



The behavioural and physiological stress responses are linked to plumage coloration in the rock pigeon (*Columbia livia*)



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ARTICLE INFO

Keywords:

Polymorphism
Predation risk
Corticosterone
Breath rate
Tonic immobility

ABSTRACT

In wild vertebrates, conspicuousness often signals a high phenotypic quality and is therefore associated with fitness benefits (“the handicap principle hypothesis”). However, conspicuous individuals usually face a higher risk of predation because they are easier to detect. Therefore, conspicuous individuals are expected to modify their behavioural and their physiological stress responses to limit the negative effect of their conspicuousness on survival. We examined the link between plumage coloration and the stress response in a bird species (the rock pigeon, *Columbia livia*) by comparing two groups of pigeons with different plumage characteristics: ‘blue-bar’ birds (lighter birds) and ‘checker’ birds (darker birds). Specifically, we measured several behavioural and physiological components of the stress response (breath rate, corticosterone, and tonic immobility). Although breath rate did not differ between ‘checker’ and ‘blue bar’ birds, the corticosterone stress response of ‘blue-bar’ birds was greater relative to that of ‘checker’ birds. Moreover, ‘checker’ birds were more likely to initiate tonic immobility relative to ‘blue bar’ birds. Therefore, this study suggests that the behavioural and physiological stress responses of wild birds may differ according to their plumage coloration. To conclude, our results suggest that plumage colorations may be functionally linked to specific behavioural and physiological sensitivities to stressors.

1. Introduction

In wild vertebrates, predation risk is a strong selective pressure that drives the physiological, behavioural and morphological adaptations of species [43]. In a context of high predation risk, conspicuous and colourful phenotypes should theoretically be selected against because of an increased risk of being detected or caught by a predator [21,26,54,76]. However, conspicuousness can also insure a higher fitness by signaling a high phenotypic quality to congeners and predators (“the handicap principle hypothesis”, [89,30]. In addition, conspicuous ornaments or coloration may even provide direct fitness advantages under specific environmental conditions by allowing individuals to better cope with some environmental challenges [13,44]. This complex and context-dependent balance between the fitness costs and benefits of specific colors has indeed been proposed to explain the occurrence of color polymorphism in wild populations [27,37].

Despite potential fitness benefits, conspicuous individuals need to cope with a higher risk of predation and, as a consequence, colourful species and individuals are expected to modify their behaviour to limit the negative effect of their conspicuousness on survival [65,70,75]. Therefore, conspicuous individuals should theoretically take less risk

than more cryptic individuals and/or they should have better physical/cognitive abilities to cope with predation risk. They should adopt specific behaviours to limit detection by predators [43]: they should also be more vigilant [43], and they should display earlier escape behaviour when a potential predator is detected [38,49,50]. In addition to these multiple behavioural changes that help individuals to avoid predation, the stress response of conspicuous individuals is also expected to differ from that of more cryptic individuals.

This ‘stress response’ involves the behavioural and physiological changes that occur in response to an acute stressor, such as a predator attack. They are mediated by hormonal and neural activations [86] and are thought to promote immediate survival when a stressor actually occurs. Importantly, the ability of individuals to mount such a stress response is known to be repeatable and heritable [3,15,22,35,74] and it is often associated with specific individual behavioural and physiological phenotypes [16,20]. Although these specific phenotypes may be advantageous in case of predator attacks, they may also incur fitness costs under other circumstances (reviewed in [42]). For example, a strong physiological stress response has been associated with reproductive failure [67]. Similarly, the activation of some behavioural stress responses is also associated with personality traits that reduce

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mating success in some species [73]. Because of this trade-off, life-history theory predicts that a high sensibility to stressor should be favoured only when its benefits outweigh its costs (e.g. when individuals may suffer from a high predation risk; [43,60]). Therefore, the stress response should theoretically be more important in conspicuous individuals relative to cryptic individuals because of a higher predation risk [6].

The stress response is associated with multiple behavioural and physiological components that can be measured in wild animals ([40,62,86,91]). First, the stress response is usually associated with ventilatory patterns that help modulating cardiovascular activity to cope with the acute stressor [28]. Therefore, breath rate has been suggested as a relevant proxy to measure the stress response of humans [28] and more recently wild vertebrates [10]. Usually, breath rate immediately increases in response to an acute stressor in humans and wild vertebrates [28,10] before to slightly decrease as the stressor is maintained [10]. Interestingly, breath rate has been related to personality and habitat in wild great tits [10,79], suggesting that this is a reliable proxy of the physiological and behavioural responses of individuals to acute stressors. Second, the occurrence of acute stressors is known to activate the Hypothalamus-Pituitary-Adrenal (HPA) axis and to result in increased circulating corticosterone levels [41,67,91]. Such an increase in corticosterone levels mediates several physiological and behavioural changes [41,67] that aim to restore homeostasis [46,62] and to promote immediate survival [6,91]. Finally, tonic immobility is known as a classic behavioural response to predation. In response to predation risk or physical restraint, individuals feign death to be able to escape when the predator relaxes its focus [23]. This behaviour is an adaptive strategy to cope with a high predation risk [20,78].

Importantly, a large inter-individual variation in these stress responses has previously been reported and this variability has been linked to environmental variables and selection processes in vertebrates (e.g. [35]). Although all these behavioural and physiological components of the stress response aim to help the organism survive a stressor, their activation is also certainly associated with costs. Therefore, these stress responses should be down-regulated when their fitness costs outweigh their fitness benefits [6,74]. Specific color increases predation risk because individuals are easier to detect and to catch, and therefore, it is predicted that the stress response of conspicuous individuals should be increased relative to more cryptic individuals to help them survive such stressors. Accordingly, recent behavioural studies have shown that color polymorphism, and more specifically head color, can be reliable signals of personality traits in Gouldian finches, *Erythrura gouldiae* [47,85]. However and surprisingly, the influence of color polymorphism on the behavioural and physiological proxies of the stress response has rarely been examined in wild birds, especially in adults

[1,17,36,64,83,85].

In this study, we examined the link between plumage coloration and the stress response by investigating simultaneously behavioural and physiological components of the stress response in a bird species, the rock pigeon (*Columbia livia*). Rock pigeons are relevant to study this question because they show a high degree of color polymorphism: Among eumelanic pigeons, some birds have a wild-like morph and are lighter ('blue-bar' birds) whereas others are overall darker and display a large amounts of black spots on their plumage ('checker' birds). Furthermore, the fitness benefits and costs of plumage color have been extensively studied in that species (e.g. [13,54]). Importantly, predation risk is related to plumage color in feral rock pigeons with lighter birds being more likely to be predated than darker individuals [58,66]. Finally, their physiological and behavioural stress responses can easily be measured [5,17]. Although hormonal and behavioural stress responses are supposed to help individuals coping with predatory events, they are also known to be associated with costs. Accordingly, rock pigeons should adjust their stress response to their risk of being predated, and thus, to their plumage color. Because lighter pigeons are more likely to be predated [58,66], we predicted that (1) breathing rate of lighter 'blue-bar' pigeons should be higher than that of darker 'checker' birds; (2) corticosterone levels of 'blue-bar' pigeons should increase to a greater extent than those of 'checker' birds in response to capture and handling; (3) 'blue-bar' birds should be more likely to initiate tonic immobility relative to 'checker' birds.

2. Materials and methods

2.1. Capture and plumage polymorphism

Within a week (June 1–June 7, 2014), thirty two pigeons were captured in a moderately urbanized area (43°34' N, 7°02' E) using Potter traps. At capture, their plumage characteristics were assessed according to previous studies [13,32,92]. First, birds were classified as eumelanic (n = 28), pheomelanic (n = 2) or white (n = 2) birds. In this population, most of pigeons are eumelanic (~92%) while pheomelanic (~4%) and white pigeons (~4%) are much less frequent. Such proportions are comparable with other populations (see [51] for other European populations). Therefore, we decided to focus only on eumelanic birds in this study (n = 28) and we did not measure the behavioural stress response of pheomelanic and white pigeons when captured. Among eumelanic pigeons, two categories of pigeons were caught in our study: Blue bar pigeons have a grey mantle with two black wing bars (n = 9, Fig. 1) and checker pigeons have a checked mantle with a significant number of black spots (n = 19; Fig. 1). We did not quantify the eumelanin level (see [13]) and we instead relied on a



Fig. 1. Pictures of a 'blue-bar' (A) and a 'checker' rock pigeon (B). Although we did not quantify the degree of eumelanin in our study, 'checker' pigeons are always much darker than 'blue-bar' pigeons.

binary classification of individuals as checker or blue-bar pigeons ([17,32,92]). This did not allow us to quantify precisely the degree of eumelanin among the checker birds but checker pigeons are always much darker than blue-bar pigeons and these two types of pigeons are clearly different and can be easily identified from a long distance (Fig. 1, see [17]). Permission to capture wild pigeons and experimental approval were granted by the French government (R45GRETA1-10).

2.2. The corticosterone stress response and molecular sexing

To measure their corticosterone response to stress, all pigeons were immediately bled after capture according to a standardized stress protocol ([87], see [5]): an initial blood sample (0.3 ml) was collected within 3 min of capture, birds were restrained in a cloth bag to mimic an acute stressor, and a second sample was taken 60 min after the first (0.3 ml). Blood samples were immediately stored at +4 °C and were centrifuged within an hour. Plasma and red cells were separated and were kept at –20 °C until laboratory analyses. Plasma corticosterone levels were determined by radioimmunoassay. Briefly, plasma corticosterone was measured in samples after ethyl ether extraction by radioimmunoassay. Duplicate aliquots of the extracts were incubated overnight at 4 °C with ³H-corticosterone and antiserum. The bound and free corticosterone fractions were separated by adding dextran-coated charcoal. After centrifugation, the bound fraction was counted in a liquid scintillation counter. All samples were run in one assay (intra-assay variation: 8.31%). The sex was determined by polymerase chain reaction (PCR) amplification of part of two highly conserved genes (CHD) genes present on the sex chromosomes at the CEBC [24].

2.3. Breath rate and tonic immobility

Immediately after the first blood sample and within 5 min of capture, the breath rate of individuals was measured [82]. Specifically, the pigeon was held in one hand and the number of breast movement was counted during 30 s (hereafter called baseline breath rate). The same procedure was repeated after the second blood sample (i.e. after 60 min of restraint, stress-induced breath rate) to monitor how an acute stressor affects breath rate [10]. In addition, a tonic immobility test was conducted immediately after the second breath rate measurement (see [20]). Briefly, the pigeon was placed on its back and was fully covered by the hand of the experimenter, who exerted light pressure on the breast of the pigeon. After 15 s, the experimenter slowly removed his hand. The pigeon was considered to be in tonic immobility if it stayed on its back for > 5 s. If the pigeon did not enter in a state of tonic immobility, the procedure was repeated up to 5 times. Pigeons were classified as initiating tonic immobility or not initiating tonic immobility in response to these tests (binary variable). In addition, we also recorded the number of trials that were necessary to initiate tonic immobility (from 1 to 5). All these measurements (breath rate and tonic immobility) were conducted by the same person (FA).

2.4. Morphometric measures and body condition

After all the behavioural and physiological measurements, all birds were weighed with a scale (± 1 g) and their wing length was measured with a ruler (± 0.5 mm). Body condition was then estimated by calculating the scaled mass index (SMI) using wing length as the body size variable, as previously detailed [55]. All birds were then released and were seen during the following days at the study site.

2.5. Statistical analyses

All analyses were performed with SAS statistical software (SAS Institute, v. 9.3.). We used General Linear Mixed Models (GLMM, proc Mixed, SAS) to determine whether (1) the standardized stress protocol had an impact on breath rate and corticosterone levels; (2) breath rate

and corticosterone levels differed between ‘checker’ and ‘blue-bar’ birds (dependent variables: corticosterone or breath rate; independent factors: sample time (baseline vs. stress-induced), sex (male vs. female), plumage (blue-bar vs. checker) and all interactions; random factor: bird identity). We then used General Linear Models (GLM, proc Glim, SAS) to test whether body condition differed between ‘checker’ and ‘blue-bar’ birds (dependent variables: body condition; independent factors: sex (male vs. female), plumage (blue-bar vs. checker) and their interaction). We then used post-hoc tests that were corrected for multiple comparisons (Tukey adjustments). For all these analyses, normality and homoscedasticity assumptions were checked by visual inspections of the residuals and by using QQ plots. Normality assumptions were not violated. Homoscedasticity assumptions were not violated except for baseline and stress-induced corticosterone levels, which had visibly unequal variances. Regarding corticosterone analyses, we therefore used the Satterthwaite method, which adjusts the degree of freedom for these unequal variances [68]. Because tonic immobility was a binary variable, we then used Generalized Linear models to test whether ‘blue-bar’ and ‘checker’ birds differed in their probability to initiate tonic immobility (Proc Genmod, distribution: binomial, link function: logit). In addition, we also analysed whether blue-bar birds initiated tonic immobility earlier relative to checker birds. Because we had right-censored data (some birds did not initiate tonic immobility after 5 trials), we used a Bayesian approach to deal with these censored data (proc Lifereg, SAS, dependent variable: number of trials before a bird initiate tonic immobility; independent factors: sex, plumage and their interaction). Finally, we examined whether all our variables of interest were related by running Spearman correlations (baseline breath rate, stress-induced breath rate, baseline corticosterone levels, stress-induced corticosterone levels, the probability to initiate tonic immobility, body condition). We corrected these analyses to take into account multiple tests (Bonferroni corrections for multiple tests).

3. Results

3.1. Breath rate

Breath rate significantly decreased in response to the stress protocol (GLMM, $F_{1,27} = 6.07$, $p = 0.021$; Fig. 2) but this decrease was not affected by sex, plumage color, and their interaction (repeated-measures ANOVA, all p -value > 0.300). Overall, there was no effect of sex, plumage color, and their interaction on baseline or stress-induced breath rate (post-hoc Tukey tests, all p -value > 0.300; Table 1, Fig. 2).

3.2. Corticosterone

Corticosterone levels significantly increased in response to the stress protocol (GLMM, $F_{1,30.6} = 64.42$, $p < 0.001$; Fig. 3) and this increase significantly differed between ‘checker’ and ‘blue bar’ birds (GLMM, $F_{1,30.6} = 4.45$, $p = 0.043$; Fig. 3). However, this corticosterone stress response was not affected by sex or any other interaction (GLMM, all p -value > 0.600). Overall, blue-bar birds had higher corticosterone levels than checker birds (GLMM, $F_{1,30.6} = 12.77$, $p = 0.001$; Fig. 3). Specifically, baseline corticosterone levels of blue bar birds were slightly higher than those of checker birds (post-hoc test, $p = 0.016$; Table 1, Fig. 3). Stress-induced corticosterone levels of blue bar birds were significantly higher than those of checker birds (post-hoc test, $p = 0.006$; Table 1, Fig. 3).

3.3. Tonic immobility

The probability to initiate tonic immobility differed between blue-bar birds and checker ones ($F_{1,26} = 4.26$, $p = 0.049$; Fig. 4). However, this probability to initiate tonic immobility was not affected by ‘sex’ and the ‘sex \times plumage color’ interaction (all p -values > 0.100). Specifically, blue bar were less likely to initiate tonic immobility than checker

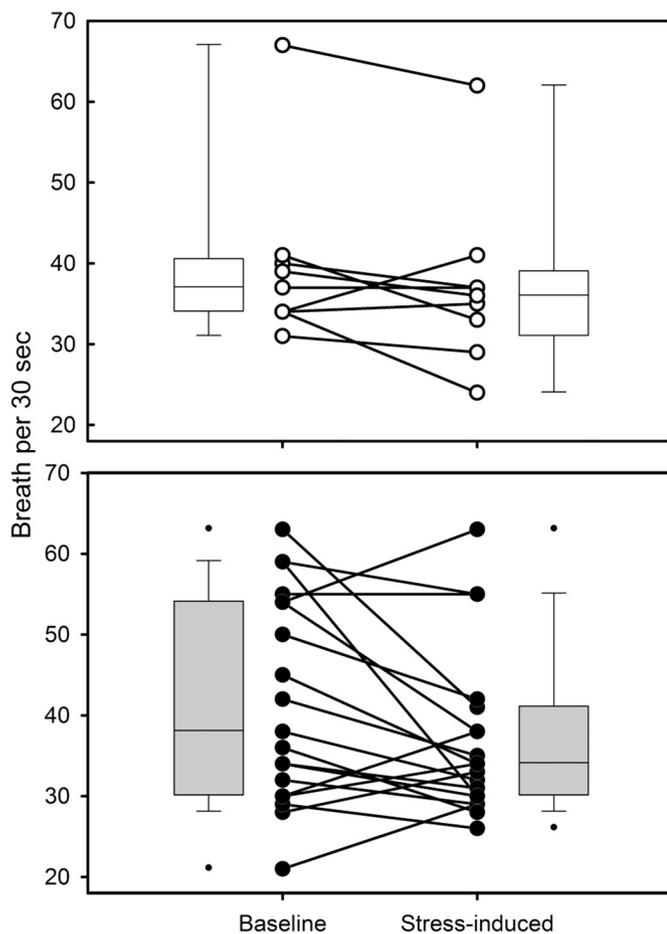


Fig. 2. Difference in breath rate between ‘blue-bar’ (A) and ‘checker’ (B) pigeons. On each graph, individual change in breath rate during the stress protocol is shown. Moreover, box-and-whisker plots represent baseline and stress-induced data: the top and bottom of the boxes represent the top and bottom quartiles, respectively; the line across the box represents the mean. The ends of the whiskers represent the fifth and ninety-fifth percentiles, and the circles represent outliers. Baseline measurements were made immediately after capture (within 5 min). Stress-induced measurements were made after a 60-min restraint protocol.

birds (Table 1, Fig. 3A).

Similarly, checker birds initiated tonic immobility earlier than blue-bar birds (Bayesian statistics, $\chi^2 = 3.92$, $p = 0.047$; Fig. 3B) but there was no influence of sex or any interaction on this variable (all p -values > 0.100).

3.4. Body condition and correlations between variables

Body condition was not affected by sex, ‘plumage color, and their interaction (GLM, all p -values > 0.200). Overall, there was therefore no difference in body condition between ‘blue-bar’ and ‘checker’ birds

Table 1

Difference in breath rates, corticosterone levels, probability to initiate tonic immobility, and body condition between blue-bar and checker pigeons.

	Blue-bar		Checker	
	Mean \pm SE	95% CI (low/high)	Mean \pm SE	95% CI (low/high)
Baseline breath rate	39.667 \pm 3.590	31.388/47.946	41.737 \pm 2.923	35.596/45.878
Stress-induced breath rate	37.111 \pm 3.525	28.981/45.241	37.000 \pm 2.353	32.056/41.944
Baseline corticosterone level	4.150 \pm 0.720	2.490/5.810	2.148 \pm 0.415	1.273/3.019
Stress-induced corticosterone level	18.010 \pm 2.486	12.276/23.744	10.238 \pm 1.375	7.350/13.127
Probability to initiate TI	0.444 \pm 0.176	0.039/0.850	0.842 \pm 0.086	0.661/1.023
Body condition	284.463 \pm 7.924	266.190/302.737	278.071 \pm 6.071	265.315/290.826

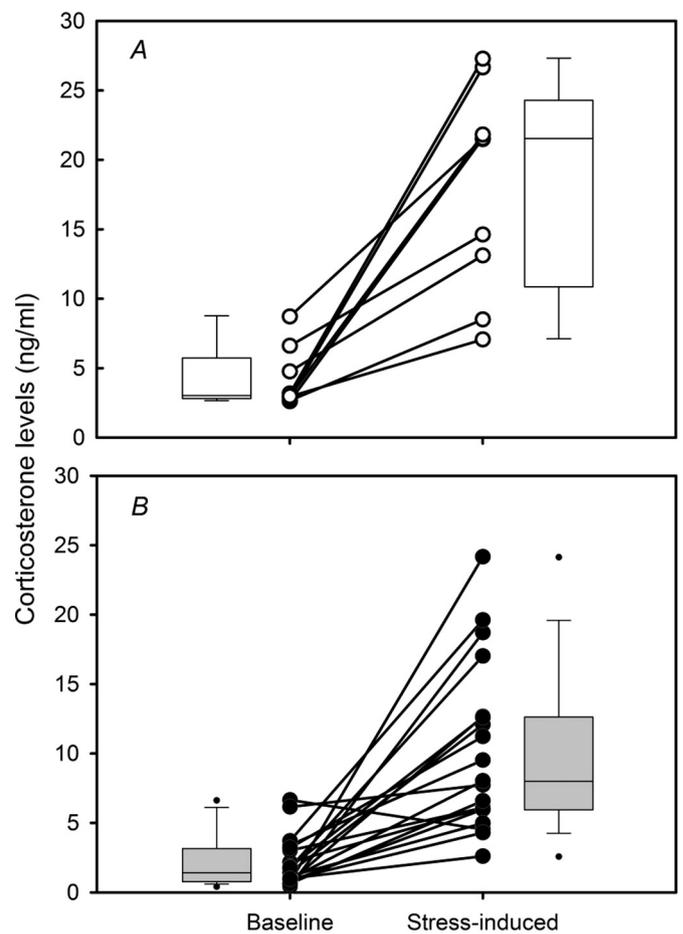


Fig. 3. Difference in corticosterone levels between ‘blue-bar’ (A) and ‘checker’ (B) pigeons. On each graph, individual change in corticosterone levels during the stress protocol is shown. Moreover, box-and-whisker plots represent baseline and stress-induced data: the top and bottom of the boxes represent the top and bottom quartiles, respectively; the line across the box represents the mean. The ends of the whiskers represent the fifth and ninety-fifth percentiles, and the circles represent outliers. Baseline measurements were made immediately after capture (within 3 min). Stress-induced measurements were made after a 60-min restraint protocol.

(Table 1).

Baseline and stress-induced breath rates were significantly correlated ($p = 0.006$) but all other variables were not correlated (all p -values > 0.500).

4. Discussion

In this study, we found that pigeons slightly differed in their behavioural and physiological stress responses depending on their plumage color. Specifically, we compared two groups of pigeons with different plumage characteristics: ‘blue-bar’ birds (lighter birds) and

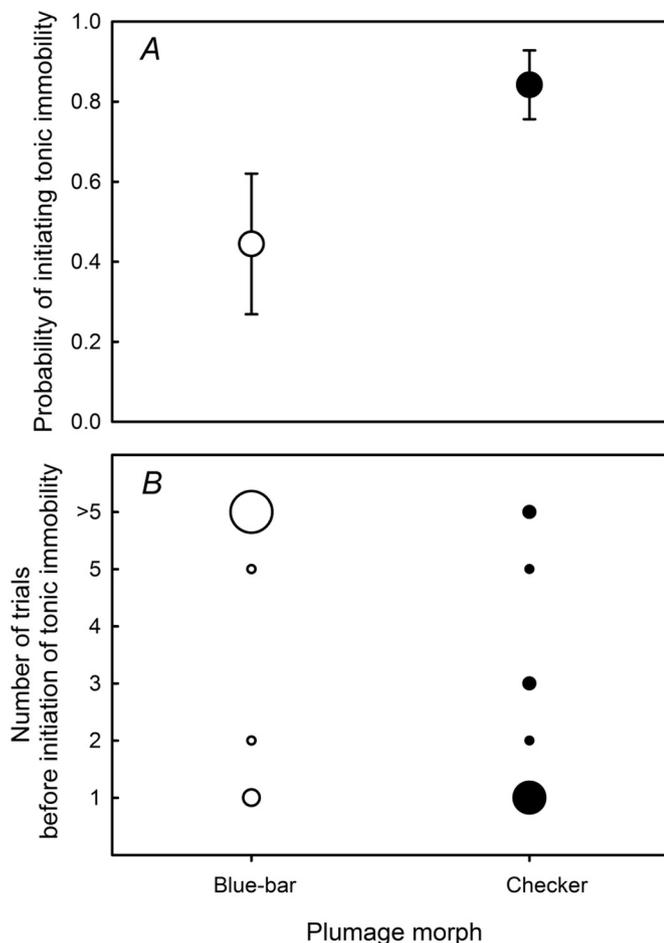


Fig. 4. Difference in the probability to initiate tonic immobility between ‘blue-bar’ and ‘checker’ pigeons (A). Mean \pm Error standards are represented. Difference in the number of trials before initiation of tonic immobility between ‘blue-bar’ and ‘checker’ pigeons (B). For each category, the size of the circle represents the percentage of individuals.

‘checker’ birds (darker birds). Although breath rate did not differ between ‘checker’ and ‘blue bar’ birds, ‘blue-bar’ birds had higher corticosterone levels relative to ‘checker’ birds (baseline and stress-induced levels). Moreover, ‘checker’ birds were more likely to initiate tonic immobility relative to ‘blue bar’ birds. Despite a relatively small sample size, this study suggests that the behavioural and physiological stress responses of wild birds may differ according to their plumage color.

4.1. Breath rate

We found that breath rate was affected by the stress of capture and tended to decrease during the stress protocol. Such decrease has previously been reported in other bird species [10; 82] and is thought to be linked to an initial sharp and temporary increase in breath rate immediately following capture. This initial and temporary increase is associated with the immediate stress response that is controlled by the autonomous nervous system [40]. Although the link between plumage characteristics and breath rate has to our knowledge never been tested in adults, previous studies found that darker nestlings had lower breath rate in some species (European kestrel, *Falco tinnunculus*, [80]; Barn owl, *Tito alba*, [81]) but not others (Barn swallow, *Hirunda rustica*, [18]). Accordingly and because lighter pigeons are more likely to be predated, we predicted that ‘blue-bar’ pigeons should have higher breath rate relative to ‘checker’ ones (prediction 1), as an adaptation to a higher predation risk. However, this hypothesis was not supported by our results, suggesting that ‘blue-bar’ and ‘checker’ pigeons do not differ to a large extent in their immediate response to an acute stressor (e.g. a

predatory event). Interestingly, previous studies have demonstrated that breath rate is linked to personality (e.g. shy vs. bold) and risk-taking behaviour [11,10,25]. Moreover, breath rate has also been suggested to be linked to the degree of stress that is experienced by wild birds in their environment [82,79,12]. Because ‘checker’ and ‘blue-bar’ pigeons had similar breath rates, our study suggests that these two categories of birds (1) may not differ dramatically in their personality, and (2) may similarly perceive and/or cope with their environment. The relationship between breath rate, personality and stress level is however inconsistent (see [11,10] for some examples) and further personality and behavioural studies are required to confirm our interpretations.

4.2. The corticosterone stress response

According to our prediction, we found that ‘blue-bar’ birds had higher baseline corticosterone levels relative to ‘checker’ birds (prediction 2), suggesting that ‘blue-bar’ and ‘checker’ birds differ in their allostatic load [41,46,62]. Overall, higher baseline corticosterone levels may suggest that ‘blue-bar’ birds are less able to cope with their environment relative to ‘checker’ birds (but see [19]). However, the origin of such elevated baseline corticosterone levels remains unidentified in our study. Moderately elevated corticosterone levels are known to activate metabolic processes that may help an individual to cope with increased energetic demands [41,61]. Such increased energetic demands may originate from multiple environmental factors, such as predation risk or food supply [88,90], which can therefore affect baseline corticosterone levels (e.g. predation risk: [14,69,72]; food supply: [7,45,59]). In our study, food supply or access to food is unlikely to explain this difference in corticosterone levels between ‘blue-bar’ and ‘checker’ birds because we did not find any difference in body condition between these two categories of birds. Instead, predation risk may be the main cause of higher baseline corticosterone levels in blue-bar birds, although other factors might also be involved (e.g. dominance rank, [52]; parasite load, [56]).

In addition, we also found that the corticosterone stress response of blue-bar birds was slightly more pronounced than that of checker birds and this resulted in significantly higher stress-induced corticosterone levels in ‘blue-bar’ birds (prediction 2). Although a larger data set would be required to confirm this pattern and to reduce the risk of type 1 error, our results support the idea that blue-bar birds may be more sensitive to stressors relative to ‘checker’ birds. Interestingly, elevated stress-induced corticosterone levels are associated with less risky behaviours in birds that have to cope with a high predation risk [53,71,84]. Moreover, elevated stress-induced corticosterone levels have been linked to better survival ability in wild birds, but only when individuals live in a constraining environment [4]. Therefore, elevated corticosterone levels might be favoured in ‘blue-bar’ birds that seem more likely to be predated than ‘checker’ birds [58,66]. Supporting the link between eumelanin plumage coloration and corticosterone regulation, previous studies have shown that darker birds mount a lower corticosterone stress response relative to lighter ones ([1,2; but see [17]) although the relationship between eumelanin plumage coloration and the corticosterone stress response seems to depend on the environmental context (e.g. [17]). Importantly, elevated corticosterone levels are also associated with fitness costs (reviewed in [67]) and lower stress-induced corticosterone levels may be favoured under specific situations [6,77]. For instance, several studies suggest that a low sensitivity to stress may be necessary to cope with the urban environment [8,48], which is characterized by multiple kinds of non-threatening anthropogenic disturbance (e.g. noise, human presence, etc.). Therefore, the lower stress-induced corticosterone levels of darker birds may be beneficial in urban areas. This could explain why the proportion of dark pigeons increases in urban areas [51] although other environmental factors are definitely also involved (food abundance: [33]; parasites: [34]; trace metal pollution: [13]).

4.3. Tonic immobility

Contrary to our prediction (prediction 3), we found that ‘checker’ birds were more likely and more rapid to initiate tonic immobility relative to ‘blue-bar’ birds. Although the link between eumelanic plumage coloration and tonic immobility has to our knowledge never been tested in adults, two studies recently found that darker nestlings were more likely to initiate tonic immobility (barn owl: [80], European kestrel: [81]), supporting therefore our results in adult pigeons. Similarly, recent studies demonstrated that several personality traits are closely associated with color polymorphism, and more specifically with head color in Gouldian finches [47,85]. Because lighter pigeons are more likely to be predated [58,66], we however predicted that ‘blue-bar’ birds should have been selected to display tonic immobility more frequently relative to ‘checker’ birds (prediction 3). How can we explain this result?

In wild birds, personality traits are often linked together and shy individuals are often more likely to initiate tonic immobility relative to bolder ones ([20,81]. Shyness may help survive predation or threats but they can also be associated with other costs [31,57]. For example, shy individuals often have a lower access to food, are less dominant, and breed less successfully than bold individuals [29,39,73]. Therefore, ‘blue-bar’ pigeons may actually survive less well because they are less able to avoid predation than checker birds [58,66] but their personality may be associated with other fitness benefits. Overall, plumage coloration may be functionally linked to specific personalities (e.g. head color, [47,85]), which may be beneficial in some environments but not others [63,64,83]. This might explain the maintenance of high plumage polymorphism in wild pigeon populations [32,33].

Acknowledgements

At the CEBC, we thank S. Ruault for her excellent technical assistance in molecular biology. This research was supported by the CNRS.

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