



No trans-generational maternal effects of early-life corticosterone exposure on neophobia and antipredator behaviour in the house sparrow

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Abstract

Conditions experienced during early development can lead to profound long-lasting changes in physiology and behaviour. The extent to which such “programming” effects are transmitted to the next generation remains largely unexplored. Here, we assessed whether maternal exposure to elevated corticosterone stress hormone during early post-natal development had an impact on neophobia and antipredator behaviour in the offspring. Our data showed that maternal early-life hormonal manipulation had no impact on offspring behavioural traits. This occurred despite the treatment associated changes to metabolism, physiology and behaviour of the study mothers up until adulthood, as previously reported.

Keywords Early-life stress · Corticosterone · Trans-generational effects · Maternal stress · Behaviour · Neophobia · Antipredator behaviour

Introduction

The early environment in which an individual develops can have profound, long-lasting, effects on behaviour (Sih 2011). Such organisational, or “programming” effects can occur as a result of environmental factors acting directly on the growing individual, or via parental effects (Mousseau and Fox 1998). Early-life adversities (e.g. low weight at birth, poor maternal care) often increase endogenous exposure to glucocorticoid (“stress”) hormones and can negatively impact the behavioural phenotype leading to increased anxiety and cognitive impairments (reviews: Cottrell and Seckl 2009; Groothuis and Trillmich 2011). However, the highly conserved nature of early-life programming strongly suggests

that adaptive phenotypic plasticity can still arise under natural selection (West-Eberhard 2003). Various theoretical models propose that early-life stress prepares individuals to better cope with challenging circumstances through future life stages (Gluckman et al. 2005; Monaghan 2008). Recent research provides some evidence supporting this possibility (reviews; Langenhof and Komdeur 2018; Moran et al. 2020). For example, exposure to stress during pre- and post-hatching development promoted explorative and risk-taking behavioural responses upon adulthood in Japanese quails (Zimmer et al. 2013). Similar effects of various early-life stressors on adult risk-taking behaviour were also reported in other species (reviewed in Moran et al. 2020). Such changes may be advantageous if they facilitate behavioural strategies that promote access to resources under harsh nutritional conditions (Zimmer et al. 2013; Langenhof and Komdeur 2018). However, the potential benefits of early-life stress on behavioural phenotypes are complex and could depend on many physiological state-behaviour interactions (Langenhof and Komdeur 2018). For instance, house sparrow adults displayed poor adult antipredator escape behaviour when exposed to corticosterone—the main avian glucocorticoid—during post-hatching development (Grace et al. 2017a). This effect, however, was moderated by individual physiological state; treated birds in poor body condition displayed no

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decrease in evasiveness compared to control birds (Grace et al. 2017a).

A novel research area concerns whether the effects of early-life environmental conditions experienced by the parental generation can be transmitted to the offspring phenotype (Burton and Metcalfe 2014). In the Japanese quail, pre-natal stress experienced by the mother led to the inheritance of a similar stress-coping phenotype in the offspring (potentially promoting risk-taking behaviours), thus supporting the possibility of induced adaptive phenotypic plasticity (Zimmer et al. 2017). However, with few exceptions (Zimmer et al. 2017; Reshetnikov et al. 2019), studies in this context remain extremely limited and have mostly been performed in domestic species. Although domestic species offer substantial practical advantages (i.e. good background knowledge on husbandry and reproduction), they often show profound changes in their behaviour compared to wild populations (e.g. Chang et al. 2009), making interpretation of the ecological role of early-life programming difficult.

Here, we assessed neophobia and antipredator behaviours of juvenile house sparrows that were produced by females that were either exposed to corticosterone, or to vehicle only, as nestlings in free-living conditions and then kept in captivity to assess the long-lasting effects of the early-life hormonal manipulation. We previously showed that the elevation of circulating corticosterone in the study females had long-lasting physiological and behavioural effects with fitness consequences that were maintained through adulthood (Grace et al. 2017a, b, 2019, 2020; Dupont et al. 2019a, b). Thus, our study design allowed us to examine the trans-generational impact of early-life corticosterone exposure on relevant behavioural traits under laboratory conditions. We predicted that the offspring of females exposed to early-life corticosterone might display high-risk behaviours (Zimmer et al. 2017; Moran et al. 2020), thus displaying reduced levels of neophobia compared to control offspring.

Materials and methods

Study subjects and early-life corticosterone exposure

In a previous experiment, we exposed house sparrow nestlings to either a corticosterone, or a placebo treatment (Grace et al. 2017a). Briefly, dozens of nest boxes were monitored in our wild study population for reproduction initiation. For all broods, half of the brood was fed with mealworms injected with corticosterone in dimethyl sulfoxide (early-corticosterone birds) while the other half was

fed with mealworms with dimethyl sulfoxide, alone (control birds). Corticosterone treatment was associated with significant elevation of circulating corticosterone concentrations. Specifically, the corticosterone treatment induced an increase of corticosterone levels within 10 min of worm ingestion and corticosterone levels remained elevated for at least 40 min (within physiological ranges, controls: ~ 10 ng/mL, early-corticosterone birds: ~ 75 ng/mL, see Grace et al. 2017a for further details). Early-corticosterone and control nestlings were collected at fledging, transferred to captivity, and hand-reared (see Grace et al. 2017a for full details). Further measurements were done to test the effects of post-natal conditions (control vs. early-corticosterone birds) on metabolism (Dupont et al. 2019a, b) and the functioning of endocrine axes (Grace et al. 2020). At adulthood, all birds were kept in 5 outdoor aviaries with food (seeds ad libitum, vitamin, salt/mineral blocks, and millet on the stalk) and water ad libitum. Control and early-corticosterone adults were kept in separate aviaries until their first reproduction (cf. next paragraph). In addition, males and females were kept separated to avoid reproduction.

Reproduction of study females and offspring rearing conditions

In 2017, early-corticosterone and control females were allowed to breed in large outdoor aviaries with wild-caught male house sparrows that were captured from our wild study population. To avoid a potential effect of housing conditions on our variables of interest, a total of 21 females from the two treatments (controls: $n = 11$, early-corticosterone birds: $n = 10$) were randomly transferred into 7 aviaries, such that each aviary contained 3 females (either 2 controls and 1 early-corticosterone female or the opposite). All females were 2 years old and were breeding for the first time to exclude potential confounding effects associated with prior reproductive experiences (Pilakouta et al. 2016). Briefly, all pairs had access to a wooden nest-box, food (cereal seeds and fly larvae) and water ad libitum. After hatching, the chicks were fed by their parents in the nest box until fledging (~ 13–14 days old). All chicks were ringed before fledging for subsequent individual identification and were then left with their parents in the aviary until 30 days of age (i.e. full nutritional independence). With the exception of the early-life hormonal administration, the chicks and their mothers experienced very similar rearing and experimental conditions at the nest. However, unlike their mothers, the chicks were not separated from their parents and transferred to indoor cages at fledging. Instead, the chicks were allowed to stay with their parents until full independence (30 days old).

This was possible in this experiment [contrary to the first experiment that focused on free-living birds (Grace et al. 2017a, b)] because these captive fledglings could be easily captured after fledging. After 30 days, all offspring were separated from their parents and transferred to another outdoor aviary. All juveniles that survived until 50 days of age were kept in captivity to assess neophobia and antipredator behaviour ($N=68$: control female = 14; control male = 8; early-corticosterone female = 25; early-corticosterone male = 21). The sample size was not balanced between the control and early-corticosterone groups because of contrasted reproductive performance between these two groups. All parental males were released back in nature at the end of the breeding event.

Offspring neophobia

At 50 days old, juveniles were transferred at 13:30 h from their aviary to an indoor room (with natural light, and constant ambient temperature, 18 °C). They were weighed with an electronic balance (± 0.1 g) and were placed in individual cages with ad libitum water, but without food. After 4 h (i.e., at 17:30 h), birds were weighed a second time, the feeder was filled with familiar food and a novel object (a small green can) was put in front of the feeder. Sparrows were therefore food-deprived for 4 h to ensure they were motivated to feed, as in previous work (Bókony et al. 2012; Liebl and Martin 2012; Zimmer et al. 2013; Bertin et al. 2018). The experimenter left the room immediately after the introduction of the novel object and sparrow behaviours were recorded with a GoPro Hero Session 4 for 1 h. One person (SMD) analysed all videos to determine a posteriori (1) the time to reach the feeder after the introduction of the novel object (in s) and (2) the time to eat from the feeder (in s). At the end of the experiment, i.e. at 18:30 h, the wing length (measured with a ruler, ± 0.05 cm) and body mass of all birds were recorded before being released into their original aviary.

Offspring antipredator behaviour

At 18:30 h, we recorded the time to capture by hand for each bird in their individual cages to estimate antipredator escape behaviour in a direct “predator” encounter (i.e. “evasiveness”). This same experimental protocol was used to measure antipredator escape behaviour in all the sparrow mothers, previously (Grace et al. 2017a). Briefly, time began when the experimenter opened the cage and stopped when the bird was captured and under control of the experimenter. The same experimenter (SMD) captured all birds to avoid a potential bias in the results.

Statistical analysis

Statistical analyses were performed in R v3.6.2 (R Core Team 2019). We used General Linear Models (GLM) or, Generalised Linear Mixed Models (GLMM using R package: “lme”) with a Gaussian error distribution. In all models, fixed factors were maternal treatment (early-corticosterone or control), sex, and the interaction between these two factors to assess potential sex-specific effects. In all GLMM, we included the mother’s identity as a random factor. In the neophobia and evasiveness models, we additionally included the change in body mass between the start and end of the test, and its interaction with sex as covariates, to assess whether “hunger” during the test influenced behaviour. We also performed similar complementary models substituting this variable for the change in body mass between transfer to single cages and the start of the neophobia test (i.e. during the 4 h food withdrawal period). As evasiveness scores were not correlated between mothers and offspring in both treatment groups (Pearson’s correlation test: $p \geq 0.38$; maternal data previously published in Grace et al. 2017a); we did not include evasiveness scores of mothers in the analyses of offspring evasiveness presented here. We log-transformed neophobic behavioural variables to improve model fit, which was assessed via graphical diagnostics of the residuals (Zuur et al. 2009). We employed a stepwise deletion of non-significant interaction terms ($p > 0.05$).

Results

Effect of maternal early-life corticosterone exposure on offspring body mass and wing length

Prior to the 4 h food deprivation, we found no difference in body mass between birds produced by early-corticosterone mothers and those produced by control mothers (Table 1a). Regardless of maternal treatment, males were heavier than females (female: 21.35 ± 0.30 g, male: 23.06 ± 0.29 g, Table 1a). Similarly, offspring wing lengths were not influenced by maternal treatment (Table 1b) and males had longer wings than females (female: 6.86 ± 0.03 cm, male: 7.03 ± 0.04 cm; Table 1b) regardless of maternal treatment.

Effect of maternal early-life corticosterone exposure on offspring neophobia and anti-predator behaviour

Only two birds did not eat during testing ($N=68$). During neophobia testing, both offspring produced by

Table 1 Results of generalised linear mixed models (GLMM) with a Gaussian error distribution to assess whether (a) the body mass, or (b) the wing length (both measured when birds were transferred into single cages) was influenced by relevant study factors

(a) Body mass	Estimate	SE	<i>df</i>	<i>t</i>	<i>p</i>
Mother ID (<i>r</i>)	0.676				
Residual	2.431				
Intercept	20.923	0.506	15.986	41.371	<0.0001
Maternal treatment (early-CORT)	0.731	0.622	11.850	1.175	0.263045
Sex (male)	1.611	0.410	62.413	3.930	<0.0003
(b) Wing length	Estimate	SE	<i>df</i>	<i>t</i>	<i>p</i>
Mother ID (<i>r</i>)	0.005				
Residual	0.027				
Intercept	6.906	0.049	14.563	139.642	<0.0001
Maternal treatment (early-CORT)	-0.079	0.060	10.173	-1.319	0.216
Sex (male)	0.206	0.042	63.131	4.843	<0.0001

The non-significant ($p > 0.05$) two-way interaction term, treatment \times sex was removed from the final models and is thus not presented here; significant fixed factors are highlighted in bold; *r* indicates the random factor (intercept) and its estimated variance

early-corticosterone mothers and control mothers reached the feeder and ate from it at similar times (Fig. 1a, b; Table 2a, b), and these behaviours were not influenced by sex, or the sex \times treatment interaction (Table 2a, b). Birds that lost more mass during the 4 h fast prior to testing (Supplementary Table S1a, b) and those that gained more mass over the 1 h testing period were quicker to reach the feeder and eat from it (Fig. 2a, b; Table 2a, b), regardless of treatment.

Although evasiveness (i.e., time to capture by hand) was slightly higher for offspring produced by early-corticosterone females than control offspring (Fig. 2c), this difference did not reach statistical significance (Table 2c). Evasiveness did not differ by sex and there were no significant sex \times treatment interactions (Table 2c). Birds that gained more mass during the antecedent neophobia testing displayed reduced evasiveness (Fig. 2c), regardless of maternal treatment (Table 2c).

Discussion

Our results clearly indicate that maternal early-life exposure to elevated corticosterone had no significant impact on offspring neophobia and antipredator escape responses in this house sparrow population. This is despite early-life hormonal manipulation of mothers leading to substantial long-lasting, or delayed effects on the mothers' stress reactivity (Grace et al. 2020), metabolism (Dupont et al. 2019a), behaviour (Grace et al. 2017a), and survival (Grace

et al. 2017b). Therefore, our data provide no support for the hypothesis of trans-generational effects of early-life stress programming through the maternal route.

We predicted that the offspring of early-corticosterone females would display reduced neophobia because previous work has shown that early-life stressors can promote risk-taking and exploratory behaviours (Zimmer et al. 2013, 2017; Moran et al. 2020). However, while this effect has been reported by some studies (Spencer and Verhulst 2007; Vallée et al. 1997), others have found no effect (Zimmer et al. 2013; Noguera et al. 2015), the opposite effect (Kalinichev et al. 2002; Vallée et al. 1997), or the effect was sex-dependent (Spencer and Verhulst 2007). Therefore, the lack of maternal treatment effect observed in our study could reflect a lack of treatment effect on maternal neophobia, a hypothesis supported by unpublished data from the mothers in this study. In Japanese quail, early-life stress had no effect on neophobia, but a strong impact on adult exploratory behaviour (Zimmer et al. 2013). Thus, early-life corticosterone exposure might have altered other fear-related behaviours that were not tested in our study, such as risk-decision making within more challenging unfamiliar environments. We also found no significant effect of maternal post-natal stress on offspring antipredator escape behaviour (i.e. evasiveness). This result was surprising given that post-natal developmental corticosterone did influence antipredator responses in the maternal generation. Specifically, early-life corticosterone exposed birds displayed decreased evasive behaviour as adults, when in good body condition (Grace et al. 2017a). Such state-behaviour interactions with

Fig. 1 Neophobic behavioural traits including **a** time to reach the feeder, or **b** time to eat the seeds since the start of neophobia test, and **c** anti-predator escape behaviour (evasiveness) in age-matched juvenile house sparrows produced by mothers fed with corticosterone during early post-natal development (early-corticosterone mothers), or produced by control mothers. Data are shown as mean \pm SE

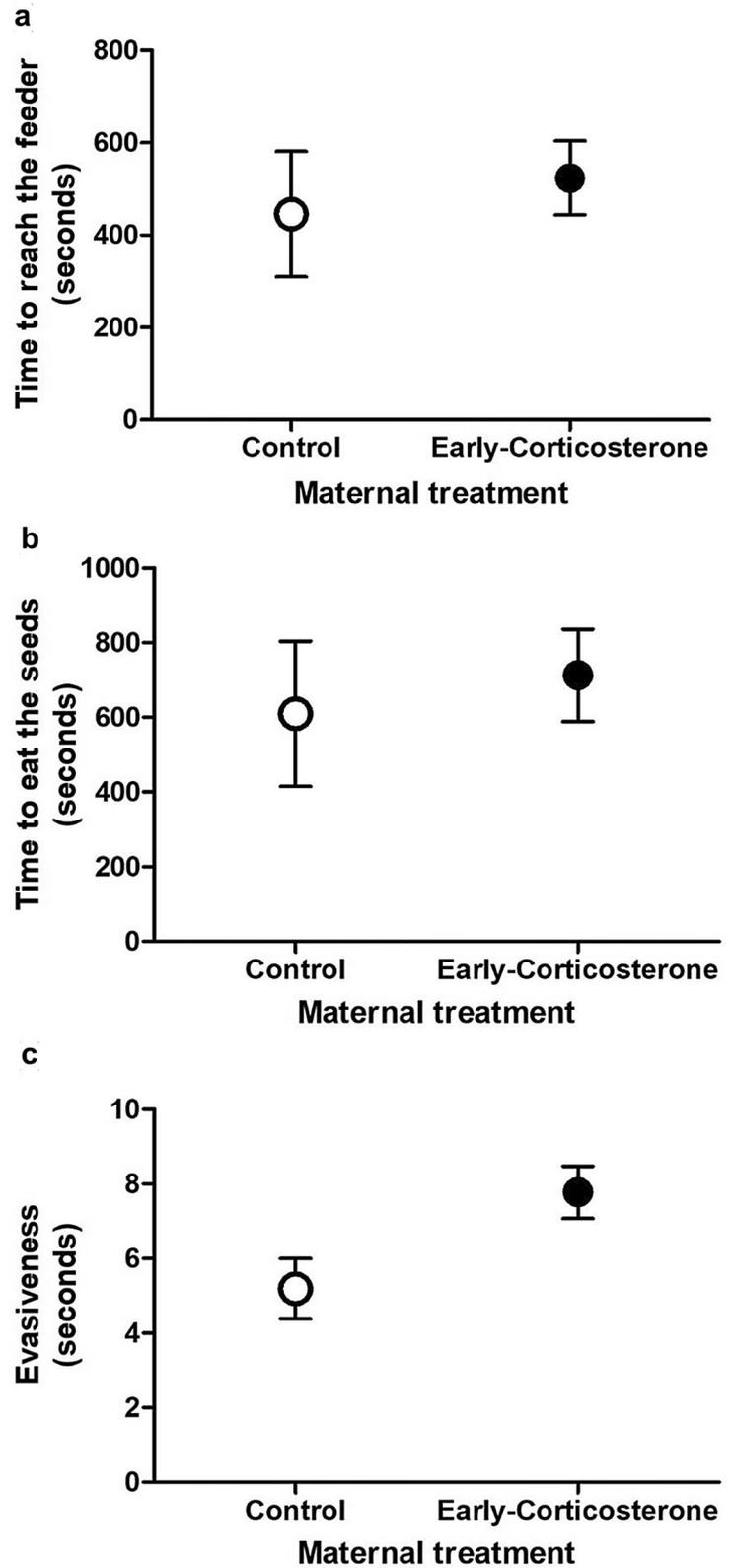


Table 2 Results of general linear models (GLM) and generalized linear mixed models (GLMM) to assess whether (a) the time to reach the feeder, (b) the time to eat the seeds, or (c) antipredator behaviour (i.e. evasiveness) was influenced by relevant study factors

(a) Time to reach the feeder	Estimate	SE	<i>t</i>	<i>p</i>	
Intercept	2.779	0.092	30.345	< 0.0001	
Maternal treatment (early-CORT)	0.136	0.083	1.638	0.106	
Mass change	- 0.431	0.062	- 6.931	< 0.0001	
Sex (male)	0.044	0.079	0.554	0.581	
(b) Time to eat seeds	Estimate	SE	<i>t</i>	<i>p</i>	
Intercept	2.924	0.098	29.795	< 0.0001	
Maternal treatment (early-CORT)	0.098	0.089	1.099	0.276	
Mass change	- 0.501	0.067	- 7.520	< 0.0001	
Sex (male)	0.116	0.085	1.367	0.176	
(c) Evasiveness	Estimate	SE	df	<i>t</i>	<i>p</i>
Mother ID (<i>r</i>)	1.730				
Residual	16.460				
Intercept	7.132	1.378	20.586	5.174	< 0.0001
Maternal treatment (early-CORT)	2.625	1.324	7.371	1.982	0.086
Mass change	- 2.441	0.876	60.730	- 2.787	0.007
Sex (male)	1.493	1.055	59.728	1.415	0.162

In all models, body mass change indicates the within-individual difference in body mass observed over neophobia testing (1 h for each bird). Non-significant two-way interaction terms between treatment and sex, and treatment and mass change ($p > 0.05$) were removed from the final models and are not presented, here; significant fixed factors are highlighted in bold. In (a) and (b) we performed GLM instead of GLMM as the variance associated with mother identity (random factor) was close to 0. For evasiveness (c) maternal identity was included as a random factor

treatment, however, emerged only when the birds were tested as adults and not as juveniles (Grace et al. 2017a). In this study we only measured evasiveness once, when the birds were 50-day-old juveniles, thus we cannot exclude the possibility that delayed effects could have been detected at later life stages. In addition, this difference between mothers and offspring might also be explained by contrasted post-natal conditions, and notably by the animal-human relationship. Indeed, mothers were handled more extensively as nestlings, transferred to captivity at fledging (~ 12–14 days old), and hand-fed until independence while the next generation was allowed to fledge naturally in their aviary and was only captured at fledging and at independence (~ 30 days old).

Growing experimental evidence points to the importance of age at breeding for the transmission of potential trans-generational effects by parents (Marasco et al. 2019; reviewed in Monaghan et al. 2020). Our study was conducted in captivity, which allowed us to minimise variation in maternal age, although we did not control for paternal age or for variation in prior reproductive effort or stress level exposure. Thus, factors associated with paternal age might have mitigated or masked potential trans-generational effects of maternal early-life stress. This could happen through paternal compensatory effects, which might occur under conditions when maternal factors enable this

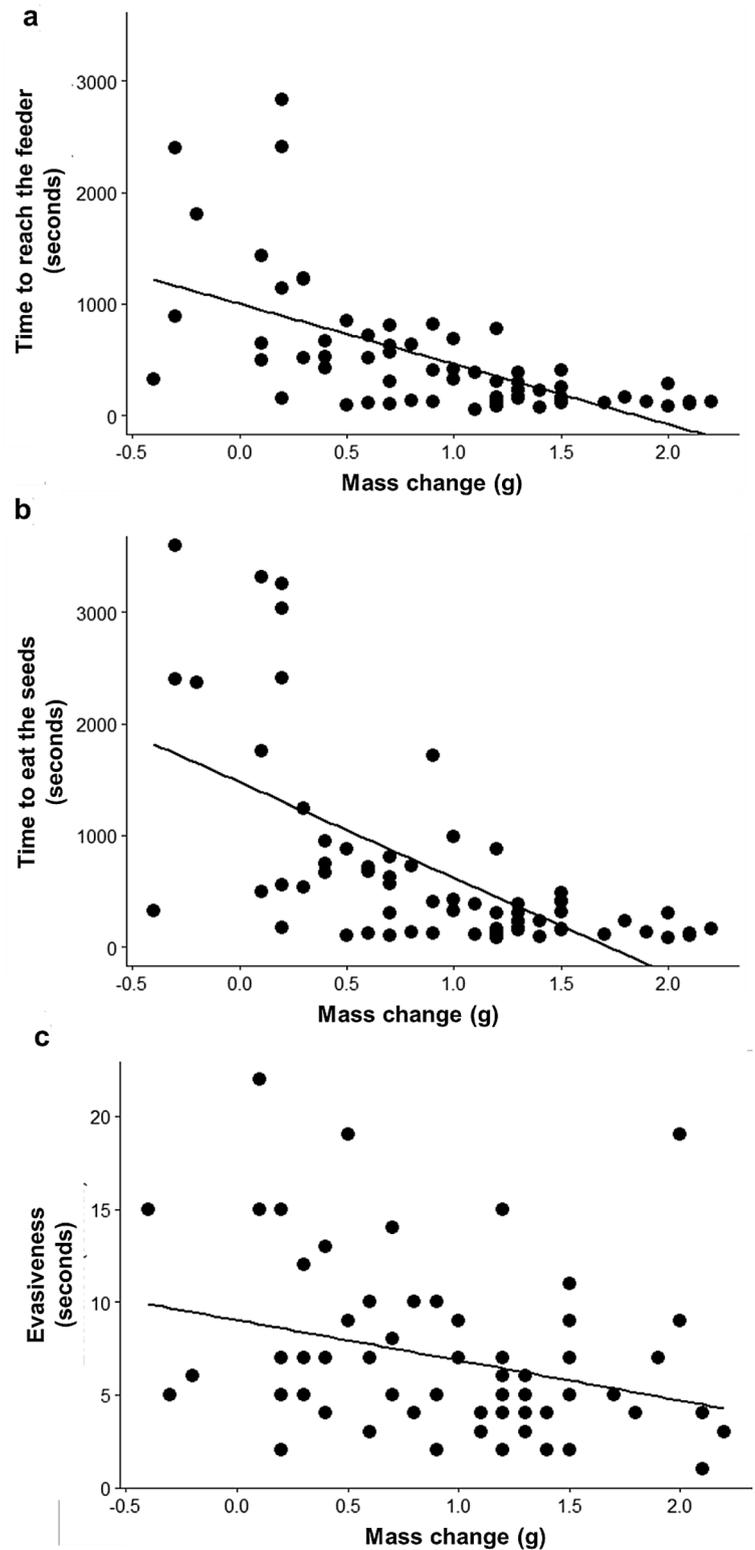
transmission to happen (Curley et al. 2011). Similarly, neophobia may be driven by paternal factors (e.g. paternal behaviour), and not (or only to a small extent) by maternal factors. In our study, we focused on maternal contribution to the next generation and wild-caught males as breeding partners because of a limited number of available captive males. Additional studies are needed to tease out both maternal and paternal effects in order to assess the relative contribution of these two routes in the transmission of early-life programming effects.

All birds were food-deprived for 4 h before behavioural testing in order to standardise hunger levels. Interestingly, however, we found consistent relationships between body mass changes and all the behavioural variables measured. These results clearly highlight that the nutritional state and motivation to eat can substantially influence individuals' risk-taking strategies. Thus we strongly recommend to rigorously consider these factors in the experimental planning of future studies.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10164-021-00712-3>.

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Fig. 2 Correlation plots of the change in body mass during neophobia testing (mass change) and the measured behavioural traits including **a** time to reach the feeder, **b** time to eat the seeds, and **c** evasiveness



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Author contributions JKG, SMD and FA contributed to the study conception and design as well as data collection. The analysis was performed by VM. The first draft of the manuscript was written by VM and SMD and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Declarations

Conflict of interest The authors have no conflicts of interest to declare.

Ethics approval Permissions to capture, sample and hold house sparrows in captivity were issued by the French government (DREAL, Poitou-Charentes, permit delivered to F Angelier) and by the Muséum National d'Histoires Naturelles. All experimental procedures were approved by the French government (R45GRETAFI-10) and Centre National de la Recherche Scientifique, and conform to guidelines set forth by the French Ministry of Higher Education and Research.

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