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ORIGINAL ARTICLE

Plumage colour predicts dispersal propensity in male pied flycatchers

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Abstract

Melanin-based colouration of tegument structures may be related to variability in the expression of certain strategies or behaviours within a species, including the propensity to disperse. This is because melanin synthesis may be physiologically linked to certain behaviours and personality traits, as proposed by the hypothesis of the pleiotropy in the melanocortin system (HPMS). During a 28-year period (1988–2015), we studied the melanin-based dorsal colouration of male pied flycatchers (*Ficedula hypoleuca*) in relation to natal dispersal movements between contrasting (pine and oak) habitats. In addition, the relationship between tonic immobility (TI), a measure of individual fearfulness towards predators, and plumage colour was examined using a shorter time series. Consistent with HPMS, males' dispersal propensity was related to their plumage colour, with the blackest individuals being more likely to disperse into a new habitat to breed. Blacker males remained for longer in TI than lighter ones. The positive relationship between plumage melanisation and TI might result from the pleiotropic effect of the melanocortin system on glucocorticoid-mediated stress and fearfulness responses as well as on eumelanin synthesis. This study provides solid empirical support for the HPMS in relation to natal dispersal behaviour.

Significance statement

Individual behaviour can be integrated with other phenotypic traits via the pleiotropic effects of some biochemical pathways. Recent research has shown connections between melanin-based colouration, personality and certain life history traits. However, the relationship between colouration and natal dispersal—a critical phase of life—has received comparatively little attention. We studied this link in the pied flycatcher, a small bird in which males exhibit considerable variation in dorsal plumage colour, ranging from brown to black. By following individuals from fledging to settlement, we show that males with a higher percentage of black feathers are more likely to disperse into novel environments than lighter males. Furthermore, we found an association between plumage melanisation and individual fearfulness to predators, possibly due to the shared pathways of melanin synthesis and stress responses. Our results highlight the potential of the interplay between melanin production and individual behaviour to explain the maintenance of colour variability in natural populations.

Keywords Adrenocorticotropin hormone · Corticosterone · Eumelanin · *Ficedula hypoleuca* · Melanocortin system · Tonic immobility

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Introduction

Dispersal is a key life history trait, with important implications for the spatial distribution, density and genetic structure of natural populations (Johnson and Gaines 1990; Bélichon et al. 1996; Holt and McPeek 1996). Dispersal movements can be classified into two main categories: breeding dispersal, in which adults change breeding sites between successive years, and natal dispersal, in which young move from their birth place to their first breeding site (Greenwood and Harvey 1982). Departure and settlement decisions of dispersers are not the result of random processes, but depend on multiple factors, such as environmental cues (e.g. habitat quality and conspecifics density; Doligez et al. 2004; Garant et al. 2005), previous experience (Davis and Stamps 2004) and phenotypic attributes, including personality (Fraser et al. 2001; Bize et al. 2017), structural size (Camacho et al. 2013, 2015), body mass (Senar et al. 2002; Garant et al. 2005) and sex (Trochet et al. 2016), among others (reviewed by Clobert et al. 2009).

Melanin-based colouration of structures in the external integument (skin, hair or feathers) may be related to the variability in the expression of certain strategies or behaviours within a species, including dispersal propensity (Ducrest et al. 2008). The synthesis of melanin is regulated by a complex system of chemical mediators, including melanocortins, a family of peptidic hormones that activate melanin synthesis, stimulating the production of eumelanin (responsible for black and grey colourations; Ducrest et al. 2008). The synthesis of pheomelanin (responsible for brownish and reddish tones; McGraw 2006) shares some pathways with eumelanin, but it is promoted by an antagonist of melanocortins—the agouti signalling protein (ASIP)—that also blocks eumelanin synthesis (Ducrest et al. 2008). Interestingly, melanocortins also mediate many other physiological functions, as well as the expression of certain behaviours (Ducrest et al. 2008). For example, melanocortins mediate the synthesis of several hormones involved in sexual behaviour, aggressiveness and territoriality (Ducrest et al. 2008). Pleiotropic effects of melanocortins might thus lead to an association between colouration and behaviour (hereafter, Hypothesis of the Pleiotropy in the Melanocortin System (HPMS); Ducrest et al. 2008; Nicolaus et al. 2016). If HPMS is correct, one would expect a link between integument colouration and certain behavioural traits and strategies related to sexual activity, exploration, aggressiveness and dominance, as it is the case for dispersal and subsequent settlement to breed in a novel environment (Dingemanse et al. 2003; Cote et al. 2010).

Although HPMS has a solid theoretical basis from which the covariance between melanic colouration and dispersal patterns can be derived (Ducrest et al. 2008; Roulin and Ducrest 2011), supporting empirical evidence is still limited to a couple of study systems. In the barn owl (*Tyto alba*), the field studies examining differences in habitat selection and dispersal behaviour between dark and pale reddish pheomelanic individuals have found that habitat selection by females, but not by males, was colour dependent (Dreiss et al. 2012; van den Brink et al. 2012a; Roulin 2013). In another study examining the relationship between plumage colouration and dispersal propensity in the common swallow (*Hirundo rustica*), Saino et al. (2014) showed that males, but not females, with brown ventral colouration were more likely to disperse than those with whitish bellies. In both cases, a greater dispersal propensity—both quantitatively and qualitatively—in the more melanised individuals was reported. These previous studies provide support for HPMS. However, further empirical evidence is needed, particularly from study models displaying traits where eumelanin is the main pigment underlying colour traits, as its synthesis is more directly enhanced by the action of melanocortins (Ducrest et al. 2008).

The links between personality-related behaviours and melanin-based colouration are at the core of the HPMS (Ducrest et al. 2008). Besides propensity to exploratory behaviours, fearfulness is a key aspect of individual personality that may influence individual propensity to disperse. Moving to an unknown habitat or territory implies facing a wider array of potential predators, and the individual strategy to cope with this kind of hazard is likely an important factor determining its success. Fearfulness response to predators is commonly measured by the tonic immobility (TI) response test (Réale et al. 2007). TI is a behaviour induced by physical restraint by which animals become temporarily paralysed as a response to capture by a perceived predator (Jones and Faure 1981; Edelaar et al. 2012). Two studies on raptor species, the barn owl and the common kestrel (*Falco tinnunculus*), have reported positive associations between the extent of eumelanin-based colouration and TI responses (van den Brink et al. 2012b,c), which may result from underlying connections between melanin synthesis and glucocorticoid physiology (van den Brink et al. 2012c). However, no study has tested so far the existence of these links in non-raptor species, like passerines, which are exposed to a wider range of potential predators and whose fearfulness responses may show a different degree of colour dependence.

Here, we assess the relationship between eumelanic plumage colouration and dispersal propensity from the natal habitat patch in a population of pied flycatchers (*Ficedula hypoleuca*) monitored over a 28-year period. We focus on one prominent chromatic feature of the plumage of pied flycatcher males, their melanin-based dorsal colouration. In autumn and winter, the sexes are almost indistinguishable as they both have a brownish plumage. Prior to spring migration, both sexes undergo partial moult, involving renewal of most body feathers (Karlsson et al. 1986; Lundberg and Alatalo 1992). Changes in the general appearance of pied flycatchers following this moult are much more noticeable in males, which acquire their characteristic ‘black and white’ nuptial plumage (Lundberg and Alatalo 1992). However, there is considerable variation in dorsal colouration within populations, ranging from completely black males to individuals with a more female-like appearance due to the presence of many pale grey/ash-brownish feathers (Fig. 1). Higher proportions of black feathers on the back suggest higher overall concentrations of both types of melanins in the plumage, but particularly imply a much higher concentration of eumelanin relative to pheomelanin (Liu et al. 2014; Galván and Wakamatsu 2016).

Fig. 1 Male pied flycatchers illustrating between-individual variation in dorsal colouration. From left to right, estimates of the percentage of black feathers on head and mantle in these birds were 5, 15, 40, 55, 85 and 95%

According to the predictions of the HPMS, we expected that more eumelanic individuals would be more likely to disperse from their natal patch and settle to breed in a novel habitat than less eumelanic individuals. In addition, we might expect that different contents of eumelanin reflect among-individual differences in behavioural traits, like TI responses. Thus, based on previous evidence on birds (van den Brink et al. 2012b,c), we predicted that more eumelanic individuals would show higher TI responses.

Methods

Study system and field procedures

Fieldwork was conducted between 1988 and 2015 in a pied flycatcher population located near La Hiruela (Madrid), Central Spain (41° 04′ N, 3° 27′ W). Field procedures and study sites are described in detail elsewhere (Camacho et al. 2015). In brief, the study area consists of two distinct habitat patches: a mature oak (*Quercus pyrenaica*) forest and a mixed pine (mostly *Pinus sylvestris*) plantation separated by a 1-km-wide strip of unsuitable breeding habitat for the species. Nest boxes (156 and 81) were provided in 1984 and 1988, in the oak and the pine forest, respectively (e.g. Camacho et al. 2013, 2015).

From mid-April, when the first migrants arrive at the study site, nest boxes were regularly checked at roughly 3-day intervals to determine exact laying and hatching dates, clutch size and number of offspring. On day 13 (hatch day = 1), when nestlings have already attained the definitive adult size (Potti and Merino 1994), they were individually marked with numbered metal rings and measured for tarsus length (to the nearest 0.05 mm) and body mass (to the nearest 0.1 g). Breeding adults were caught while incubating (females only) or while feeding chicks (both sexes) with a spring trap installed inside the nest box (Camacho et al. 2017). Breeding individuals were aged as 1 year old or at least 2 years old based on their plumage characteristics (Karlsson et al. 1986; Potti and Montalvo 1991a; Lundberg and Alatalo 1992) and measured for standard morphological traits.

Dispersal behaviour

Pied flycatchers generally return to their natal site to breed regardless of the habitat type, but previous studies on this population have shown that over 25% of them move to the alternative habitat patch between the year of birth and the year of first breeding (Camacho et al. 2013, 2016). Less than 2% of adults change habitats later in life (Camacho et al. 2013), suggesting that critical dispersal events occur during natal dispersal. For this reason, only first-time breeders of known origin (i.e. ringed as nestlings) are considered in this study. For the purposes of this study, natal dispersal is defined as a change of patch irrespective of the distance between the natal nest box and the first breeding nest box. Because of the small scale of our study area, the likelihood of changing habitats is not determined by proximity of the natal nest box to the adjacent forest patch (Camacho et al. 2016). Furthermore, the treatment of dispersal as a habitat shift, as opposed to dispersal distance, has been found to be biologically relevant in previous studies on this population, as it depended on both individual (e.g. sex, body size, natal experience) and environmental (e.g. local breeding density) factors (Camacho et al. 2013, 2016). First-time breeders were classified into ‘dispersers’, defined as those that move from their natal patch to breed in the adjacent one, and ‘philopatric’, defined as those that return to their natal patch to breed. Dispersal outside the study area is an extremely rare event (pers. obs. from non-systematic explorations of surrounding areas) and, therefore, is unlikely to bias the results of this study. Males stemming from manipulated broods for experimental purposes (e.g. cross-fostering) were removed from the dataset.

Colour measurements

Following previous studies on the pied flycatcher (e.g. Drost 1936; Lundberg and Alatalo 1992; Lehtonen et al. 2009; Laaksonen et al. 2015), dorsal colour was visually estimated in the field as the percentage of the area of head and mantle covered by non-black feathers (brownish, grey or white), excluding the rump and the white forehead patch. To minimise observer bias, colour measurements were done blind to individual dispersal status. Data on bigamous males ($n = 19$)

captured twice within the same year were used to confirm the consistency of colouration estimation (repeatability = 0.81, $p < 0.001$; Lessells and Boag 1987). Between-observer repeatability, estimated from a subset of 30 dorsal photos (similar to those of Fig. 1) independently scored by two of us (JP and DC), was also high ($R = 0.90$, $p < 0.001$). Because this study focuses on the production of black plumage, we used the reciprocal of the variable originally recorded in the field to give a more intuitive appreciation of plumage blackness than the original brownness estimates. For brevity, this character will be referred to hereinafter as 'blackness'. Also, we will refer to males scored high in blackness as 'blacker' or 'darker' males, as opposed to 'lighter' or 'browner' males, as those are the most common appreciations to the human eye, as also described in the literature on the species (Lundberg and Alatalo 1992).

Tonic immobility

Between 2010 and 2014, we subjected male pied flycatchers to TI tests. For measuring TI, once morphological measurements were collected, each male was placed on its back on a 13 × 13 cm cardboard square in a quiet, shaded place. After making sure the individual stopped moving, the observer released the grip of the bird, set a timer, carefully moved 2–4 m away and recorded the time elapsed until the bird eventually 'escaped'. TI measurements were taken by the same observer (CC) to avoid potential bias. It is important to note that TI tests were done blind to colour scores as, to avoid undesirable disturbances, TI tests were performed at some distance from where morphological and colour measurements were taken. Because of concerns for the welfare of birds, as well as due to time constraints derived from the simultaneous capture of numerous birds, 3 min was set as the upper limit to TI recording. To determine this time limit, the duration of the TI test was progressively reduced from 20 to 3 min during a pilot trial performed in 2010. Only 8% of the birds that remained in TI for longer than 3 min turned back by themselves before being 'awoken' by us ($n = 15$ out of 188 birds), indicating that a 3-min trial is long enough to capture variability in TI in this pied flycatcher population.

Data analyses

To investigate the relationship between individual colouration and dispersal propensity, we fitted a generalised linear mixed model (GLMM, binomial distribution, logit link function) including the natal dispersal status (0 = philopatric, 1 = disperser) as a binary response variable and blackness of the dorsal region as an explanatory variable. In addition, we included in the models other factors that could affect the motivation of birds to disperse. Breeding density in the pine and the oak forest, measured as the number of nest boxes occupied by pied flycatchers in each patch, was included as separate covariates to control for the effects of nest site competition (Garant et al. 2005; Camacho et al. 2015). Laying date, which is an accurate proxy for the arrival date in our study population (Potti and Montalvo 1991a), was also included as a covariate to account for the potential effect of delayed phenology (e.g. decreasing nest site availability as the season progresses).

Dispersal propensity might vary depending on the habitat of origin (Camacho et al. 2016). In addition, the intensity of competition for nest sites in the source and/or destination habitats might act as a confounding factor. Thus, habitat of origin and its interaction with breeding density in each habitat patch were included as fixed effects. The interaction between percent black and habitat of origin was also fitted as a fixed effect. Body size, measured as tarsus length, was included as a covariate, as it is known to influence the direction of dispersal of pied flycatchers moving between the two study habitats (Camacho et al. 2013). Due to the large variation in the age of first reproduction in the study population (1–3 years; Potti and Montalvo 1991b), male age was also included as covariate in the model. Year was fitted as a random effect to account for temporal heterogeneity in environmental conditions throughout the study period.

The distribution of the TI data was markedly bimodal, implying that individuals either 'awoke' at some time during the 3-min trial or had to be awoken after this time (45 and 55%, respectively, $n = 319$ individuals). Following previous studies showing divergent selection for long or short duration of TI in birds (Mills and Faure 1991, 2000), individuals were categorised as 0, if they escaped, or 1, if they were flushed. To test for an association between plumage colouration and TI, we used a generalised linear model (GLM, binomial distribution, logit link function), including TI as a binary response variable and percent black as a covariate. In addition, dispersal status, breeding habitat and the age at first breeding were included in the model as controlling factors. Because some birds could not be given the opportunity to enter TI due to disturbances (e.g. passing car noise) during induction attempts, we ran the same model after excluding individuals that righted themselves less than 10 s after the onset of the attempt to make sure that our results were not confounded by TI induction failure.

GLMMs were performed in R version 3.2.4 (https://www.r-project.org) using the function *glmer* of the 'lme4' package (Bates et al. 2011). Sample sizes may differ among analyses because not all data were taken for all individuals. Model selection was carried out by stepwise removal of non-significant terms from a saturated model (i.e. containing all main effects and interactions). Before interpreting the output of the GLMMs, we systematically performed model diagnostic statistics to avoid misleading conclusions based on statistical artefacts. To this end, we checked the assumptions about the distribution of residuals through diagnostic plots and examined collinearity or the presence of influential cases. These analyses did not show any obvious deviation from GLMM assumptions or any collinearity problems.

Data availability The datasets analysed during the current study are available from the corresponding author on reasonable request.

Results

Males' dispersal propensity was related to their plumage colour, as the blackest individuals were more likely to disperse into a new habitat to breed (Table 1; Fig. 2). Natal dispersal between habitats was also affected by population density in the non-natal site, but this effect varied depending on the habitat of origin (Table 1). Males born in the pine forest showed a greater propensity to disperse to the adjacent oakwood as population density in the oakwood decreased. In contrast, the dispersal decisions of males born in the oakwood appeared to be independent of changes in breeding density in the destination habitat. No effect of the age of first reproduction, breeding phenology or body size was detected (Table 1).

TI was measured for 319 different males, including first-time and experienced breeders. Blackness of the dorsal region was positively associated with the TI duration, i.e. blacker males remained for longer in TI than browner males (GLM: estimate ± SE = 0.013 ± 0.006, $z = 2.39$, $p = 0.017$), after excluding the non-significant effects of dispersal status, breeding habitat and age at first breeding. Further analysis excluding males that escaped within the first 10 s confirmed that the association between mantle colour and TI result was not confounded by potentially unsuccessful TI induction attempts (GLM: estimate ± SE = 0.015 ± 0.007, $z = 1.99$, $p = 0.046$, $n = 144$ males).

Discussion

We have shown associations between the plumage colouration of male pied flycatchers and two behavioural traits, the propensity to disperse between contrasting habitats and TI response. Darker males were more likely to leave their natal site and settle in a new habitat than those with a less eumelanic colouration (e.g. appearing greyer or browner at some distance), thus supporting the predictions of HPMS (Ducrest et al. 2008). In addition, darker males remained for longer in TI than lighter males, in what can be interpreted as additional evidence in support of HPMS. We will briefly discuss these issues in turn.

Increased eumelanin synthesis may be associated with the expression of certain behavioural traits, such as aggressiveness and physical and sexual activity, as mediated by the pleiotropic action of melanocortins (Ducrest et al. 2008). These traits are often identified as 'bold' behavioural syndromes, and may be related to greater dispersal propensities (Dingemanse et al. 2003; Cote et al. 2010). Two previous studies have examined individual variation in dispersal tendency with respect to the extent of melanic plumage colouration (van der Brink et al. 2012a; Saino et al. 2014). In both study systems, more melanised individuals had higher dispersal propensity, in seeming consistency with the results of this study and the HPMS. However, beyond the melanin content of feathers in general, our results on male pied flycatchers are the first evidence of a relationship between dispersal propensity and the relative concentration of eumelanin over pheomelanin in the plumage.

Darker pied flycatchers returning to breed for the first time in the study area had a higher tendency to leave their natal patch and settle in a new habitat, after controlling for other factors influencing natal dispersal, such as population density and differences in the dispersal propensity due to the natal

Table 1 Results of the GLMM analysing the effect of blackness of male dorsal plumage, measured as the percentage of black feathers on head and mantle, on dispersal propensity between habitats. The effects of body size (tarsus length), age at first breeding, breeding phenology (laying date), habitat of origin and population density in the natal and the non-natal habitat are also shown

	Estimate	SE	Z	P
Intercept	− 5.846	1.397	− 4.19	*< 0.001*
Blackness	0.018	0.007	2.76	*0.006*
Body size	0.066	0.187	0.35	0.725
Age at first breeding	0.111	0.123	0.90	0.370
Breeding phenology	0.001	0.015	0.07	0.943
Population density in natal habitat	0.017	0.044	0.39	0.700
Population density in non-natal habitat	0.053	0.024	2.21	*0.027*
Habitat of origin	3.713	1.176	3.16	*0.002*
Percentage black × habitat of origin	0.012	0.014	0.874	0.382
Population density in natal habitat × habitat of origin	− 0.005	0.033	− 0.15	0.884
Population density in non-natal habitat × habitat of origin	− 0.038	0.015	2.53	*0.012*

Number of individuals = 644; number of years = 25. Statistics and P values of non-significant terms are those obtained by adding them individually to the final models, in which only significant predictors were retained. P values < 0.05, shown in italics, were considered statistically significant

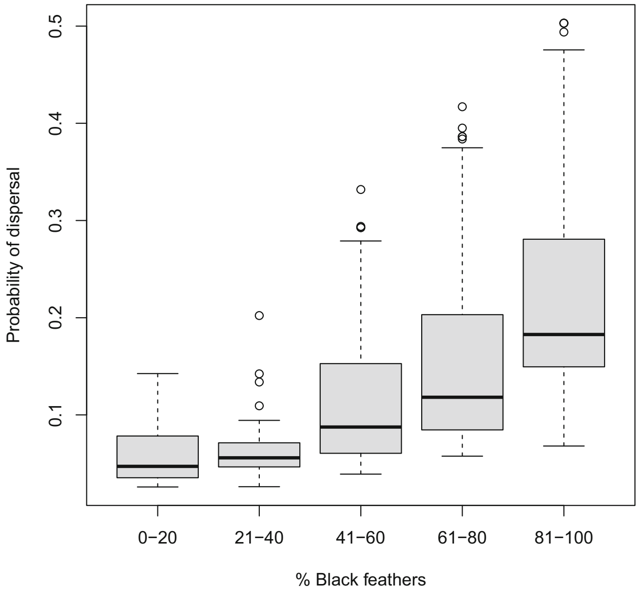

Fig. 2 Relationship between blackness of dorsal plumage, measured as the percentage of black feathers on head and mantle, and probability of dispersal in male pied flycatchers. Fitted values from the GLMM are shown. Shown are the median (central line in box), the upper and lower hinges (edges of the box approximating the first and third quartiles), the whiskers (defined as 1.5× the hinge spread) and outliers (open circles)

habitat type (see Camacho et al. 2016 for a discussion on these issues). The pleiotropic effects of melanocortins also involve higher testosterone levels, a hormone that has also been shown to influence natal dispersal behaviour (e.g. Nunes et al. 1999; Tschirren et al. 2007). Males moving from their birthplace to the adjacent patch may suffer from lower familiarity with their new environment, which probably limits their ability to acquire a suitable territory. Under this context, higher testosterone levels could confer darker males a greater competitive ability to acquire and defend a nest site in non-familiar areas.

Darker pied flycatchers persisted for longer in TI than lighter ones, suggesting a link between colouration and individual personality (van den Brink et al. 2012b). However, according to previous studies on other species displaying variable extensions of melanin-based colouration in their plumage (van den Brink et al. 2012a, b; Nicolaus et al. 2016), this result may appear inconsistent with the expected overall ‘bolder’ personality of darker individuals. It should be noted, however, that TI measures individual fearfulness responses towards a potential predator, which is probably weakly or not related to other components of individual personality more closely involved in dispersal, like nest defence, exploratory behaviour or responsiveness to novel stimuli (e.g. Réale et al. 2007; van den Brink et al. 2012a; Wuerz and Krüger 2015; Nicolaus et al. 2016; Bize et al. 2017). In fact, the positive relationship between plumage darkness and TI may result from the pleiotropic effect of the melanocortin system both on glucocorticoid-mediated stress and fearfulness responses on one hand and on eumelanin synthesis on the other (Ducrest et al. 2008; Almasi et al. 2010).

As noted by the HPMS, eumelanin synthesis is activated by a series of melanocortins, including the adrenocorticotropin hormone (ACTH). ACTH is also a key component of the hypothalamic-pituitary-adrenal axis, where it promotes the production and release of corticosterone by the cortex of the adrenal glands, thereby triggering physiological responses to stressful situations. Importantly, corticosterone-based stress responses and TI appear positively associated, as shown by studies in captivity on breeding lines artificially selected for long and short TI or by further correlational studies from poultry (reviewed in Cockrem 2007). Therefore, the positive association between TI and plumage melanisation in male flycatchers found here is consistent with the general framework proposed by the HPMS, as both the biochemical regulation of eumelanin synthesis and the expression of fearfulness against predators may share common pathways, ultimately connected by physiological stress responses. These interconnections make sense in the context of the colour-dependent propensity to disperse found here, as plumage colour may ultimately reflect variation in the coping styles of individuals exposed to environmental challenges (Cockrem 2005; Carere et al. 2010; Roulin and Ducrest 2011).

Conclusion

Our results indicate that eumelanic plumage colouration predicts natal dispersal behaviour of male pied flycatchers, such that more eumelanic males are more likely to change habitats during dispersal than lighter ones. We also found an association between the plumage colouration and TI, possibly as a result of the shared pathways of melanin synthesis and stress responses. Further studies testing the predicted differences in the hypothalamic-pituitary-adrenal axis function among individuals varying in eumelanin-based colouration are nevertheless needed to confirm our results. In addition, studies using a set of standard battery of behavioural tests (e.g. Réale et al. 2007) are required to obtain a more complete characterisation of the personality of individuals in relation to eumelanin-based colouration. Ultimately, this will allow a better understanding of the ecological implications of the HPMS and its potential to explain the maintenance of melanin-based colour variability under variable ecological scenarios.

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Compliance with ethical standards

Ethical approval Birds were caught and ringed under licences from the Ringing Office of the Spanish Ministry of Agriculture, Food, Fisheries and Environment. All work was subject to review by the ethical committees at the Doñana Biological Station and the CSIC headquarters (Spain) and adhered to Spain standard requirements.

Conflict of interest The authors declare that they have no conflict of interest.

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