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ORIGINAL ARTICLE

Time available for moulting shapes inter- and intra-specific variability in post-juvenile moult extent in wheatears (genus *Oenanthe*)

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Abstract

Moult is a vital and endogenously controlled process in the avian life. However, birds may modulate their feather renovation properties, such as the extent of moult, based on exogenous factors. Despite the large body of knowledge about moult patterns, numerous questions remain unclear. In this study, we aimed to improve our knowledge about the factors that affect variation in the extent of the post-juvenile moult in passerines by performing inter- and intra-specific comparative analyses. We assessed the effect of internal and external factors on passerines' moult by comparing post-juvenile moult extent among 16 wheatear species (genus *Oenanthe*) from the Palearctic Ecozone. The tested factors included migration distance used as a proxy of time available for moulting and habitat type. We also explored the relationship between the extent of the moult, migration distance, and sex in the Northern Wheatear *Oenanthe oenanthe* across a latitudinal gradient in Western Europe. The results indicate that post-juvenile moult extent in wheatears was negatively related to migration distance, such that species with shorter migration distances moult extensively compared to long-distance migratory species. In contrast, the extent of post-juvenile moult in the *Oenanthe* genus was not related to preferred habitat type (arid or non-arid) of the species. Migration distance was also related to post-juvenile moult extent in the Northern Wheatear, with fewer renewed feathers in northern populations. However, the extent of the post-juvenile moult did not differ between sexes. Thus, our results support that time constraints affect moult extent in long-distance migratory species and populations.

Keywords Migratory behaviour · Moult strategy · Northern wheatear · Passerine · Sex effect

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Zusammenfassung

Die für die Mauser zur Verfügung stehende Zeit bestimmt die zwischen- und innerartlichen Unterschiede im Umfang der post-juvenilen Mauser bei Steinschmätzern (Gattung Oenanthe)

Die Mauser ist ein lebenswichtiger und endogen gesteuerter Vorgang im Leben eines Vogels. Aber Vögel können äußeren Umständen folgend die Eigenheiten ihrer zu erneuernden Federn und auch das Ausmaß der Mauser verändern. Trotz unseres umfangreichen Wissens über die Muster, nach denen die Mauser abläuft, sind noch viele Fragen ungeklärt. Wir zielten in unserer Studie darauf ab, durch intra- und innerartliche vergleichende Analysen mehr über die Faktoren zu erfahren, die die Unterschiede im Ausmaß der post-juvenilen Mauser von Singvögeln beeinflussen. Hierfür bewerteten wir den Einfluss interner und externer Faktoren auf die Mauser von Singvögeln, indem wir den Verlauf der Mauser bei 16 paläarktischen Steinschmätzerarten (Gattung *Oenanthe*) miteinander verglichen. Zu den untersuchten Faktoren gehörte die Strecke, die die Vögel auf ihrem Zug normalerweise zurücklegen, als Stellvertreter für die Zeit, die ihnen für die Mauser zur Verfügung stand, und ihren jeweiligen Habitattyp. Für den Steinschmätzer (*Oenanthe oenanthe*) untersuchten wir außerdem entlang eines Breitengrad-Gradienten in Westeuropa den Zusammenhang zwischen Ausmaß der Mauser, Zugstrecke und Geschlecht. Die Ergebnisse deuten darauf hin, dass das Ausmaß der Mauser bei Steinschmätzern negativ mit der Zugstrecke korreliert, dass also Kurzstreckenzieher intensiver als Langstreckenzieher mausern. Im Gegensatz dazu stand das Ausmaß der Mauser in der Gattung *Oenanthe* in keinem Zusammenhang mit dem bevorzugten Habitattyp (trocken oder nicht-arid) der jeweiligen Art. Beim Steinschmätzer hing das Ausmaß der post-juvenilen Mauser von der Zugstrecke ab, wobei bei nördlicheren Populationen weniger Federn erneuert wurden. Zwischen den Geschlechtern gab es dagegen keinen Unterschied im Ausmaß der Mauser. Somit bestätigen unsere Ergebnisse, dass bei langstreckenziehenden Arten und Populationen zeitliche Einschränkungen einen Einfluss auf das Ausmaß der Mauser haben.

Introduction

Moult, defined as the process by which birds regularly renew their plumage, contributes to the appearance of a bird's plumage over time and is one of the key, energy-demanding processes in the avian annual cycle (Stresemann and Stresemann 1966; Ginn and Melville 1983; Lindström et al. 1993; Zuberogoitia et al. 2018). As a result, the moult conflicts with, and is temporally constrained by, the other two important annual routine events in the avian life cycle, reproduction, and migration. Feather replacement is a process under endogenous control (Berthold and Querner 1982; de la Hera et al. 2013). However, birds show considerable flexibility and are able to modulate their moult properties (e.g., moult speed or extent) according to exogenous factors, such as photoperiod and resource or time availability (Noskov and Rymkevich 1985; Borras et al. 2004; Chabot et al. 2018). Thus, passerines display inter- and intra-specific differences in moult strategies (Jenni and Winkler 2020). For example, a limited-extent partial moult has been described for species and populations living in northern latitudes due to less time available for moulting after the breeding season (Jenni and Winkler 2020; Kiat and Sapir 2017). This time constraint is exacerbated in migratory species and populations, and therefore, migration distance has been commonly studied in relation to inter-specific differences in moult patterns (Hall et al. 2004; De la Hera et al. 2009; Kiat and Sapir 2017).

Juveniles of most Western Palearctic passerine species perform a feather moult during the first months of their life (Jenni and Winkler 2020). This moult occurs before autumn migration or cold season onset and is known as the post-juvenile moult. The extent of the post-juvenile moult may vary from the renewal of body-only plumage to complete moulting of the entire plumage (Stresemann and Stresemann 1966; Ginn and Melville 1983). Feather moulting in this early stage of a bird's life is needed to replace the looser textured, nest-grown feathers with adult-type feathers (Jenni and Winkler 2020). The extent of the post-juvenile moult may influence breeding success during the first breeding season (e.g., by affecting plumage functionality or visual communication; Hill 1991, Jenni and Winkler 2020). Despite its evolutionary and ecological importance (Kiat et al. 2019), the extent of the post-juvenile moult has been less studied than other properties related to the moult of adult birds (e.g., the speed and duration of primary moult; Crates et al. 2015, Kiat and Izhaki 2016).

A considerable inter- and intra-specific variation in the extent of the post-juvenile moult has been found, even at small spatial scales (Gargallo 2013). For example, a larger extent of the post-juvenile moult has been described for males of several species (Crates et al. 2015; Chabot et al. 2018; Jenni and Winkler 2020), for early hatching individuals that benefit from more favourable conditions (Bojarinova et al. 1999), and for those populations with shorter migration distances, due to more time available for moulting (Morganti et al. 2013; Kiat and Izhaki 2016; Kiat and Sapir 2017). Availability of resources, habitat quality, and predictability may also determine the number of feathers moulted: more productive and predictable habitats may support more extensive post-juvenile moults than low quality and unpredictable habitats (Borras et al. 2004; Barta et al. 2008; Kiat and Izhaki 2016). However, the factors affecting the extent of the post-juvenile moult are complex and still numerous questions remain unclear (Bojarinova et al. 1999; Crates et al. 2015).

In this study, we aimed to unravel the factors that affect the variation in post-juvenile moult extent in passerines by making an inter- and intra-specific comparison. Therefore, the scope of the present study was twofold. Our first objective was to explore whether the extent of the post-juvenile moult differs between species according to evolutionary and ecological factors. We analysed the effect of the time available for moulting and habitat type on the extent of the post-juvenile moult. We assessed whether time available for moulting determines the extent of the post-juvenile moult on wheatears, due to time constraints on moulting patterns (Morganti et al. 2013; Kiat and Izhaki 2016). We used migration distance as a proxy of time available for moulting (de la Hera et al. 2010; Kiat et al. 2019), since previous studies have found that long-migratory populations of wheatears spent less time at the breeding area, and therefore have less time available for moulting. For example, Northern Wheatear populations in Canada spent around 87 days at the breeding area before a migration trip of around 14,500 km (Bairlein et al. 2012; Schmaljohann et al. 2012a), while populations from southern Sweden and Germany spent more than 110 days before covering distances of 5160 and 4100 km, respectively (Arlt et al. 2015; Schmaljohann et al. 2012b). Thus, we expected a larger number of moulted feathers in resident or short-distance migratory species than that of long-distance migrants. We also hypothesised that the moult can be constrained by the aridity of the habitat, which may reduce availability of resources (Gaston 1981; Borras et al. 2004; Pérez-Granados 2020), and thus, we explored if birds living in less harsh conditions may perform a more extensive post-juvenile moult. In the second objective, we complemented the inter-specific comparison with an intra-specific analysis. We assessed whether the variation in the extent of the post-juvenile moult of a sexually dimorphic migratory passerine, the Northern Wheatear (*Oenanthe oenanthe*), was related to differences in migration distance and sex. We predicted that individuals breeding closer to wintering areas may moult a larger number of feathers than those breeding farther away, due to shorter migration distances, allowing to spent more time at the breeding area and, thus, longer time availability for moulting (before migration). In addition, based on the assumption that the post-juvenile moult may differ between sexes according to sexual selection (Norris 1990; Safran and McGraw 2004; Jenni and Winkler 2020), we predicted that Northern Wheatear males would moult a larger number of feathers than females, because males show more ornamented plumage patterns and perform sexual displays (Currie 1998). Hence, males may benefit more from extensive moults during the post-juvenile, but also during the pre-breeding moult.

Materials and methods

Study species

We used the wheatears, passerines in the genus *Oenanthe* (Vieillot 1816, Family Muscicapidae), as a study species group. The wheatears is a group of 28 species (Del Hoyo et al. 2019) for which previous studies have found morphological differences among species in relation to their migratory behaviour and foraging habitats (Kaboli et al. 2007). Therefore, we consider wheatears to be an adequate target group of species to assess the relevance of different factors in the extent of the post-juvenile moult in passerines. Post-juvenile moult extent was examined for 1481 museum specimens and 290 living birds (1769 individuals in total), belonging to 16 species (Table 1).

The wheatears are characteristic species in arid and open habitats of the Palearctic and Afrotropical ecozones, with only one species extending to the Nearctic (Del Hoyo et al. 2019). The genus includes species with different distribution patterns, body sizes, and migration strategies (from sedentary to extremely long-distance migrants; Shirihai and Svensson 2018). Adults of all wheatear species perform a complete post-breeding moult in the breeding areas and before autumn migration or cold season onset, while juveniles perform a partial post-juvenile moult promptly after fledging and before autumn migration. In most of the studied species, this post-juvenile moult takes place between July and August, and involves body feathers, wing coverts, and tertials, but not remiges or rectrices (Jenni and Winkler 2020; Shirihai and Svensson 2018). In addition, only 3 out of the 16 studied species (*Oenanthe oenanthe, O. hispanica,* and *O. isabellina*) also perform a pre-breeding moult in winter (Shirihai and Svensson 2018). This moult involves few feathers that are easily distinguished from those renewed in the post-juvenile moult (Svensson 1992; Jenni and Winkler 2020). We considered first-year and second-years individuals (EURING codes 3 and 5, respectively) that had finished their post-juvenile moult. Wheatears were trapped at their breeding grounds (most of them were trapped during May and August).

Information about migration distance (km) and preferred habitat of each species (summarised as "Arid/Non-Arid") were obtained from the published literature (Table 1; BirdLife International and NatureServe 2014; Shirihai and Svensson 2018; Del Hoyo et al. 2019). The migration distance was calculated as the orthodromic distance between the mid-breeding and the mid-wintering areas of each species according to the distribution maps provided by BirdLife International and NatureServe (2014) (Table 1). The mid-breeding and mid-wintering coordinates of each species were estimated by the equation:

Table 1 Number of specimens examined, migration distance, and preferred habitat per each *Oenanthe* species considered in the inter-specific comparison

	Number of specimens	Migration distance (km)	Preferred habitat	Extent of the post-juvenile moult
O. oenanthe (oe)	420	8000	No arid	3.57 ± 2.04
O. hispanica (hi)	312	2500	No arid	9.02 ± 1.88
O. pleschanka (pl)	207	5400	No arid	7.53 ± 2.04
O. deserti (de)	156	2500	Arid	8.40 ± 2.76
O. leucopyga (lo)	107	0	Arid	9.88 ± 3.26
O. lugens (lu)	104	200	Arid	13.74 ± 2.38
O. leucura (le)	94	0	No arid	9.25 ± 2.63
O. finschii (fi)	90	1600	No arid	14.52 ± 2.09
O. isabellina (is)	67	4500	No arid	6.52 ± 2.45
O. monacha (mn)	42	0	Arid	11.05 ± 2.17
O. cypriaca (cy)	36	2400	No arid	12.94 ± 2.60
O. picata (pi)	32	900	No arid	12.72 ± 2.70
O. moesta (mo)	32	600	No arid	12.69 ± 2.52
O. chrysopygia (ch)	26	1100	No arid	10.69 ± 2.28
O. melanura (me)	25	0	Arid	14.64 ± 1.87
O. xanthoprymna (xa)	19	1300	No arid	10.68 ± 2.58
Total	1769			

Mean (± standard deviation) extent of the post-juvenile moult (number of feathers moulted) of each species is also shown. The letters among brackets after the species name refer to the acronyms used for each species in Fig. 1

$$\mathrm{Min}_{\mathrm{Lat}} + \left(\frac{\mathrm{Max}_{\mathrm{Lat}} - \mathrm{Min}_{\mathrm{Lat}}}{2}\right) \Big/ \mathrm{Min}_{\mathrm{Log}} + \left(\frac{\mathrm{Max}_{\mathrm{Lon}} - \mathrm{Min}_{\mathrm{Lon}}}{2}\right),$$

where $\mathrm{Min}_{\mathrm{Lat}}$ and $\mathrm{Max}_{\mathrm{Lat}}$ are minimim and maximum latitude, while $\mathrm{Min}_{\mathrm{Lon}}$ and $\mathrm{Max}_{\mathrm{Lon}}$ are minimum and maximum longitude of the distribution range of the species for each period. An extended description of the preferred habitat of each species can be found in Supplemental Table S1.

The intra-specific comparison was done using the Northern Wheatear as a study species model. We chose this species, because it has the longest migration distance and largest distribution area among the wheatears. Post-juvenile moult extent of the Northern Wheatear was collected at seven different breeding sites (May–August, regions hereafter) located in five countries along a latitudinal gradient in Western Europe (Sweden, Denmark, United Kingdom, Switzerland, and two populations in northern Spain and one in central Spain, Supplemental Table S2). For each population, we estimated the migration distance between trapping location and the mid-wintering areas of the species as explained above. For museum specimens without precise location data, we used the centre of the country where they were collected as a rough estimate of latitude of trapping location (Supplemental Table S2).

Moult data

Post-juvenile moult data were obtained after a careful examination of one of the wings of first-year wheatears trapped or inspected in museums. We trapped wheatears using flat spring traps with food bait (Pérez-Granados and Seoane 2018). In some cases, we employed species-specific playback equipment to attract birds into the traps. All examined wheatears were sexed and aged, when possible, based on a combination of several plumage characteristics, which include colour, texture, and moult limits (Svensson 1992; Jenni and Winkler 2020). In all cases, we annotated whether each of the greater coverts (10 feathers), tertials (3 feathers), alula (3 feathers), carpal covert (1 feather), primary coverts (9 feathers), primaries (10 feathers), and secondaries (6 feathers) had been moulted (scored as 1) or had remained unmoulted (scored as 0). Additionally, we estimated the moulting proportion of both lesser and medium coverts (scored from 0 to 1). For each individual, we summed the total number of moulted feathers to obtain a final score of post-juvenile moult extent per tested individual (maximum possible score of 43). None of the birds examined moulted any primary covert or primary during the post-juvenile moult and only three individuals (0.17% of the total) moulted the innermost secondary.

Statistical analyses

Because species-specific traits are known to be phylogenetically conserved, we used phylogenetic generalised least square (PGLS) regression (Freckleton et al. 2002) to account for non-independence among species due to shared evolutionary history. We examined the strength of phylogenetic non-independence using the maximum-likelihood value of the scaling parameter Pagel's λ (Pagel 1997). Pagel's λ is a multiplier of the off-diagonal elements of the variance–covariance matrix that PGLS uses to model interdependence among species. This ranges from 0 (no phylogenetic signal) to 1 (strong phylogenetic signal corresponding to a Brownian motion model of evolution). The wheatears' phylogenetic tree was obtained from an analysis of global bird diversity (Jetz et al. 2012) and built using BirdTree.org data (Rubolini et al. 2015; Supplemental Figure S1). We fitted univariate regression models using the mean score at species level of the post-juvenile moult extent as the response variable and migration distance, and preferred habitat as predictors. Models were weighed by within-species variances (Garamszegi 2014, see Supplemental Script S1). We ranked models according to their Akaike Information Criterion modified for small sample sizes (AICc; Akaike 1987). Models within two ΔAICc units were considered equally plausible (Burnham and Anderson 2002) (see Supplemental Script S1).

For the intra-specific analysis, we fitted mixed models to examine the effects of migration distance and sex on the extent of the moult in the Northern Wheatear. First, we considered the moult score of 262 individuals of Northern Wheatear and fitted a linear mixed model using migration distance as a predictor and region (seven categorical levels) as a random factor. This allowed us to evaluate variations in the score of the post-juvenile moult extent related to migration distance, but taking into account possible particularities of the seven regions we sampled: Sweden, Denmark, United Kingdom, Switzerland (Southern Alps), and Spain (Cantabrian Range, Pyrenees and Iberian Range, see also Supplemental Figure S2). With the subset of sexed individuals ($n = 175$), we then fitted a mixed model using sex, migration distance, and its interaction as predictors and location (five regions: Denmark, Southern Alps. Cantabrian Range, Pyrenees, and Iberian Range) as a random factor. Analyses (two-tailed, critical $\alpha = 0.05$) were performed using R (version 3.4.1, R Development Core Team 2014; package 'lme4' for mixed models, Bates et al. 2015; packages 'ape' and 'nlme' for PGLS, Paradis and Schliep 2018; Pinheiro et al. 2019, 'rr2' for r^2, Ives and Li 2018).

Results

Inter-specific level

The post-juvenile moult extent of the wheatears was mainly related to migration distance (Table 2). Moult extent varied negatively with migration distance, such that species with shorter migration distances moulted more feathers ($\beta = -0.82$, $F_{1,14} = 37.48$, $p < 0.0001$, $R^2 = 0.73$; Fig. 1). For example, the mean score of moult extent among Northern Wheatears, a long-distance migratory species, was 3.57, while the mean scores for resident species (*O. leucopyga*, *O. leucura*, *O. monacha,* and *O. melanura*) ranged from 9.25 to 14.64 (Fig. 1, Table 1). In contrast, the post-juvenile moult extent was not well explained by preferred habitat type (Table 2).

Intra-specific level

Mean moult extent of Northern Wheatear populations were related to migration distance. Birds from northern latitudes showed a less extensive moult than those breeding closer to the wintering grounds, i.e., the populations from southern Europe ($\beta = -1.774$, $t_{6.75,} = -3.60$, $p = 0.0093$, $n = 262$ individuals; Fig. 2). Individuals from Sweden, the site with the longest migration distance, showed a mean score of the post-juvenile moult of 2.43, while moult data from individuals studied in the Iberian System (in Central Spain, the site with the shortest migration distance) yielded a mean score of 6.27 (Fig. 2, Supplemental Table S2). Sex was not associated with the extent of the moult of the Northern Wheatear, with males moulting a similar number of feathers as females ($\beta = -0.022$, $t_{167.76} = 0.006$, $p = 0.99$, $n = 175$ individuals; Fig. 3).

Table 2 AICc values for phylogenetic least squares regressions built to explain post-juvenile moult extent in 16 wheatear species (genus *Oenanthe*)

Explanatory variable	K	AICc	ΔAICc
Migration distance (weighed)	3	66.04	0
Null model (unweighed)	2	80.17	14.13
Null model (weighed)	2	83.79	17.76
Habitat type (weighed)	3	86.34	20.30

All models had one explanatory variable. We tried both weighed (by within-species variance) and unweighed models, but show here only the more plausible of these. Results of analyses for null models (built with just the intercept) are also included. In all cases, Pagel's $\lambda = 1$

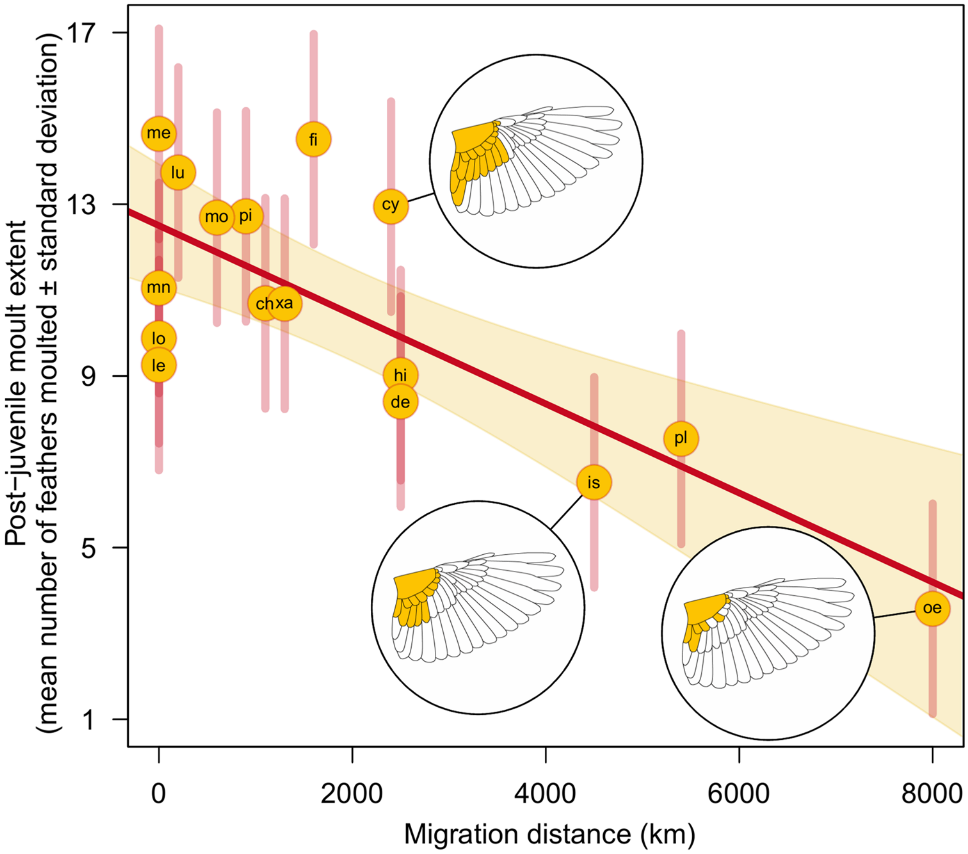

Fig. 1 The effect of migration distance (km) on the extent of the post-juvenile moult (mean ± SD number of feathers moulted) among 16 wheatear species (genus *Oenanthe*) in the Palearctic Ecozone. The letters in each data-point represent the specific species (see Table 1). The circled insets depict examples of moult extent in three species. The solid red line shows the linear regression between migration distance and extent of the post-juvenile moult, and 95% Confidence Intervals are shown in light red

Discussion

We provide new insights on the ecological factors that influence the inter- and intra-specific differences in the post-juvenile moult extent in passerines, focussing on the members of the *Oenanthe* genus. Our results strongly suggest that time available for moulting shapes the post-juvenile moult in wheatears through a negative relationship between the extent of the moult and the migration distance at species and population levels.

The post-juvenile moult extent of wheatears was significantly related to migration distance, with juveniles of long-distance migratory species moulting more feathers than sedentary or short-distance migratory species (Fig. 1). However, further research is needed at a population level for most of the wheatear species. Our results are based on migration distances calculated as straight lines between the mid-breeding and the mid-wintering areas of each species. However, some of species have large breeding and wintering areas and, thus, our estimated migration distances should be considered just as a proxy of the time available for moulting for each species or populations.

Interestingly, the post-juvenile moult extent of the Northern Wheatear populations was also affected by migration distance (Fig. 2). Individuals of populations with longer migration distances moult fewer feathers than those of populations with shorter migration distances. This finding is likely related to the fact that long-migratory populations of the Northern Wheatear spend less time in the breeding area when compared to short-migratory populations (Schmaljohann et al. 2012a, b; Arlt et al. 2015). Long-migratory populations leave the wintering area at similar dates or even later than short-migratory ones and their spring migration can be 10–20 days longer. Thus, the time spent at breeding grounds notably differs among Northern Wheatear populations, from 87 days in Alaska to 130 days in Germany (see detailed data in Arlt et al. 2015). Our results agree with our prediction and are in line with previous studies on time constraints for moulting in long-distance migratory species (Chabot et al. 2018; Kiat et al. 2019).

The observed variability in the extent of moult in juvenile wheatears at the inter- and intra-specific levels reflects an adaptive flexibility, in part as a response to time constraints (Hall and Tullberg 2004). Several factors have been reported to be involved in the time constraints experienced among wheatear species, as well as among populations of the same species in different latitudes. The post-juvenile moult extent shows intra-specific or even intra-population differences depending on the hatching and moult starting dates, because individuals that hatch earlier have more time available for

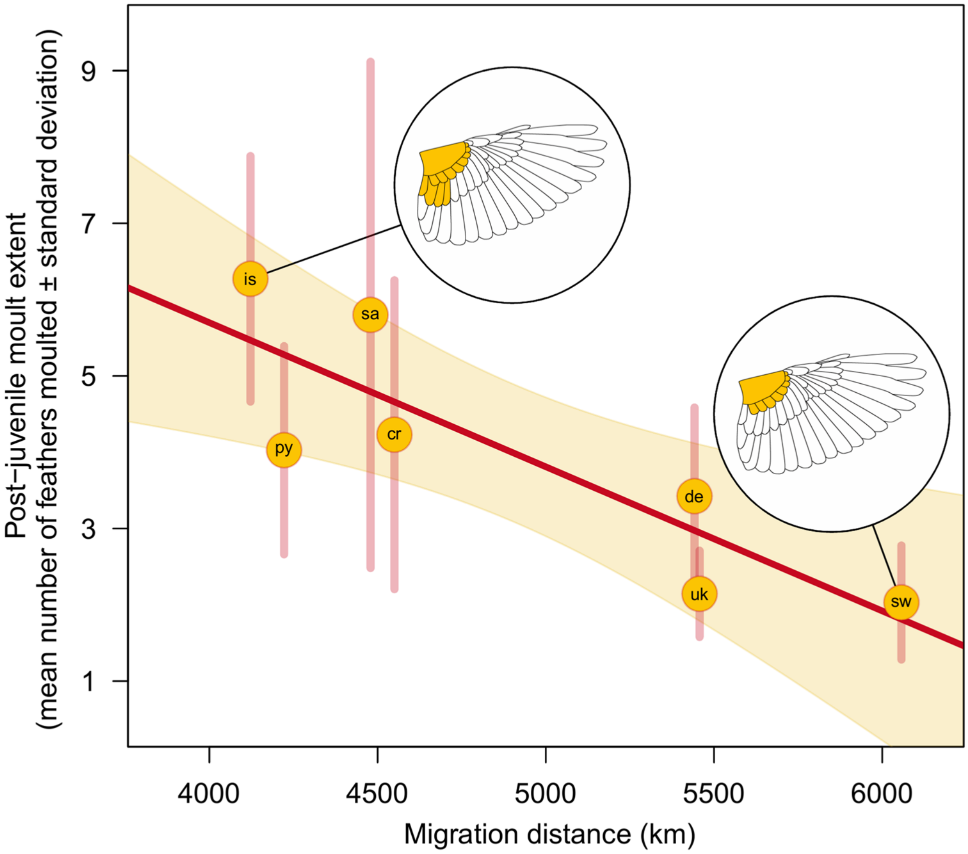

Fig. 2 The effect of migration distance (km) on the extent of the post-juvenile moult (mean ± SD number of feathers moulted) among seven populations of Northern Wheatear (*Oenanthe oenanthe*) in Western Europe. The letters in each data-point represent the specific population (see Supplemental Figure S2). The circled insets depict examples of moult extent in two populations. The solid red line shows the linear regression between migration distance and extent of the post-juvenile moult, and 95% Confidence Intervals in light red

moulting before the start of migration or the onset of winter (Newton 1966; Dhondt 1973; Bojarinova et al. 1999). In addition, the renewal of the feathers depends on the time available to gather the necessary resources, including those required for the pre-migration stage (Kiat and Sapir 2017), but it is unclear whether an extensive moult also demands more time to gain experience to efficiently obtain these resources (Norman 1990).

Contrary to our expectations and previous findings, we did not find a significant sex effect on the post-juvenile moult extent of the Northern Wheatear (Senar et al. 1998; Crates et al. 2015; Chabot et al. 2018). Extensive post-juvenile moults often involve plumage traits in males that are considered to be sexually selected (Norris 1990; Safran and McGraw 2004). We therefore expected males of sexually dimorphic species, such as the Northern Wheatear, to moult more feathers than females. Jenni and Winkler (2020) reviewed the extent of the post-juvenile moult in 22 passerine species and found that in 13 species (59%) males moulted more feathers than females. These authors stated that males may invest more in post-juvenile moult than females to achieve a more adult-like plumage for contests during winter and the following breeding season (Jenni and Winkler 2020). However, Northern Wheatear females and males of our studied populations moulted a similar number of feathers as registered in a sedentary species, Black Wheatear (*Oenanthe leucura,* Pérez-Granados 2020). These findings suggest that the relationship between sex and the extent of the moult varies between species (Norman 1997, Jenni and Winkler 2020). Such inter-specific variability regarding sex might be also related to the extent of the pre-breeding moult (Jenni and Winkler 2020). The Northern Wheatear undertake this moult in winter, after the post-breeding migration, and involves even fewer feathers than the post-juvenile moult (Shirihai and Svensson 2018; Jenni and Winkler 2020). Our unpublished data from three Iberian regions support such pattern ($n = 132$, mean number of moulted feathers ± SD = 0.89 ± 0.96), and therefore, we expected a negligible relationship with sex and the post-juvenile moult.

Wheatears are very sensitive to habitat quality at a local scale during the breeding season (Arlt and Part 2008). However, and contrary to our predictions, habitat type did not correlate with the post-juvenile moult extent in our study species. Juvenile wheatears living in dry habitats (mainly deserts) moulted a similar number of feathers in their post-juvenile moult as species that occupy non-arid habitats characterised by higher productivity during the breeding season (e.g., mountain areas). However, this lack of a general effect may be due to our classification of habitats (with just

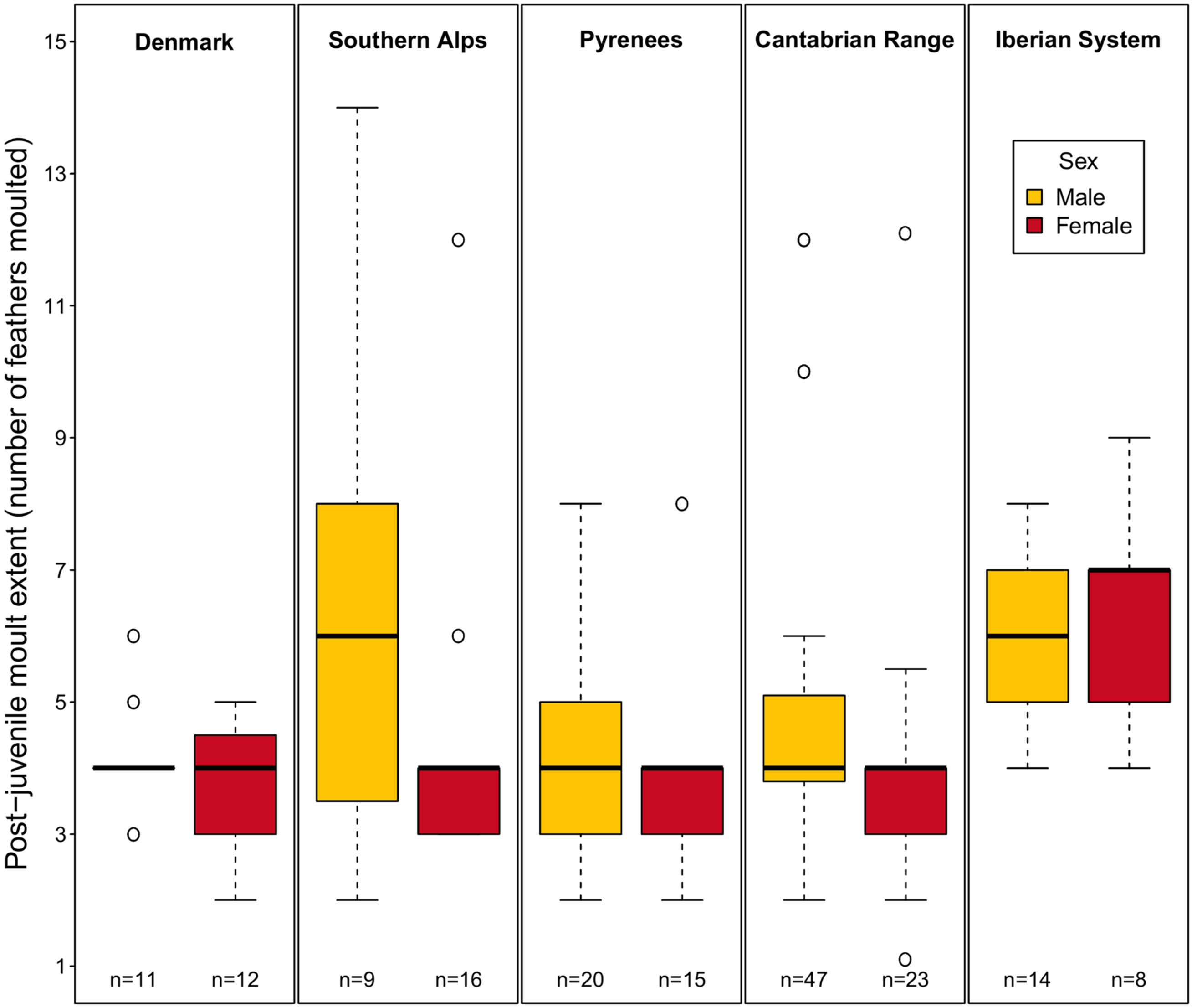

Fig. 3 The sex-dependent difference in extent of the post-juvenile moult (number of feathers moulted) among seven Northern Wheatear (*Oenanthe oenanthe*) populations. The box-plots display the fifth, twenty-fifth, fiftieth (median), seventy-fifth, and ninety-fifth percentiles of the data

two habitat types) or the fact that most wheatear species are indeed able to thrive in a wide environmental range including deserts (Shirihai and Svensson 2018; Del Hoyo et al. 2019).

Our study provides evidence for the factors that influence the post-juvenile moult extent in passerines. The results of this study indicate a strong relationship between moult and time available for moulting, which is related to migration distance, both important, highly energy-demanding processes in the avian annual cycle (Schmaljohann et al. 2012a). Further research should investigate the moult extent in other species or moult types (e.g., among populations of species with wide distribution ranges) to better evaluate the inter- and intra-specific differences (Hall and Thullberg 2004; Chabot et al. 2018), and include factors not considered in our study, such as photoperiod and hatching date. The importance of sex in moult extent should also be assessed to determine putative fitness consequences (Bojarinova et al. 1999; Podofillini et al. 2019).

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Data availability The data used in this study are archived on Figshare repository and can be accessed at: https://figshare.com/s/0ea2e130431436e1e000.

Code availability Code employed can be accessed at: https://figshare.com/s/02471a47d281cf292a6d.

Compliance with ethical standards

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

Ethics approval This study was performed under regular ringing permits from the Israel Nature and Parks Authority (NPA; ringing-permit A258) and General Directorate of Biodiversity and Environmental Quality of Spain (permits 530356, 530406, and 530465) and Federal Office for the Environment of Switzerland (permit reference F044-0799).

Consent to participate All researchers involved in the study are co-authors and consented voluntary to be part of the present manuscript.

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