Post-juvenile moult of the Red Crossbill *Loxia curvirostra*: differences in relation to sex and colour patterns

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The study of moult has received increased scientific attention due to its interdependence with other life-history aspects and its value as a reliable proxy of a bird's fitness. Here, we perform a detailed description of post-juvenile partial moult of a Red Crossbill Loxia curvirostra population exploiting Scots Pine Pinus sylvestris forests in the Pyrenees, southern Europe, with data from more than 1700 moult records. Crossbills within the tested population had replaced all or most median coverts and the six innermost greater coverts (GCs; 70-87%), decreasing outwards. Just 10% of the birds had renewed GC1. Tertials were renewed in half the cases and, exceptionally, some tail feathers, secondaries, primaries or primary coverts were renewed (less than 10%). Post-juvenile partial moults were more extensive in Pyrenean crossbills compared to crossbills in northern Europe, and in females compared to males. Among males, there were differences in moult extent dependent on colour, from greater to lesser extent: patchy, red, orange and yellow. Several factors could underlie these differences, such as climate, food availability or stability (explaining latitudinal differences), hormonal and sexual selection processes (explaining sex-dependent variation), hatching date or oxidative stress associated with the expression of colour patterns.

Key words: Loxia, moult in birds, avian colouration, moult extent

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Feathers are dead structures that wear and, therefore, progressively lose their structural and functional properties. Consequently, that wear compromises essential functions for the bird, such as the flying capacity, thermoregulation or visual communication (Jenni & Winkler 2020). As a result, all birds renew their feathers with a higher or lower frequency, in most species once a year, as in passerines. Moulting feathers is energetically costly, and so is timed to not overlap with other energydemanding activities like reproduction and migration (Lindström et al. 1993, Hemborg et al. 1998, Hemborg 1999). Birds are expected to adjust their moult to the time and strategy best adapted to current circumstances (Newton & Rothery 2009, Jenni & Winkler 2020). For example, first-year birds in some European sedentary species undergo a complete post-juvenile moult, where they renew all feathers because they have a wide temporal window after fledging and before winter, given that these species often breed relatively early within the season (Ginn & Melville 1983, Kiat & Izhaki 2016, Jenni & Winkler 2020). By contrast, in most migratory species, juveniles undergo a partial moult, often affecting just the body and some wing coverts, due to the narrow temporal window from fledging to the start of migration. Variation in moult also occurs within the same species, where different populations may have a greater or lesser extent of feathers renewed. Even between individuals, moult extent, ergo, the number of feathers replaced, can differ depending on the birds' physical condition. Besides this variation, however, most birds show predictable moults as a result of optimal evolutionary adaptation (Barta et al. 2006).

Moult of European passerines is reasonably well described for northern and central European populations (e.g. Svensson 1998, Jenni & Winkler 2020), but there is still a considerable gap in the understanding of moult in populations in southern Europe. Many passerines conduct a post-juvenile partial moult soon after fledging and before the winter period. During this partial moult, several but not all feathers are replaced, including all body feathers, tail feathers and a variable number of wing feathers, including smaller, median and greater coverts, tertials and, more rarely, some primaries, primary coverts or even some secondaries (Jenni & Winkler 2020, Svensson 1998). Understanding such variation in how many feathers are moulted during partial moult is important because the moult pattern is ultimately associated with the environment, and from here we can analyse how ecological and evolutionary drivers like climate change can affect essential biological processes within a bird's life history (Kiat et al. 2019). Since, in general, southern European passerines have more time to breed and moult (the climatologic summer is longer than at higher latitudes), studies suggest that southern European birds can have more extensive partial moults (Jenni & Winkler 2020, Kiat et al. 2021).

With this study we intend to contribute to our knowledge on moulting and colouration in birds in southern Europe, making use of a long-term dataset of 20 years collected in Spain on Red Crossbills Loxia curvirostra (hereafter, crossbill), a suitable model species due to its large variability in moulting and colouration. Crossbills undergo a partial moult in their first year of life (post-juvenile partial moult), with which they pass from a full juvenile plumage to an adult-like plumage with juvenile feathers mostly retained in their wings and tail (Jenni & Winkler 2020, Svensson 1998). Crossbills are specialist foragers who strongly depend on the annual fluctuations in seed production of the conifers they feed on (Cramp & Perrins 1994). Consequently, their life cycle is adapted to seed availability (both temporally and spatially). They start to breed in winter, mainly from December until March/April, when cones open (Cramp & Perrins 1994) with an additional (opportunistic) second laying attempt in summer or autumn (Clouet 2000, Alonso & Arizaga 2011). Red Crossbills moult in summer but most do not overlap this process with the breeding period (Alonso & Arizaga 2011, Fernández-Eslava et al. 2020). Spain hosts a number of crossbill populations differing in their vocal, morphological or genetic traits, all of which are driven by trophic specialization (Edelaar et al. 2012, Björklund et al. 2013, Parchman *et al.* 2018). In parallel, moult could also vary among individual birds and zones (populations) in response to different selection pressures, such as the seed availability of different conifers and trophic resource stability. For example, the Aleppo Pine *Pinus halepensis* has a much more stable annual and interannual productivity than other conifers, such as Scots Pine *P. sylvestris* (Tapias *et al.* 2004). Therefore, describing the moult within these populations (associated with different conifer species) is a first but essential step to studying ecological and evolutionary relationships and environmental aspects. Overall, it contributes to our general aim of understanding how crossbills are adapted to key trophic resources and how these modulate their life history traits.

It is relatively common in northern and central European crossbills to find birds with so-called 'eccentric' moults, i.e. an extensive partial moult where up to a few primaries, secondaries or primary coverts are replaced (Jenni & Winkler 2020). Overall, however, we expect that owing to their southern distribution with longer summers and/or more stable seed production in many southern European conifer species (Parchman *et al.* 2018), these eccentric partial moults could be relatively more frequent in Spanish crossbills compared to northern European crossbills.

The main breeding season of crossbills in Iberia is between February and May (late winter/early spring) and their moult takes place soon after breeding, peaking in June (Alonso & Arizaga 2011, Fernández-Eslava et al. 2020). However, when food is abundant, they can lay a second opportunistic clutch in summer (August/September), and if this occurs, adults can suspend their moult to breed and resume moulting after the second clutch (Fernández-Eslava et al. 2020). We can find birds from these clutches with juvenile plumage almost every month throughout the year (Alonso & Arizaga 2011). For this reason, it is yet unknown whether all juvenile birds moult within the same period of the year or whether we can detect two or more moulting peaks, which would correspond to the main two breeding peaks potentially existing within a year (see Bojarinova et al. 1999). Another interesting point is whether there could be a relationship between the partial moult (and its extent) and the dominant colour among crossbill males. Male crossbills range in colour patterns from yellow to red, passing through orange and a patchy colouring, which includes both vellow and red feathers (Fernández-Eslava et al. 2020). The timing of post-juvenile partial moult could depend on birth date or be non-synchronous, so the moulting process in different seasons might give distinct plumage



Examples of two Red Crossbill colour morphs; above a yellow male and below a red male (photos DA, Navarra, Spain).

colours. Some authors relate the different plumage colours to the amount of carotenoids available in the diet (del Val et al. 2014) because they could change over the months due to the pinecone seed maturation (pinecones are green in spring but ripen in autumn; Jenni & Winkler 2020). An alternative explanation for the different plumage colours is the available time before winter and, therefore, differences in moult speed and investment of moulting resources between springborn and summer-born individuals. In the Two-barred Crossbill Loxia leucoptera, a species taxonomically close to the Red Crossbill, Deviche (2000) related the moult extent to colour and age (skull ossification) in juveniles. He observed that the red-plumaged juvenile males had a more extensive partial moult than the nonred males, even though both groups were apparently of a similar age. He concluded that the colour of the plumage was not related to the birth date of the birds. However, due to a limited sample size, he could not test for differences between individuals of other colourations, such as, for example, between orange and yellow morphs or those with a mixture of red and yellow feathers.

In this paper, we will provide a detailed description of the post-juvenile partial moult in a crossbill population exploiting Scots Pine forests in the Pyrenees in southern Europe. One of our hypotheses is that southern European crossbills perform a more extensive postjuvenile moult than their northern counterparts. This may be because the summer season is longer in the south, so the birds have more time to moult. Also, we predict that the extent of post-juvenile moult in crossbills could vary between the sexes and in relation to the colour patterns of males. In some species, differences in the extent of post-juvenile moult between males and females have been reported, with more extensive moults in males (Gosler 1991, Rymkevich & Bojarinova 1996, Senar et al. 1998, Bojarinova et al. 1999) that could be related to reproductive effort (Crates et al. 2015). On the other hand, the extent of the post-juvenile partial moult has been related to the hatching date. Specifically, field and experimental studies show that juvenile birds hatched early in the breeding season start moulting earlier and have more extensive post-juvenile partial moults (Rymkevich & Bojarinova 1996, Serra et al. 2007, Ryzhanovskiy 2017). Because feather colour is acquired during moult, differences in moult extent and colour could be related. If this is so, we could expect that the colour will also depend on the moment of birth (spring-born or summer-born). But it is likely not the only factor, since the relationship between the post-juvenile moult extent and plumage colour in birds has also been shown to be linked to individual quality (Senar et al. 1998, López et al. 2005, Crates et al. 2015). The variation in the extent of post-juvenile moult may have potentially important ecological and behavioural implications, which have not been explored to their fullest in the avian literature.

METHODS

Study area and data collection

This study was carried out in the western Pyrenees (Navarra, north of Spain). Crossbills were sampled at two nearby sampling points: Uztarroz (42°53'N, 01°00'W, 1340 m.a.s.l.) and Bigüezal (42°40'N, 01°08'W, 1100 m.a.s.l.). The data from these two sites were lumped for the analyses and considered as a single sampling unit because they are only separated 30 km in a straight line and sampling sites were found in mature forests of the same conifer species, Scotch Pine (Loidi & Báscones 2006).

The sampling protocol consisted of visiting each sampling site once every two weeks, during the whole

annual cycle, from 1997 to 2020, with gaps due to bad weather or logistics. At each locality, we always used the same number of mist nets (length: Uztarroz: 12 m, Bigüezal: 24 m), always placed at fixed sites within each locality. Mist nets were open for four hours, starting at dawn. Mist nets were placed around areas where birds gathered to ingest minerals (salt deposits at Bigüezal, cattle rail composed of stones at Uztarroz). Once captured, each bird was ringed, sexed and aged, following Svensson (1998). According to feather colour, form and wear, crossbills were aged as first/ second year birds (EURING code 3 or 5) when they showed a full or partial juvenile plumage. In this latter case of partial moult, birds still retained juvenile feathers, showing a partial moult with a limit between the new and old (juvenile) feathers in their wing and tail. Crossbills were aged as adults (EURING code 4, 6, or a higher code for older birds), if they had performed a complete post-breeding moult, hence they had no juvenile feathers left (Jenni & Winkler 2020). For our analyses in this study, we used only first/second year birds.

Many birds showed a finished post-juvenile partial moult at the time of capture so that we could complete a moult record for each. Overall, we compiled 1757 moult records (females: 636, males: 1121). On the moult record, wing and tail feathers were scored as 1 if they were old (non-moulted feather, nest-grown feather) and 5 if they were new (moulted feather). For crossbills with their post-juvenile moult finished, we built three categories to classify their moult extent (Figure 1): (1) Rm: Reduced moult, whether the partial moult involved just the minor and median coverts, (2) Nm: Normal moult, with also some (eventually, all) greater coverts moulted, tertials and alula feathers, (3) Em: Eccentric moult, whether the partial moult also involved a variable number of rectrices, secondaries, primaries or primary coverts (defined above in the introduction).

Additionally, we recorded whether these first/ second-year birds were moulting or still had full juvenile plumage. Thus, we distinguished three states of moult: (1) with totally juvenile plumage, (2) during their moult or with partially changed plumage or (3) with the post-juvenile moult finished. We calculated the percentage in each state over the course of the year (Figure 2).

In addition, we recorded the colour of the male crossbills. We used four colour categories: yellow, orange, red and patchy. The latter comprised birds with a variable number of yellow and red/orange feathers. The visual assessment of the colour is known to corre-



Figure 1. Three patterns of post-juvenile moult in male Red Crossbills. (A) Reduced post-juvenile moult (Rm), showing moult of limited extent, replacing body feathers and some marginal coverts. The rest of the wing has juvenile feathers. Recognizable as second year bird by having all median coverts and juvenile greater coverts fringed whitish. (B) Normal postjuvenile moult (Nm), replacing body feathers, marginal coverts, 3-8 median coverts and 5-9 greater coverts. Rest of wing juvenile. Recognizable as a second-year bird by having some median coverts and juvenile greater coverts fringed whitish. (C) Eccentric post-juvenile moult (Em), replacing body feathers, marginal coverts, median coverts, greater coverts, tertials and 4-9 primaries. Rest of wing juvenile. Recognizable as first year by the whitish fringed carpal covert and the fact that only one of the primary coverts (PC7) has been renewed (photos DA, 4 April 2004, Navarra, Spain).

late very well with colour measures recorded by colorimetry (del Val *et al.* 2009). A single observer (DA) recorded all measurements, including colour group. Previous work in which individuals were classified into these four colour categories proved to be highly repeat-

Table 1. Chi-squared test of the relationship between the state of observed moult in first/second year birds (full juvenile plumage, moulting and finished post-juvenile moult) and the annual season.

		Full juvenile plumage	Moulting	Finished post-juvenile moult
Spring	Observed	293.0	417.0	994.0
	Expected	288.8	471.9	943.3
	Residuals	0.2	-2.5	1.7
Summer	Observed	126.0	250.0	34.0
	Expected	69.5	113.5	227.0
	Residuals	6.8	12.8	-12.8
Autumn	Observed	97.0	94.0	164.0
	Expected	60.2	98.3	196.5
	Residuals	4.7	-0.4	-2.3
Winter	Observed	22.0	118.0	565.0
	Expected	119.5	195.2	390.3
	Residuals	-8.9	-5.5	8.8



Figure 2. Phenological distribution of post-juvenile moult progress in a Scots Pine-associated Pyrenean population of Red Crossbills. Completed post-juvenile moult, active post-juvenile moult (that is, with a mixture of juvenile plumage and new plumage) and fully-grown juvenile plumage without post-juvenile feathers. Sample sizes are shown above the bars.

able when measured twice (separated by one week) by observer DA, who recorded all measurements without knowing the identity of the bird (Spearman's r = 0.96, P < 0.001; Cantarero *et al.* 2020).

Statistical analyses

We used chi-square tests to investigate if there was an association between the division of birds over the moult categories (reduced, normal and eccentric moult) and (1) timing of the season, (2) sex of the bird and (3) the male colour categories. Recaptured birds in the same period of moult were excluded. To test for the existence of significant differences, we employed Pearson chi-square tests using R v. 4.2.2 based on contingency tables which showed the number of observed and expected individuals (Tables 1–3) for each categorical variable.

RESULTS

Throughout the year, we found birds in the first/second year of life with three different plumages depending on their moult (Figure 2): juvenile plumage, plumage in active partial moult and plumage showing a finished partial moult. We found variations in the proportion of these three plumages throughout the different seasons of the year (χ^2_6 = 599.61, *P* < 0.001; see Table 1 and Figure 2). During the winter months (December to February), most crossbills were captured with an already completed partial moult, while in summer (June to August), birds were mainly observed with an active partial moult (Table 1, Figure 1). Birds with full juvenile plumage occurred along the whole annual cycle, though they tended to be proportionally more abundant around summertime (Table 1, Figure 2).

For already finished partial moults, we observed that, overall, crossbills within the tested population had replaced all (100%) of the lesser and most (>80%) of the median coverts, and the greater coverts (GC) up to GC6 (70-87%; numbered from inner- to outermost; Figure 3). GC renewal decreased from GC5 to GC1 (just 10% of the birds had renewed GC1). Tertials were renewed less frequently (up to 50%) and the rest of wing feathers (secondaries, primaries, primary coverts), only exceptionally (<10%). Tail feathers were replaced in a small proportion of the birds (Figure 3).

The extent of the observed moult was found to be sex-dependent ($\chi^2_2 = 24.26$, P < 0.001), with the females undergoing more eccentric moults (Em) than the males (Table 2, Figure 3). Among males, we also found variation among the colour groups ($\chi^2_6 = 137.25$, P < 0.001), with the yellow crossbills moulting

MALES

S6 S5 S4 S3 S2 S1

CC

P1 P2 P3 P4 P5 P6 P7 P8 P9

fewer feathers, the patchy ones being more likely to perform eccentric moults, while the red and orange morphs where more likely to perform normal moults (Table 3, Figure 4).

DISCUSSION

Despite all the information that moulting data can provide us about the life history of birds or in relation to other processes during the annual cycle, few descriptive studies have been carried out on this topic. With this in-depth study on post-juvenile moulting in an Iberian Red Crossbill population, we want to provide

MiC

MeC

T9

Т8

S7

information that we hope will help to understand other life-history characteristics, such as colour variation, the quality of individuals or adaptative strategies that develop, for example, in response to climate change.

Crossbills have a main reproductive peak at the end of winter (February–March; see Alonso & Arizaga 2011), while the main season of post-juvenile moult occurs well outside of the breeding period, namely in summer (higher percentage of active post-juvenile moults in June–September, see Figure 2), roughly coinciding with the time when adult crossbill moult within this same population (Fernández-Eslava *et al.* 2020). This suggests that it is in this period when crossbills find the best conditions to moult, either because they

PC

P10





Table 2. Chi-squared test of the relationship between sex of the birds and the extent of the observed moult for birds who finished their post-juvenile moult (Reduced, Normal and Eccentric).

			Females	Males
	Reduced	Observed	66.0	144.0
		Expected	76.0	134.0
		Residuals	-1.1	0.9
ktent	Normal	Observed	489.0	909.0
lt ey		Expected	506.1	892.0
Mou		Residuals	-0.8	0.6
	Eccentric	Observed	81.0	68.0
		Expected	53.9	95.1
		Residuals	3.7	-2.8

Table 3. Chi-squared test of the relationship between male colouration and the extent of the observed moult for birds who finished their post-juvenile moult (Reduced, Normal and Eccentric).

			Yellow	Patchy	Orange	Red
	Reduced	Observed	44.0	38.0	49.0	13.0
		Expected	14.3	28.3	19.4	60.4
Ļ		Residuals	7.9	1.8	-0.8	-6.1
tten	Normal	Observed	59.0	158.0	255.0	437.0
lt ey		Expected	90.0	178.4	259.5	381.1
[non]		Residuals	-3.3	-1.5	-0.3	2.9
	Eccentric	Observed	8.0	24.0	16.0	20.0
		Expected	6.7	13.4	19.4	28.5
		Residuals	0.5	2.9	-0.8	-1.6



Figure 4. Post-juvenile moult extent according to male colouration in Red Crossbills. The extent of moult is ordered from reduced moult (Rm) with zero greater coverts moulted to normal moult (Nm) with 1–10 greater coverts moulted to eccentric moult (Em).

find optimal nutritional sources or find the best temporal adjustment in order to avoid overlap with other energy-demanding life history aspects.

The extent of post-juvenile partial moult in our population is larger than in crossbills from northern Europe (Jenni & Winkler 2020). One of the main differences was that in our population every feather could potentially be moulted. Northern European crossbills were reported never to moult the innermost primary coverts (PC1-3) and the outermost secondaries (S1-5; Jenni & Winkler 2020), whilst up to a 10% of the crossbills we studied had moulted these feathers. Another remarkable difference was the alula: Jenni & Winkler (1994) observed that only up to 10% of birds moulted these feathers; whilst we observed that c. 80% and 50% of the birds had moulted their first and second alula, respectively. Finally, we also found that our crossbills were more likely to moult some secondaries. Interestingly, both in northern and southern Europe, the replacement of tail feathers is exceptional (but see Benkman & Young 2020). Overall, however, we obtain a pattern typical for several finch species and other passerine birds: that the extent of partial moult tends to be higher at lower European latitudes (Kiat & Izhaki 2016, Kiat et al. 2021) probably because the climate at southern localities allows broader temporal windows with conditions favourable to moult (Jenni & Winkler 2020).

Moult extent also varied in relation to sex, with females replacing more feathers (i.e. females undergo eccentric partial moults more frequently), see Table 2 and Figure 3. Causes underlying this difference remain unknown to us, so we can no more than advance some potential explanations. A first possibility could be that the male ornamentation supposes an added cost. For example, in the House finch Carpodacus mexicanus, a species with a colour pattern similar to the Red Crossbill, it was detected that males without food restriction develop redder and more intense plumage. These observations show an energetic cost of carotenoid utilization in generating colourful plumage (Hill 2000). In line with this, it is possible that male crossbills, by expending energy resources to produce colourful plumage, have fewer reserves than females to shed their feathers during their post-juvenile moult. A second possibility, which to date has not been tested, could be that the hormonal balance of females could promote eccentric partial moults more frequently than in males, who have different hormones. Alternatively, reproductive differences between sexes could also play a role (Figuerola & Jovani 2001). In particular, crossbills in our Pyrenean population can show an opportunistic reproduction in mid-summer, well after their main breeding period, which lasts from mid-winter to spring (Alonso & Arizaga 2011, Fernández-Eslava et al. 2020). In this summer breeding period, it is relatively common to find first-year females (showing juvenile feathers) with brood patches (Alonso & Arizaga 2011). This reproduction occurs during the moulting period, and probably the moult will be suspended like in older birds undergoing complete moults (Kiat et al. 2019, Fernández-Eslava et al. 2020). If so, then it is possible that, as a consequence of re-activating the moulting process after breeding, females could replace more feathers than expected, thus giving rise to the eccentric (extensive) partial moult. In contrast, first-year males have not been observed breeding (i.e. showing cloacal protuberance) in this opportunistic summer breeding period (DA pers. obs.). This suggests that males are less likely to breed in their first year of life, which would be compatible with the hypothesis that females which show eccentric moults are those which suspend their partial moult for an opportunistic breeding trial in summer. First-year males may be outcompeted from such first-year breeding attempts by males that already have a sub-adult or adult fully-grown plumage (coloured body plumage), which could be a reason underlying the observed difference in moult extent between the sexes.

Within the colour categories, we found that males with lighter colours (i.e. yellow as compared to orange, patchy and red crossbills) replaced fewer feathers (Table 3, Figure 4). On the opposite end of the spectrum, patchy crossbills were found to be particularly prone to undergo eccentric partial moults (Table 3, Figure 4). Overall, it can be stated that crossbills hatching during the first months of the year would have a lot of time to moult, which would allow them to perform more extensive partial moults. It is also possible that some birds, born in late summer (e.g. September), that undergo partial moult at the end of the year (e.g. November) and develop a very short extent of the moult (Rm), again perform a partial moult the following year, but this time, eccentrically and exhibiting a patchy plumage (yellow from November and red-orange from the summer of next year). On the other hand, orange and red males usually show moults of standard extent (Nm; the most frequent in the population). Therefore, they are likely to make their partial moult in the main season, that is, when most individuals are in active moult (in our case, June-September) with sufficient time available (before winter). Based on their moult extent at the time of catching, we hypothesize that orange and red coloured male crossbills would be birds hatched in late winter/ earlier spring (main reproductive period), whilst the yellow birds could mostly come from the opportunistic broods in summer. This schedule may fit rather well with the two moult peaks detected for the crossbills that undergo a partial moult within this population (Alonso & Arizaga 2011).

In conclusion, we observed that juvenile Pyrenean crossbills associated with Scots Pine forests show more extensive partial moults than in northern Europe and females moulted more extensively compared to males. Among males, orange and red colour morphs showed more extensive moult compared to yellow individuals, while patchy birds exhibited a proportionally higher degree of eccentric moults. Causes underlying these differences could be complex ranging from factors such as variation in hatching date, climate, food availability and stability (explaining latitudinal differences) to hormonal and sexual-selection processes (explaining sex-dependent variation). Understanding the exact mechanisms behind moult variation is needed to better understand life-history strategies and trade-offs in birds and the constraints and flexibility they have in response to environmental change.

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SAMENVATTING

Onderzoek naar de rui van vogels heeft in de loop van de jaren steeds meer aandacht van onderzoekers gekregen. Het vervangen van veren bij vogels is namelijk een proces dat interfereert met verschillende andere aspecten in het vogelleven. Het verloop van het ruiproces is bovendien een goede maatstaf voor de conditie van de vogel. Wij onderzochten in 1997-2020 in de Grove Dennen Pinus sylvestris bossen in de Spaanse Pyreneeën in detail de post-juveniele partiële rui van meer dan 1700 Kruisbekken Loxia curvirostra. Van de onderzochte vogels die de rui al hadden beëindigd, hadden alle de kleine vleugeldekveren geruid, >80% de middelste vleugeldekveren en 70-87% 1-6 van de binnenste grote vleugeldekveren (aantal nieuwe veren afnemend van buiten naar binnen: binnenste grote vleugeldekveer slechts in 10% van de gevallen vernieuwd). Tertials waren in de helft van de gevallen nieuw. Slechts nu en dan waren enkele handpennen, handpendekveren, armpennen en staartpennen vernieuwd. De rui was bij vrouwtjes uitgebreider dan bij mannetjes en bij de Pyreneese Kruisbekken ook uitgebreider dan bij vogels in het noorden van Europa. Bij mannetjes varieerde de kleur van vlekkerig-gekleurd, rood, oranje tot geel, en was in deze volgorde gecorreleerd met de mate van vleugelrui. Aan deze variatie kunnen in beginsel verschillende factoren ten grondslag liggen, zoals verschillen in klimaat, voedselbeschikbaarheid en -voorspelbaarheid en broedseizoen (bij verschillen tussen noord en zuid), variatie in hormonale en seksuele selectieprocessen (bij verschillen tussen mannetjes en vrouwtjes) en uitkomstdatum of oxidatieve stress geassocieerd met de expressie van kleur.

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