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ORIGINAL ARTICLE

Estimation of moult duration in birds with suspended moults: the case of the Red Crossbill and its relation to reproduction

Blanca Fernández-Eslava[1,2] · Daniel Alonso[2] · David Galicia[1] · Juan Arizaga[2]

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Abstract

Suspended moult is a relatively common phenomenon in birds, but it has remained relatively ignored for a long time in studies dealing with moulting process. Furthermore, the new and increasing number of models used to estimate moult duration systematically omit the fact that suspended moults can occur and that they significantly alter parameter estimates. Taking suspended moults into account is critical to obtain reliable moult-associated parameter estimates, which is fundamental given the demographic and evolutionary consequences of moult in birds. The main goal of this work is to develop a standardised method useful for characterising the main moulting parameters (such as the duration and starting date) of bird species that perform suspended moults. Additionally, with the aim of delving into our understanding of when and why suspended moults happen, we study their relationship with the occurrence of second breeding attempts in summer. We used data obtained from a Red Crossbill population in the Pyrenees during a period of 17 years. We observed that the percentage of crossbills undergoing suspended moult was approximately 50% during summer (July–August) and that moult suspension ultimately gives rise to a lengthened moulting period. Underhill–Zucchini models assume a time-linear replacement of feathers, overestimating the moult duration. Based on these same modelling approaches, we proposed a method to calculate the real moult duration after removing the time during which the moult was suspended. We also obtained evidence supporting the idea that crossbills suspend their moult as a strategy that could increase their breeding output in summer. The method proposed here can be used as a tool for working with species that undergo suspended moults.

Keywords *Loxia* · Moult in birds · Non-linear moults · Underhill–Zucchini models

Zusammenfassung

Schätzung der Mauserdauer bei Vögeln mit unterbrochener Mauser am Beispiel des Fichtenkreuzschnabels und der Zusammenhang mit der Fortpflanzung

Eine unterbrochene Mauser ist ein bei Vögeln relativ häufig auftretendes Phänomen, das aber in den Untersuchungen zur Mauser lange Zeit außer Acht gelassen wurde. Außerdem ignorieren die vielen neuen Modelle zum Einschätzen der Mauserdauer systematisch die Tatsache, dass eine Unterbrechung der Mauser auftreten und dies einen erheblichen Einfluss auf die Parameter zum Einschätzen der Dauer haben kann. Solche Verschiebungen zu berücksichtigen ist sehr wichtig, um verlässliche, mit der Mauser zusammenhängende Parameter für die Abschätzung der Dauer zu erhalten, die wiederum für die demografischen und evolutionsbiologischen Auswirkungen der Mauser bei Vögeln wichtig ist. Ziel dieser Untersuchung war die Entwicklung einer standardisierten Methode, mit deren Hilfe man für diejenigen Vogelarten, bei denen eine unterbrochene Mauser vorkommt, die wichtigsten Merkmale wie z.B. den Beginn und die Dauer der Mauser bestimmen kann. Zum

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✉ Blanca Fernández-Eslava
bfernandez@alumni.unav.es

[1] Department of Environmental Biology, Universidad de Navarra, 31009 Pamplona, Spain

[2] Department of Ornithology, Aranzadi Sciences Society, Zorroagagaina 11, 20014 Donostia-S. Sebastián, Spain

besseren Verständnis dafür, wann und warum eine unterbrochene Mauser vorkommt, untersuchten wir darüber hinaus einen Zusammenhang mit dem Auftreten eines zweiten Brutversuchs im Sommer. Wir verwendeten hierfür Daten, die über 17 Jahre hinweg in einer Fichtenkreuzschnabel-Population in den Pyrenäen gewonnen worden waren. Für diese konnten wir feststellen, dass der Anteil an Fichtenkreuzschnäbeln mit unterbrochener Mauser im Sommer (Juli-August) etwa 50% betrug und schließlich zu einer verlängerten Mauserdauer führte. Die Underhill-Zucchini-Modelle gehen von einem zeitlinearen Ersatz von Federn aus und überschätzen dabei die Dauer der Mauser. Auf einem gleichen Modellansatz basierend schlagen wir eine Methode zur Berechnung der tatsächlichen Mauserdauer vor, aus der die Zeit der Unterbrechung herausgerechnet wird. Wir erhielten auch Belege für die Annahme, dass Fichtenkreuzschnäbel ihre Mauser möglicherweise aus strategischen Gründen unterbrechen, um so ihren Bruterfolg im Sommer zu vergrößern. Die von uns hier vorgestellte Methode kann als Hilfe für Untersuchungen an solchen Arten verwendet werden, bei denen eine unterbrochene Mauser vorkommt.

Introduction

Time allocation to different processes demanding a high amount of energy across the annual cycle is critical to ensure individual survival and/or reproductive output (Farner 1964). Therefore, the phenological patterns of life-history aspects such as moulting, breeding, and migration in birds have been fixed very accurately through natural selection. The understanding of the variability and flexibility in the start and duration of any of such process is critical to have a better comprehension of how animals are able to cope with variable environments and face new scenarios in a changing world (Helm and Gwinner 2006).

In most small passerines, there is little or no temporal overlap between breeding and moulting, hence allowing these two important events to coexist in the annual cycle with minimal energetic stress for the bird (Jenni and Winkler 1994). Nevertheless, individuals that overlap moult and reproduction are not uncommon, although the most common scenario is to stop moulting temporarily to alternate between these two processes (Snow and Snow 1964; Stresemann and Stresemann 1966; Porkert and Hromádko 2012). The physiological relationships between reproduction and the activation or inhibition of moulting are not yet resolved, but it is known that high concentrations of testosterone in birds delay, prevent, or stop the moult (Nolan et al. 1992; Dawson 1994, 2005; De Ridder et al. 2002). This break in moult results in identifiable feather generations, which provide us with valuable information to study this phenomenon. Information regarding when and why the process of suspended moult occurs and how long it takes is vital to better understand the effects of potential environmental factors driving the demographic and evolutionary processes of species to the extent that they influence parameters such as survival and the fitness of individuals.

Suspended moult can be defined as a complete moulting process that, prior to its end, is interrupted for a period of time to be resumed afterwards. Moult suspension is a relatively common phenomenon in several bird species, especially those in which the moulting period overlaps with breeding and/or migration processes. In some Palaearctic warblers that overwinter in Africa, suspension occurs during the autumn migration period and is resumed after arrival to the African winter quarters (Mead and Watmough 1976; Aidley and Wilkinson 1987; Norman 1998; Kulaszewicz and Jakubas 2015). In other birds, such as a number of boreal seed-eating passerines, the occurrence of suspended moults is also common as an adaption to facultative reproductive events (Hahn 1995, 1998; Hahn et al. 2004). Some authors have also noted that this phenomenon may be more frequent than previously stated in both migratory and non-migratory species due to the scarcity of studies about its occurrence (Ryder and Wolfe 2009).

As a main rule, the time needed to replace the primary flight feathers is equal to or less than the time needed to replace all the plumage; hence, an index accounting for the degree of replacement of the primaries can be used as a surrogate for the duration of the complete moulting process (Ginn and Melville 1983). Several methods use such indices to calculate the duration of the entire moulting process. The simplest method is to adjust a regression line of moulting scores according to date (Pimm 1976), although this method calculates the start and end dates for the population as a whole instead of an average bird. To solve this problem, Underhill and Zucchini (1988) developed a model using the maximum-likelihood method that incorporates data from both moulting and non-moulting birds. Rothery and Newton (2002) proposed a binary regression method, which is similar to the maximum-likelihood estimator, but the birds are scored simply as “moulting” or “non-moulting”. More recently, Rohwer and Broms (2012) presented a novel method that calculates parameters using a higher number of variables, such as the gap between the feathers of moulting birds, the growth rate of primaries, and their length. However, the feather growth rate is difficult to obtain directly, because it requires recaptures of still-moulting birds, or an approximation through feather growth bands must be carried out (Michener and Michener 1938; Grubb 2006; De La Hera et al. 2011). Overall, both regression models and the models developed by Underhill and Zucchini (1988) (or more recent approaches based on these models) assume that the moult index must increase linearly with time, its duration is similar among individuals, and the starting date of the moult has a normal distribution. These models have been proven to be very accurate and useful for populations or species that perform a continuous, linear moulting process (Newton and Rothery 2000; Remisiewicz et al. 2009). However, populations or species that undergo suspended moults may not adhere to one or more of the previously mentioned criteria; for instance, the moult index may not have a linear relationship with time. Therefore, estimates of the duration and starting date of moult in species that perform suspended moulting processes are commonly unreliable (Symes and Wilson 2008), and it is necessary to expand the models to take into account the particular characteristics of suspended moult, because its unawareness is still a reality.

The Red Crossbill (*Loxia curvirostra*) is an excellent model for studying the phenomenon of suspended moults. As a general rule, juvenile crossbills perform a partial moult in their first year of life that affects their body feathers, some wing coverts and the tail, while adults undergo a complete moult (Jenni and Winkler 1994; Svensson 1998). Suspended moults are common in adults, and the suspension period can be so long that some authors even talk about two moult periods in crossbills: the main one occurs at the end of the summer and a second one in mid-winter or spring (Weber 1953; Newton 1972; Rymkevich 1990). Studies conducted on Mediterranean populations, however, often refer to a single, though rather long, moulting period from mid-spring to September (Massa 1987) or even to November (Alonso and Arizaga 2011). This high geographical variability among populations is likely to be associated with ecological conditions (e.g., feeding sources and climatic conditions) that also vary geographically but, overall, highlight the existence of suspended moults in crossbills. These birds present high trophic specialisation, because they feed on seeds of very specific conifer species. Many conifers have irregular cone crops; hence, they produce huge amounts of cones that can be opportunistically exploited by crossbills only in some years. In these years, secondary opportunistic breeding attempts often occur as well. It is suggested that it is in such years when, due to the second breeding attempts, suspended moults become more common (or appear among a higher proportion of individuals). In Iberian crossbills, the main breeding period takes place in winter–spring, but a second one can happen in summer (around August), although the occurrence of this second breeding period is much more irregular (Alonso and Arizaga 2011).

Here, we show how Underhill–Zucchini models behave for a population with suspended moults, and using this information, we develop a useful and standardised method to characterise the main moulting parameters (such as the duration and starting date) in bird species that perform suspended moults. To carry out this objective, we use the data and experience acquired during 17 years of monitoring a Red Crossbill population in the Pyrenees. Additionally, and with the aim of deeply understanding when and why suspended moults happen, we study their relationship with the occurrence of second breeding attempts in summer. Moulting data collected from Citril Finches (*Carduelis citrinella*), a regional sympatric species showing no suspended moults, were also used for comparative purposes.

Methods

Study area and data collection

All crossbills used in this study were captured from two locations in the western Pyrenees in northern Spain: Bigüezal (42° 40′ N, 1° 07′ W; 1096 masl) and Uztarroz (42° 52′ N, 1° 00′ W; 1383 masl). Additionally, Citril Finches were captured at these localities, since they share the same habitat, but two localities were added from the Iberian System to increase the sample size of the latter species: El Royo (41° 54′ N, 2° 38′ W; 1069 masl) and Villoslada de Cameros (42° 06′ N, 2° 40′ W; 1064 masl). The vegetation at all these sites is dominated by Scots pine (*Pinus sylvestris*), and some patches of mountain meadows appear within the forest.

Captures were made periodically, with one sampling day per week in the Pyrenees and one sampling day every other week in the Iberian System, during a period of 4 h starting at dawn and 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 (salt deposits). The salt deposits remain active for the entire annual cycle and are used to complement the diet of livestock within the region.

The period considered in this study was from 1999 to 2016 for crossbills and from 2001 to 2017 for Citril Finches. All data were collected by one of the authors (DA). Once captured, each bird was ringed, and its sex and age were determined (Svensson 1998). We only considered adults in this study. The stage of the moult was recorded according to the degree of development of the primary feathers (P1–P9, numbered from innermost to outermost; P10 is very marginal in size and was not considered) of the right wing (Ginn and Melville 1983): 0, old still non-moulted feather; 1, absent or in pin; 2, $< 1/3$ grown; 3, 1/3 to 2/3 grown; 4, $> 3/4$ grown; 5, fully newly grown. The sum of the scores for the primaries ranges from 0 for a bird without any feather changes to 45 if the nine primaries are new (Underhill and Zucchini 1988). These values were transformed to a scale of 0–1 (1 equates to 45 points, all new feathers). In females, the presence of brood patches was scored from 0 to 5 (Pinilla 2000): 0, no brood patch; 1, incipient developing brood patch; 2, almost-grown brood patch; 3, fully developed brood patch; 4, regressing brood patch; 5, re-feathering brood patch.

Criteria for differentiating suspended and interrupted moult

According to Jenni and Winkler (1994) and Svensson (1998), we considered a moult event to be suspended when feathers were replaced in the typical regular sequence (starting from P1 to P9) of complete moult, which, however, stopped at a certain primary feather (in most cases, almost half of the primaries were unmoulted). Thus, in this case, we can find two generations of feathers: the new one (inner primaries), composed fully of newly grown feathers (code 5), and the old one (outer primaries, code 0), which is composed of old, worn feathers. In suspended moults of crossbills, moreover, it is rather common to find that all or most of the secondaries and rectrices are unmoulted (DA, pers. obs.). The moult will resume later up to the end.

In contrast, a moult event was identified as interrupted when it followed the typical, regular sequence of a complete moult, where, however, some isolated feathers (either in the primaries and, most commonly, in the secondaries and/or rectrices) remained unmoulted. In this case, the moult will not continue later.

Moult analyses

The following parameters were estimated: duration, starting date, and standard deviation (SD) of this date, following the models developed by Underhill and Zucchini (1988) and recently implemented in R (Erni et al. 2013). These models assume that moulting is a continuous, linear process over time. A priori, consequently, a suspended moult would not fit this pattern, because the process is stopped for a period of time, with it being resumed later. However, it is likely to be linear before the suspension of the moult.

Underhill and Zucchini consider three different types of models depending on how the birds are classified. In type 1, the individuals are labelled into three categories that correspond with birds that are still non-moulting, birds that are in active moult, and those that have finished moulting. The type 2 model is similar to the type 1 model, but moulting birds are given a feather score from 0 to 5. In the type 3 model, only moulting birds are given a feather score (from 0 to 5), hence ignoring birds that are not moulting. For our analytical purposes, we assumed that birds undergoing suspended moult were birds in active moult; hence, 0 was assigned to the feathers that had not yet been moulted and 5 to those that had already been moulted.

We used these three methodological alternatives in this work. Models were run for the set of primaries as a whole (P1–P9) and for all the possible subsets resulting from progressively incorporating primaries (that is, P1–P2, P1–P3… P1–P8) to determine at which primaries the moult is suspended. In this way, we can calculate the duration of each feathers range and check if there are important changes in the moult progression to detect the suspended moult. In populations with continuous moulting process, without pauses, the estimation of the duration of these intervals must increase linearly as we add primaries. Otherwise, we would be facing a suspended moult.

In species in which different primary outer feathers vary greatly in length with respect to the inner ones which are shorter, it is appropriate to correct for this variation, taking into account the feather mass (Summers et al. 1983; Underhill and Joubert 1995). Thus, the total score of a bird obtained visually can be converted to a 'feather mass score' (FMS) or can be calculated with the 'percentage feather mass grown' (PFMG: Summers et al. 1983), reflecting the percentage of new feather material produced by weight. However, this may not be the case for Red Crossbills, for which all primaries are very similar in weight. Regardless, a preliminary analysis taking into account these weights did not indicate any noticeable difference compared to the method used in this work.

Results

Proportion of birds with suspended moults

Throughout the sampling years, adult crossbills were captured in active moult in almost every month of the year, except in January and February, with a peak in June, when 63% of the population was moulting (Fig. 1). At the same time, we observed that the percentage of birds in active moult did not fit a normal distribution pattern, because after June, a plateau that lasted from July to September was observed (Fig. 1). Coinciding with these months, there was a high percentage of birds exhibiting suspended moults (ca. 50% in July–August), as shown in Fig. 1.

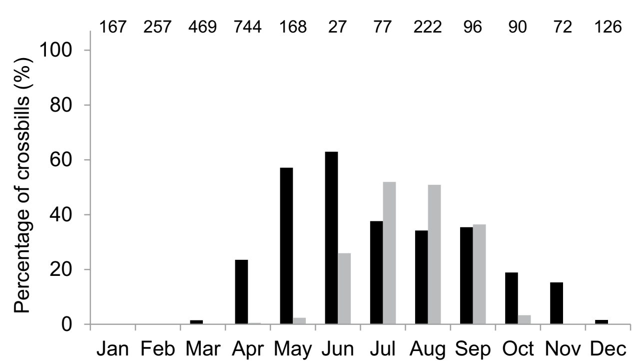

Fig. 1 Percentage of Red Crossbills: black bars are percentage of moulting crossbills (without those in suspended moult) and grey bars are percentage of crossbills with suspended moults. Total sample sizes of adult crossbills are shown on the top axis

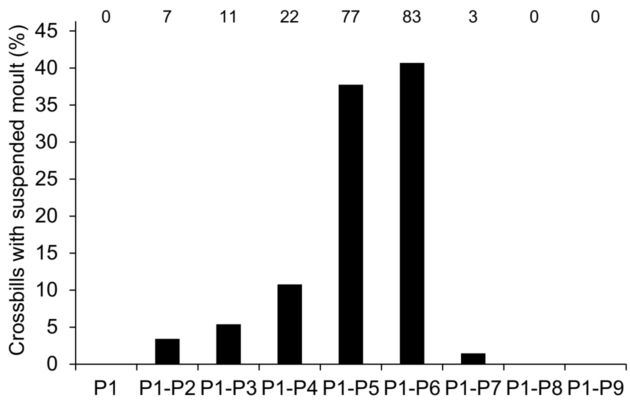

Fig. 2 Percentages of only those Red Crossbills undergoing suspended moult that have moulted a number of primaries before suspension. Total sample sizes of suspended moults are shown on the top axis

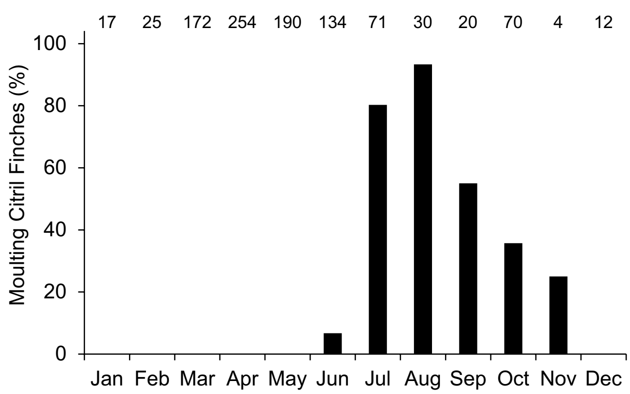

Fig. 3 Percentage of actively moulting Citril Finches each month. Total sample sizes of adult Citril Finches are shown on the top axis

Most crossbills with moult suspension suspended their moult at primaries P5 or P6 (ca. 80%), with only a minor proportion doing so at P2–P4 or P7, and none of them suspended the moult at P1 or P8–P9 (Fig. 2).

Adult Citril Finches were trapped in active moult during a shorter period, between June and November, reaching a moulting peak in August (when just over 90% of the population was moulting, Fig. 3). Unlike crossbills, no suspended moults were recorded, highlighting that the moult was continuous in this species and likely linear.

Estimation of the moult parameters

For crossbills, the estimated moulting starting date was remarkably variable among model types. The type 1 and 2 models provided similar estimates, indicating that the moult began by mid-May (Table 1). The type 3 model, however, indicated that the moult may have started rather earlier (beginning of April). In Citril Finches, however, the starting date of the moult was similar among models (mid-July) (Table 2).

With regard to the moulting duration in crossbills, the type 1 and 2 models showed an increasing duration of the moult as we added an increasing number of primaries, up to 136.8 days of duration (SE 2.9) for the type 1 model and 147.4 days (SE 2.6) for the type 2 model. However, the duration did not fit a linear trend as we added more feathers (Fig. 4a). Between P5 and P7, we detected an increase in the slope, which may be attributed to a high proportion of birds that would suspend their complete moult at this moment. In contrast, in the case of the Citril Finch, the observed pattern followed a linear trend (Fig. 4b), demonstrating that in this species, the process is continuous and linear over time. The time which Citril Finches spent replacing their plumage according to the type 1 and 2 models was 80.9 days (SE 3.4) and 82.2 days (SE 2.4), respectively.

In the type 3 model, in which only birds in moult are considered (and in our case, birds in suspended moult as well), the estimated duration was absolutely different from that according to the other two model types. In this case, the duration for crossbills was assessed to be much longer (211.7 days, SE 7.6 days) (Table 1). In addition, unlike in Fig. 4a, the duration of the moult was observed to decrease as more primaries were added until P5 was added because after P6, the estimate increased as more primaries were included (Fig. 5), resulting in a u-shaped curve. This effect is caused by the suspended moult. Before suspension, these birds have only one active feather; therefore, the moult progresses slowly with respect to a normal one in which there are several active feathers. When it is resumed, there is again only one active feather, so the model also shows a slowed moult in relation to the normal process. During the suspension, these birds are not taken into account in the calculation. Consequently, the indices calculated for suspended moults change abruptly from high values (with 5–6 first feathers), underestimating the moult duration, to low values (considering the greater part or all of the primaries), giving a longer duration than expected.

In the Citril Finch, the type 3 model indicated an overall shorter moulting period in comparison to the type 1 and 2 models, with only 66.8 days (SE 6.7). Regardless, it is important to note that the duration of the moult was found to increase linearly as we added more primaries (except for P1–P2; Fig. 5), contrasting with the u-shaped pattern found in crossbills.

Correction of moult duration

According to Figs. 2 and 5, it can be stated that, in this population of crossbills, the moult was suspended mainly at P5 and P6; hence, until P4, we assume that it followed a linear replacement pattern. Therefore, only for the first

Table 1 Estimates of primary moult parameters obtained by fitting the different Underhill-Zucchini models from data of Red Crossbills. Means are in bold and standard errors are below the means. Units of estimates are days from 1 January

	Type 1				Type 2				Type 3			
	n	Duration	Start	SD	*n*	Duration	Start	SD	*n*	Duration	Start	SD
P1	2515	**34.6**	**131.7**	**33.5**	2515	**32.3**	**131.8**	**34.4**	248	**207.5**	**106.7**	**33.5**
		1.9	1.5	6.1		1.8	1.5	6.2		7.5	3.9	6.0
P1–P2	2515	**39.6**	**131.7**	**33.5**	2515	**39.1**	**131.9**	**33.9**	269	**225.4**	**41.3**	**84.2**
		2.1	1.5	6.0		2.0	1.5	6.0		66.1	29.1	40.7
P1–P3	2515	**47.7**	**130.7**	**32.0**	2515	**49.5**	**130.5**	**31.7**	302	**131.1**	**98.1**	**48.0**
		2.2	1.4	5.7		2.1	1.4	5.4		31.7	14.8	18.5
P1–P4	2515	**57.8**	**132.2**	**34.3**	2515	**62.5**	**130.9**	**32.2**	341	**104.1**	**115.1**	**35.4**
		2.4	1.5	6.1		2.2	1.4	5.4		20.8	10.0	11.4
P1–P5	2515	**72.4**	**134.3**	**37.1**	2515	**79.0**	**131.3**	**32.8**	406	**87.9**	**126.0**	**28.7**
		2.6	1.6	6.7		2.3	1.4	5.4		15.9	8.1	7.9
P1–P6	2515	**100.0**	**137.0**	**41.1**	2515	**105.0**	**131.1**	**34.4**	531	**100.9**	**125.1**	**27.9**
		2.9	1.8	7.5		2.3	1.4	5.4		12.0	6.3	6.0
P1–P7	2515	**128.3**	**136.3**	**40.0**	2515	**129.1**	**129.8**	**33.8**	644	**138.0**	**116.1**	**29.6**
		2.9	1.8	7.4		2.3	1.3	5.2		8.6	4.7	5.3
P1–P8	2515	**134.3**	**135.7**	**39.1**	2515	**140.0**	**130.8**	**34.0**	663	**181.9**	**106.9**	**31.9**
		2.9	1.7	7.3		2.4	1.4	5.2		7.4	4.1	5.8
P1–P9	2515	**136.8**	**135.2**	**38.4**	2515	**147.4**	**132.8**	**34.7**	670	**211.7**	**105.7**	**33.5**
		2.9	1.7	7.2		2.6	1.4	5.3		7.6	3.9	6.1

Table 2 Estimates of primary moult parameters obtained by fitting the different Underhill-Zucchini models from data of Citril Finches. Means are in bold and standard errors are below the means. Units of estimates are days from 1 January

	Type 1				Type 2				Type 3			
	n	Duration	Start	SD	*n*	Duration	Start	SD	*n*	Duration	Start	SD
P1	999	**26.3**	**187.5**	**11.3**	999	**25.6**	**187.4**	**12.4**	63	**115.2**	**137.1**	**33.5**
		2.3	1.5	3.4		2.4	1.5	3.4		51.3	27.2	21.0
P1–P2	999	**28.6**	**187.4**	**10.9**	999	**28.6**	**187.8**	**11.4**	67	**29.9**	**188.9**	**12.9**
		2.4	1.5	3.3		2.4	1.4	3.2		19.6	9.9	7.6
P1–P3	999	**36.0**	**187.6**	**11.8**	999	**35.8**	**188.3**	**11.7**	77	**15.4**	**199.3**	**7.5**
		2.7	1.5	3.5		2.5	1.4	3.2		12.6	6.4	4.6
P1–P4	999	**42.6**	**187.8**	**12.4**	999	**42.4**	**188.9**	**12.0**	84	**18.3**	**201.7**	**7.6**
		3.0	1.6	3.7		2.7	1.4	3.2		11.1	5.6	4.0
P1–P5	999	**50.0**	**188.5**	**15.0**	999	**51.6**	**189.4**	**13.5**	89	**31.5**	**198.9**	**9.0**
		3.4	1.8	4.2		2.9	1.5	3.4		0.0	0.0	1.6
P1–P6	999	**61.7**	**188.9**	**16.1**	999	**61.6**	**189.4**	**14.1**	100	**35.4**	**199.6**	**8.6**
		3.5	1.9	4.4		2.7	1.5	3.4		NA	NA	1.5
P1–P7	999	**66.8**	**189.1**	**16.5**	999	**67.8**	**189.7**	**14.0**	106	**42.5**	**200.2**	**9.1**
		3.4	1.9	4.6		2.6	1.5	3.3		1.8	1.6	2.4
P1–P8	999	**70.7**	**189.4**	**17.3**	999	**73.1**	**190.0**	**13.9**	112	**57.0**	**197.5**	**9.7**
		3.4	1.9	4.8		2.5	1.5	3.2		6.8	3.2	2.7
P1–P9	999	**80.9**	**190.3**	**19.6**	999	**82.2**	**190.2**	**14.5**	131	**66.8**	**197.3**	**9.9**
		3.4	2.1	5.5		2.4	1.5	3.4		6.7	3.1	2.5

four intervals (from P1–P2 to P1–P5), it could be extrapolated how long the moult would last for a population that may not suspend their complete moult. The differences in moulting duration between the results obtained by projection and the ones derived from the type 1 and 2 models allow us to estimate the period during which the moult remains suspended (Fig. 4c). If the type 1 model is used, a period of 23 days is predicted, while the type 2 model indicates a period of 16 days. In Citril Finches, however, the projection and the estimated duration of the moult were similar, because this species does not perform suspended moults (Fig. 4d).

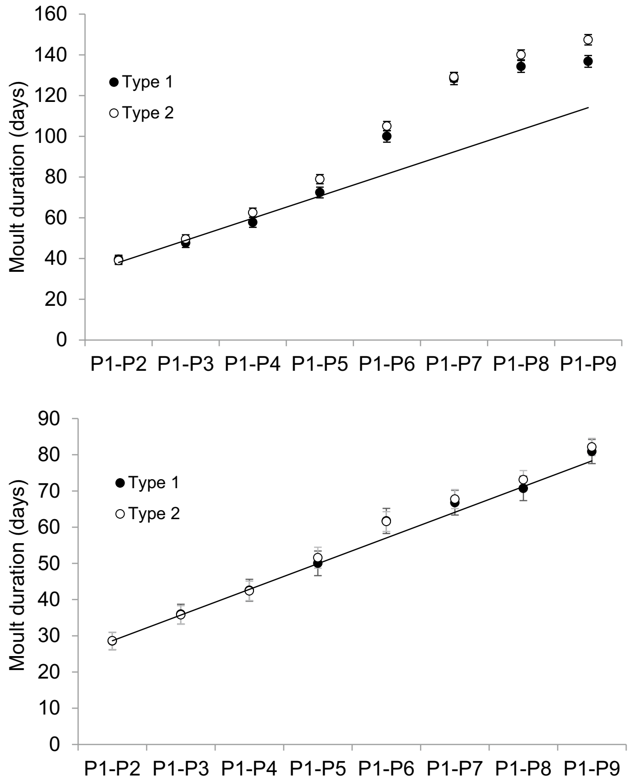

Fig. 4 Moult duration (±SE) in Red Crossbills and Citril Finches (above and below, respectively) using type 1 and 2 models. The duration is assessed for an increasing number of primary feathers. The continuous line shows the extrapolation of moulting duration in crossbills and Citril Finches (above and below, respectively) using the first four intervals (P1–P2, P1–P3, P1–P4, and P1–P5) with the type 1 model

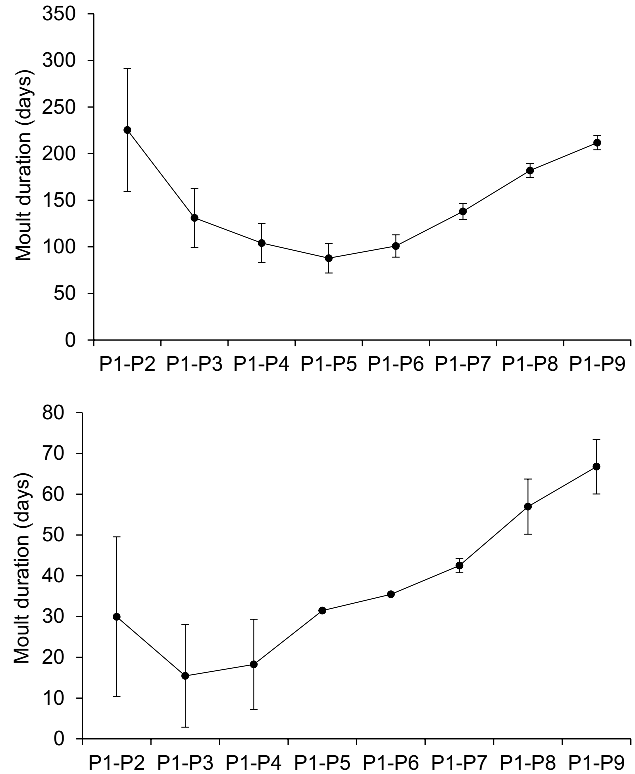

Fig. 5 Moult duration (±SE) in Red Crossbills and Citril Finches (above and below, respectively) using the type 3 model. The duration is assessed for an increasing number of primary feathers

Relationship between reproduction and suspended moult

The proportion of crossbills undergoing suspended moult was found to increase with the proportion of female crossbills caught with brood patches scored 1–4 in July–September (Fig. 6), i.e., the years with the highest proportion of summer-breeding birds were those in which we also detected the highest proportion of suspended moults within the population.

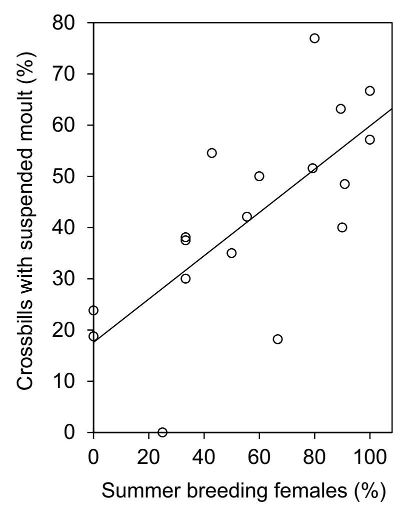

Fig. 6 Correlation between breeding females of crossbills with brood patches scored as 1–4 and the total number of crossbills undergoing suspended moult ($F_{1,16}=15.89$, $P=0.001$, $r^2=0.46$)

Discussion

To the best of our knowledge, this work is the first to analyse the suspended moult in crossbills in detail and the first to propose a methodology to estimate the duration of suspended moults in birds, which can, hence, be applied to a broad range of species that undergo this type of complex moulting process. The number of individual birds undergoing a suspended moult and its duration can be critical traits in a population, with unknown effects on or ecological correlates with other life-history aspects or driving environmental factors. In this context, our method can be relevant in studies addressing the relationship between the moulting process and its effects on a bird's annual cycle and its evolutionary and demographic consequences (Newton 2006).

Suspended moult was found to be a very common phenomenon in crossbills, as in the months of July or August, more than half of the population had suspended the moult. These months exactly overlap with the existence of opportunistic breeding attempts in summer (Alonso and Arizaga 2011), and the yearly variation in the proportion of crossbills with suspended moult was found to be positively correlated with the proportion of active breeding crossbills in summer. Therefore, we obtained evidence supporting the idea that Red Crossbills suspend their moult as a strategy to increase their breeding output in summer, i.e., to avoid great overlap between two processes that demand a high amount of energy, which compromises their own survival and that of their offspring (Hemborg and Lundberg 1998; Hemborg 1999). This variability may be due to environmental factors, such as the availability of food (seeds), as in years with exceptionally good harvests, the number of individuals that carry out a second lay during summer months may increase. Therefore, future research should deepen the understanding of the relationships among annual forest mass productivity, reproduction, and moult.

Nevertheless, a significant fraction of captured crossbills did not undergo suspended moult, which might suggest that some individuals likely maintain a linear moulting process, as do Citril Finches. Our data, however, do not support the hypothesis that Red Crossbills have two seasons of moulting, as seems to occur at higher latitudes (Weber 1953, 1972; Newton 1972; Rymkevich 1990). This difference is likely shaped by the different phenological rhythms of each population, which in turn depend on the productive rhythms of the coniferous species on which they feed (pine in the case of Pyrenean Red Crossbills; spruce in the case of Nordic Red Crossbills) (Benkman 1990; Clouet 2000).

Estimation of the suspension period duration requires a detailed analysis of the moulting duration of all primaries, since it is first necessary to determine at which primaries there is a higher probability of suspending the moult. However, this assessment is highly sensitive to the type of Underhill–Zucchini model used. Models based on recording non-moulting and moulting birds (type 1 and 2) provided similar moulting duration estimates (ca. 140 days), and the progression of duration estimation as we added primaries was similar: linear for only the first four intervals (up to P5). However, it is likely that the most reliable estimate was obtained with the type 1 model, since Newton and Rothery (2000) demonstrated biased assessment when they used the type 2 and 3 models, and slight deviations from linearity can have critical effects on the results (Rothery et al. 2001), especially for type 3 models, which are based only on active moult scores. Notably, in our case, the moult duration was misestimated by almost 2 weeks for Citril Finches when we used the type 3 model and even by 2 months and a half for crossbills. Newton and Rothery (2000) reported that the type 3 model still showed a high correlation between moult starting date and duration, but it must be acknowledged that these two parameters are not calculated independently, so a long moulting duration is directly linked with an early starting date.

Recently, Rohwer and Broms (2012) published a new method that allows the analysis of moult based on the hollow primary intervals, the lengths of the feathers, and their growth rates. This method requires the feathers to be lost sequentially but not necessarily from P1. Therefore, it can be used to estimate moult duration for a variable number of primaries and to estimate the starting date of moults beginning more or less simultaneously at several primary feathers. The method, therefore, resolves well the estimation of the duration of moults with several moulting centres in the primaries, but it cannot estimate the duration of a suspension period in the moult and, therefore, how long the total period lasts. In addition, the growth rate of the feathers and the intensity of the moult can vary individually and during different phases of a moult event (De La Hera et al. 2011). Such variation in the growth rate is particularly expected in species that undergo suspended moults, when just before and after the suspension; when a single feather is growing, the growth rate of these feathers could slow down.

The models of Underhill and Zucchini (1988) have some previously discussed drawbacks, but they have the advantage of using data that are very easy to collect in the field and easy to standardise across various observers, which, overall, allows comparisons among species, sites, or years (Underhill et al. 1989; Craig et al. 2010; Barshep and Manu 2013). For this reason, we propose that the type 1 Underhill–Zucchini model but following our methodology can be used to estimate the duration of suspended moults, including both the time of active moulting and the period of suspension. Another advantage of using our methodology is that even in populations where observers do not detect suspended moults, we might suspect that they really occur in the population, because a preliminary analysis of our database eliminating suspended moults has shown similar results to those in this article.

In conclusion, we observed that suspended moults were rather common in our studied population of crossbills and that the moult was suspended around P5–P6. The application of the Underhill–Zucchini models provided us with a duration of 137 moulting days (type 1), but once the suspension period was estimated, the real active moulting period decreased to 114 days, which is 23 days shorter. The method used to obtain the duration of the suspension has been explained in detail and can be used as a tool for working with species that undergo suspended moults. The results of this work have potential applications in a broad range of fields, including evolutionary biology, ecology, and demography.

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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 methodology; DA collected the data; BF and DG analysed the data; BF, JA, and DG led the writing of the manuscript. All authors contributed critically and gave final approval for publication. We 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.

Compliance with ethical standards

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

References

Aidley DJ, Wilkinson R (1987) Moult of some palaearctic warblers in northern nigeria. Bird Study 34(3):220–225. https://doi.org/10.1080/00063658709476964

Alonso D, Arizaga J (2011) Seasonal patterns of breeding, moulting, and body mass variation in Pyrenean Common Crossbills Loxia curvirostra curvirostra. Ring Migr 26(1):64–70. https://doi.org/10.1080/03078698.2011.587253

Barshep Y, Manu SA (2013) Breeding phenology and moult of the endemic Bannerman's Weaver Ploceus bannermani. Ostrich 84(3):231–233. https://doi.org/10.2989/00306525.2013.863235

Benkman CW (1990) Intake rates and the timing of crossbill reproduction. Auk 107:376–386. https://doi.org/10.2307/4087622

Clouet M (2000) The breeding biology of the common crossbill loxia curvirostra in the central pyrenees. Bird Study 47(2):186–194. https://doi.org/10.1080/00063650009461174

Craig AJFK, Bonnevie BT, Oschadleus HD (2010) Regional patterns in moult and sexual dimorphism of adult southern red bishops euplectes orix in Southern Africa. Ostrich 81(2):123–128. https://doi.org/10.2989/00306525.2010.488357

Dawson A (1994) The effects of daylength and testosterone on the initiation and progress of moult in Starlings *Sturnus vulgaris*. Ibis 136:335–340. https://doi.org/10.1111/j.1474-919X.1994.tb01104.x

Dawson A (2005) The effect of temperature on photoperiodically regulated gonadal maturation, regression and moult in starlings—potential consequences of climate change. Funct Ecol 19(6):995–1000. https://doi.org/10.1111/j.1365-2435.2005.01061.x

De La Hera I et al (2011) How much variation in the molt duration of passerines can be explained by the growth rate of tail feathers? Auk 128(2):321–329. https://doi.org/10.1525/auk.2011.10181

De Ridder E et al (2002) Short-and long term effects of male-like concentrations of testosterone on female european starlings (*Sturnus vulgaris*). Auk 119(2):487–497. https://doi.org/10.2307/4089894

Erni B et al (2013) moult: an R Package to analyze moult in birds. J Stat Softw 52(8):1–23. https://doi.org/10.18637/jss.v052.i08

Farner D (1964) The photoperiodic control of reproductive cycles in birds. Am Sci 52(1):137–156

Ginn HB, Melville DS (1983) Moult in birds. British Trust for Ornithology, Tring

Grubb TC (2006) Ptilochronology: feather time and the biology of birds. Oxford University Press, Oxford

Hahn TP (1995) Integration of photoperiodic and food cues to time changes in reproductive physiology by an opportunistic breeder, the red crossbill, *Loxia curvirostra* (Aves: Carduelinae). J Exp Zool 272(3):213–226. https://doi.org/10.1002/jez.1402720306

Hahn TP (1998) Reproductive seasonality in an opportunistic breeder, the red crossbill, *Loxia curvirostra*. Ecology 79(7):2365–2375. https://doi.org/10.2307/176828

Hahn TP et al (2004) Physiological responses to photoperiod in three cardueline finch species. Gen Comp Endocrinol 137(1):99–108. https://doi.org/10.1016/j.ygcen.2004.02.014

Helm B, Gwinner E (2006) S40-2 Timing of molt as a buffer in the avian annual cycle 1 Molt as a timing buffer in the annual cycle 2 Fitness implications of molt as a timing buffer 3 Precisely timed post-juvenal molt in captive stonechats. Acta Zool Sin 52:703–706

Hemborg C (1999) 'Sexual differences in moult-breeding overlap and female reproductive costs in pied flycatchers, *Ficedula hypoleuca*. J Anim Ecol. https://doi.org/10.1046/j.1365-2656.1999.00295.x

Hemborg C, Lundberg A (1998) Costs of overlapping reproduction and moult in passerine birds: an experiment with the pied flycatcher. Behav Ecol Sociobiol 43:19–23. https://doi.org/10.1007/s002650050462

Jenni L, Winkler R (1994) Moult and ageing of European passerines. Academic Press, London

Kulaszewicz I, Jakubas D (2015) Factors affecting post-breeding moult in the Savi's warbler *Locustella luscinioides* in Northern Poland. Ardea 103(1):61–68. https://doi.org/10.5253/arde.v103i1.a6

Massa B (1987) Variations in Mediterranean Crossbills *Loxia curvirostra*. Bull Br Ornithol Club 107(3):118–128

Mead CJ, Watmough BR (1976) Suspended moult of trans-saharan migrants in Ieria. Bird Study 23(3):187–196. https://doi.org/10.1080/00063657609476500

Michener H, Michener JR (1938) Bars in flight feathers. Condor 40(4):149–160. https://doi.org/10.2307/1363421

Newton I (1972) Finches/I. Newton. London: Collins (New naturalist ; 55)

Newton I (2006) Movement patterns of Common Crossbills Loxia curvirostra in Europe. Ibis 148(4):782–788. https://doi.org/10.1111/j.1474-919X.2006.00585.x

Newton I, Rothery P (2000) Timing and duration of moult in the bullfinch *Pyrrhula purrhula*: an appraisal of different analytical procedures. Ibis 142:65–74. https://doi.org/10.1111/j.1474-919X.2000.tb07685.x

Nolan V et al (1992) Testosterone and avian life histories: effects of experimentally elevated testosterone on prebasic molt and survival in male dark-eyed juncos. Condor 94(2):364–370. https://doi.org/10.2307/1369209

Norman SC (1998) Post-nuptial moult variation in the Willow Warbler *Phylloscopus trochilus* in relation to breeding. Bird Study 45(2):226–231. https://doi.org/10.1080/00063659809461094

Pimm SL (1976) Estimation of the duration of bird molt. Condor 78(4):550. https://doi.org/10.2307/1367104

Pinilla J (2000) Manual para el anillamiento científico de aves. SEO/BirdLi, Madrid

Porkert J, Hromádko M (2012) A record of breeding-moulting overlap in the Common Redstart *Phoenicurus phoenicurus*. Bird Study 59(3):380–382. https://doi.org/10.1080/00063657.2012.683987

Remisiewicz M et al (2009) Extended primary moult as an adaptation of adult Wood Sandpipers *Tringa glareola* to their freshwater habitats in southern Africa. Ardea 97:271–280. https://doi.org/10.5253/078.097.0302

Rohwer S, Broms K (2012) Use of feather loss intervals to estimate molt duration and to sample feather vein at equal time intervals through the primary replacement. Auk 129(4):653–659. https://doi.org/10.1525/auk.2012.12096

Rothery P, Newton I (2002) A simple method for estimating timing and duration of avian primary moult using field data. Ibis 144(3):526–528. https://doi.org/10.1046/j.1474-919X.2002.00072.x

Rothery P et al (2001) The timing and duration of moult in adult *Starlings Sturnus* vulgaris in east-central England. The Ibis 143(3):435–441. https://doi.org/10.1111/j.1474-919X.2001.tb04944.x

Ryder TB, Wolfe JD (2009) The current state of knowledge on molt and plumage sequences in selected Neotropical bird families: a review. Ornithol Neotrop 20(1):1–18

Rymkevich TA (1990) Moult of Passerines of NorthWestern USSR. Leningrad University Press, Leningrad

Snow DW, Snow BK (1964) Breeding seasons and annual cycles of trinidad land-birds. Zoologica 49:1

Stresemann E, Stresemann V (1966) Die mauser der vögel. J Ornithol 107:1–448

Summers RW, Swann RL, Nicoll M (1983) The effects of methods on estimates of primary moult duration in the redshank tringa totanus. Bird Study 30(2):149–156. https://doi.org/10.1080/00063658309476790

Svensson L (1998) Guía para la identificación de los paseriformes de Europa. SEO/Bird L, Madrid

Symes CT, Wilson JW (2008) Primary moult patterns and morphometrics in the Green-winged *Pytilia Pytilia* melba. Ostrich 79(1):87–90. https://doi.org/10.2989/OSTRICH.2008.79.1.12.367

Underhill LG, Joubert A (1995) Relative masses of primary feathers. Ring Migr 16(2):109–116. https://doi.org/10.1080/03078698.1995.9674099

Underhill LG, Zucchini W (1988) A model for avian primary moult. Ibis 130(3):358–372. https://doi.org/10.1111/j.1474-919X.1988.tb00993.x

Underhill LG et al (1989) The biannual primary moult of adult willow warblers *Phylloscopus trochilus* in Europe and Africa: an application of a new technique. Ostrich 60:16. https://doi.org/10.1080/00306525.1989.9639609

Weber H (1953) Bewirkung des Farbwechsels bei männlichen Kreuzschnäbeln. J Ornithol 94(3–4):342–346. https://doi.org/10.1007/BF01922518

Weber WC (1972) Birds in cities: a study of populations, foraging ecology and nest-sites of urban birds. University of British Columbia, Vancouver. https://doi.org/10.14288/1.0101293