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Source: Ardea, 108(1) : 21-29

Published By: Netherlands Ornithologists' Union

URL: https://doi.org/10.5253/arde.v108i1.a6

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Post-juvenile and post-breeding moult of the Black Wheatear *Oenanthe leucura* in south-eastern Spain: slowed down due to climatic aridity?

Cristian Pérez-Granados



Pérez-Granados C. 2020. Post-juvenile and post-breeding moult of the Black Wheatear *Oenanthe leucura* in south-eastern Spain: slowed down due to climatic aridity? Ardea 108: 21–29. doi:10.5253/arde.v108i1.a6

Despite increasing interest in moult in birds, there are still clear gaps in our knowledge of this topic. For example, many aspects of the moult of several European passerines remain unknown. Here, I describe the extent of the post-juvenile and the post-breeding moult of Black Wheatears *Oenanthe leucura* in south-eastern Spain and analyse the possible influence of ecological factors on moult in this species. The post-juvenile moult of Black Wheatears involved a variable number of greater coverts (six in most cases), but tertials, alula feathers and the carpal covert were also moulted frequently. Primaries were never moulted, while secondaries and tail feathers were moulted in 1.5% of 65 birds. The number of feathers moulted in the post-juvenile moult was not related to sex or individuals' body size. The post-breeding moult occurred between late June and mid-November and followed the typical sequence of European passerines. It had a mean duration of 145 days, with no differences between sexes or years. The body condition of wheatears did not decrease as the moult advanced. The duration of the post-breeding moult of Black Wheatears was almost double the mean duration described for European passerines and is among the longest period ever described for passerines. The resident status and medium size of the species may partly explain the long duration of the post-breeding moult, but the low seasonality and high aridity of the study area seem to be the main drivers of the pattern found.

Key words: feather, moult strategy, passerine, resident, seasonality

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Moult, reproduction and migration are the three major events in avian life cycles (Newton 2009). Feathers may constitute up to 30% of lean dry body mass of birds (Jenni & Winkler 1994), and therefore, moult is recognised as a highly energy-demanding activity (Murphy 1996, Swaddle & Witter 1997). Moreover, moult affects plumage functionality by reducing thermoregulation and flight performance and, consequently, may have an impact on individuals' fitness (Swaddle & Witter 1997, de la Hera *et al.* 2011). In the last few decades, there has been an increasing interest in understanding the moult of birds (e.g. Newton 2009, Kiat *et al.* 2019), and for some groups, such as the European passerines, detailed information is available for several species (Svensson 1992, Jenni & Winkler 1994).

Nonetheless, there are still clear gaps in our knowledge and the moult process of some European passerines remains undescribed. This lack of information is even more evident for bird species and populations inhabiting southern Europe. Most of our current knowledge about the moult of European passerines stems from northern European species or northern populations (Svensson 1992, Jenni & Winkler 1994). However, the moult pattern of birds in southern Europe may differ from those in northern areas (Sanz 1999, Hemborg *et al.* 2001), due to different weather and climatic conditions.

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Feather moult has a strong genetic character (Berthold & Querner 1982), but species and individuals usually show great plasticity, likely as an adaptation to different ecological conditions (Hasselquist *et al.* 1988). For example, migratory species usually have a less extensive post-juvenile moult or perform post-breeding moult at greater speed than resident birds, since moult is time-constrained by migratory behaviour (reviewed by Kiat *et al.* 2018). Among other factors, the moult of birds is affected by (1) body mass, since larger birds usually take longer to complete post-breeding moult in comparison to related, but smaller, species (Jenni & Winkler 1994), (2) sex and reproduction, because males and un-paired birds may invest more time and energy in moulting due to, usually, less effort being expended during the breeding period (Chabot *et al.* 2018, Grissot *et al.* 2019), and (3) habitat, with birds of the same species living under more suitable conditions moulting a greater number of feathers (Borras *et al.* 2004, Barta *et al.* 2008).

The Black Wheatear *Oenanthe leucura* is a resident, medium-sized (35 and 38 g, for females and males, respectively) passerine distributed in the Iberian Peninsula and North Africa (Moreno 2012). In the Iberian Peninsula, the species is more abundant in the south and south-eastern area, selecting sites with large number of sunshine days per year and less precipitation (Carrascal & Palomino 2006). The Black Wheatear mainly inhabits low-vegetation, stony and arid habitats (Moreno 2012). Juvenile Wheatears perform a partial post-juvenile moult in their first summer that usually involves a reduced number of wing coverts while adult birds perform a complete post-breeding moult (Jenni & Winkler 1994). The complete post-breeding moult entails a larger cost than the post-juvenile moult due to the larger number and larger size of feathers involved (Jenni & Winkler 1994). The biometry and plumage pattern of the species is relatively well known (Møller *et al.* 1995, Pérez-Granados & Seoane 2018). However, the extent of the post-juvenile moult and timing of the complete post-breeding moult is not well known (Svensson 1992, Jenni & Winkler 2004, Blasco-Zumeta & Heinz 2019).

This study has three main goals: (1) to provide the first detailed description of the post-juvenile moult of the Black Wheatear and assess how it is effected by sex and body size, (2) to estimate the post-breeding moult duration and speed of the Black Wheatear, and (3) to evaluate the effect of sex and date on body condition during the post-breeding moult.



Serra Grossa (Sierra de San Julián) is an arid mountainous area (height 161 m) with eroded slopes and abandoned quarries around Alicante. Here, the Black Wheatear acquires densities of up to 4 breeding birds/10 ha (photo CPG, 14 February 2015, Alicante, Spain).

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METHODS

Study area

The study was carried out in two arid mountainous areas with eroded slopes around the city of Alicante (38°21'N, 0°27'W) in south-eastern Spain, where the species reaches densities of up to 4 birds/10 ha (Pérez-Granados & Pérez 2018). Sites were separated by 2.5 km, located at 100 m a.s.l. and had a mean annual temperature of 18.3°C and a mean annual precipitation of 311 mm (Spanish State Meteorological Agency 2019). Fieldwork took place during July–October of the years 2014–2016, after the breeding season. Data on post-breeding moult were only collected during the years 2014 and 2015. Mean daily temperature during the study period and years considered was 24.7°C, while mean total precipitation was 95.9 mm (Spanish State Meteorological Agency 2019).



First-year male Black Wheatear in breeding habitat (photo CPG, 22 July 2014, Alicante, Spain).

Bird ringing and moulting data

Black Wheatears were caught using small spring-traps baited with Morio Worms *Zophobas morio* and with the aid of a playback within their territories during the first two hours after sunrise. Birds were ringed to avoid pseudoreplication, weighed with a precision scale (accuracy 0.1 g) and their tarsus length was measured with digital callipers (accuracy 0.01 mm) in order to estimate body condition index (see below). All individuals were sexed and aged as immatures (birds that had not yet undergone a complete moult) or adults (birds undergoing a complete moult) according to plumage characteristics (Svensson 1992).



Pattern of the post-breeding moult of a first-year male Black Wheatear. This bird had completed moult of P1–P6 and S1, and P7 and S2 were growing, S3 was starting to grow and P8–10 and S4–S6 were not moulted (photo CPG, 11 September 2017, Alicante, Spain).

Post-juvenile moult data were obtained by examining the left side of the tail and the left wing of 65 immature birds (40 males and 25 females) trapped during 2014 and 2016. I recorded whether each tail feather, greater covert, tertial, alula, carpal covert, primary covert, primary and secondary wing feather was moulted (scored as 1) or not (scored as 0). The total number of feathers moulted (extent of the moult hereafter) was used as a response variable in subsequent analyses. I also annotated the extent of the post-breeding moult of adult birds trapped performing a complete post-breeding moult (20 males and 12 females in 2014 and 22 males and 16 females in 2015). I followed a standard moult card proposed by Ashmole (1962). Old feathers were scored as 0, new, fully-grown feathers were scored as 5 and growing feathers were given a score from 1 to 4 according to the percentage of feather growth (Ashmole 1962, Newton 2009). Tertials were not included in the study since they are usually moulted as a separate unit (Jenni & Winkler 1994). In the Black Wheatear, the moult of secondaries can be completed before the moult of primaries, and therefore both types of feathers were included in the study (Table

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S1). The sum of the feathers' scores was used as a response variable in subsequent analyses (active moult score, hereafter).

Statistical analyses

Tarsus length and body mass were z-standardised prior to analyses to make means zero and to ensure equal variance. Due to sexual dimorphism in the species (Pérez-Granados & Seoane 2018), *z*-standardization was carried out using specific formulae for each sex. Body condition of adult birds was estimated using the scaled mass index (Peig & Green 2009), following the equation:

$$M^{i} = M_{i}\left(\frac{T_{o}}{T_{i}}\right)B_{SMA},$$

where M_i and T_i are the body mass and the tarsus length of individual i, respectively, B_{SMA} is the scaling exponent estimated by the Standardized Major Axis (SMA) regression of M on T. T_o is an arbitrary value of T (i.e. the arithmetic mean value for each sex), and M^i is the predicted body mass for individual i when the linear body measure is standardized to T_o.

In subsequent analyses, immature individuals trapped in different years were analysed together, while adult birds trapped in different years were treated as independent. A Generalised Linear Model (family Poisson) was fitted to assess the relationship between the extent of the post-juvenile moult using body size and sex as predictors. I did not include body condition in this analysis, since the body condition of immature birds may depend on several uncontrolled factors (e.g. parents' quality, hatching date; Jenni & Winkler 1994, Bojarinova *et al.*1999).

Duration of post-breeding moult for each sex and year was estimated by regressing Julian date against the active moult score. I opted for applying a simple regression equation in order to compare the moult duration estimated in the current study with that obtained in other published studies, which used the same or similar methodologies (Snow 1969, Ginn & Melville 1983, Matthysen 1986, Jenni & Winkler 1994). The datasets generated and analysed in the current study are available online (doi.org/10.6084/m9.figshare.9715697.v1). To assess whether or not post-breeding moult differed between sexes and years, I fitted a linear model using the active moult score as a response variable and Julian date, year, sex and the interaction date × sex as predictors. Finally, I fitted a linear model using standardised body condition of adult birds as a response variable and date and sex as predictors to assess whether or not body condition of Black Wheatears changed during the moulting period. In four cases, it was possible to assess records from the same male during the course of a single moult (Table S1). These data were used to estimate the change in the active moult score over time, as an independent measure of moult speed. Although this could lead to

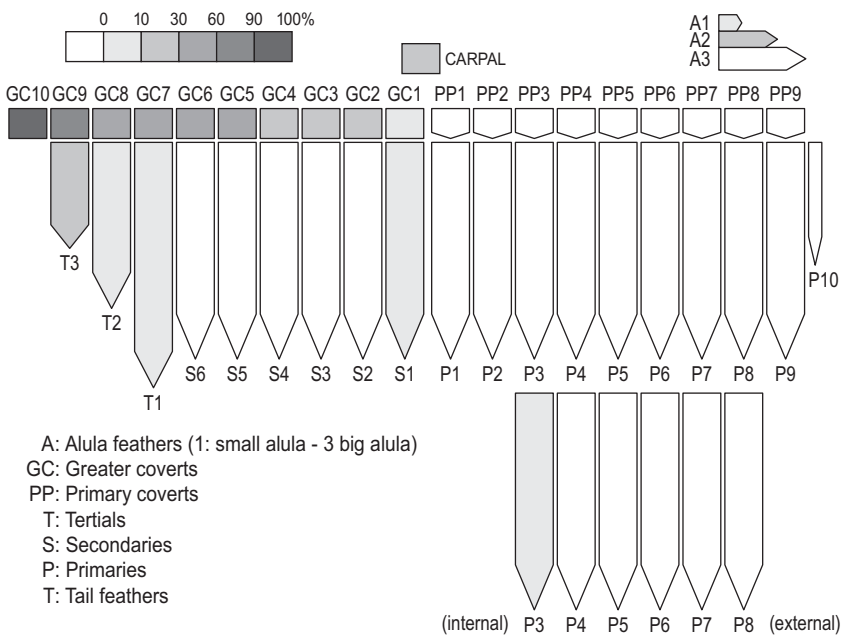


Figure 1. Extent of the post-juvenile moult on the wing and tail of Black Wheatears in south-eastern Spain.

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pseudo-replication in the dataset, I treated recaptures as statistically independent. Due to the large number of days elapsed between the two recaptures (mean of 30 days), I assumed that the active moult score of the same bird could differ between retrapping dates according to individual trade-offs.

Statistical analyses were performed in R v. 3.4.1 (R Development Core Team 2014). B_{SMA} was calculated using the R package 'lmodel2' (Legendre2014). Model performances were evaluated by visually checking the residuals and no heteroscedasticy or non-linear responses were found.

RESULTS

Post-juvenile moult

The post-juvenile moult of Black Wheatears involved a mean (±SE) number of 7.40 ± 0.38 feathers (Figure 1). The six internal greater coverts were the only feathers moulted in more than 50% of examined birds. Tertials, alula feathers and/or the carpal covert were often moulted (Figure 1). Only one individual moulted a secondary and another moulted a tail feather. Primaries and primary coverts were never moulted (Figure 1). The extent of the post-juvenile moult neither varied significantly with body size nor differed significantly with sex (Table 1).

Post-breeding moult

All trapped adult birds were moulting and none of them completed moulting during the study period (3 July – 31 October; Table S2). The post-breeding moult of Black Wheatears seems to occur between late June and mid-November (Figure 2) and follows the typical sequence of European passerines, beginning with the shedding of the innermost primary followed by primaries moulted in descending order and secondaries (starting when the fifth or sixth primary is lost) in

Table 1. Results of a Generalised Linear Model testing the effect of sex and tarsus length (used as a proxy of body size) and their interaction, on the extent of the post-juvenile moult of Black Wheatears in south-eastern Spain.

Variable	Estimate	SE	*Z*-value	*P*
Intercept	1.928	0.076	25.28	<0.001
Sex (male, female = 0)	0.106	0.095	1.11	0.265
Tarsus length (mm)	–0.026	0.076	–0.34	0.736
Sex (male) × tarsus (female = 0)	0.167	0.096	1.74	0.081

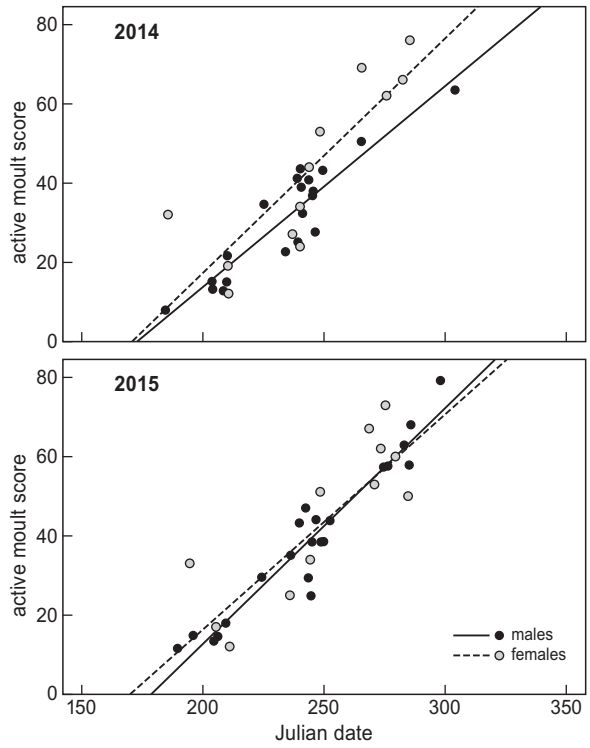


Figure 2. Active moult scores plotted against Julian date for male and female Black Wheatears trapped in 2014 (top) and 2015 (bottom) in south-eastern Spain. Equations for each sex and year can be found in Table S3.

Table 2. Results of interindividual linear models testing (A) the effect of sex and year on post-breeding moult duration of Black Wheatears in south-eastern Spain, and (B) the change in body condition over time.

Variable	Estimate	SE	*Z*-value	*P*
(A) post-breeding moult duration				
Intercept	–93.813	13.452	–6.974	<0.001
Date	0.555	0.052	10.483	<0.001
Sex (male, female = 0)	–6.694	17.043	–0.393	0.696
Year (2015 = 0)	–0.173	2.007	–0.087	0.931
Date × sex (male, female = 0)	0.012	0.069	0.183	0.835
(B) body condition				
Intercept	–0.0916	1.051	–0.087	0.931
Date	0.0003	0.004	0.070	0.940
Sex (male, female = 0)	–0.0220	0.247	–0.090	0.927

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ascending order. The post-breeding moult of males extended over 140–158 days while females took 135–147 days (Figure 2 and see Table S3 for detailed values per sex and year). According to the linear model, there were no differences in post-breeding moult duration between sexes and years (Table 2). Likewise, body condition did not change during the moulting season (Table 2). Examination of the four males caught more than once within the same moult provided a mean increase in active moult score of 0.483 points per day (see Table S2). Mean change in body mass for retrapped males was 0.3 g (range: –1.5 – 3.3 g).

DISCUSSION

In this work, I provide the first description of the post-juvenile and post-breeding moult of Black Wheatears and evaluate the effect of sex and body measurements on both types of moult. The extent of the post-juvenile moult of Black Wheatears in south-eastern Spain is smaller compared to other sedentary Palearctic Wheatears typically found in arid environments, such as the White-crowned Wheatear *O. leucopyga*, the Hooded Wheatear *O. monacha* and the Blackstart *O. melanura* (range of 7.9–12.6 feathers moulted; Yosef Kiat pers. comm.). The extent of post-juvenile moult was not related to sex nor to individual body size, which suggests that post-juvenile moult in the studied species may have a marked genetic character (Berthold & Querner 1982). A large number of previous studies have found a more extensive post-juvenile moult in males of other passerines (e.g. Bojarinova *et al.* 1999, Chabot *et al.* 2018), since plumage traits are usually more often exhibited by males and may be sexually selected (Safran& McGraw 2004). We expected this to be true for the Black Wheatear, which performs visual sexual displays (Moreno 2012). However, a previous study on the species highlighted that immature males may use their tail pattern, with smaller black bars, as a signal of subordination towards adult birds in order to reduce confrontations (Pérez-Granados & Seoane 2018). If this hypothesis is also valid for the wing pattern, immature males may avoid moulting a large number of the feathers they use for signalling subordination.

The start time and duration of the post-breeding moult of Black Wheatears did not differ between sexes or years, which may be related to the similar contribution made by each sex during reproduction (Moreno 2012). Moult duration depends mainly on migratory behaviour and size of the bird. The post-breeding moult of resident passerines usually takes longer than that of migratory birds, and usually ranges between 60 and 85 days for passerines lighter than 20 g (Jenni & Winkler 1994). Larger passerines, such as the Common Starling *Sturnus vulgaris* and thrushes *Turdus* spp., usually take up to 60–100 days to complete post-breeding moult (Snow 1969, Ginn & Melville 1983, Matthysen 1986). However, the duration of post-breeding moult of Black Wheatears was much longer than that described for starlings and thrushes, even though wheatears are smaller. Post-breeding moult duration is even longer than that described for some of the largest European passerines (range of 92–110 days for Eurasian Jay *Garrulus glandarius* and Eurasian Magpie *Pica pica*; Ginn & Melville 1983, Jenni & Winkler 1994), and can only be compared to the duration described for some species of the genus *Corvus* (e.g. 140–145 days for the Common Raven *C. corax* and 105–172 days for the Carrion Crow *C. corone* and the Rook *C. frugilegus*; Jenni & Winkler 1994). It is worth highlighting that the approach employed here does not take into account different masses of moulted feathers which may have some consequences in the interpretation of obtained results.

Previous studies have proposed rapid moult rates in passerines as an adaptation to seasonal environments, in order to moult within the time window of more favourable conditions (Bensch *et al.* 1991). Southern Spain is characterised by low seasonality, high aridity and limited resource availability (Valera *et al.* 2011). Therefore, the slow moult rate of the Black Wheatear may be an adaptation to arid conditions, and could be a common strategy in arid-adapted bird species (Wyndham 1981, Zann 1985). This assumption is partially supported by the fact that the post-breeding moult was 15 days quicker in 2015 than in 2014 (Table S3), and the amount of precipitation between July and October in Alicante city during 2015 was much higher (49.8 mm in 2014 and 142.2 mm in 2015; Spanish State Meteorological Agency 2019). Agonistic behaviour may also have an impact on the timing of moult, with more aggressive species moulting at a slower rate (Dow 1973), because of their need for territory defence during the moulting period (Dhont 1973, Matthysen 1986). The Black Wheatear is a territorial and aggressive species, with both sexes usually approaching playbacks very quickly and sometimes attacking trapped birds (own obs.). Heterospecific aggression also seems to be common in this species (Moreno 2012). Therefore, the aggressive and territorial behaviour of the species may contribute to the slow rate of post-breeding moult.

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The long duration of the post-breeding moult may explain the absence of a relationship between individuals' body condition and date. In areas with low-seasonality and limited resources during the moulting period, as in south-eastern Spain (Bru & Garcia-Marí 2008, Valera *et al.* 2011), resident birds may decide to moult over a longer period. A slow moult may allow birds to create heavier feathers (de la Hera *et al.* 2010) and reduce the daily amount of energy dedicated to moulting and, at the same time, minimise the negative effect of moulting on plumage functionality (Swaddle & Witter 1997, de la Hera *et al.* 2011). Future studies should compare moult pattern in this and other passerines within a gradient of aridity to understand the possible effects of aridity on moult. Alternatively, experimental studies manipulating water and food availability could be used to understand the role of aridity on the moult of birds.

ACKNOWLEDGEMENTS

This paper is dedicated to Gregorio Pérez for his invaluable assistance. I am also in debt to Roque Belenguer and Germán M. López-Iborra for their help. I am grateful to two anonymous reviewers whose comments helped to improve the manuscript. I wish to thank the Servicio de Vida Silvestre of Conselleria d´Infraestructures, Territorii Medi Ambient for ringing permits, and Carlos Ponce and Juancho Calleja for teaching me to be an expert ringer and for all their comments that improved this work. I want to thank Nieves Herrero García for her work on the written English. This study was carried out without public or private funding and all costs were assumed by the author.

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SAMENVATTING

Ondanks de toenemende belangstelling voor rui bij vogels zijn er nog steeds duidelijke hiaten in onze kennis over dit onderwerp. Zo zijn bijvoorbeeld veel aspecten van de rui van verschillende Europese zangvogels nog onbekend. In deze studie beschrijf ik de postjuveniele en de postnuptiale rui van Zwarte Tapuiten *Oenanthe leucura* in 2014–2016 in Zuidoost-Spanje en analyseer ik de invloed die ecologische factoren op de rui bij deze soort kunnen hebben. De postjuveniele rui van de Zwarte Tapuit in dit onderzoek betrof een variabel aantal armpendekveren (in de meeste gevallen zes), maar tertials, duimvleugelveren en carpale dekveer werden ook vaak geruid. Handpennen werden nooit geruid en armpennen en staartveren slechts in 1,5% van de 65 vogels. Het aantal geruide veren tijdens de postjuveniele rui was niet gerelateerd aan geslacht of grootte van de vogel. De postnuptiale rui vond plaats tussen eind juni en half november en verliep zoals bij veel andere Europese zangvogels het geval is. Deze rui duurde gemiddeld 145 dagen (zonder verschillen tussen geslachten of jaren). De lichaamsconditie van de tapuiten nam niet af naarmate de rui vorderde. De duur van de postnuptiale rui van de Zwarte Tapuiten is bijna het dubbele van de gemiddelde duur beschreven voor Europese zangvogels en is hiermee een van de langstdurende die ooit voor zangvogels beschreven is. Hun bestaan als standvogel en hun grootte kunnen gedeeltelijk de lange duur van de postnuptiale rui verklaren. De kleine seizoenfluctuaties van het klimaat en de sterke droogheid van het studiegebied lijken echter de belangrijkste factoren van het gevonden patroon te zijn.

Corresponding editor: Allert Bijleveld
Received 4 December 2019; accepted 3 March 2020

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SUPPLEMENTARY MATERIAL

Table S1. Status of the flight moult and body mass change (first capture – retrapping) for four Black Wheatear males retrapped within the same moulting season. Moult status 'moulted' refers to new fully grown feathers, while code refers to percentage of grown feather for growing feathers (according to Ashmole 1962). Feathers not included in the table have to be considered as old.

Weight change (g)	Score change (days)	Capture date	Flight moult status	Recapture	Flight moult status
–0.8	17 (37)	29/07/2014	(P1–P3 moulted, P4 code 4, P5 code 2)	4/09/2014	(P1–P6 moulted, P7 code 1) (S1 moulted, S2 code 2)
–1.5	22 (37)	29/07/2014	(P1–P2 moulted, P3 code 3, P4 code 2)	4/09/2014	(P1–P5 moulted, P6 code 4, P7 code 1) (S1 moulted, S2 code 2)
0.2	9 (20)	13/08/2014	(P1–P6 moulted, P7 code 1) (S1 code 1)	2/09/2014	(P1–P6 moulted, P7 code 4, P8 code 1) (S1 code 4, S2 code 2)
3.3	10 (26)	12/08/2015	(P1–P4 moulted, P5 code 4, P6 code 2, P7 code 1) (S1 code 2)	7/09/2015	(P1–P6 moulted, P7 code 2) (S1 moulted, S2 code 2)
0.3	58 (120)		58/120 equals an increase of 0.483 points per day (i.e. 165 days to complete the flight moult)		

Table S2. Status of the flight moult for the first and last birds trapped each year in active moult. Moult status refers as 'moulted' to new fully grown feathers, while code refers to percentage of grown feather for growing feathers (according to Ashmole 1962). Feathers not included in the table have to be considered as old.

First capture	Moult status	Last capture	Moult status
03/07/2014	(P1 moulted, P2 code 3)	31/10/2014	(P1–P8 moulted, P9 code 1) (S1–S4 moulted, S5–S6 code 1)
05/07/2015	(P1–P5 moulted, P6 code 4, P7 code 1) (S1 code 3)	25/10/2015	(P1–P10 moulted) (S1–S5 moulted, S6 code 4)

Table S3. Summary table of regressing active moult score against Julian date for each sex and year. Number of birds trapped for each class is between parenthesis. Number of days needed, and starting and end time to complete the flight moult was estimated through the specified equation.

Year	Sex	Equation	Duration	Moulting time
2014	Male (20)	SCORE = –87.784+0.5078×Date	158	22 June – 27 November
	Female (12)	SCORE = –92.262+0.5435×Date	147	19 June – 13 November
2015	Male (22)	SCORE = –106.163+0.5949×Date	140	29 June – 9 November
	Female (16)	SCORE = –101.227+0.5924×Date	135	20 June – 3 November

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