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Tail pattern variation in the Black Wheatear (*Oenanthe leucura*).

**Cristian Pérez-Granados**¹, # and **Javier Seoane**¹


# Corresponding author: E-mail address: cristian.perezg@uam.es. Tel: +34 (914978271). Fax: +34 (914978001).

**Abstract**

Delayed plumage maturation occurs in birds by retaining subadult plumage until after their first breeding season. We analysed data from 114 Black Wheatears (*Oenanthe leucura*) trapped during 2014-2016 in Southeastern Spain. We explored whether biometric measurements, and more specifically tail pattern, differ among age and sex classes, and its relation to delayed plumage maturation. Males and adults were heavier and had longer wings and tails than females and juveniles, respectively. Adult birds had longer terminal black tail bars than juveniles, which suggests a potential dominance signaling function for the tail pattern. Further research is needed to investigate the relationship of these traits to sexual selection and dominance in Black Wheatear.

**Keywords:** Biometry, delayed plumage maturation, dominance signal, sexual selection.
Delayed plumage maturation (DPM hereafter) is a widespread age-dependent trait, defined by the delayed acquisition of definitive plumage by 1st-year individuals (subadults hereafter) until after their first breeding season (Cucco and Malacarne 2000). Subadults with DPM are usually sexually mature and can potentially breed, which creates an interesting evolutionary problem about what is their advantage for maintaining distinctive non-adult plumages. DPM might allow subadults to avoid confrontations with adults by honestly signaling subordination, increase their fitness by sneak a foothold on a territory, or by decreasing their detectability by making them more cryptic (see an extensive review in Cucco and Malacarne 2000). DPM has also an impact in other interesting age-dependent traits, usually related to mate attraction and male competition, such as body size or the presence of colourful plumage (e.g. Barber and Wright 2017).

The Black Wheatear (*Oenanthe leucura*), a medium-sized passerine, is known for its stone carrying behaviour performed a few days prior to egg laying (Moreno et al. 1994; Aznar and Ibáñez-Agulleiro 2016). Females carry stones to nest sites (Aznar and Ibáñez-Agulleiro 2016) and in males this behaviour appears to represent a form of post-mating sexual display allowing the adjustment of reproductive effort by females (Moreno et al. 1994). Pair formation in the species has been related to male displays, when males sing from prominent locations, with their wings and tails erect in a “vertical plane” (Moreno 2016). This suggests that tail pattern could play a key role in mate choice in the Black Wheatear, as has been proposed for other species (e.g. Kose and Möller 1999).

Adult Black Wheatears perform a fully post-breeding moult (July-October), while juveniles undergo a post-juvenile partial moult (July), involving only a few internal greater wing coverts (Pérez-Granados 2017). Thus, subadults show DPM by
maintaining a large number of wing coverts and the flight and tail feathers until after the
first breeding season (Senar et al. 1998). Previous studies have suggested that wing
loadings of the species have been modified by selection pressures related to stone
carrying display (Møller et al., 1995). To our view, these characteristics make the Black
Wheatears a good case study to explore the adaptive significance of DPM and inter-
individual differences in biometry.

In this study we aimed to comprehend the role of the terminal black tail bar of Black
Wheatears as a potential signal. We hypothesized that adult birds would have larger
terminal bars than juveniles if bars play a main role in signaling dominance. If bars play
a role in sexual selection, we expect that males would have larger terminal bars than
females. We also explored biometric differences between age and sex classes and
provide the first data of juvenile Black Wheatear biometry.

Material and Methods

Study area

The field work took place from July to November 2014-2016 in three arid localities
around Alicante city (38°21’N, 0°29’ W, southeastern Spain). Localities were separated
by 7.2 ± 5.1 km, located at 100 m a.s.l. and had a mean annual temperature of 18°C and
mean annual precipitation of 300 mm. Black Wheatears were caught in the two first
hours after dawn, using small spring-traps baited with tenebrionids. Birds were attracted
with the aid of an mp3 and a Radioshack amplifier. Birds were banded and maximum
wing length, length of the eighth primary (P8 hereafter) and tail length were taken with
specified rulers (accuracy 0.5 mm). Tarsus length and the length of the terminal black
bar from the tip to the end of the black area on the outer (external tail bar hereafter, Fig.
1) and innermost (central tail bar hereafter, Fig. 1) rectrices, taking the maximum
parallel length to the rachis, were measured with dial calipers (accuracy 0.01 mm).
Individuals were weighed with a precision scale (0.1 g). Birds were sexed and aged by plumage characteristics (Pérez-Granados 2017), and were categorised as juveniles or adults (after at least one complete moult cycle).

**Statistical analyses**

We built linear models for each biometric measurement as the response variable, and sex, age and its interaction as explanatory factors. We included tarsus length --a surrogate for body size-- as a controlling covariate (wing length was used instead as a controlling covariate when testing differences in tarsus length and tail length when testing differences in the size of the terminal black tail bar). All birds trapped were analyzed together, since there was no difference in body mass between individuals captured in different months, years or sites (ANOVA test, Month $F_{5,106} = 1.58$, $P = 0.17$; Year $F_{2,109} = 1.22$, $P = 0.30$; Site $F_{2,109} = 0.19$, $P = 0.98$). The level of significance was $p < 0.05$ and results were expressed as mean ± SE. Continuous variables were log-transformed. The analyses were done with R 3.2.1 (R Development Core Team 2014).

**Results**

In total, 114 Black Wheatears were captured, of which 59 were juveniles (38 males [64.4%], 21 females [35.6%]) and 55 were adults (34 males [61.8%] and 21 females [38.2%]). We trapped a larger number of males (Pearson’s Chi-squared test with Yates $= 3.50$, $P = 0.06$), but we captured a similar number of birds of each age (Pearson’s Chi-squared test with Yates $= 0.02$, $P = 0.89$), and a similar proportion of each sex within age groups (Pearson’s Chi-squared test with Yates $= 0.05$, $P = 0.81$). In all analyses, age and sex interaction was never significant (Online Resource 1). Once body size was controlled, we found that males were heavier and had larger wings, tarsus and tail length than females (Table 1). Likewise, adult birds were heavier and had larger wings and tails than juveniles, but tarsus length did not differ with age (Table 1). Once the tail
length of individuals was controlled for, adult birds had significantly longer central tail bars than juveniles (Table 1). We also found that males had smaller external tail bars than females (Table 1).

*Discussion*

DPM causes subadult and adult individuals have to face the challenging choices of the breeding season showing different plumages. Age-differences found in the size of the terminal black bars in the Black Wheatear suggest that tail pattern may play a role in signalling dominance, which might allow subadults to honestly show subordination towards adults (Senar et al. 1998, Hawkins et al. 2012). The tail pattern may contribute to the establishment of social hierarchies, which has been reported to diminish the intensity and frequency of intraspecific agonistic aggressions in birds, thus avoiding a waste of time and energy (VanderWerf and Freed 2003). DPM might also be used in mate choice. Hence, adult birds that are probably more dominant and experienced should also select mates of similar ages because of the well-known positive relationship between longevity and fitness, which explains the evolution of age-assortative mating (e.g. Lack 1968).

Males had shorter external tail bars than females, but no differences between sexes were found in the central tail bar, which is three times larger (more conspicuous) than the external bar. It might also be related to the possible use of tail pattern as signalling dominance in the Black Wheatear. If that is the case, subadult males might also be more interested to clearly show their subordination with smaller tail bars, since males are usually more aggressive than females in the studied species (Moreno 2016).

Biometric differences found in Black Wheatears were similar to those described in many other European passerines: adult and males are larger than juveniles and females, respectively (e.g. Alatalo et al. 1984). Larger wings and tails in males, particularly in
the case of adult individuals, agree with the hypothesis of a specific adaptation to the astonishing stone carrying display (Møller et al. 1995). Adult females might also be larger due to ontogenetic processes (Badyaev 2002), but might also be related to stones carried by females for nest support (Aznar and Ibáñez-Agulleiro 2016). Shorter wings in juvenile birds might be a response to increase their survival probability early in life, by improving their manoeuvrability and ability to evade predators (e.g. Alatalo et al. 1984). The use of songs to attract individuals has been criticized for biasing captures in several ways (e.g. De la Hera et al. 2017), but we captured a similar number of adults and subadults and a similar proportion of each sex within age groups was captured. This suggests that the biometry data compiled might be considered as representative of the general population at our study localities. A caveat is that birds were not captured during the breeding season, as it could be argued that level of tail feathers abrasion may be different in autumn and spring, which may affect signalling. However, dominance signalling may act during the whole year due to the territorial character and resident status of the studied species (Moreno 2016). We assume that abrasion of feathers did not differ among individuals according to age categories and thus abrasion would not interfere with signalling at breeding period. However, if juvenile birds showed higher abrasion of feathers due to lower feather quality, this would increase the potential signalling dominance in spring.

Our research on Black Wheatear has given evidence that tail pattern and biometry differed after the first complete moult. We suggest that tail pattern could be used for the recognition of older birds by a quick screening of the plumage. However, we have no empirical evidence that smaller tail bars reduces aggression by adults toward subadults, and thus further research is needed to evaluate the adaptive significance of DPM in the Black Wheatear. The best evidence would come from studies testing the relationship of
these traits and aggressive response or mate choice, or from experimental manipulations of the size of the terminal tail bar to test its effect on reproductive fitness, or aggressive response between individuals.

Acknowledgements

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References


Table 1: Summary table of biometric measurements and body mass of Black Wheatears (*Oenanthe leucura*) trapped in Alicante, Spain, according to age and sex. Data are presented as mean ± SE, N and range in parentheses. P shows the significant differences between age and sex classes, according to linear models and type-II partitioning of variances for the measurement, after considering a surrogate for body or tail size as a controlling variable, including age, sex and interaction as predictors: S — sex (male/female); A — age (adult/juvenile); * — p < 0.05; ** — p < 0.01; *** — p < 0.005. P8 refers to the length of the eight primary feather. See detailed analyses in Online Resource 1.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Juveniles</th>
<th>Adults</th>
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<td>Female</td>
<td>Male</td>
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<td>Mean ± SD, N (min-max)</td>
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<tr>
<td>Wing length (mm)</td>
<td>94.6 ± 2.5, 21 (91.0 - 101.0)</td>
<td>99.0 ± 2.0, 38 (94.0 - 103.5)</td>
<td>96.6 ± 1.9, 19 (93.5 - 99.5)</td>
<td>100.3 ± 2.3, 24 (96.0 - 104.0)</td>
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<td>S***</td>
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<td>P8 (mm)</td>
<td>71.7 ± 1.8, 20 (69.0 - 76.0)</td>
<td>75.1 ± 1.8, 37 (71.0 - 79.0)</td>
<td>73.7 ± 2.0, 17 (69.0 - 76.0)</td>
<td>76.3 ± 2.7, 25 (71.5 - 81.0)</td>
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<td>S***</td>
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<td>Tail length (mm)</td>
<td>68.7 ± 2.4, 21 (64.0 - 73.0)</td>
<td>71.1 ± 2.5, 36 (67.0 - 79.0)</td>
<td>70.1 ± 3.4, 20 (66.0 - 78.5)</td>
<td>73.7 ± 2.4, 34 (68.0 - 80.0)</td>
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<td>Tarsus length (mm)</td>
<td>27.2 ± 0.8, 21 (25.1 - 28.6)</td>
<td>27.8 ± 0.8, 38 (26.3 - 30.0)</td>
<td>27.1 ± 1.0, 21 (25.5 - 28.8)</td>
<td>27.8 ± 1.1, 34 (26.3 - 30.3)</td>
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<td>S***</td>
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<tr>
<td>Body mass (g)</td>
<td>34.3 ± 1.7, 20 (31.6 - 38.3)</td>
<td>37.5 ± 2.2, 38 (32.5 - 41.4)</td>
<td>35.3 ± 2.8, 20 (30.3 - 41.2)</td>
<td>38.3 ± 2.0, 34 (32.7 - 41.7)</td>
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<td>Central tail bar</td>
<td>33.6 ± 1.3, 21 (31.0 - 35.5)</td>
<td>34.0 ± 3.7, 34 (22.5 - 39.2)</td>
<td>36.1 ± 1.8, 20 (23.2 - 38.8)</td>
<td>36.4 ± 3.0, 34 (30.0 - 42.9)</td>
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<td>length (mm)</td>
<td>A***</td>
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<td>External tail bar</td>
<td>11.4 ± 1.3, 21 (9.6 - 14.3)</td>
<td>10.8 ± 1.6, 36 (7.0 - 13.8)</td>
<td>12.8 ± 1.4, 20 (10.2 - 15.4)</td>
<td>13.3 ± 1.2, 34 (10.1 - 16.0)</td>
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<td>length (mm)</td>
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Fig. 1. Tail pattern of the Black Wheatear (*Oenanthe leucura*). The length of the terminal black tail bars measured (external tail bar and central tail bar) are also shown. Measures were taken considering the maximum parallel length from the tip to the end of the black area on the rachis. Photographer: Cristian Pérez-Granados.