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ORIGINAL ARTICLE

# Moult performance varies in relation to colour patterns in crossbills

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**Abstract**

Carotenoid-based ornamentation can vary greatly among individual birds of the same population. This variability might consider the timing and duration of moult. Crossbills (genus *Loxia*) show large variation in their colour patterns, ranging from dull yellow to red. Thus, they provide an excellent avian model for testing whether the timing and duration of their moult are associated with their dominant colour patterns. Using a dataset of more than 1900 crossbills captured in the Pyrenees (Spain), we observed that individuals with red feathers started their primary moult early, while those with yellow feathers started moult on an average of 18 days later. We also found that yellow crossbills were more likely to suspend moults (i.e. temporally interrupt moult), postponing a part of the moult until September. These differences in the moulting process may be related to plumage colour, which reflect individual condition.

**Keywords** *Loxia* · Moult in birds · Non-linear moults · Plumage colouration · Carotenoids · Underhill-Zucchini models

**Zusammenfassung**

**Mauserverlauf variiert im Zusammenhang mit Farbmustern bei Kreuzschnäbeln**

Die auf Carotinoiden basierende Ornamentik kann bei einzelnen Vögeln derselben Population stark variieren. Diese Variabilität könnte mit dem Zeitpunkt und der Dauer der Mauser zusammenhängen. Kreuzschnäbel (Gattung *Loxia*) zeigen große Unterschiede in ihren Farbmustern, die von stumpfem Gelb bis zu Rot reichen. Sie eignen sich daher hervorragend als Vogelmodell, um zu untersuchen, ob der Zeitpunkt und die Dauer der Mauser mit den vorherrschenden Farbmustern zusammenhängen. Anhand eines Datensatzes von mehr als 1900 Kreuzschnäbeln, die in den Pyrenäen (Spanien) gefangen wurden, konnten wir feststellen, dass Individuen mit roten Federn ihre primäre Mauser früh begannen, während jene mit gelben Federn im Durchschnitt 18 Tage später mit der Mauser begannen. Außerdem stellten wir fest, dass gelbe Kreuzschnäbel ihre Mauser eher verschieben (d. h. die Mauser zeitlich unterbrechen) und einen Teil der Mauser auf September verschieben. Diese Unterschiede im Mauserprozess könnten mit der Gefiederfarbe zusammenhängen, die den individuellen Zustand widerspiegelt.

## Introduction

In many birds, males show conspicuous colour patterns that are obtained from the metabolization of carotenoid-based pigments (Prum 1999). Carotenoid-based colouration, ranging from yellow to orange and red, in the animal kingdom has evolved as an honest signal showing the quality of the individual in social and sexual contexts (e.g. Lehtonen et al. 2011). These carotenoids, however, cannot be synthetized de novo; hence, they must be acquired via the intake of yellow pigments. The concentration of such pigments in the organism can depend on several factors, such as the physiological capacity of accumulation and the type of diet. Furthermore, the availability of these carotenoids can vary seasonally or because of habitat quality (Arriero and Fargallo 2006; Ferns and Hinsley 2008); these pigments can constitute a limited resource during some periods in the annual cycle (Hill 2006). Thus, only the best foragers, with the best individual quality, and capability to adjust moult

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when these pigments are most abundant in the environment, may be able to present the brightest colour patterns (Hill and Montgomerie 1994; Hill et al. 2002; Hill 2006). Getting a colourful plumage is more complex in those species that transform yellow pigments into red ones. The metabolism behind the colour transformation (e.g. by adding ketones through oxidation to produce red keto-carotenoids) is highly energy demanding, which would augment the honesty of this colour signal (Hill 2000). Moreover, this transformation is associated with mitochondrial breathing (Johnson and Hill 2013), so the red ornaments may appear only in birds capable of obtaining sufficient pigments through the diet, allocating energy for their transformation, and having optimal mitochondrial functionality.

The Red Crossbill (*Loxia curvirostra*; hereafter, crossbills) is an excellent avian model to test the relationship between carotenoid-based colour patterns and other life-history aspects, including moult. Male crossbills show carotenoid-based colours, varying from yellow to orange and red, in several parts of their body, including the throat, mantle, and rump (Stradi 1998). This great variation could be caused by individual differences in the timing of the post-breeding moult: males moulting at the end of the summer/autumn tend to show a higher proportion of red colouration, in comparison with those that moulting earlier, which would acquire a more yellow colouration (Weber 1972; Ginn and Melville 1983; del Val et al. 2014). Theoretically, the red colouration late in the season may reflect a high amount of carotenoid-based pigments in the crossbills' diet due to a shift from old to new conifer cones (Newton 1972). Notably, in Iberia, the new cones of key conifers for crossbills, such as the Scots Pine (*Pinus sylvestris*), are fully grown in late spring and early summer, when old cones had dropped the seed (Ceballos and Ruiz de la Torre 1979). During this time of year, captured crossbills often have resin stuck to their beaks because they feed on new green cones (pers. obs.). As the season progresses, the cones turn brown until they reach full maturity in November (Ceballos and Ruiz de la Torre 1979), by which time the post-breeding moult of the crossbills is completed (Fernández-Eslava et al. 2020).

However, these studies have omitted that crossbills can suspend, and later resume, this moult (Jenni and Winkler 2020). Our recent study of the same population revealed that a remarkable proportion of the birds suspended their post-breeding moult (i.e. temporally interrupt moult of body and flight feathers), typically at the time that they are replacing the middle primary feathers (P5–P6, numbered in descending order) (Fernández-Eslava et al. 2020). Suspended moults have been associated with a second, opportunistic breeding in crossbills around mid-summer; hence, the post-breeding moult is resumed by the end of the autumn once the second breeding is completed (Fernández-Eslava et al. 2020). The suspended moult phenomenon could give rise to, or be associated with, the occurrence of different colour patterns. For example, the concentration of carotenoids in blood can vary seasonally (del Val et al. 2014), so the amount of carotenoids deposited in the feathers, and hence the feathers' colour, may vary depending on when they grow. On the other hand, moult is a highly energy-demanding process, so individual quality can play a role in moult progress and might be reflected in the colour of feathers.

The relationship between plumage colour and moult has been poorly investigated, not only in crossbills but also in most birds even though the growth and colour-acquisition of new feathers share the same physiologic processes (Hill 2006). Studying the relationship between colour and moult would allow us to determine the most important factors that influence the acquisition of colour, and understand its relationship with other vital processes that also demand a high amount of energy. The fact that crossbills suspend their moult due to a second clutch (Fernández-Eslava et al. 2020) can help us investigate the limitations of birds to carry out reproduction and moult without deteriorating their physical condition. Individual condition, in case of crossbills, appears to be reflected in the colour of their ornamentation. With this study, we contribute to filling this gap in our understanding of the relationships between moult and colouration. The main purpose of our work was to determine whether the start and duration of the post-breeding moult varied among male crossbills with different colour patterns. Our hypothesis is that moult would start on an optimal date in high-quality individuals, i.e. the red crossbills, than in the lower-quality yellow ones (Fernández-Eslava et al. 2021a, b). This optimal date would occur within our studied population in May–June (Fernández-Eslava et al. 2020) when the growth of green cones is at its peak, and a large part of the population is in active moult. We also expect that the high quality of the red males would allow them to carry out a second breeding without suspending the moult, most likely only slowing down this process. In terms of duration, we expect that the yellows would suspend the moult to cope with breeding and perform a rapid moult that would impair the acquisition of the red colour during feather synthesis. To test this hypothesis, we used a dataset with 1911 male adult crossbills captured from 1999 to 2022 in two nearby sampling localities in the Pyrenees (Spain).

## Methods

### Study area and data collection

All crossbills used in this study were captured at two locations in the western Pyrenees in northern Spain: Bigüezal (42° 40′ N, 1° 07′ W; 1096 m asl) and Uztarroz (42° 52′ N, 1° 00′ W; 1383 m asl). The vegetation at these two sites is dominated by Scots pine, with some patches of meadow scattered across the forest matrix. Captures were conducted periodically, with one sampling day per fortnight, during the whole annual cycle, from 1999 to 2022. Some gaps within this long sampling series occurred due to logistical difficulties or extreme bad weather (e.g. snowfalls hampering the access to sampling localities). Overall, however, we obtained a representative sample of male adult crossbills captured with active and non-active moult across the entire year ($n = 1911$ male adult crossbills; for details see Fig. 1).

Crossbills were sampled during a 4-h period beginning at dawn, with the same number of mist nets within each sampling site. Mist nets were placed around sites where birds attend daily to feed on salt deposits provided for the cattle. One of the authors (DA) collected all data. Once captured, each bird was ringed and its sexed and aged (Svensson 1998). We only considered adult males in this study. We considered as adults the males that have undergone at least their first complete moult, i.e. hatched more than one year before capture (EURING age category 4 or 6). The stage of moult was recorded according to the degree of development of the primary feathers (P1 to P9, numbered from innermost to outermost; P10 is reduced and was not considered) of the right wing: 0, old non-moulted feather; 1, absent or in pin; 2, < 1/3 grown; 3, 1/3 to 2/3 grown; 4, > 3/4 grown; and 5, fully newly grown (Ginn and Melville 1983). The sum of the scores for the primaries ranges from 0 for a bird without any feather moulted to 45 if the nine primaries are new (Underhill and Zucchini 1988). These values were transformed to a scale of 0–1 (1 = moult score 45 points, all feathers new). In bird species where the length and, therefore, mass of the outer- and innermost primaries vary substantially, the total moult score should be corrected for the feathers mass (Summers et al. 1983; Underhill and Joubert 1995). Crossbills, however, have primaries of similar size and mass, so their moult score does not need to be corrected for this factor (Fernández-Eslava et al. 2020).

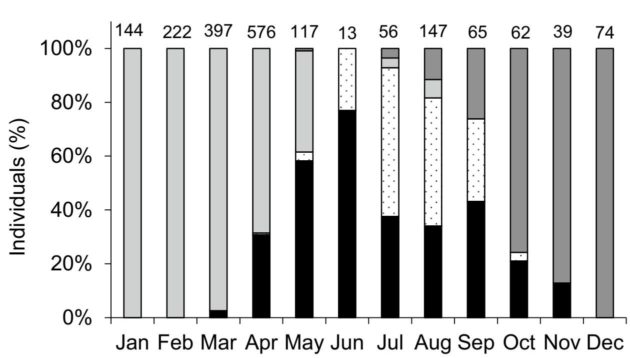


**Fig. 1** Percentages of moulting crossbills (black bars), those with suspended moults (dotted pattern) percentage before moult (light grey), and after moult (dark grey). Total sample size = 1911

The body plumage colour of males was classified into four categories: yellow, patchy (i.e. yellow and orange patches), orange, and red. This qualitative visual inspection of body colour has been proved to be methodologically reliable (del Val et al. 2009). Furthermore, the same person (DA) assigned the colour category to all birds. A repeatability test showed that the author was able to assign the colour consistently (Spearman's $r = 0.96$, $P < 0.001$, $n = 47$; for details see also Cantarero et al. (2020). Besides, we wanted to know the males' reproductive state at capture, so we recorded the presence or absence of the cloacal protuberance as a binomial variable.

## Moult analyses

The time birds need to replace the primary flight feathers overlaps with the time needed to replace all the plumage (Jenni and Winkler 2020). Therefore, the index of primary moult can be used as a proxy of the duration of the moult of all flight feathers (Ginn and Melville 1983). The currently most-used, classical approach to assess the duration and start date of the moult, was provided by Underhill and Zucchini (1988). This method assumes that the moult progresses linearly, with a similar duration between individuals, and the start date of the moult has a normal distribution (Underhill and Zucchini 1988). Crossbills, however, typically do not fit these general rules, since they often suspend their moult (Fernández-Eslava et al. 2020). To face this problem, we proposed a method to estimate moult duration in birds undergoing suspended moult, such as crossbills (Fernández-Eslava et al. 2020). Generally, crossbills suspend their moult in P5–P6, so Fernández-Eslava et al. (2020) extrapolated moult duration after considering a linear progression from P1 to P5 (see explanation below and in Fernández-Eslava et al. (2020).

First, we calculated moult parameters (start date, duration, and standard deviation of the start date) for each colour group (yellow, patchy, orange, and red) with the Underhill and Zucchini (UZ) method for all primaries (P1–P9) jointly (Underhill and Zucchini 1988; Erni et al. 2013). This method allows up to five model approaches (Underhill and Zucchini 1988, Underhill et al. 1990). Based on previous study of the same population (Fernández-Eslava et al. 2020), we decided apply for data type 1 model, in which individual birds are allocated to three categories: (1) birds that have not yet moulted, (2) birds that are actively moulting, and (3) those that have finished moulting (Underhill and Zucchini 1988). Birds in suspended moult were categorized as birds in active moult. Subsequently, UZ models were run for all primaries (P1–P9), also including colour as a factor (in one, two, or three of the estimated moult parameters, with all the possible combinations considered). All tested models were ranked according to their Akaike Information Criterion value (AIC). Models that differed in less than 2 AIC units were considered to fit to the data equally well (Anderson et al. 1998).

Moult duration, however, is overestimated with UZ models for populations undergoing suspended moult (Fernández-Eslava et al. 2020). Therefore, we additionally assessed moult duration for each colour group using the approach proposed by Fernández-Eslava et al. (2020). This approach basically uses UZ models to estimate moult duration; however, despite considering all primaries (P1–P9), duration is calculated for all the possible primary subsets resulting from a progressive adding of primaries (i.e. P1, P1–P2, P1–P3, P1–P4… up to P1–P9). After that, we are able to create a plot that shows the cumulative duration of moult as we add primaries. In birds having suspended moult, this figure typically shows an 'S' shape, due to the temporal 'jump' occurring when moult is suspended at a given primary feather (Fernández-Eslava et al. 2020). Within our crossbill population, this 'jump' occurs after P5 (until then, the moult has a linear progression) (Fernández-Eslava et al. 2020), so to estimate moult duration after removing the time in which the moult is suspended, we made an extrapolation from a linear model based on estimating moult duration until P1–P5 primary subsets.

## Results

The best model (i.e. the one with the lowest AIC) showed that feather colour was significant at explaining variation in the moult start date and its standard deviation (Table 1). Patchy crossbills began to moult before any other colour group (24 Apr, SD: 17.5 days), and the yellow crossbills were the last ones to begin moult (19 May, SD: 43.8 days; Fig. 2). Overall, yellow crossbills began to moult 23 days later than the patchy ones, and 18 days later than the red ones (Fig. 2). Likewise, an analysis of

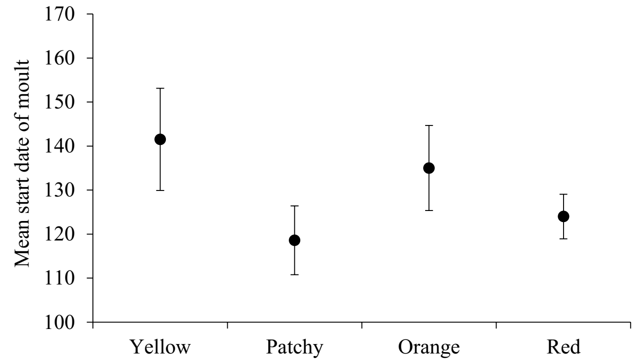


**Fig. 2** Mean start date of moult and its confidence intervals (95%) for P1–P9, using the UZ type 1 model in crossbills by colour category. Reference date: 1 = January 1st

the moult parameters for the P1-P5, which is the stage before the suspension, with colour as an explanatory variable, confirmed the differences found in the beginning of the moult (for more information, see Fig. S1 of the supplementary material).

Moult duration did not vary significantly between colour categories if we considered all primary feathers (P1–P9) without the correction for the suspended moult (Table 1; see also Table S1 in supplementary material and 2). This analysis gave a duration of 145 days (SE: 3.9 days) for our sample population, without differences between colour groups. However, after estimating moult duration by progressively adding more and more feathers (i.e. P1, P1–P2, P1–P3… P1–P9) within each colour group, differences among these groups increased (Figs. 3, 4). After P5, no group fitted the expected linear progression of a moult pattern without any suspension, typical of many passerines (Fig. 3). However, the moult duration of red crossbills was close to the linear pattern, whereas moult of yellow crossbills was remarkably far from this linearity (Fig. 3), which indicated that suspended moult was more common in yellow birds. Supporting this finding, we also detected that 18% of captured yellow birds suspended moult, while it was 2% among the red birds (Fig. 5).

Extrapolating the total moult duration using the cumulative duration until P5 from Fig. 3 (i.e. before birds suspend the moult), we found differences in the moult progress between the colour categories (Fig. 4). The red crossbills took 46 more days to complete P1–P9 moult (127 days) than yellow crossbills (81 days). Furthermore, the analysis of the moult parameters for P1–P5 before any moult suspension showed that yellow crossbills took 29 days less to complete this first part of the moult (for more information, see Fig. S2 of the supplementary material).

**Table 1** Different UZ type 1 models calculated for P1–P9 with colour factor as a covariate for indicated moult parameters and model ranking by AIC. The best model is marked with a bold face

| Model | Moult parameters | | | df | AIC |
|---|---|---|---|---|---|
| | Duration | Start | SD of start | | |
| m1 | | Colour | Colour | 9 | 1031.72 |
| m2 | Colour | Colour | Colour | 12 | 1036.96 |
| m3 | Colour | | Colour | 9 | 1044.47 |
| m4 | | Colour | | 6 | 1047.51 |
| m5 | | | Colour | 3 | 1047.72 |
| m6 | | | | 3 | 1050.16 |
| m7 | Colour | | | 6 | 1050.62 |
| m8 | Colour | Colour | | 9 | 1052.21 |

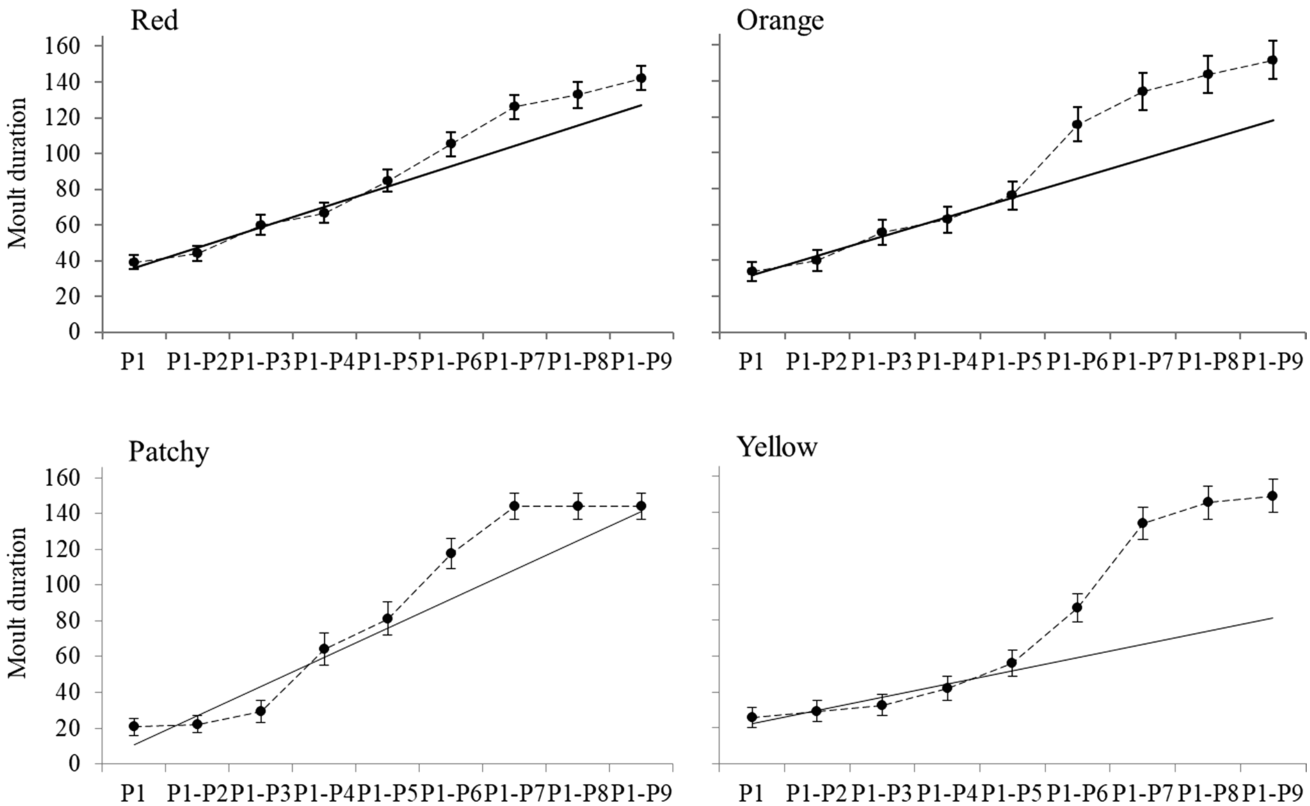


**Fig. 3** Moult duration (± SE) in four colour groups of crossbills, using the UZ type 1 model (circles) and its extrapolation (black line). The durations estimated for an increasing number of primary feathers, indicated at the X-axis

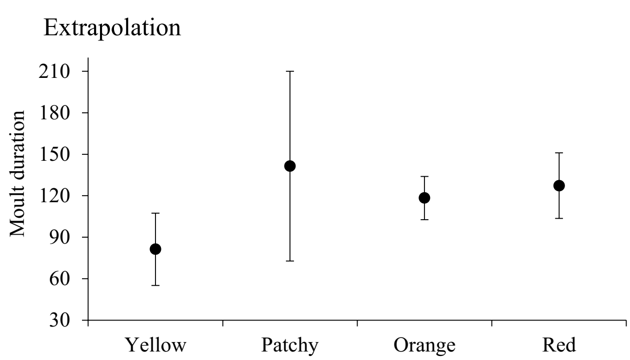


**Fig. 4** Moult duration (± 95% CI) in crossbills, extrapolated using the moult duration estimates for the intervals before primary moult suspension for each colour group from the UZ model, indicated by Fig. 3 (P1; P1–P2; P1–P3; P1–P4; P1–P5)

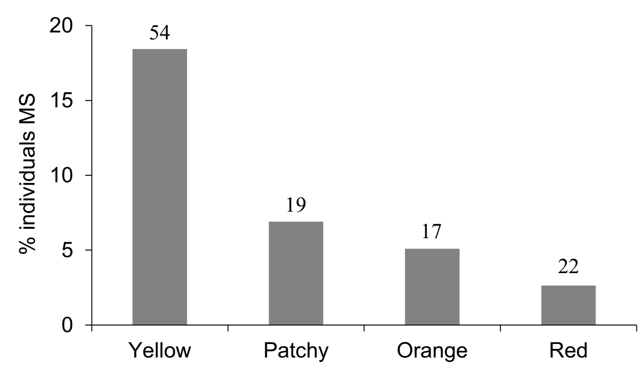


**Fig. 5** Percentage of adult male crossbills undergoing suspended moults in each colour group. Total sample size = 112 individuals

## Discussion

Active moult within our crossbill population was peaked in June, suggesting that this would be an optimal moment to face this energy-demanding process (Fig. 1). This could occur either because birds would be at their metabolic optimum after breeding or because the birds would try to moult during high availability of nutrients (i.e. maximum size of green cones) and avoid overlapping another highly energy-demanding process of reproduction (Jenni and Winkler 2020). A second smaller peak of moulting occurred in September, which presumably reflected resuming moult by those individuals that had suspended their moult due to an opportunistic breeding in summer (Fernández-Eslava et al. 2020). Our results clearly show that yellow crossbills start to moult later than birds with other colour patterns (either patchy or red) (Figs. 2 and S1). Thus, it appears that patchy and red crossbills are able to take better advantage of the first period of moult, in particular, the first half of May. On the contrary, yellow crossbills are destined to acquire duller colours as they start moult in late May and prolong it until the end of the summer, mostly as a result of suspended moult (Fig. 5). Orange males begin moulting at an intermediate time between reds and yellows. This distribution of moult timing among the colour groups indicates that the red coloration is acquired at the beginning of the moult period.

In House Finches (*Haemorhous mexicanus*), a passerine similar to crossbills in terms of plumage colour synthesis, the redness has also been related to moult. For example, moult intensity in house finches peaked earlier in the season in red individuals, suggesting that redder males start their moult earlier (Hutton et al. 2021). Similarly, Blue-black Grassquits (*Volatinia jacarina*), starting their moult earlier, acquire more saturated colour patterns, because males who moult earlier in the season are in better nutritional conditions and can invest more energy into synthesis of new feathers and allocate more nutrients to generate more intense colours than the less fit males (Hill and Montgomerie 1994; Hill 2000; Maia and Macedo 2011).

Our results considering the start date of moult for birds do not fit with the findings obtained by del Val et al. (2014) from a nearby population of crossbills in Central Pyrenees, where yellow birds start moult before other colour groups. In their study, however, the authors did not consider the fact that especially yellow birds have suspended moults, which could generate a bias (Fernández-Eslava et al. 2020). If these other authors had classified a bird with a suspended moult as a bird that has ended its moult, in the result the estimated moult duration would be reduced and start date would be biased for such a moult event. In addition, these authors calculated the beginning of the moult as the mean start date, instead of the start date for the average bird. Anyway, del Val et al. (2014) detected a main peak of moult in August, not in June as we found (Fig. 1), so we cannot reject the possibility that their sample comprised a different crossbill population than ours (Parchman et al. 2018). However, we emphasized that crossbills show a complex moult pattern, with a high proportion of individuals suspending moult, which must be considered from a methodological standpoint (Fernández-Eslava et al. 2020).

Our results also show that, in yellow birds, the moult duration of the first five feathers (P1–P5) and its extrapolation over P1–P9 was shorter, especially compared to the red birds (Fig. 4). Therefore, it is likely that the yellows increase their rate of feather replacement and synthesis before the cold season arrives. This acceleration could explain why a yellow plumage develops in some birds, as rapid moult has been related to lower colour saturation (Ferns and Hinsley 2008). The photoperiod appears to have a similar effect since birds experimentally exposed to a shorter daylength moult faster and produce fewer coloured feathers and less colour saturation than the control birds (Serra et al. 2007).

Interestingly, we also detected that the highest proportion of suspended moults was found in yellow crossbills. Suspended moult in crossbills is related to a second clutch in summer (Hahn et al. 2004; Fernández-Eslava et al. 2020), so it seems illogical that precisely those birds of presumably poorer individual quality (yellow ones, as compared to red) would be the ones laying a second clutch. The reasons for this phenomenon remain unknown to us, so we can only offer some plausible explanations: (1) yellow crossbills show higher percentage of suspended moults because they are lower-quality birds than the red ones. Indeed, the red ornamentation of the plumage is a reliable signal of quality in these birds (Cantarero et al. 2020), which in turn is reflected in other aspects such of their biology as the higher survival rate (Fernández-Eslava et al. 2021a, b). Adult individuals with yellow feathers might be old individuals since the male plumage becomes less red with age, that is, they tend to be patchy or yellow (Fernández-Eslava et al. 2021b). However, there is no evidence that birds can suspend moulting and resume it later just because they are too weak to finish the moult in one go. (2) Yellow crossbills would be less fit, and thus worse prepared for opportunistic reproduction during moult than red crossbills. In other words, dealing with extra energy expenditure on breeding can lead to a depletion of energy resources in yellow males, which would be more prone to suspend the moult than the red ones. Opportunistic reproduction is frequent in this species (Jenni and Winkler 2020). Besides, it is related to the suspension of moult. In fact, in a previous study in the same population, it was shown that the years with the highest percentage of females with brood patch during the summer were also the years with the highest percentage of birds with suspended moult (Fernández-Eslava et al. 2020). For that reason, it is likely that red crossbills, which are better-quality birds, may be able to finish their moult, avoiding suspending it, even if they attempt a second, opportunistic brood in summer, in contrast to yellow ones. (3) Red-coloured crossbills are likely to have a more successful reproduction in winter/spring (main breeding season for the species in the Pyrenees), as compared to yellow crossbills. Therefore, this last group of birds would be more likely to attempt a second clutch in summer (not necessary for red birds), with the corresponding delay and suspension of moult. However, the proportion of males with cloacal protrusion during the summer months was similar among all colour groups, so all colour groups seem equally disposed to summer breeding (Table 2). (4) Red and yellow crossbills may belong to different sympatric populations. Resident crossbills with

**Table 2** Chi-squared test comparing the frequencies of the presence of the cloacal protrusion (CP) between the colour groups of male crossbills ($\chi^2 = 0.1611$, $df = 3$, $P = 0.9836$)

| | Yellow | Patchy | Orange | Red | |
|---|---|---|---|---|---|
| CP | | | | | |
| Yes | 9 | 10 | 24 | 6 | Observed |
| | 8.89 | 9.37 | 24.02 | 6.73 | Expected |
| | 0.038 | 0.207 | −0.004 | −0.28 | Residuals |
| No | 28 | 29 | 76 | 22 | Observed |
| | 28.11 | 29.63 | 75.98 | 21.27 | Expected |
| | −0.021 | −0.116 | 0.002 | 0.157 | Residuals |

presumably duller feathers (Massa 1987; Cramp and Perrins 1994) may try a second clutch in summer, as they would have a foraging apparatus (i.e. bill morphology) optimized to open the green cones which appear in summer. By contrast, the red crossbills may belong to a more mobile population or subpopulation, breeding in winter/spring, but leaving the area after moulting, looking for a better-suited food resource. This idea is partly supported by the proportion significantly lower of red individuals in the summer months than in the winter and spring months (colour score x calendar month $\chi^2 = 57.56$, $df = 30$, $P < 0.001$).

In conclusion, our results suggest that the development of red feathers in male crossbills occurs at an optimal time for moulting and is probably a feature of better-quality individuals. This finding agrees with the concept of honest advertising of individual quality by the colour saturation. The differences between individuals in costs of plumage production will only allow fit males with the sufficient resources to invest in red ornament development. In crossbills, an early moult is essential for producing highly saturated red plumage, while a late and fast moult is associated with yellow plumage likely of a poorer quality. To our knowledge, this is one of a few studies that have linked the timing and characteristics of moult with colour patterns. Additional studies should delve into the environmental factors driving the differences that seem to exist between the intra-population differences in timing of the moult (early and late) and those found between populations (see the contrast with del Val et al. 2014). These differences in colouration related with moult could be related to the amount of carotenoids that the birds can obtain during at different times of the year, in relation to the ripening of pinecones, species of pines, or the quality of habitat and forest.

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s10336-023-02116-1.

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**Author contributions** All the authors participated in the conception and design of the work; DA, BF, and JA conceived the ideas and designed the methodology; DA collected the data; BF and DG analysed the data; BF, JA, and DG led the writing of the manuscript. All the authors contributed critically and gave final approval for publication. The authors also declare that the article is original and that it has not been submitted anywhere other than your journal. We would of course be ready to provide further information about our data and methods if desired.

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## Declarations

**Ethics statement** This study was conducted under permission from the Departamento de Desarrollo Rural, Medio Ambiente and Administración Local de Navarra, Spain. All data were collected by DA, who has licences for handling animals for scientific purposes.



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