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Physiology

Within-individual plasticity explains age-related decrease in stress response in a short-lived bird

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A crucial problem for every organism is how to allocate energy between competing life-history components. The optimal allocation decision is often state-dependent and mediated by hormones. Here, we investigated how age, a major state variable affects individuals' hormonal response to a standardized stressor: a trait that may reflect allocation between self-maintenance and reproduction. We caught free-living house sparrows and measured their hormonal (corticosterone) response to capture stress in consecutive years. Using a long-term ringing dataset, we determined the age of the birds, and we partitioned the variation into within- and among-individual age components to investigate the effects of plasticity versus selection or gene flow, respectively, on the stress response. We found large among-individual variation in the birds' hormone profiles, but overall, birds responded less strongly to capture stress as they grew older. These results suggest that stress responsiveness is a plastic trait that may vary within individuals in an adaptive manner, and natural selection may act on the reaction norms producing optimal phenotypic response in the actual environment and life-history stage.

1. Introduction

Age is a major state variable that influences life-history decisions. In iteroparous animals, the trade-off between reproduction and survival results in a decreasing residual reproductive value with age; therefore, an optimal resource allocation strategy should favour an increment in current reproductive investment as individuals become older. Glucocorticoid hormones, which are released in elevated amounts in response to environmental challenges (commonly referred to as 'stressors'), suppress reproduction and enhance survival [1]. Life-history theory, therefore, predicts that when the value of the current reproduction is high relative to the value of future reproduction and survival, as expected in older adults, the stress response should be attenuated to ensure that reproduction is not inhibited [1].

Several studies have tested this prediction and found reduced corticosterone response in older individuals [2,3]. For example, in some long-lived birds, it has been shown that older individuals captured in a single reproductive season responded less strongly to a standardized stressor than younger individuals [4,5]. However, all these studies have used a cross-sectional approach, by measuring the hormonal stress response of individuals of different age in a population. This approach does not allow disentangling the effects of individual plasticity from selection and/or gene flow, because the results may indicate either that

Table 1. *A priori* candidate models of individual differences in corticosterone levels. K , number of parameters in the model; DIC, deviance information criterion; Δ DIC, difference between DIC value of a given model and the model with the lowest DIC. The random structure denotes the formula used in the MCMCglmm analyses, while the description gives a verbal explanation of the models. Models differ only in their random-effects structure.

model	K	DIC	Δ DIC	random structure	description
model 1	9	2226	109	$\sim \text{ring}$	random intercept only: individuals differ in average hormone levels
model 2	10	2194	76	$\sim \text{us(trait) : ring}^a$	random intercept and random slope: individuals differ in stress response
model 3	12	2117	0	$\sim \text{us(trait} \times \text{within-individual_age) : ring}$	random intercept and random slope: individuals respond differently to change in their age

^a'trait' is a reserved name in MCMCglmm nomenclature that refers to the stress level here. 'ring' is the individual ID.

individuals dampened their stress responses with age, or that individuals with higher stress response had higher mortality and did not reach an advanced age. Furthermore, even if individuals show a consistently dampened stress response with increasing age, large among-individual variation may mask such an effect in a cross-sectional analysis.

Here, we investigated for the first time the age-related differences in the stress response in a short-lived passerine species, the house sparrow (*Passer domesticus*), using a longitudinal dataset, where several individuals were sampled in consecutive years. We used within-group centring in linear mixed models to separate the effects of individual plasticity and selection and/or gene flow and quantify their contribution to variation in corticosterone levels.

2. Material and methods

This study was carried out between May 2005 and June 2007 at the Centre d'Études Biologiques de Chizé, France (46.14706 N, 0.425646 W). This population is subject to long-term monitoring, whereby almost all chicks and a large proportion of adults were ringed each year from 1998 onwards. Breeding sparrows were captured in their nest-boxes, when their nestlings were 7–12 days old. Immediately after capture, a small blood sample (50–100 μ l) was collected from the brachial vein and a subsequent sample was collected 30 min later. Corticosterone concentrations were measured as detailed in [6].

We analysed 181 stress responses from 143 individuals. From 33 individuals, we collected corticosterone data from multiple years. Age of the birds ranged 1–8 years. To separate within- and among-individual effects of age, we used within-individual centring [7], i.e. we broke down the effect of age into two components: within-individual variation, calculated as the mean-centred values of age within each individual, and among-individual variation, represented by the mean age of each individual in the dataset. Initial and stress-induced corticosterone were analysed in Bayesian linear mixed models using the 'MCMCglmm' package in R [8,9]. We used initial and stress-induced corticosterone levels as dependent variables in the same model, with stress level as a fixed factor. This model allows the analysis of reaction norms [10], whereas the interaction between stress level and within- or among-individual age effects can be interpreted as the age-dependent differences in stress response, i.e. the degree to which the difference between initial and stress-induced corticosterone varies with age within and among individuals.

We built three candidate models that differed in their random-effects structure (table 1). The simplest model assumed only a random intercept, which was necessary to control for

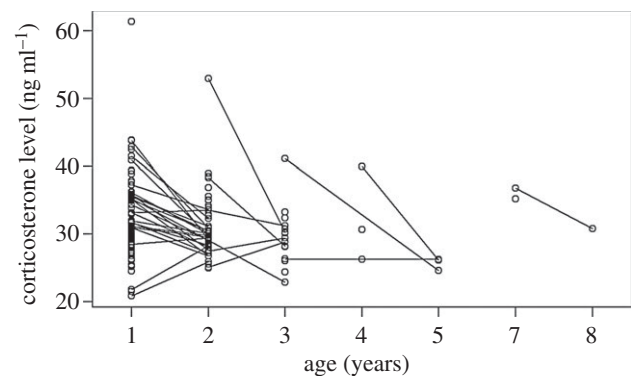


Figure 1. Individual differences in predicted values of stress-induced corticosterone levels in house sparrows as a function of their age at sampling. Lines connect the same individuals.

the repeated nature of the data. The second model assumed a random intercept and slope. The last model assumed that individuals differ in their age-dependent change in stress response. All models were fitted with the same fixed-effects structure: the models contained both age components (within- and among-individual variation), and their interaction with the stress level (initial versus stress-induced). Controlling for variation in breeding date, or restricting the analyses to only the first 2 years for those birds that were sampled in 3 years, or to birds that were first ringed as adults, did not alter our conclusions (see the electronic supplementary material).

We used inverse Wishart priors (a weakly informative prior, which allows for minimal influence on the posterior distributions) and a residual variance structure separately for initial and stress-induced corticosterone. We compared candidate models using the deviance information criterion (DIC) [8]. We report the parameter estimates (posterior means) and corresponding 95% credibility interval (CI) values. We provide raw repeatabilities (R_M following [11]).

3. Results

The model including a random intercept, a random slope, and random slope \times within-individual age effect interaction received the most support out of the candidate models (table 1). This means that (i) the initial corticosterone levels, (ii) the corticosterone stress response and (iii) the change of this stress response with increasing age differ significantly among individuals (figure 1). The fixed-effects part of the model showed that at the population level, initial corticosterone

Table 2. Parameter estimates (posterior means and 95% CI) of the best supported model (table 1). Italicized font indicates CI not overlapping with zero.

	posterior mean	lower 95% CI	upper 95% CI
<i>initial corticosterone (intercept)</i>	5.58	4.75	6.45
<i>stress level (stress-induced)</i>	25.91	23.16	28.51
within-individual age	0.15	−1.54	1.82
among-individual age	−0.14	−0.55	0.28
<i>stress level × within-individual age</i>	−4.54	−8.22	−0.73
stress	0.39	−1.02	1.67
level × among-individual age			

levels did not vary with age either among or within individuals, whereas the stress response decreased with among-individual ageing but individuals with different ages did not differ in their stress response (table 2 and figure 2). Overall, neither initial nor stress-induced corticosterone levels were repeatable (initial: $R = 0.005$ [0; 0.092], stress-induced: $R = 0.001$ [0; 0.096]).

4. Discussion

This study provided three key results. First, we found that the age of the individuals affected their stress response: as individuals became older, they responded less strongly to a standardized stressor. Second, this decrease in the stress response was only due to within-individual age effects, and despite a large range in ages for a short-lived bird, we could not detect any among-individual age effect that would be a characteristic of ongoing natural selection on the stress response. Finally, we found significant among-individual variation in the age-dependent change in stress response.

The finding that the stress response of house sparrows decreases with age is in accordance with previous studies that found reduced maximum glucocorticoid response to stress in older individuals in a wide variety of taxa [2,3]. However, a general negative correlation between age and stress response may arise from two very distinct processes: within-individual changes (e.g. habituation or plasticity) and among-individual variation (due to natural selection and/or gene flow). We found that only the within-individual component of age explained significant variation of the stress response. Why would individuals respond less strongly to the same stressor as they grow older? We propose three alternative hypotheses. First, it is possible that birds habituate to the capture procedure. A previous study on Eastern bluebirds (*Sialia sialis*) found that a single previous exposure to capture-handling stress had a negative effect on the subsequent capture-handling stress response [12]. Following this rationale, if our results were the consequences of habituation, we would expect that naive birds that were captured for the first time would have higher stress-induced

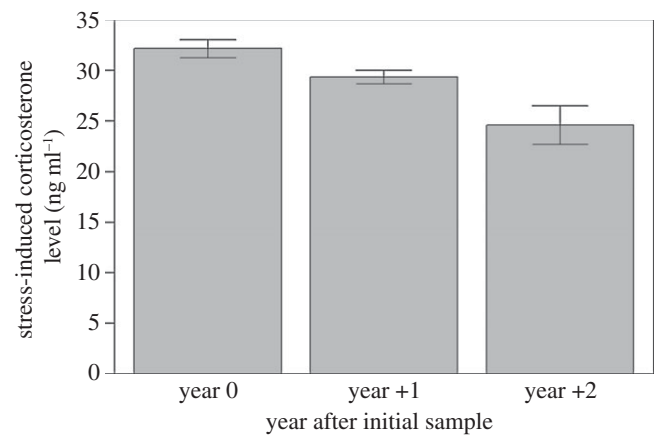


Figure 2. Means \pm 95% CI of predicted stress-induced corticosterone levels in house sparrows. The stress response becomes weaker as individuals grow older (table 2). Year 0 is the first sample of 146 individuals. In years +1 and +2, 32 and 3 individuals were sampled again 1 and/or 2 years after the initial capture, respectively. The results remained qualitatively the same without considering the year +2 samples (electronic supplementary material, table S3).

corticosterone levels than those that were of the same age but had been exposed to capture and handling before, but we found no such effect ($t_{99} = 0.02$, $p = 0.981$).

The second possibility is that the capacity to mount a robust stress response decreases with age. Such a decline in stress responsiveness has been observed in laboratory animals and in one long-lived bird species, although data on other species do not support this idea [2]. If senescence causes a decline in the capacity of mounting a stress response, we would detect this effect in the among-individual comparisons (except if senescence occurs at different ages in different individuals), but older individuals had similar corticosterone levels to their younger counterparts (figure 1).

Finally, the within-individual decline with age is most likely a consequence of phenotypic plasticity, whereby individuals adjust their stress response to their actual life-history and environmental conditions. This individual plasticity resulted in an overall lack of repeatability of hormone levels, corroborating other studies that found limited or context-specific repeatability [13–16]. If individuals are highly plastic in their hormonal response to environmental stimuli [10], then natural selection is expected to act on the hormonal strategies (i.e. physiological reaction norms) rather than the hormone levels. In this case, evolution would select for phenotypically plastic hormonal strategies that can produce the optimal phenotypic response under a wide range of environments. It remains to be tested to what extent the different individual responses to ageing represent alternative optimal strategies.

Ethics. Ethical approval was granted by the Deux-Sèvres Veterinary Service (no. 79–2).

Data accessibility. Data are available from the Dryad repository: <http://dx.doi.org/10.5061/dryad.rg0s0>.

Authors' contributions. Á.Z.L., V.B., M.G., F.A. and O.C. collected field data, Á.Z.L. designed the study, analysed the data and drafted the manuscript. Á.Z.L. and M.G. participated in hormone assays. O.C. coordinated the study. All authors contributed to writing and gave final approval for publication.

Competing interests. We declare we have no competing interests.

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