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Frédéric Angelier, Charline Parenteau, Colette Trouvé, Nicole Angelier

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

Frédéric Angelier*, Charline Parenteau, Colette Trouvé, Nicole Angelier

*Centre d’Etudes Biologiques de Chizé, CNRS-ULR, 79360 Villiers en Bois, France*

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* Author for correspondence: angelier@cebc.cnrs.fr
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 behavioral and physiological sensitivities to stressors.

Key-words: polymorphism, predation risk, corticosterone, breath rate, tonic immobility
Introduction

In wild vertebrates, predation risk is a strong selective pressure that drives the physiological, behavioural and morphological adaptations of species (Lima & Dill 1990). 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 (Endler 1978; Godin & McDonough 2003; Stuart-Fox et al. 2003; Palleroni et al. 2005). However, conspicuousness can also insure a higher fitness by signalling a high phenotypic quality to congeners and predators (“the handicap principle hypothesis”, Zahavi 1975; Hill 1990). 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 (Losey et al. 1997; Chatelain et al. 2016). 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 (Gray & McKinnon 2007; Karpestam et al. 2016).

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 (Ruell et al. 2013; Schuett et al. 2015; Stevens 2015). 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 (Lima & Dill 1990): they should also be more vigilant (Lima & Dill 1990), and they should display earlier escape behaviour when a potential predator is detected (Katz et al. 2015; Møller et al. 2011, 2016). 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 (Wingfield 2003) 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 (Evans et al. 2006; Angelier et al. 2011; Cockrem 2013; Jenkins et al. 2014; Stedman et al. 2017) and it is often associated with specific individual behavioural and physiological phenotypes (Edelaar et al. 2012; Cockrem 2007). Although these specific phenotypes may be advantageous in case of predator attacks, they may also incur fitness costs under other circumstances (reviewed in Lima 1998). For example, a strong physiological stress response has been associated with reproductive failure (Sapolsky et al. 2000). Similarly, the activation of some behavioural stress responses is also associated with personality traits that reduce mating success in some species (Smith and Blumstein 2008). 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; Lima & Dill 1990; Rödl et al. 2007). Therefore, the stress response should theoretically be more important in conspicuous individuals relative to cryptic individuals because of a higher predation risk (Angelier & Wingfield 2013).

The stress response is associated with multiple behavioural and physiological components that can be measured in wild animals (Koolhas et al. 1999; Wingfield 2003; Wingfield et al. 1998; Romero et al. 2009). First, the stress response is usually associated with ventilatory patterns that help modulating cardiovascular activity to cope with the acute stressor (Grossman 1983). Therefore, breath rate has been suggested as a relevant proxy to measure the stress response of humans (Grossman 1983) and more recently wild vertebrates (Carere & Van Oers 2004). Usually, breath rate immediately increases in response to an acute stressor in humans and wild vertebrates (Grossman 1983; Carere & Van Oers 2004) before to slightly decrease as the stressor is maintained (Carere & Van Oers 2004). Interestingly, breath rate has been related to personality and habitat in wild great tits (Carere & Van Oers 2004; Torne-Nogueira et al. 2014), 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 (Wingfield et al. 1998; Sapolsky et al. 2000; Landys et al. 2006). Such an increase in corticosterone levels mediates several physiological and behavioural changes (Sapolsky et al. 2000; Landys et al. 2006) that aim to restore homeostasis (McEwen & Wingfield 2003; Romero et al. 2009) and to promote immediate survival (Wingfield et al. 1998; Angelier & Wingfield 2013). 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 (Forkman et al. 2007). This behaviour is an adaptive strategy to cope with a high predation risk (Thompson et al. 1981; Edelaar et al. 2012).

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. Jenkins et al. 2014). 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 (Angelier & Wingfield 2013; Stedman et al. 2017). 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 behavioral studies have shown that color polymorphism, and more specifically head color, can be reliable signals of personality traits in Gouldian finches, *Erythrura gouldiae* (Mettke-Hoffmann 2012; Williams et al. 2012). However and surprisingly, the influence of colour polymorphism on the behavioral and physiological proxies of the stress response has rarely been examined in wild birds, especially in adults (Almasi et al. 2010; Roulin & Ducrest 2011; Williams et al. 2012; Jenkins et al. 2013; Vitousek et al. 2014a; Corbel et al. 2016).

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. Palleroni et al. 2005; Chatelain et al. 2016). Importantly, predation risk is related to plumage color in feral rock pigeons with lighter birds being more likely to be predated than darker individuals (Récapet et al. 2013; Santos et al. 2015). Finally, their physiological and behavioural stress responses can easily be measured (Angelier et al. 2016; Corbel et al. 2016). 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 (Récapet et al. 2013; Santos et al. 2015), 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.

**Materials and methods**

*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 (Jacquin et al. 2011; Recapet et al. 2013; Chatelain et al. 2016). 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 Obukhova 2007 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 Chatelain et al. 2016) and we instead relied on a binary classification of individuals as checker or blue-bar pigeons (Jacquin et al. 2011; Recapet et al. 2013; Corbel et al. 2016). 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 Corbel et al. 2016). Permission to capture wild pigeons and experimental approval were granted by the French government (R45GRETAF1-10).

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 (Wingfield et al. 1992, see Angelier et al. 2016): 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 (Fridolfsson and Ellegren 1999).

**Breath rate and tonic immobility**

Immediately after the first blood sample and within 5 minutes of capture, the breath rate of individuals was measured (Van Oers & Carere 2007). Specifically, the pigeon was held in one hand and the number of breast movement was counted during 30 seconds (hereafter called baseline breath rate). The same procedure was repeated after the second blood sample (i.e. after 60 minutes of restraint, stress-induced breath rate) to monitor how an acute stressor affects breath rate (Carere and van Oers 2004). In addition, a tonic immobility test was conducted immediately after the second breath rate measurement (see Edelaar et al. 2012). 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 seconds, the experimenter slowly removed his hand. The pigeon was considered to be in tonic immobility if it stayed on its back for more than 5 seconds. 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).

**Morphometric measures and body condition**

After all the behavioral 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 (Peig and Green 2009). All birds were then released and were seen during the following days at the study site.

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 Glm, 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 (Satterthwaite 1946). 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).

Results

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).

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).

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 x plumage color’ interaction (all p-values > 0.100). Specifically, blue bar were less likely to initiate tonic immobility than checker 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).

**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).

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

**Discussion**

In this study, we found that pigeons slightly differed in their behavioral 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 ‘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.
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 (Carere & Van Oers 2004; Van Oers et al. 2007) 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 (Koolhaas et al. 1997). 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*, Van den Brink 2012a; Barn owl, *Tito alba*, Van den Brink et al. 2012b) but not others (Barn swallow, *Hirunda rustica*, Corti et al. 2017). 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 (Carere et al. 2001; Carere & Van Oers 2004; Fucikova et al. 2009). Moreover, breath rate has also been suggested to be linked to the degree of stress that is experienced by wild birds in their environment (Van Oers & Carere 2007; Torne-Noguera et al. 2014; Charmantier et al. 2017). 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 Carere et al. 2001; Carere & Van Oers 2004 for some examples) and further personality and behavioural studies are required to confirm our interpretations.
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 (McEwen & Wingfield 2003; Landys et al. 2006; Romero et al. 2009). 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 Dickens & Romero 2013). 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 (Romero 2002; Landys et al. 2006). Such increased energetic demands may originate from multiple environmental factors, such as predation risk or food supply (Zanette et al. 2014; Wright & Fokidis 2016), which can therefore affect baseline corticosterone levels (e.g. predation risk: Scheuerlein et al. 2001, Sheriff et al. 2011, Clinchy et al. 2013; food supply: Lynn et al. 2010; Riechert et al. 2014; Angelier et al. 2015). 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, Ode et al. 2015; parasite load, Raouf et al. 2006).

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 behaviors in birds that have to cope with a high predation risk (Seltmann et al. 2012; Ouyang et al. 2012; Vitousek et al. 2014b). 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 (Angelier et al. 2009). Therefore, elevated corticosterone levels might be favoured in ‘blue-bar’ birds that seem more likely to be predated than ‘checker’ birds (Récapet et al. 2013; Santos et al. 2015). Supporting the link between eumelanic plumage coloration and corticosterone regulation, previous studies have shown that darker birds mount a lower corticosterone stress response relative to lighter ones (Almasi et al. 2010, 2013; but see Corbel et al. 2016) although the relationship between eumelanic plumage coloration and the corticosterone stress response seems to depend on the environmental context (e.g. Corbel et al. 2016). Importantly, elevated corticosterone levels are also associated with fitness costs (reviewed in Sapolsky et al. 2000) and lower stress-induced corticosterone levels may be favoured under specific situations (Angelier & Wingfield 2013; Taff and Vitousek 2016). For instance, several studies suggest that a low sensitivity to stress may be necessary to cope with the urban environment (Møller 2008; Bonier 2012), 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 (Obukhova 2007) although other environmental factors are definitely also involved (food abundance: Jacquin et al. 2012; parasites: Jacquin et al. 2013; trace metal pollution: Chatelain et al. 2016).

**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: Van den brink et al. 2012a, European kestrel: Van den brink et al. 2012b), 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 (Williams et al. 2012; Mettke-Hoffmann 2012). Because lighter pigeons are more likely to be predated (Récapet et al. 2013; Santos et al. 2015), 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 (Edelaar et al. 2012; Van den brink et al. 2012b). Shyness may help survive predation or threats but they can also be associated with other costs (Houston et al. 1993, Réale et al. 2007). For example, shy individuals often have a lower access to food, are less dominant, and breed less successfully than bold individuals (Smith & Blumstein 2008; Kontiainen et al. 2009; Habig et al. 2017). Therefore, ‘blue-bar’ pigeons may actually survive less well because they are less able to avoid predation than checker birds (Récapet et al. 2013; Santos et al. 2015) but their personality may be associated with other fitness benefits. Overall, plumage coloration may be functionally linked to specific personalities (e.g. head color, Mettke-Hoffmann 2012; Williams et al. 2012), which may be beneficial in some environments but not others (Roulin 2004; Roulin & Ducrest 2011; Vitousek et al. 2014a). This might explain the maintenance of high plumage polymorphism in wild pigeon populations (Jacquin et al. 2011, 2012).

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References


Table 1: Difference in breath rates, corticosterone levels, probability to initiate tonic immobility, and body condition between blue-bar and checker pigeons.

<table>
<thead>
<tr>
<th></th>
<th>Blue-bar</th>
<th>Checker</th>
<th></th>
<th>Blue-bar</th>
<th>Checker</th>
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<tr>
<td></td>
<td>Mean ± SE</td>
<td>95% CI (Low/High)</td>
<td>Mean ± SE</td>
<td>95% CI (Low/High)</td>
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<td>Baseline breath rate</td>
<td>39.667 ± 3.590</td>
<td>31.388 / 47.946</td>
<td>41.737 ± 2.923</td>
<td>35.596 / 45.878</td>
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<td>Stress-induced breath rate</td>
<td>37.111 ± 3.525</td>
<td>28.981 / 45.241</td>
<td>37.000 ± 2.353</td>
<td>32.056 / 41.944</td>
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<td>Baseline corticosterone level</td>
<td>4.150 ± 0.720</td>
<td>2.490 / 5.810</td>
<td>2.148 ± 0.415</td>
<td>1.273 / 3.019</td>
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<td>Probability to initiate TI</td>
<td>0.444 ± 0.176</td>
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<td>0.842 ± 0.086</td>
<td>0.661 / 1.023</td>
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<td>Body condition</td>
<td>284.463 ± 7.924</td>
<td>266.190 / 302.737</td>
<td>278.071 ± 6.071</td>
<td>265.315 / 290.826</td>
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Figure legends

**Figure 1:** Pictures of a ‘blue-bar’ (A) and a ‘checker’ rock pigeon (B). Although we did not quantify the degree of eumelanism in our study, ‘checker’ pigeons are always much darker than ‘blue-bar’ pigeons.

**Figure 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 minutes). Stress-induced measurements were made after a 60-mins restraint protocol.

**Figure 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 minutes). Stress-induced measurements were made after a 60-mins restraint protocol.

**Figure 4:** Difference in the probability to initiate tonic immobility between ‘blue-bar’ and ‘checker’ pigeons (A). Mean ± 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.
Fig. 1
Highlights

- We examined the link between plumage coloration and the stress response in wild pigeons.
- Plumage color had no influence on breath rate.
- Darker pigeons had lower corticosterone levels.
- Darker pigeons were more likely to initiate tonic immobility.
- The stress response of wild pigeons differ according to their plumage coloration.