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Pigeons in the sun: Thermal constraints of eumelanic plumage in the rock pigeon (*Columba livia*)

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ABSTRACT

In wild vertebrates, several species exhibit eumelanic color polymorphism with the coexistence of dark and light morphs. The maintenance of such polymorphism suggests the existence of a selective balance between the morphs and a large body of literature has reported the costs and benefits of darker plumage coloration in birds. Among them, it has been suggested that melanin and dark plumage could entail high energetic costs especially under hot and sunny climates. However, to my knowledge, the thermal constraints of sun exposure have rarely been studied in polymorphic species. Here, we tested the impact of eumelanic plumage coloration on plumage and body temperatures, and evaporative cooling behavior in the polymorphic rock pigeon (*Columbia livia*). We experimentally exposed light and dark pigeons to direct sun radiation for 1 h while a few birds were maintained in the shade as controls. We found that sun exposure was associated with increased plumage temperature, and this effect was greater for darker pigeons. In addition, we found that sun exposure was also associated with higher cloacal temperature but for dark pigeons only. Finally, light and dark pigeons were more likely to show cooling evaporative behavior when exposed to sun and as their cloacal temperature increases. Altogether, these results suggest that darker pigeons may have a lower ability to cope with heat and solar radiations and that dark plumage can be associated with thermal costs in this polymorphic species.

1. Introduction

Eumelanin is a pigment, which is responsible for the black and grey coloration of the epidermis, hair, feather, and scales in vertebrates (Hill and McGraw, 2006). In wild vertebrates, several species exhibit eumelanic color polymorphism with the coexistence of several morphs characterized by specific colors or patterns. Because this color polymorphism is heritable and under genetic control (Roulin, 2004; McKinnon and Pierroti, 2010), the maintenance of such polymorphism suggests the existence of a selective balance between the morphs, and all morphs should respectively benefit and suffer from specific fitness advantages and costs (Galeotti et al., 2003; Roulin, 2004; Meunier et al., 2011).

In that context, a large body of literature has studied and reported the costs and benefits of eumelanin-based coloration in birds (Roulin, 2004, 2016). For example, much attention has been paid to the link between eumelanic color polymorphism, predation risk and parasitism (reviewed in Cote et al., 2018; Karpestam et al., 2016), and a few studies have shown that specific morphs are less likely to be predated or parasitized than others (Santos et al., 2005; Jacquin et al., 2013). More recently, there has been a growing interest into the functional link between eumelanic color and several organismal systems (reviewed in Ducrest et al., 2008) and several studies have reported a close link between melanin and physiological mechanisms, such as immunity (Jacquin et al., 2011; Gangoso et al., 2015a) or stress regulation (Almasi et al., 2010; Angelier et al., 2018). Similarly, eumelanic morphs have also been associated with specific personality and behavioral patterns (Van den Brink et al., 2012; Mateos-Gonzalez and Senar, 2012; Angelier et al., 2018) with potential consequences on risk-taking strategy and social dominance (Gangoso et al., 2015b). Importantly, these links between melanin and the functioning of organismal systems may explain why darker birds perform better in some environments, but are selected against in others (Meunier et al., 2011).

In addition, melanin has also structural and chemical properties, which confer specific characteristics to the plumage. For example, melanin pigments increase the strength of the feathers and melanic feathers wear more slowly than non-melanic feathers (Roulin, 2007), providing obvious benefits in terms of plumage quality or plumage resistance to feather bacteria. Melanin is also known to bind to heavy metals, and thus, melanic plumage has been suggested as an effective

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way to get rid of these contaminants by depositing them into inert feathers (Chatelain et al., 2014). It has also been suggested that melanin and darker plumage could entail higher energetic costs especially under hot and sunny climates (Roulin, 2014). Specifically, plumage color is likely to influence resistance to heat because darker colors absorb more illuminating light, and thus heat up more (Stuart-Fox et al., 2017). Therefore, lighter plumage color may possibly be associated with better ability to cope with heat and high solar radiation. Importantly, and in addition to the other aforementioned factors, this potential higher energetic cost of darker plumage could also play a role in the maintenance of eumelanic color polymorphism in wild populations (Galvan et al., 2018; Romano et al., 2019).

The impact of pigmentation on thermal constraints or thermal needs has been extensively studied in ectotherms, which highly depend on thermoregulation to complete their life-history cycle (reviewed in Clusella-Trullas et al., 2007, 2008; Stuart-Fox et al., 2017). However, this topic has been much less studied in endotherms (Oswald and Arnold, 2012), and to my knowledge, a few studies only have investigated the impact of eumelanic color plumage on the ability of birds to cope with solar radiation and heat (Hochscheid et al., 2002; Margalida et al., 2008). Darker plumage may be detrimental in warmer and sunnier regions if it affects thermoregulation (Delhey, 2018) but we currently lack experimental data to fully assess the thermal costs of eumelanic color plumage in polymorphic bird species.

In this study, I tested the impact of eumelanic plumage coloration on plumage and body temperatures in the polymorphic rock pigeon (*Columbia livia*). The rock pigeon is a very relevant model because it shows a high eumelanic color plumage polymorphism: 5 eumelanic morphs can be found in the wild including 'white', 'blue-bar', 'checker', 'T-pattern', and 'spread' pigeons (from the palest to the darkest, see Vickrey et al., 2018). In addition, the polymorphism of rock pigeons shows an important spatial pattern (Obukhova, 2007): most southern European populations of rock pigeons usually show a higher frequency of lighter birds, suggesting that darker pigeons may actually suffer from hot and dry environments. To test this hypothesis, I conducted an experiment and exposed light (blue-bar) and dark (T-pattern and checker) pigeons to direct sun radiation ('sun-exposed birds') during 1 h while a few birds were kept in the shade ('control birds'). I then measured their plumage and body temperatures and I also monitored whether they exhibit evaporative cooling behavior or not. I predicted that (1) sun-exposed darker pigeons will have higher plumage and body temperature relative to lighter pigeons; (2) body temperature will be significantly and positively correlated with plumage temperature; (3) sun exposure and darker plumage will be associated with a higher probability to exhibit evaporative cooling behavior.

2. Methods

2.1. Study site, birds and plumage color

Twenty-three birds were captured in summer in a moderately urbanized landscape in Southern France, (43°34′N, 7°02′E) using Potter traps between 7:00 and 9:00 from August 4 to August 7, 2018. Immediately after capture, birds were classified as eumelanic, pheomelanic or white birds according to their plumage characteristics (Jacquin et al., 2011; Chatelain et al., 2016; Angelier et al., 2018). Pheomelanic and white birds were released at capture because they represent only a very small percentage of the study population and the number of such individuals were too limited to test the influence of their plumage color on plumage and body temperature. Eumelanic birds were identified as light ('blue-bar') or dark ('checkers' and 'T-pattern') birds (called hereafter 'plumage color') according to their plumage color and pattern: Blue-bar birds have the wild-type plumage, which consist in a uniform light grey plumage with two black wing bars. In contrast, checker and T-pattern birds have a similar grey plumage, but the wings are covered with some dark black spots (checker) or are almost entirely black (T-pattern pigeons). In this experiment, I kept only the T-pattern birds, and the checker birds that had a very high density of dark spots on their wings in order to have two contrasted groups of birds (i.e. light and dark pigeons). Immediately after capture, all birds were transferred to individual cages with water and food ad libitum in a shady place. They were left undisturbed until 14:00 so that they could habituate to their individual cage until the sun exposure experiment.

2.2. Sun exposure experiment

At 14:00, all birds and their individual cages were placed on a terrace in either a sunny place or a shady place (with no direct sun exposure). The 'sun exposure experiment' consisted therefore in placing birds either in direct sun exposure or in the shade with three distinct groups of birds (hereafter called, light sun-exposed birds (blue-bar birds), $n = 8$; dark sun-exposed birds (checker and T-pattern birds), $n = 9$; control birds, $n = 6$). The control group could not be split in two groups according to plumage color because of limited sample size (3 light birds and 3 dark birds only). The terrace was protected from wind and air temperature was always between 31 and 34 °C during the experiment. During the sun exposure experiment, the sky was perfectly clear with no cloud. All experimental and control birds were left undisturbed in their individual cages during 1 h. After 1 h, the birds were removed from their cage and their plumage temperature was immediately measured (within 10 s of capture) by using an infrared thermometer (Testboy, TV325, Germany) on the central part of their back, which is covered by their wings. Their cloacal temperature was then measured (within 2 min of capture) by using a thermometer with an external temperature probe, which was gently inserted in the bird's cloaca (called hereafter 'cloacal temperature'). Just before removing the birds from their cage, their evaporative cooling behavior was also monitored. Specifically, the birds were observed from a distance with binocular during 2 min and their gular fluttering behavior was monitored (binomial variable: expressing gular fluttering or not). Gular fluttering consists in repeated fast motions of the neck/throat while the beak is open. Gular fluttering is a specific behavior, which is known to allow heat dissipation through evaporative cooling in birds (Smith et al., 2015).

2.3. Statistical analyses

All analyses were performed with SAS statistical software (SAS Institute, v. 9.4.). Firstly, I compared plumage and cloacal temperature between the three groups (control birds, sun-exposed light birds, and sun-exposed dark birds) by using ANOVAs. Secondly, I tested whether cloacal temperature was explained by plumage temperature by running linear regressions (dependent variable: cloacal temperature, independent variable: plumage temperature). Thirdly, I ran Chi-squared tests to test if gular fluttering behavior was more apparent in one of the three groups of birds. Finally, I tested whether plumage or cloacal temperatures were linked to the probability of showing gular fluttering behavior by using logistic regressions. The assumptions of equal variances and normal residuals were met for all models and regressions.

3. Results

Plumage temperature significantly differed between the three groups of pigeons (ANOVA, $F_{2,20} = 38.42$, $P < 0.001$; Mean ± SE, control: 35.47 ± 0.53, sun-exposed dark birds: 45.89 ± 1.00, sun-exposed light birds: 42.80 ± 0.61; Fig. 1A). Specifically, sun-exposed dark and light birds had higher plumage temperature than control birds (dark: $\chi^2 = 75.66$, $p < 0.001$, light: $\chi^2 = 35.68$, $p < 0.001$; Fig. 1A). Dark sun-exposed birds also had higher plumage temperature than light sun-exposed birds ($\chi^2 = 7.82$, $p = 0.005$ Fig. 1A). Cloacal temperature significantly differed between the three groups of pigeons (ANOVA, $F_{2,20} = 5.47$, $P = 0.013$, Mean ± SE, control: 40.98 ± 0.29, sun-exposed dark birds: 41.83 ± 0.13, sun-exposed light birds: 41.3 ± 0.15; Fig. 1B). Specifically, sun-exposed

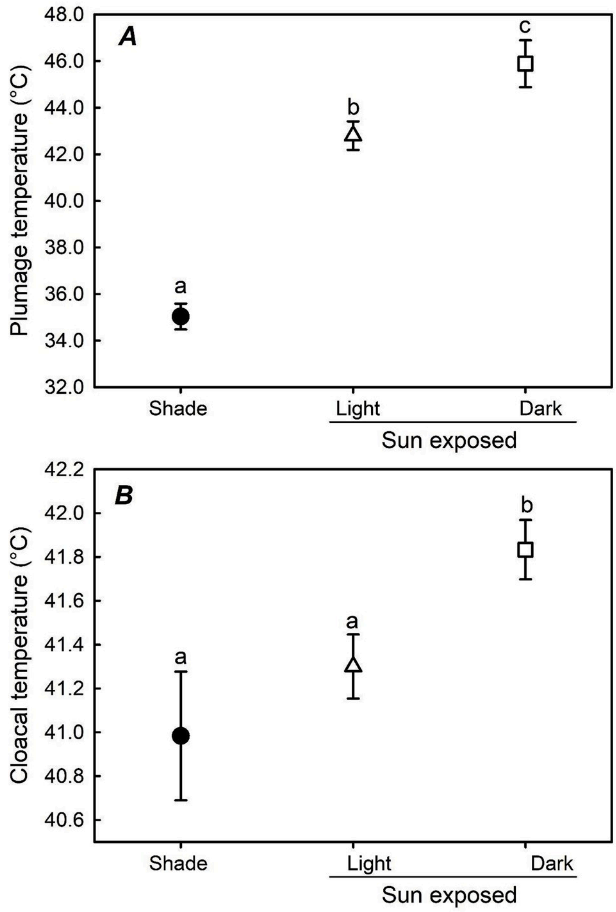

Fig. 1. Influence of the sun exposure experiment and plumage color on (A) plumage temperature; (B) cloacal temperature in rock pigeons. Black dots represent the pigeons that were maintained in the shade (n = 6) while white dots represent the pigeons that were exposed to the sun. Triangle and square symbols respectively represent sun-exposed light (n = 8) and sun-exposed dark pigeons (n = 9). Mean ± Error standards are represented. Different letters indicate significant differences.

dark pigeons had higher cloacal temperature than control birds (χ^2 = 10.18, p = 0.001; Fig. 1B) but cloacal temperature did not significantly differ between sun-exposed light birds and controls (χ^2 = 1.35, p = 0.246; Fig. 1B). Dark sun-exposed birds also had higher cloacal temperature than light sun-exposed birds (χ^2 = 4.72, p = 0.029; Fig. 1B). Cloacal temperature was significantly and positively related to plumage temperature ($F_{1,21}$ = 17.35, P < 0.001, r^2 = 0.452) and this relationship hold true when considering sun-exposed birds only ($F_{1,15}$ = 9.53, P = 0.007, r^2 = 0.389).

The probability to show gular fluttering significantly differed between the three groups of pigeons (χ^2 = 8.75, p = 0.013; Fig. 2A). Specifically, the probability to show gular fluttering significantly differed between controls and sun-exposed dark birds (χ^2 = 8.73, p = 0.003; Fig. 2A) and between controls and sun-exposed light birds (χ^2 = 3.95, p = 0.046; Fig. 2). However, the probability to show gular fluttering behavior did not significantly differ between sun-exposed light birds and sun-exposed dark birds (χ^2 = 1.47, p = 0.226; Fig. 2A). The probability to show gular fluttering behavior was significantly explained by plumage temperature (logistic regression, χ^2 = 6.42, p = 0.011) and cloacal temperature (logistic regression, χ^2 = 7.62, p = 0.006). When considering sun-exposed birds only, the probability to show gular fluttering behavior was still significantly explained by cloacal temperature (logistic regression, χ^2 = 5.51, p = 0.019; Fig. 2B), but not by plumage temperature (logistic regression, χ^2 = 0.70, p = 0.404).

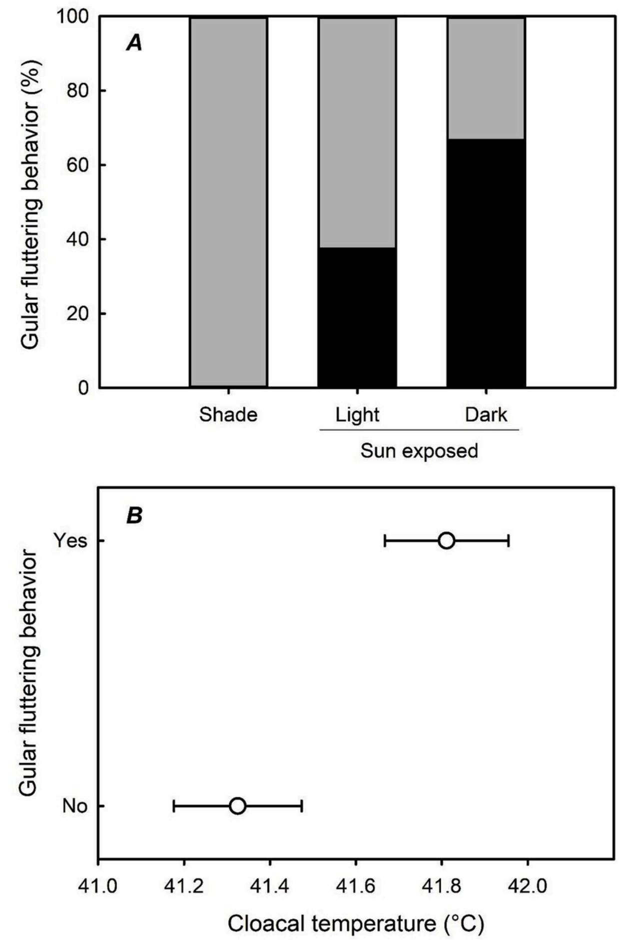

Fig. 2. (A) Influence of the sun exposure experiment and plumage color on the proportion of individuals showing evaporative cooling behavior (gular fluttering). Black squares represent the percentage of individuals showing gular fluttering behavior while grey squares represent the percentage of individuals that did not show this behavior. (B) Influence of cloacal temperature on the probability to show gular fluttering behavior for sun-exposed pigeons. Mean ± Error standards are represented. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

4. Discussion

In this study, plumage color had an impact on plumage and body temperatures in the polymorphic rock pigeon. As predicted, darker individuals had higher plumage temperature than their paler counterparts when exposed to solar radiations. When exposed to solar radiations, darker individuals also had slightly higher cloacal temperature than paler individuals while paler individuals exposed to solar radiations had similar cloacal temperature to the birds that stayed in the shade (control birds). This suggests that darker pigeons may have a lower ability to cope with heat and solar radiations than their paler counterparts. In addition, pigeons were more likely to show cooling evaporative behavior when exposed to the solar radiations and as their cloacal temperature increases. Altogether, these results suggest that darker plumage can be associated with thermal costs in sunny environments.

4.1. Plumage and body temperature

As expected, sun-exposed birds had a higher plumage temperature than the birds that stayed in the shade (i.e. control birds), confirming that the experimental treatment was associated with increased solar radiation and heat. Interestingly, plumage color had also a strong impact on plumage temperature for sun-exposed birds as the plumage of dark birds was hotter than the plumage of light birds. This confirms that darker plumages absorb more solar radiation and may be associated with higher heating rates, especially when directly exposed to the sun (Stuart-Fox et al., 2017). Accordingly, Hochscheid et al. (2002) have previously reported that white adults had a lower plumage temperature than black chicks in a seabird species, the Cape gannet (*Morus capensis*). Importantly, sun-exposed dark pigeons had a higher cloacal temperature than sun-exposed light birds and than birds who stayed in the shade (i.e. controls); cloacal temperature was not different between sun-exposed light birds and controls.

This suggests that lighter plumage may attenuate the thermal constraints associated with solar radiation and heat, as suggested in other studies in mammals with fur color polymorphism (e.g. Hetem et al., 2009). Because increased cloacal temperature could be associated in the long-term with overheating, with multiple physiological costs (reviewed in Huey et al., 2012), and even with mortality in extreme cases (McKecknie and Wolf, 2010), dark pigeons may not afford to stay for extended periods in sunny and hot places. However, the difference in body temperature between sun-exposed light and dark pigeons was limited to ~0.5 °C in this study. Moreover, cloacal temperature of these sun-exposed pigeons remains within the natural range of body temperature for this species (Bittencourt et al., 2015), suggesting that the impact of sun exposure on body temperature was limited for these birds. Previous studies have shown that a slight fever is energetically expensive in birds and can increase the risk of dehydration (Marder and Arieli, 1988; Marais et al., 2011; Nilsson et al., 2016) but the biological impact of such a small change in body temperature remains to be determined and definitely deserves future studies (Dawson & O'Connor, 1996).

Despite a higher plumage temperature, sun-exposed light birds did not have a significantly higher body temperature than control birds. Because of the small sample size, I may not have been able to detect a significant difference in cloacal temperature between these two groups (type 2 error) and it is therefore necessary to remain cautious regarding the interpretation of these results. Importantly, all experimental pigeons were exposed to the sun for a limited period (1 h) and with ad libitum access to water. These conditions may have not been constraining enough to induce a significant and detectable increase of body temperature in blue-bar pigeons. This suggests that light plumage might effectively attenuate the thermal constraints associated with high solar radiation and heat in the short term (at least 1 h) and when individuals have access to water. However, this attenuation may disappear in case of prolonged sun exposure (>1 h) and when the individuals have no access to water. Future studies should now examine with a larger sample size the combined impacts of plumage color, water accessibility, and duration of sun exposure on body temperature.

Unfortunately, the sample size was too low to test if such difference in plumage and cloacal temperatures occur when the birds are maintained in the shade (i.e. control birds). However, control birds had plumage temperatures, which were close to ambient temperature and much lower than the plumage temperature of all sun-exposed birds. In addition, the cloacal temperature of control pigeons was within the natural range of body temperature for this species (Bittencourt et al., 2015), suggesting that control pigeons were not overheating when maintained in the shade.

Although darker tegument and increased tegument temperature can be beneficial in some species or under specific circumstances (Clusella Trullas et al., 2007; Roulin, 2014; Stuart-Fox et al., 2017; Pinkert and Zeuss, 2018), this study also suggests that sun exposure and heat can represent a thermal constraint for dark birds. Therefore, the thermal costs and benefits of plumage color might be involved in the spatial distribution of specific morphs in the rock pigeon (Obukhova, 2007).

4.2. Gular fluttering behavior

Although increased body temperature is recognized as a way to save water during heat exposure in birds (Tieleman and Williams, 1999; Schleucher et al., 2001; Nilsson et al., 2016), birds cannot afford to increase their body temperature over a specific sublethal value because of the associated physiological and survival costs (Huey et al., 2012). For example, an increase of body temperature is known to result in an increased metabolism, especially in birds (23% increase in energy expenditure per °C in ducks, Marais et al., 2011). In order to cope with extreme heat, birds and pigeons use panting and gular fluttering behavior, which allow them to cool down by increasing their water evapotranspiration (Dawson, 1982; Tielemans and Williams, 2002; Smith et al., 2015). Accordingly, I found not only that sun-exposed birds were more likely to show gular fluttering behavior than controls, but also that the probability to show this cooling behavior was positively associated with cloacal temperature. This supports the idea that gular fluttering behavior allows sun-exposed birds to limit the impact of solar radiation on body temperature (~0.5 °C increase in this study), and thus, to keep their body temperature within the natural range for this species (Bittencourt et al., 2015).

Surprisingly and despite the difference in plumage and body temperatures between dark and light birds, there was not any significant difference in gular fluttering behavior between these two groups of birds. I may not have been able to detect a significant difference in behavior between these two groups, especially because categorical behavioral data often requires large sample sizes to detect significant differences (Garamszegi, 2016). Because, as described before, the cloacal temperature of sun-exposed blue-bar birds did not significantly differ from that of controls, gular fluttering behavior may be effective enough to regulate the body temperature of light birds for a short period (1 h). In contrast, and despite gular fluttering behavior, sun-exposed dark birds had a slightly higher cloacal temperature than control birds (and sun-exposed light birds). This suggests that gular fluttering behavior may not be sufficient to regulate body temperature in dark birds exposed to heat and sun because their darker plumage is associated with higher plumage temperature and heat transfer. Future studies are now required to confirm this result and to investigate the impact of long-term sun exposure (>1 h) on body temperature of the different morphs of rock pigeons.

Importantly, thermoregulatory behavior and physiology can have a high incidence on heat load, limiting therefore the potential influence of plumage color on plumage and body temperatures (Huey et al., 2012; Stuart-Fox et al., 2017). For example, previous studies showed that species or individuals may use shady shelters and reduce their activity in case of high solar radiation and heat (Huey et al., 2012; Rowe et al., 2013; Schweizer et al., 2019). In this study, the objective was to experimentally test the influence of plumage color on plumage and body temperatures. To do so, the experimental birds were exposed to direct sun with no possibility to select and hide in a shady place. Therefore, it is not possible to rule out that darker pigeons may adopt specific activity schedule (e.g. being active during cooler morning and evening; Rowe et al., 2013) or specific behaviors (e.g. resting in a shady place, Huey et al., 2012), which attenuate the impact of their dark plumage on body temperature. Further studies should therefore test whether polymorphic rock pigeons adopt contrasted thermoregulatory behaviors according to their plumage color.

Declarations of competing interest

We declare no conflict of interest.

CRediT authorship contribution statement

Frédéric Angelier: Formal analysis, Data curation, Writing - original draft.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtherbio.2020.102601.

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