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

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10 **Abstract**

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

20

21 **Keywords:** Biometry, delayed plumage maturation, dominance signal, sexual selection.

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23

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

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

46 Adult Black Wheatears perform a fully post-breeding moult (July-October), while
47 juveniles undergo a post-juvenile partial moult (July), involving only a few internal
48 greater wing coverts (Pérez-Granados 2017). Thus, subadults show DPM by

49 maintaining a large number of wing coverts and the flight and tail feathers until after the
50 first breeding season (Senar et al. 1998). Previous studies have suggested that wing
51 loadings of the species have been modified by selection pressures related to stone
52 carrying display (Møller et al., 1995). To our view, these characteristics make the Black
53 Wheatears a good case study to explore the adaptive significance of DPM and inter-
54 individual differences in biometry.

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

61 **Material and Methods**

62 **Study area**

63 The field work took place from July to November 2014-2016 in three arid localities
64 around Alicante city (38°21'N, 0°29' W, southeastern Spain). Localities were separated
65 by 7.2 ± 5.1 km, located at 100 m a.s.l. and had a mean annual temperature of 18°C and
66 mean annual precipitation of 300 mm. Black Wheatears were caught in the two first
67 hours after dawn, using small spring-traps baited with tenebrionids. Birds were attracted
68 with the aid of an mp3 and a Radioshack amplifier. Birds were banded and maximum
69 wing length, length of the eighth primary (P8 hereafter) and tail length were taken with
70 specified rulers (accuracy 0.5 mm). Tarsus length and the length of the terminal black
71 bar from the tip to the end of the black area on the outer (external tail bar hereafter, Fig.
72 1) and innermost (central tail bar hereafter, Fig. 1) rectrices, taking the maximum
73 parallel length to the rachis, were measured with dial calipers (accuracy 0.01 mm).

74 Individuals were weighed with a precision scale (0.1 g). Birds were sexed and aged by
75 plumage characteristics (Pérez-Granados 2017), and were categorised as juveniles or
76 adults (after at least one complete moult cycle).

77 **Statistical analyses**

78 We built linear models for each biometric measurement as the response variable, and
79 sex, age and its interaction as explanatory factors. We included tarsus length --a
80 surrogate for body size-- as a controlling covariate (wing length was used instead as a
81 controlling covariate when testing differences in tarsus length and tail length when
82 testing differences in the size of the terminal black tail bar). All birds trapped were
83 analyzed together, since there was no difference in body mass between individuals
84 captured in different months, years or sites (ANOVA test, Month $F_{5,106} = 1.58$, $P = 0.17$;
85 Year $F_{2,109} = 1.22$, $P = 0.30$; Site $F_{2,109} = 0.19$, $P = 0.98$). The level of significance was p
86 < 0.05 and results were expressed as mean \pm SE. Continuous variables were log-
87 transformed. The analyses were done with R 3.2.1 (R Development Core Team 2014).

88 **Results**

89 In total, 114 Black Wheatears were captured, of which 59 were juveniles (38 males
90 [64.4%], 21 females [35.6%]) and 55 were adults (34 males [61.8%] and 21 females
91 [38.2%]). We trapped a larger number of males (Pearson's Chi-squared test with Yates
92 = 3.50, $P = 0.06$), but we captured a similar number of birds of each age (Pearson's Chi-
93 squared test with Yates = 0.02, $P = 0.89$), and a similar proportion of each sex within
94 age groups (Pearson's Chi-squared test with Yates = 0.05, $P = 0.81$). In all analyses, age
95 and sex interaction was never significant (Online Resource 1). Once body size was
96 controlled, we found that males were heavier and had larger wings, tarsus and tail length
97 than females (Table 1). Likewise, adult birds were heavier and had larger wings and
98 tails than juveniles, but tarsus length did not differ with age (Table 1). Once the tail

99 length of individuals was controlled for, adult birds had significantly longer central tail
100 bars than juveniles (Table 1). We also found that males had smaller external tail bars
101 than females (Table 1).

102 **Discussion**

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

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

121 Biometric differences found in Black Wheatears were similar to those described in
122 many other European passerines: adult and males are larger than juveniles and females,
123 respectively (e.g. Alatalo et al. 1984). Larger wings and tails in males, particularly in

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

143 Our research on Black Wheatear has given evidence that tail pattern and biometry
144 differed after the first complete moult. We suggest that tail pattern could be used for the
145 recognition of older birds by a quick screening of the plumage. However, we have no
146 empirical evidence that smaller tail bars reduces aggression by adults toward subadults,
147 and thus further research is needed to evaluate the adaptive significance of DPM in the
148 Black Wheatear. The best evidence would come from studies testing the relationship of

149 these traits and aggressive response or mate choice, or from experimental manipulations
150 of the size of the terminal tail bar to test its effect on reproductive fitness, or aggressive
151 response between individuals.

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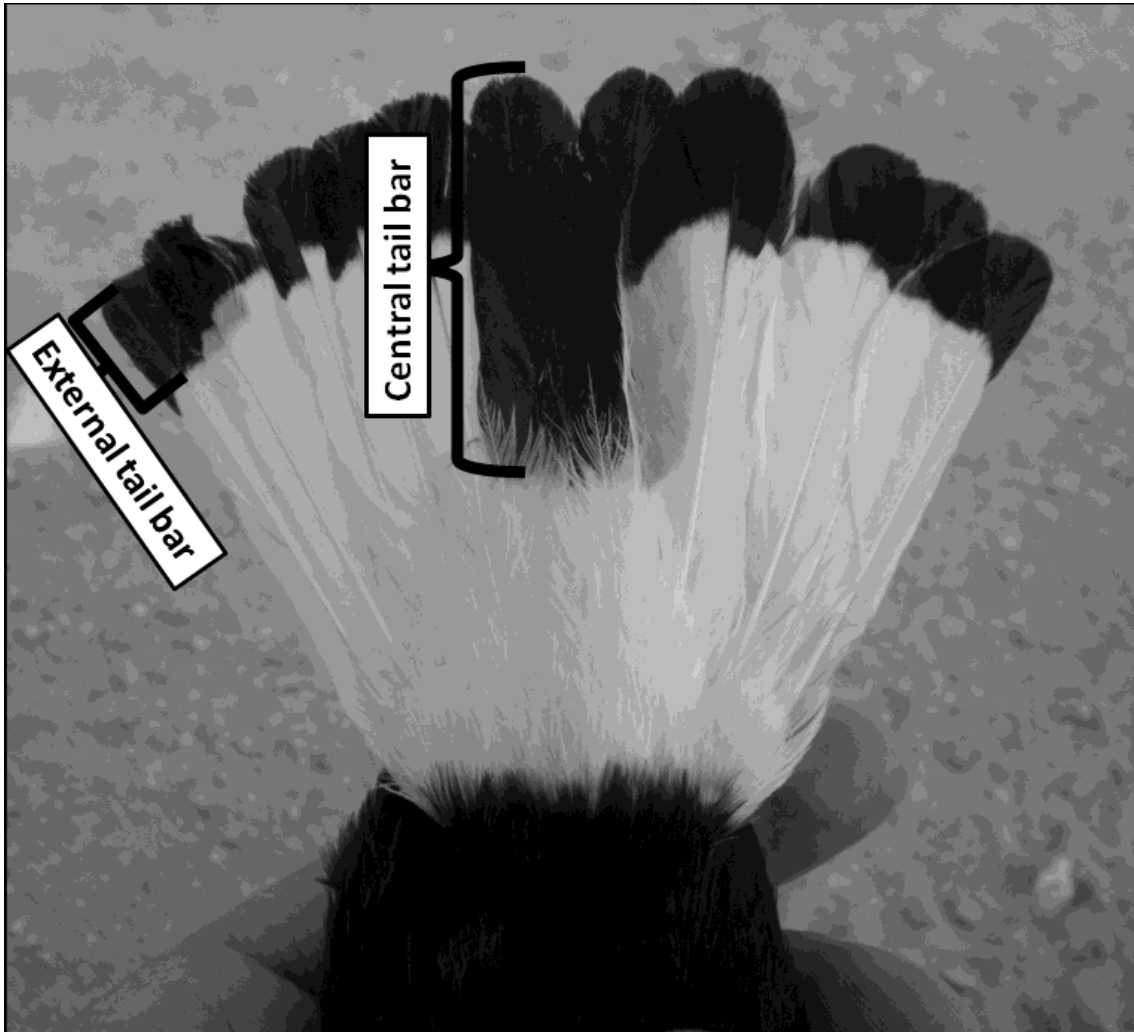
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196

197 **Table 1:** Summary table of biometric measurements and body mass of Black Wheatears
 198 (*Oenanthe leucura*) trapped in Alicante, Spain, according to age and sex. Data are
 199 presented as mean \pm SE, N and range in parentheses. P shows the significant differences
 200 between age and sex classes, according to linear models and type-II partitioning of
 201 variances for the measurement, after considering a surrogate for body or tail size as a
 202 controlling variable, including age, sex and interaction as predictors: S — sex
 203 (male/female); A — age (adult/juvenile); * — $p < 0.05$; ** — $p < 0.01$; *** — $p <$
 204 0.005 . P8 refers to the length of the eight primary feather. See detailed analyses in
 205 Online Resource 1.

Measurement	Juveniles		Adults		P
	Female	Male	Female	Male	
Mean \pm SD, N (min-max)					
Wing length (mm)	94.6 \pm 2.5, 21 (91.0 - 101.0)	99.0 \pm 2.0, 38 (94.0 - 103.5)	96.6 \pm 1.9, 19 (93.5 - 99.5)	100.3 \pm 2.3, 24 (96.0 - 104.0)	S*** A***
P8 (mm)	71.7 \pm 1.8, 20 (69.0 - 76.0)	75.1 \pm 1.8, 37 (71.0 - 79.0)	73.7 \pm 2.0, 17 (69.0 - 76.0)	76.3 \pm 2.7, 25 (71.5 - 81.0)	S*** A***
Tail length (mm)	68.7 \pm 2.4, 21 (64.0 - 73.0)	71.1 \pm 2.5, 36 (67.0 - 79.0)	70.1 \pm 3.4, 20 (66.0 - 78.5)	73.7 \pm 2.4, 34 (68.0 - 80.0)	S*** A***
Tarsus length (mm)	27.2 \pm 0.8, 21 (25.1 - 28.6)	27.8 \pm 0.8, 38 (26.3 - 30.0)	27.1 \pm 1.0, 21 (25.5 - 28.8)	27.8 \pm 1.1, 34 (26.3 - 30.3)	S***
Body mass (g)	34.3 \pm 1.7, 20 (31.6 - 38.3)	37.5 \pm 2.2, 38 (32.5 - 41.4)	35.3 \pm 2.8, 20 (30.3 - 41.2)	38.3 \pm 2.0, 34 (32.7 - 41.7)	S*** A**
Central tail bar length (mm)	33.6 \pm 1.3, 21 (31.0 - 35.5)	34.0 \pm 3.7, 34 (22.5 - 39.2)	36.1 \pm 1.8, 20 (33.2 - 38.8)	36.4 \pm 3.0, 34 (30.0 - 42.9)	A***
External tail bar length (mm)	11.4 \pm 1.3, 21 (9.6 - 14.3)	10.8 \pm 1.6, 36 (7.0 - 13.8)	12.8 \pm 1.4, 20 (10.2 - 15.4)	13.3 \pm 1.2, 34 (10.1 - 16.0)	A*** S*

207 **Fig. 1.** Tail pattern of the Black Weather (*Oenanthe leucura*). The length of the
208 terminal black tail bars measured (external tail bar and central tail bar) are also shown.
209 Measures were taken considering the maximum parallel length from the tip to the end of
210 the black area on the rachis. Photographer: Cristian Pérez-Granados.



211