($\chi^2=26.68$, $df=17$, $p=0.038$, RMSEA index = 0.110, BIC = -40.104). Therefore, we used the same model structure with unidirectional paths. This model had a better fit to the data ($\chi^2=24.40$, $df=17$, $p=0.101$, RMSEA index = 0.088, BIC = -44.33). Model specification, standardized coefficients and corresponding significance values are summarized in Table 2. Subsequently, we simplified the model by omitting paths with p values greater than 0.1. The resulting final path model had substantially better fit ($\chi^2=37.29$, $df=32$, $p=0.23$, RMSEA index = 0.054, BIC = -92.082), and was qualitatively largely consistent with the initial model (i.e. all significant paths remained significant with very similar path coefficients, and two marginally non-significant path became significant in the new model). The final path model is shown in Fig. 2.

To test again the potential bidirectional relationships between hormones and behavior, an alternative initial model was also considered including unidirectional paths from baseline corticosterone to baseline feeding and from stress-induced corticosterone to baseline feeding, but the fit of this model was again poor ($\chi^2=22.81$, $df=32$, $p=0.088$, RMSEA index = 0.092, BIC = -37.83), and these 'hormone to behavior' paths were not significant ($p=0.756$ and $p=0.251$ respectively).

Baseline male feeding behavior and body size of the chicks

Neither the date in the season, nor the bib size of males was related to their baseline feeding rate, however, baseline feeding rate decreased with increasing brood sizes. Brood sizes decreased with date. The body mass of the chicks measured at day 7 were positively related to male baseline feeding rate (Table 2, Fig. 2).

Corticosterone levels of males

Baseline corticosterone levels were only related to handling time, even though the mean handling time was 2.78 min (range: 1.65–

Table 2
Initial path model of the relationship between behavior, corticosterone levels and external variables in male house sparrows.

	Path	Standardized coefficient	p
Date	→Brood size	−0.35	0.005
Date	→Chick mass	−0.16	0.241
Date	→Baseline feeding	0.13	0.327
Date	→Baseline corticosterone	0.05	0.747
Date	→Stress-induced corticosterone	0.10	0.510
Date	→Post-stress feeding	0.08	0.287
Date	→Temperature	0.65	0.000
Brood size	→Chick mass	0.02	0.900
Brood size	→Post-stress feeding	0.35	0.000
Brood size	→Stress-induced corticosterone	0.26	0.043
Brood size	→Baseline corticosterone	0.07	0.614
Brood size	→Baseline feeding	−0.29	0.032
Baseline feeding	→Chick mass	0.36	0.008
Baseline feeding	→Baseline corticosterone	−0.14	0.306
Baseline feeding	→Post-stress feeding	0.45	0.000
Baseline feeding	→Stress-induced corticosterone	−0.12	0.374
Chick mass	→Baseline corticosterone	0.09	0.466
Chick mass	→Stress-induced corticosterone	0.13	0.315
Bib	→Baseline feeding	−0.03	0.820
Bib	→Baseline corticosterone	0.11	0.399
Bib	→Post-stress feeding	−0.30	0.000
Bib	→Stress-induced corticosterone	0.22	0.085
Handling time	→Baseline corticosterone	0.43	0.000
Temperature	→Baseline corticosterone	−0.18	0.287
Temperature	→Stress-induced corticosterone	−0.33	0.054
Baseline corticosterone	→Stress-induced corticosterone	−0.01	0.958
Baseline corticosterone	→Post-stress feeding	−0.40	0.000
Stress-induced corticosterone	→Post-stress feeding	−0.34	0.000

4.51 min). Selecting data points only where the first blood sample was taken within 3 min showed that corticosterone levels tended to increase already during the first 3 min of blood sampling ($p = 0.088$). Therefore, we used all baseline corticosterone values and kept handling time in the model to statistically control for this effect. Capture date, brood size, bib size and feeding rate of males were all unrelated to baseline corticosterone levels (Table 2, Fig. 2).

Stress-induced corticosterone levels were affected by maximal daily temperature. As expected, daily temperature significantly

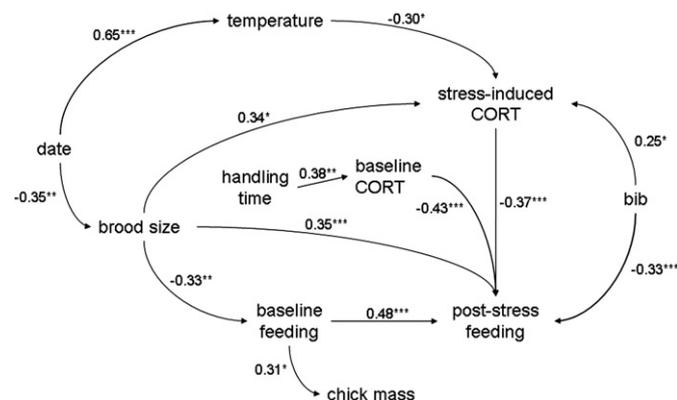


Fig. 2. Path diagram of the final path analysis. Arrows indicate direct linear relationships between explanatory and response variables. Standardized path coefficients and their significance are shown above the paths. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

increased with the date. Brood size and bib size were positively related to stress-induced corticosterone levels. The effect of bib size was marginally non-significant in the initial model ($p = 0.079$, Table 2), but became significant in the final model (Fig. 2). Baseline feeding rate did not influence the stress-induced corticosterone levels (Table 2, Fig. 2).

Post-stress feeding effort of males

Post-stress feeding rate was significantly lower than baseline feeding rate (mean difference was -0.90 feedings/h/chick, $t_{22} = -3.43$, $p = 0.002$). The path analysis revealed that post-stress feeding rate was influenced by several factors. Baseline feeding rate had a strong positive effect on the post-stress feeding rate. Brood size was related positively, whereas bib size of males was related negatively to the post-stress feeding rate. Taking into account these effects, the corticosterone levels (both baseline and stress-induced) still significantly predicted the males' post-stress feeding rate (Table 2, Fig. 3).

Discussion

In this study, we investigated the natural variation in the feeding effort of male house sparrows and its relation to an experimentally induced stress response. Our key question was whether the magnitude of stress response affected the parental behavior of males in the period after the acute stressor. We found that the higher the males' corticosterone levels were, the lower their post-stress feeding rate was. Since we were interested in the natural variation of these traits, we also asked what factors may have influenced the corticosterone levels and the parental behavior of the parents. We discuss these results in turn.

First, we found that the baseline male feeding rate was an important predictor of nestling body mass. In accordance with this finding, Hoi et al. (2003) also found that the best predictor of the body size and mass of the chicks was the male feeding rate alone. Since nestling body mass is related to fledging and recruitment success, these results indicate that variation in feeding rate of males has direct fitness consequences in this species. Therefore it is important to know whether acute stress has immediate consequences on parental behavior, and how male parents may resist these effects.

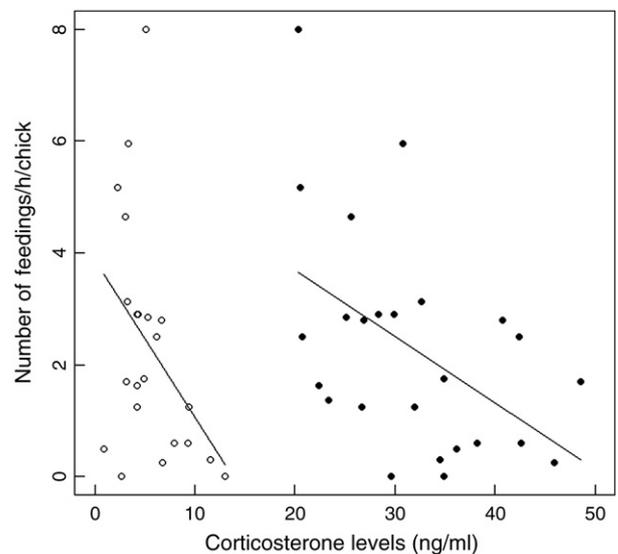


Fig. 3. Relationship between baseline corticosterone (open circles) and stress-induced (filled circles) corticosterone levels and the post-stress chick feeding rate of male house sparrows. Males mounting a more robust stress response had a lower post-stress parental feeding contribution.

We also found that the per capita feeding rate was lower in large broods, a result corroborated by other studies (e.g. Nakagawa et al., 2007a,b) which indicates that parents are constrained in their provisioning capacity. Nevertheless, the relationship between chick body mass and male feeding rate was significant in the path model controlling for this brood size effect. Apart from the brood size, we found no factor that may have confounded our analysis of the feeding rate.

Second, we found that baseline feeding rate did not explain variation in corticosterone levels. One may have predicted a positive relationship between feeding rate and baseline corticosterone, because increased energetic demands may induce elevated baseline corticosterone levels (Landys et al., 2006). However, male house sparrows show consistent individual behavioral differences in feeding rate across breeding seasons and years (Schwagmeyer and Mock, 2003; Nakagawa et al., 2007a; see also later), therefore males with high feeding rate may be well prepared for the energetic demands of chick provisioning. Furthermore, in a previous study of this population, even in response to a brood size enlargement, we found no elevation of baseline corticosterone levels of the parents (Lendvai et al., 2007). We acknowledge that the 'noise' due to the handling time is higher for baseline corticosterone than for the stress-induced levels, therefore it may be more difficult to detect any significant differences. However, baseline feeding rate was also unrelated to stress-induced corticosterone levels. Our previous experiments on this population showed that stress response may be modulated mainly in terms of the brood value and not the parental workload (Lendvai et al., 2007; Lendvai and Chastel, 2008).

We found that the maximum daily temperature had a negative effect on the stress-induced corticosterone levels. This result suggests that when the meteorological conditions are challenging, i.e. when the temperature falls below what is expected in the season, the birds up-regulate their stress response. One may argue that in inclement weather the survival probability of the chicks drops considerably, as was shown in the house sparrow (Ringsby et al., 2002). As the survival prospects of the chicks are lower in inclement weather, the value of the current brood becomes lower, and parents may consequently up-regulate their stress response (Lendvai et al., 2007; Lendvai and Chastel, 2008). Although this explanation is still possible, the fact that we found a similar negative relationship between the daily temperature and stress response in fledgling house sparrows (Lendvai et al., 2009b) suggests a more general phenomenon. Due to the increased thermoregulation in cold weather, the energetic costs of coping with a stressor may be higher which may be mirrored by a higher stress response (Romero et al., 2000).

Finally, we found that the post-stress feeding rate of males was shaped in a complex manner, under the influence of several effects. The best predictor of the post-stress feeding rate of males was how they had provisioned their chicks before the stress. This result is consistent with a number of other studies and corroborates the high individual consistency of male parental care in this species (Schwagmeyer et al., 2002; Schwagmeyer and Mock, 2003; Nakagawa et al., 2007a). The remarkable consistency of male parental behavior over time and across different stages of parental care (Kopisch et al., 2005) is by definition an indication of a behavioral syndrome or animal personality (Groothuis and Carere, 2005; Sih et al., 2004). Current research on animal personalities classifies individuals based on behavioral axes including activity, boldness, exploration, aggressiveness and sociability (Réale et al., 2007). If we are to accept that consistent individual behavioral differences over time and across situations define animal personalities (Réale et al., 2007), it leaves us with the intriguing possibility that parental care would form another behavioral axis in some species. Moreover, this notable consistency characterizes only male parents in the house sparrow; therefore personality profiles would not necessarily be matched in the two sexes. Recent models suggest that animal personalities arise by individual differences in the "solution" of life-

history trade-offs (Wolf et al., 2007; Biro and Stamps, 2008) that are mediated by physiological systems such as glucocorticoid and other hormones (Biro and Stamps, 2008). Since males and females may face different life-history trade-offs, it is possible that different personality profiles may coexist in the same species. It is currently unknown how parental care is linked to other personality traits in male house sparrows, but current research suggest that avian personalities may be related to the physiological stress response (reviewed by Cockrem (2007), see also Lendvai et al., in press). We found here that baseline feeding rate was not related to either baseline or stress-induced corticosterone levels, which suggests that in male house sparrows the stress response is not or not strongly constrained by the personality of the focal individual.

However, after controlling for the baseline parental effort, post-stress feeding rate was strongly negatively related to the corticosterone levels: i.e. individuals having high baseline and responding strongly to the capture–handling stress showed less parental effort than individuals with a moderate stress response (Fig. 3). This result shows that even subtle natural variation in the corticosterone levels may induce differences in the post-stress parental behavior. Although the role of corticosterone as a mediator in life-history trade-offs is routinely discussed in the literature (e.g. Wingfield et al., 1995, 1998; Ricklefs and Wikelski, 2002; Heidinger et al., 2006; Blas et al., 2007), and the results of several studies (e.g. showing seasonal modulation of the stress response, reviewed by Romero (2002)) are consistent with this notion, however, very few studies have investigated the actual relationship between the corticosterone levels and parental care (Breuner et al., 2008, see also Introduction). In this study, we chose to explore the natural variation in corticosterone and parental care. Individual variation is often overlooked in studies of avian stress response and is merely used to assess the confidence limits of estimates of hormone levels (Williams, 2008, but see e.g. Carere et al. (2003), Wada et al. (2008), Almasi et al. (2008) and Miller et al. (2009)). Here we showed that natural individual variation in corticosterone levels is not just 'noise' in the data, but is a meaningful source of variation that may influence parental decisions.

Corticosterone is just one part of the physiological machinery controlling behavior. The effects of corticosterone are modulated by receptor numbers and the corticosterone binding globulin (CBG), therefore, these factors may interact to form the physiological stress response (Breuner and Orchinik, 2001; Love et al., 2004). In the house sparrow, the CBG levels are not modulated during acute stress (Breuner et al., 2006), and taking into account the CBG levels in baseline and stress-induced corticosterone levels did not alter the conclusions drawn from total corticosterone levels (Fokidis et al., 2009). However, corticosterone may also interact with other hormones in the regulation of parental behavior (Chastel et al., 2005; Angelier et al., 2007). Recent results suggest that the effects of corticosterone on parental behavior may be indirect with the interplay of prolactin (Angelier et al., 2009), and it may be an important direction for future studies.

Finally, we found that the bib size of the males was related to two important variables. Males with large bibs mounted a more robust stress response and they fed their chicks less frequently after the stress than small bibbed males. The function of the male's bib in a reproductive context is still unclear. On the one hand, it is well established that the size of the bib is a reliable indicator of dominance (a so called badge of status: Møller, 1987; Solberg and Ringsby, 1997; Liker and Barta, 2001; Hein et al., 2003; Bókony et al., 2006). On the other hand, the role of the bib in signaling parental investment is controversial, with different studies reporting positive, negative or no relationship between bib size and parental care, and with a recent experiment suggesting that bib size has no role in signaling parental qualities (Nakagawa et al. (2007b) and references therein). Interestingly, in our study, bib size was not related to baseline feeding rate, but we found a strong negative relationship between bib size and

post-stress feeding and a weaker positive relationship between bib size and stress-induced corticosterone levels. These results indicate that the badge itself may not be an indicator of parental quality in normal conditions, but rather may be related to males' stress sensitivity: males with small bibs may be more resistant to stress than their larger-bibbed counterparts. It is noteworthy that this finding contradicts the predictions of a recent study suggesting that the degree of eumelanin coloration may be a signal of adaptation to poor environments and the ability to cope with stressful factors in that environment (Roulin et al., 2008; see also Kittilsen et al. (2009)). However, the eumelanin coloration of house sparrows (the bib) and that of barn owls (black wing spots) is under different control: while the sparrows' bib is at least partly testosterone-dependent (Evans et al., 2000; Buchanan et al., 2001), the degree of eumelanism is independent from the circulating testosterone levels in the barn owls (*Tyto alba*) (Roulin et al., 2004). Testosterone levels generally have a negative effect on parental motivation, but this effect may be masked during normal conditions. Our message is that natural variation in response to an acute stress may amplify these motivational differences, and (probably in concert with other hormones) influence parental decisions of the individuals.

In previous experiments in the house sparrow we showed that individuals are able to modulate their corticosterone stress response in function of the brood value (Lendvai et al., 2007; Lendvai and Chastel, 2008). Here, we showed that corticosterone levels are related to parental behavior, and thus may have direct consequences on fitness. Therefore, the ability itself to flexibly modulate the stress response may be an important, but poorly studied trait in life-history evolution.

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References

Almasi, B., Roulin, A., Jenni-Eiermann, S., Jenni, L., 2008. Parental investment and its sensitivity to corticosterone is linked to melanin-based coloration in barn owls. *Horm. Behav.* 54, 217–223.

Angelier, F., Moe, B., Weimerskirch, H., Chastel, O., 2007. Age-specific reproductive success in a long-lived bird: do older parents resist stress better? *J. Anim. Ecol.* 76, 1181–1191.

Angelier, F., Clément-Chastel, C., Weckler, J., Gabrielsen, G.W., Chastel, O., 2009. How does corticosterone affect parental behaviour and reproductive success? A study of prolactin in Black-legged kittiwakes. *Funct. Ecol.* 23, 784–793.

Biro, P.A., Stamps, J.A., 2008. Are animal personality traits linked to life-history productivity? *Trends Ecol. Evol.* 23, 361–368.

Blas, J., Bortolotti, G.R., Tella, J.L., Baos, R., Marchant, T.A., 2007. Stress response during development predicts fitness in a wild, long lived vertebrate. *PNAS* 104, 8880–8884.

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.

Bókony, V., Lendvai, Á.Z., Liker, A., Angelier, F., Wingfield, J.C., Chastel, O., 2009. Stress response and the value of reproduction: are birds prudent parents? *Am. Nat.* 173, 589–598.

Breuner, C.W., Orchinik, M., 2001. Seasonal regulation of membrane and intracellular corticosteroid receptors in the house sparrow brain. *J. Neuroendocrinol.* 13, 412–420.

Breuner, C.W., Lynn, S.E., Julian, G.E., Cornelius, J.M., Heidinger, B.J., Love, O.P., Sprague, R.S., Wada, H., Whitman, B.A., 2006. Plasma-binding globulins and acute stress response. *Horm. Metab. Res.* 38, 260–268.

Breuner, C.W., Patterson, S.H., Hahn, T.P., 2008. In search of relationships between the acute adrenocortical response and fitness. *Gen. Comp. Endocrinol.* 157, 288–295.

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* 268, 1337–1344.

Carere, C., Groothuis, T.G.G., Mostl, E., Daan, S., Koolhaas, J.M., 2003. Fecal corticosteroids in a territorial bird selected for different personalities: daily rhythm and the response to social stress. *Horm. Behav.* 43, 540–548.

Chastel, O., Lacroix, A., Weimerskirch, H., Gabrielsen, G., 2005. Modulation of prolactin but not corticosterone responses to stress in relation to parental effort in a long-lived bird. *Horm. Behav.* 47, 459–466.

Cockrem, J.F., 2007. Stress, corticosterone responses and avian personalities. *J. Ornithol.* 148, 169–178.

Dittami, J., Hoi, H., Sageder, G., 1991. Parental investment and territorial sexual-behavior in male and female reed warblers – are they mutually exclusive? *Ethology* 88, 249–255.

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.

Fokidis, H.B., Orchinik, M., Deviche, P., 2009. Corticosterone and corticosteroid binding globulin in birds: relation to urbanization in a desert city. *Gen. Comp. Endocrinol.* 160, 259–270.

Groothuis, T.G.G., Carere, C., 2005. Avian personalities: characterization and epigenesis. *Neurosci. Biobehav. Rev.* 29, 137–150.

Hatch, M.L., Westneat, D.F., 2007. Age-related patterns of reproductive success in house sparrows *Passer domesticus*. *J. Avian Biol.* 38, 603–611.

Hegner, R.E., Wingfield, J.C., 1987. Effects of experimental manipulation of testosterone levels on parental investment and breeding success in male house sparrows. *Auk* 104, 462–469.

Heidinger, B.J., Nisbet, I.C.T., Ketterson, E.D., 2006. Older parents are less responsive to a stressor in a long-lived seabird: a mechanism for increased reproductive performance with age? *Proc. R. Soc. Lond. B* 273, 2227–2231.

Hein, W.K., Westneat, D.F., Poston, J.P., 2003. Sex of opponent influences response to a potential status signal in house sparrows. *Anim. Behav.* 65, 1211–1221.

Hoi, H., Vaclav, R., Slobodova, D., 2003. Postmating sexual selection in house sparrows: can females estimate “good fathers” according to their early paternal effort? *Folia Zool. Brno* 52, 299–308.

Ketterson, E.D., Nolan Jr, V., 1999. Adaptation, exaptation, and constraint: a hormonal perspective. *Am. Nat.* 154, S4–S25.

Ketterson, E.D., Nolan Jr, V., Wolf, L., Ziegenfus, C., 1992. Testosterone and avian life histories – effects of experimentally elevated testosterone on behavior and correlates of fitness in the dark-eyed junco (*Junco-hyemalis*). *Am. Nat.* 140, 980–999.

Kitaysky, A.S., Wingfield, J.C., Piatt, J.F., 2001. Corticosterone facilitates begging and affects resource allocation in the black-legged kittiwake. *Behav. Ecol.* 12, 619–625.

Kittilsen, S., Schjolden, J., Beitnes-Johansen, I., Shaw, J.C., Pottinger, T.G., Sørensen, C., Braastad, B.O., Bakken, M., Øverli, Ø., 2009. Melanin-based skin spots reflect stress responsiveness in salmonid fish. *Horm. Behav.* 56, 292–298.

Kopisch, A.D., Schwagmeyer, P.L., Mock, D.W., 2005. Individual consistency in parental effort across multiple stages of care in the house sparrow, *Passer domesticus*. *Ethology* 111, 1062–1070.

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.

Lendvai, Á.Z., Chastel, O., 2008. Experimental mate-removal increases the stress response of female house sparrows: the effects of offspring value? *Horm. Behav.* 53, 395–401.

Lendvai, Á.Z., Giraudeau, M., Chastel, O., 2007. Reproduction and modulation of the stress response: an experimental test in the house sparrow. *Proc. R. Soc. Lond. B* 274, 391–397.

Lendvai, Á.Z., Barta, Z., Chastel, O., 2009a. Conflict over parental care in house sparrows: do females use a negotiation rule? *Behav. Ecol.* 63, 1189–1196.

Lendvai, Á.Z., Loiseau, C., Sorci, G., Chastel, O., 2009b. Early developmental conditions affect stress response in juvenile but not in adult house sparrows (*Passer domesticus*). *Gen. Comp. Endocrinol.* 160, 30–35.

Lendvai, Á.Z., Bókony, V., Chastel, O., in press. Coping with novelty and stress in free-living house sparrows. *Journal of Experimental Biology*.

Li, C.C., 1975. Path Analysis: a Primer. Boxwood press.

Liker, A., Barta, Z., 2001. Male badge size predicts dominance against females in House Sparrows. *Condor* 103, 151–157.

Lindström, K.M., Hasselquist, D., Wikelski, M., 2005. House sparrows (*Passer domesticus*) adjust their social status position to their physiological costs. *Horm. Behav.* 48, 311–320.

Love, O.P., Breuner, C.W., Vézina, F., Williams, T.D., 2004. Mediation of corticosterone-induced reproductive conflict. *Horm. Behav.* 46, 59–65.

McCloughlin, J.W., Jawor, J.M., Ketterson, E.D., 2007. Natural variation in a testosterone-mediated trade-off between mating effort and parental effort. *Am. Nat.* 170, 864–875.

Miller, D.A., Vleck, C.M., Otis, D.L., 2009. Individual variation in baseline and stress-induced corticosterone and prolactin levels predicts parental effort by nesting mourning doves. *Horm. Behav.* 56, 457–464.

- Møller, A.P., 1987. Variation in badge size in male house sparrows *Passer domesticus*: evidence for status signalling. *Anim. Behav.* 35, 1637–1644.
- Nakagawa, S., Gillespie, D.O.S., Hatchwell, B.J., Burke, T., 2007a. Predictable males and unpredictable females: sex difference in repeatability of parental care in a wild bird population. *J. Evol. Biol.* 20, 1674–1681.
- Nakagawa, S., Ockendon, N., Gillespie, D., Hatchwell, B., Burke, T., 2007b. Does the badge of status influence parental care and investment in house sparrows? An experimental test. *Oecologia* 153, 749–760.
- R Development Core Team, 2006. R: A language and environment for statistical computing. R Foundation for Statistical Computing, ISBN 3-900051-07-0, URL <http://www.R-project.org>, Vienna, Austria.
- Réale, D., Reader, S.M., Sol, D., McDougall, P.T., Dingemanse, N.J., 2007. Integrating animal temperament within ecology and evolution. *Biol. Rev.* 82, 291–318.
- Ricklefs, R.E., Wikelski, M., 2002. The physiology/life-history nexus. *TREE* 17, 462–468.
- Ringsby, T., Saether, B., Tufto, J., Jensen, H., Solberg, E., 2002. Asynchronous spatiotemporal demography of a house sparrow metapopulation in a correlated environment. *Ecology* 83, 561–569.
- Romero, L.M., 2002. Seasonal changes in plasma glucocorticoid concentrations in free-living vertebrates. *Gen. Comp. Endocrinol.* 128, 1–24.
- Romero, L.M., 2004. Physiological stress in ecology: lessons from biomedical research. *Trends Ecol. Evol.* 19, 249–255.
- Romero, L.M., Reed, J.M., Wingfield, J.C., 2000. Effects of weather on corticosterone responses in wild free-living passerine birds. *Gen. Comp. Endocrinol.* 118, 113–122.
- Romero, L.M., Cyr, N.E., Romero, R.C., 2006. Corticosterone responses change seasonally in free-living house sparrows (*Passer domesticus*). *Gen. Comp. Endocrinol.* 149, 58–65.
- Roulin, A., Muller, W., Sasvari, L., Dijkstra, C., Ducrest, A.L., Riols, C., Wink, M., Lubjuhn, T., 2004. Extra-pair paternity, testes size and testosterone level in relation to colour polymorphism in the barn owl *Tyto alba*. *J. Avian Biol.* 35, 492–500.
- Roulin, A., Gasparini, J., Bize, P., Ritschard, M., Richner, H., 2008. Melanin-based colorations signal strategies to cope with poor and rich environments. *Behav. Ecol. Sociobiol.* 62, 507–519.
- Schwagmeyer, P.L., Mock, D.W., 1997. How to minimize sample sizes while preserving statistical power. *Anim. Behav.* 54, 470–474.
- Schwagmeyer, P.L., Mock, D.W., 2003. How consistently are good parents good parents? Repeatability of parental care in the house sparrow, *Passer domesticus*. *Ethology* 109, 303–313.
- Schwagmeyer, P.L., Mock, D.W., 2008. Parental provisioning and offspring fitness: size matters. *Anim. Behav.* 75, 291–298.
- Schwagmeyer, P.L., Mock, D.W., Parker, G.A., 2002. Biparental care in house sparrows: negotiation or sealed bid? *Behav. Ecol.* 13, 713–721.
- Sih, A., Bell, A., Johnson, J.C., 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.* 19, 372–378.
- Silverin, B., 1980. Effects of long-acting testosterone treatment on free-living pied flycatchers, *Ficedula hypoleuca*, during the breeding period. *Anim. Behav.* 28, 906–912.
- Silverin, B., 1986. Corticosterone-binding proteins and behavioral effects of high plasma levels of corticosterone during the breeding period in the pied flycatcher. *Gen. Comp. Endocrinol.* 64, 67–74.
- Sinervo, B., 1999. Mechanistic analysis of natural selection and a refinement of Lack's and Williams's principles. *Am. Nat.* 154, 26–42.
- Sinervo, B., Svensson, E., 1998. Mechanistic and selective causes of life history trade-offs and plasticity. *Oikos* 83, 432–442.
- Solberg, E.J., Ringsby, T.H., 1997. Does male badge size signal status in small island populations of house sparrows, *Passer domesticus*? *Ethology* 103, 177–186.
- Stearns, S.C., 1992. *The Evolution of Life Histories*. Oxford University Press, New York.
- Szentirmai, I., Székely, T., Komdeur, J., 2007. Sexual conflict over care: antagonistic effects of clutch desertion on reproductive success of male and female penduline tits. *J. Evol. Biol.* 20, 1739–1744.
- Trivers, R.L., 1972. Parental investment and sexual selection. In: Campbell, B. (Ed.), *Sexual Selection and the Descent of Man, 1871–1971*. Aldine, Chicago, pp. 136–179.
- Van Roo, B.L., 2004. Exogenous testosterone inhibits several forms of male parental behavior and stimulates song in a monogamous songbird: the blue-headed vireo (*Vireo solitarius*). *Horm. Behav.* 46, 678–683.
- Wada, H., Salvante, K., Stables, C., Wagner, E., Williams, T., Breuner, C., 2008. Adrenocortical responses in zebra finches (*Taeniopygia guttata*): individual variation, repeatability, and relationship to phenotypic quality. *Horm. Behav.* 53, 472–480.
- Williams, G.C., 1966. Natural selection, the costs of reproduction and a refinement of Lack's principle. *Am. Nat.* 100, 687–690.
- Williams, T.D., 2008. Individual variation in endocrine systems: moving beyond the 'tyranny of the Golden Mean'. *Philos. Trans. R. Soc.* 363, 1687–1698.
- Wingfield, J.C., 1994. Modulation of the adrenocortical response to stress in birds. In: Davey, K., Peter, R., Tobe, S. (Eds.), *Perspectives in Comparative Endocrinology*. National Research Council of Canada, Ottawa, Canada, pp. 520–528.
- Wingfield, J.C., Sapolsky, R., 2003. Reproduction and resistance to stress: when and how. *J. Neuroendocrinol.* 15, 711–724.
- Wingfield, J.C., O'Reilly, K., Astheimer, L., 1995. Ecological bases of the modulation of adrenocortical responses to stress in Arctic birds. *Am. Zool.* 35, 285–294.
- 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.
- Wolf, M., van Doorn, G.S., Leimar, O., Weissing, F.J., 2007. Life-history trade-offs favour the evolution of animal personalities. *Nature* 447, 581–584.