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Gabriel Gargallo

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ORIGINAL ARTICLE

Feather selection and replacement patterns demonstrate that Goldfinches *Carduelis carduelis* fix postjuvenile moult extent prior to moult initiation

Gabriel Gargallo

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Abstract Birds undergoing a partial moult have to make important decisions regarding moult extent, pattern and sequence. Moreover, since partial moults are usually subject to a great degree of individual variability, the mechanisms controlling and organising such moults can be particularly complex. In the present paper, I investigate the feather selection and replacement process involved in partial postjuvenile moult in the Goldfinch *Carduelis carduelis*. Moult patterns observed after moult completion indicate that birds select the feathers to be replaced according to a predetermined order of moult priorities. However, the sequence of feather replacement, both within and between feather tracts, differs markedly from this order of moult priorities, varying individually to be adjusted to the final moult extent. These results indicate that, prior to or at the beginning of moult, each bird fixes with precision which feathers will be replaced. These findings have important implications for the interpretation of partial and incomplete moult patterns and for our understanding of the underlying factors controlling moults.

Keywords Partial moult · Moult extent · Moult sequence · Postjuvenile moult · Goldfinch · *Carduelis carduelis*

Zusammenfassung

Federauswahl und Muster der Federerneuerung zeigen, dass Stieglitze (*Carduelis carduelis*) ihre Jungmauser vor dem Mauserbeginn festlegen

Vögel mit einer Teilmauser müssen wichtige Entscheidungen zu Umfang, Muster und Ablauf ihrer Mauser treffen. Darüber hinaus sind die Mechanismen, die die Mauser steuern, vermutlich recht komplex, da die Teilmauser normalerweise einen großen Spielraum in der individuellen Variabilität aufweist. In dieser Publikation untersuche ich den Vorgang von Auswahl und Austausch der Federn in der Jungmauser des Stieglitz (*Carduelis carduelis*). Das Muster der Mauser, wie nach ihrem Abschluss festgestellt, legt nahe, dass die Vögel ihre Federn nach einer vorab festgelegten Reihenfolge von „Mauser-Prioritäten" ersetzen. Allerdings weicht die Reihenfolge des Federaustauschs bei gleichen, aber auch bei unterschiedlichen, Federtypen merklich von dieser Reihenfolge der „Mauser Prioritäten" ab und variiert individuell, um dann zum abschließenden Ergebnis der Mauser zu führen. Diese Resultate weisen darauf hin, dass noch vor, oder direkt bei, Beginn der Mauser jeder Vogel genau festlegt, welche Federn ersetzt werden sollen. Die Ergebnisse haben wichtige Implikationen für die Interpretation der Muster von Teilmauser oder unvollständiger Mauser, wie auch für unser Verständnis derjenigen Faktoren, die die Mauser steuern.

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G. Gargallo (✉)
Catalan Ornithological Institute, Museu de Ciències Naturals,
Passeig Picasso s/n, 08003 Barcelona, Spain
e-mail: anella@ornitologia.org

Introduction

The complete moult of a whole plumage requires very complex neurophysiological mechanisms that control and

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coordinate feather replacement (Payne 1972). However, in passerines, the sequence of the complete moult is largely fixed (the so-called 'basic sequence'; Ginn and Melville 1983), and thus all birds undertaking a complete moult largely follow the same predetermined feather replacement rules. Partial moults include by definition only part of the plumage (Jenni and Winkler 1994); nevertheless, this generates a new set of requirements, which can be added to those already applying to complete moults, and include the selection of the number of feathers to be replaced (i.e. moult extent) and the sequence in which these will be replaced (i.e. moult sequence). Thus, even in birds undertaking moults of limited extent, the underlying mechanisms can be particularly complex. However, given the potentially huge number of different moult patterns produced by partial moults (cf. Jenni and Winkler 1994; Pyle 1997), the study of this process can help to identify the true nature and limits of variability in moult patterns, a key factor in the understanding of the evolution of moult strategies (cf. Rohwer et al. 2009).

Both sex and different environmental and energetic constraints can influence the extent of partial moults (Gosler 1991; Jenni and Winkler 1994; Bojarinova et al. 1999; Flinks 1999). However, much of the individual variation observed in postjuvenile moult extent in European passerines seems to respond to variations in the time available for moulting in summer/early autumn, in turn due to differences in geographical origin and hatching dates (reviewed in Jenni and Winkler 1994). A large body of experimental data indicates that in these species partial moult extent, like timing and duration, is largely controlled by a genetically fixed time programme that is modified by the photoperiod (Gwinner 1986; Jenni and Winkler 1994; Noskov and Rymkevich 1985). However, the number of different combinations of feathers that can be replaced to attain a specific moult extent is huge (given the large number of feathers that form the plumage of a bird). Birds therefore have to select not only the quantity but also which feathers in particular will be replaced.

Within a given species, the role and emplacement of each feather (Dwight 1900; Newton 1964; Mester and Prünte 1982; Ginn and Melville 1983; Jenni and Winkler 1994), its replacement costs, and eventually the feather generation to which it belongs, will usually differ and so the advantages of replacing each particular feather will also vary. In fact, given the high cost associated with feather replacement and the vital role of moult in determining plumage appearance and quality (Jenni and Winkler 1994; Senar 2006; Pap et al. 2007), birds should be under strong selection pressure to choose with precision which feathers have to be replaced. Given that the number of feathers replaced varies between individuals, this selection cannot be fixed, but birds may select feathers according to a predetermined order of moult priorities, and so the greater the number of feathers to be replaced (i.e. the larger the moult extent), the greater the number of lower priority feathers that will be replaced. Support for this view comes from the fact that, in many European passerines studied after the completion of a partial moult, the lower the renewal frequency of a given feather, the greater the extent of the moult tends to be in the birds that have renewed that particular feather (Richter 1972; Herremans 1988; de la Cruz et al. 1992; Jenni and Winkler 1994; Pilastro et al. 1996; Gargallo 1995, 1996, 1997, and unpublished data). Even so, the question of the existence of an order of moult priorities has never been formally explored.

The study of the rules of feather replacement is vital if we are to identify crucial details regarding the moult strategies of birds and the underlying mechanisms that govern moult processes (Rohwer 2008; Rohwer et al. 2009). Thus, given the variable nature of partial moults, the study of moult sequences can be particular useful when attempting to understand these mechanisms. Unfortunately, the sequence of feather replacement in partial moults is particularly poorly known (Jenni and Winkler 1994), and important questions such as how and to what point moult sequences are adjusted to different levels of extension (i.e. which feathers will replaced by each individual) still remain largely unexplored.

In the present paper, I study the postjuvenile moult of the flight feathers in the Goldfinch *Carduelis carduelis* in an attempt to understand how birds select and replace feathers during partial moults with a large degree of individual variability. Goldfinches moult between July and October; adults undertake a complete postnuptial moult, while first-year birds undertake a partial postjuvenile moult that is very variable in extent. Some birds replace only their body feathers, marginal and median wing coverts or some greater coverts, while others renew almost all or practically all their plumage (Mester and Prünte 1982; Cramp and Perrins 1994; Jenni and Winkler 1994; Gargallo and Clarabuch 1995). As suggested by the moult patterns observed in many European passerines, I hypothesise that, given the large degree of individual variability in postjuvenile moult extent, Goldfinches follow a predetermined order of moult priorities when selecting which feathers to replace. Yet, birds do not necessarily have to moult feathers using a sequence of replacements that matches the order of moult priorities. Often moult sequences have been deduced from moult patterns observed after moult completion (cf. Jenni and Winkler 1994; Pyle 1997), on the assumption that the order of moult priorities and feather replacement was the same. If birds moult following the order of moult priorities, they ensure that, even if the moult is interrupted, the feathers with the highest moult priority will be replaced (Fig. 1a). However, the renewal of

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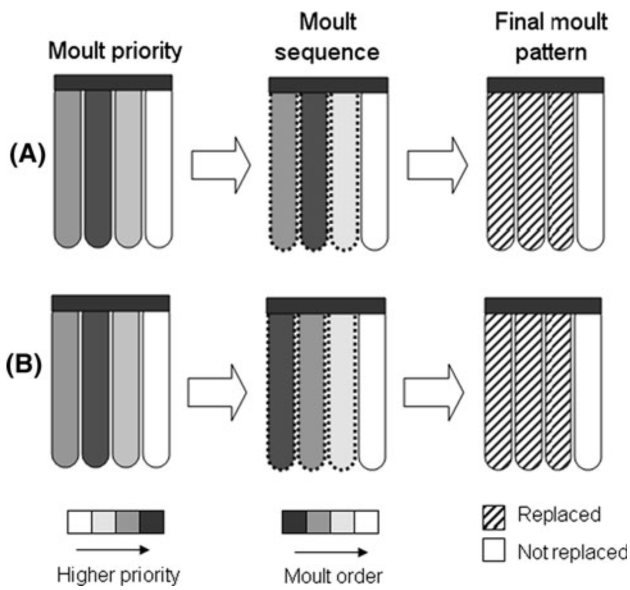

Fig. 1 Birds undertaking a partial moult may select the feather to be replaced according to a predetermined order of moult priorities. However, when birds actively replace these feathers, the replacement sequence may or not match this order. The relevance of this difference is explained in this example using a hypothetical bird with four primaries. According to the moult priorities of this hypothetical case, if only one of the feathers is replaced, it will be feather number 3. If two feathers are replaced, these will be feathers 2 and 3, while feathers number 1 and 4 are only replaced if three and four feathers, respectively, are renewed. Assuming that this particular bird is going to replace four feathers, these may be replaced following a moult sequence that matches (**a**), or not (**b**), the order of moult priorities. If, after the replacement of only two feathers, the moult is interrupted, the feathers that end up being replaced will be those with the highest order of moult priority in the first case (**a**) but not in the second case (**b**). Therefore, birds actively replacing feathers following the order of moult priorities ensure that any eventual interruption of their moult will always result in the replacement of the feathers with the highest moult priority (**a**). However, if the moult sequence does not follow the order of moult priorities, birds may benefit by replacing feathers according to a sequence that may be more efficient energetically and/or aerodynamically (e.g. by replacing all feathers descendantly and using only one moult focus; **b**)

feathers following the order of moult priorities may be impractical or less efficient in energetic or aerodynamic terms (Fig. 1b). Moreover, to date, there is no evidence to suggest that partial moults are more prone than complete moults to be interrupted as a direct response to external constraints (cf. Murphy et al. 1988).

I tested these hypotheses by studying moult patterns of Goldfinches trapped during and after postjuvenile moult. The sample of birds trapped after postjuvenile moult completion was used to determine an expected order of moult priorities and to test its validity by checking the consistency of individual moult patterns. In addition, the sample of birds trapped during moult was used to determine the moult sequence and to test whether or not it matched the order of moult priorities. The implications of the system of feather selection and replacement observed in the Goldfinch are discussed in relation to the control and organization of partial moults in birds.

Methods

Study area and data collection

Goldfinches were studied in Ibiza (Balearic Islands, Spain) between 1993 and 1996. Birds were trapped using mist-nets and aged according to Gargallo and Clarabuch (1995). A total of 279 first-year birds and 82 adults were studied while in active moult (September; approximately the middle of the moult season) and 83 first-year birds after moult completion (mid-October–December). Moult cards were filled in for each bird and feathers were scored following Ginn and Melville (1983). Only data on the moult of flight feathers (i.e. remiges and rectrices) are analysed here (left side only). The outermost primary (P10) was not taken into account due to its very small size.

Analytical approach

If birds follow a strict order of moult priorities, the higher a given feather is in the order of moult priority, the higher should be its renewal frequency. Therefore, by using birds trapped after moult completion, I was able to calculate the moult frequency of each feather and to construct an 'expected order of moult priorities'. I constructed expected priority orders for all the flight feathers, the remiges and each feather tract separately. Feathers with the same moult frequency were given identical priority order. Subsequently, by calculating the number of feathers that appeared to have been replaced out of order (i.e. not matching the expected order of priorities), I estimated both for birds captured during moult and after moult completion to what extent the moult patterns shown by each individual bird matched the expected order of moult priorities. Obviously, if birds moult according to a strict order of moult priorities, then, regardless the total number of feathers renewed, all feathers replaced by each individual bird will always appear as the highest in the list of priorities. Consequently, the frequency of appearance of feathers found to have been renewed 'incorrectly' (i.e. out of order) in birds trapped after moult completion will provide a good estimate of the degree to which birds follow a given order of moult priorities. On the other hand, in birds studied in active moult, the frequency of appearance of feathers replaced 'incorrectly' reveals to what extent the moult sequence matches the order of moult priorities.

For the purposes of this study, I considered an 'erroneously replaced feather' (or simply an 'error') to be any

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feather that appeared renewed even though a feather with a higher moult priority (i.e. feathers with a higher moult frequency) had been left unmoulted. It is worth noting that this parameter is fixed by convention, since we have no way of knowing which particular feather has really been incorrectly replaced. The number of errors observed was calculated for all the flight feathers, the remiges and each feather tract separately in birds trapped during moult and after moult completion. For each calculation, sample sizes varied, since only birds with some feathers replaced were considered in each case. Confidence limits for the number of errors observed were calculated by bootstrapping with replacement following Sokal and Rohlf (1995). A total of 1,000 re-samplings were carried out in each case.

Given that the number or errors that can occur in each feather is limited by the renewal frequency of the other feathers, the observed number of errors was compared with the estimated number of errors expected to occur by chance alone. According to the definition of 'error' used here, the probability of a given feather being erroneously replaced is equal to the probability that at least one of the feathers with a higher priority of moult was left unmoulted. Thus, except for feathers with priority 1 (since by definition the probability of error in these cases is 0), the number of errors expected to occur for each feather was calculated using the formula

$$E = N\left[1 - \prod_{i=1}^{k} F_i\right]$$

where E is the number of errors expected to occur, N the frequency of renewal of the feather in birds trapped after moult completion and F the renewal probability of the ith feather in the k group. The k group includes all feathers taken into consideration with a higher moult priority than the one for which errors are calculated. The renewal probability of each feather was calculated as its moult frequency divided by the sample size. The number of errors expected to occur were calculated for all flight feathers, the remiges and each feather tract separately. For each calculation, moult frequencies and sample sizes varied, since only birds with some replaced feathers were considered. To establish confidence limits for the number of errors expected by chance, I conducted a sampled randomisation procedure (Sokal and Rohlf 1995). For each case (i.e. flight feathers, remiges and each feather tract), I first randomly created a 'source' population 100 times greater than the original but with the same renewal frequency for each feather (in percentage) as in the original sample. Then, I resampled with replacement from this source population a total of 1,000 samples of n individuals (with n equal to the original sample size). The total number of errors observed in each of these 1,000 random samples was calculated and 95 % confidence limits were estimated following Sokal and Rohlf (1995).

The moult sequence of the sample of birds trapped during moult (September) was studied using a modified version of the procedure described by Yuri and Rohwer (1997) and Rohwer (2008). Accordingly, each primary, secondary, tertial and rectrix was categorised as follows:

1. Nodal. Nodal feathers identify a moult focus. Feathers were classified as nodal when their moult score was higher than any of the adjacent feathers. Nodal feathers were sub-classified as primary nodes when their moult score was higher than that of all the other feathers in the tract.
2. Descendant (proximal to distal). Feathers were classified as descendant when their moult score was lower than that of the adjacent proximal feather and both feathers were already replaced (i.e. new or growing).
3. Ascendant (distal to proximal). Feathers were classified as ascendant when their moult score was higher than that of the adjacent proximal feather and both feathers were already replaced (i.e. new or growing).

Furthermore, in order to determine the moult sequence between the different feather tracts, I studied the relationship in the progression of moult between tertials, rectrices and primaries. In order to compare moult progressions directly, I only included in these analyses birds actively moulting all three feather tracts. Since the size of the flight feathers varies greatly, moult extent and progression were calculated in terms of renewed feather mass (Underhill and Zucchini 1988). Thus, the flight feathers of an adult Goldfinch were dried for 24 h at 80 °C and weighed to the nearest 0.01 mg. In birds in active moult, the mass of growing feathers was estimated from their relative growth stage as inferred from the moult score according to Underhill and Zucchini (1988). Throughout this paper, primaries are numbered descendantly, secondaries (and tertials) ascendantly and rectrices from the centre outwards.

Results

Moult priorities

The renewal frequency of flight feathers observed after moult completion shows that tertials were fully renewed in most cases, rectrices and to a lesser extent primaries were also frequently moulted, while secondaries were only rarely moulted (Tables 1, 2). Other than in two cases, in which P9 was replaced together with P3–7 and P2–7, birds that moulted more than one primary ($n = 40$) had a continuous block of renewed feathers. Assuming a descendant moult sequence (see below), moult focus was nearly

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Table 1 Frequency of moult of flight feathers in Goldfinches *Carduelis carduelis* trapped after postjuvenile moult completion and during moult

	S9	S8	S7	S6	S5	S4	S3	S2	S1	P1	P2	P3	P4	P5	P6	P7	P8	P9	R1	R2	R3	R4	R5	R6
After moult completion ($n = 83$)																								
Frequency	79	83	77	8	4	2	1	2	2	6	7	12	25	42	45	27	7	9	79	69	43	46	51	66
%	95.2	100.0	92.8	9.6	4.8	2.4	1.2	2.4	2.4	7.2	8.4	14.5	30.1	50.6	54.2	32.5	8.4	10.8	95.2	83.1	51.8	55.4	61.4	79.5
During moult ($n = 279$)																								
Frequency	143	239	61	0	1	1	3	11	14	28	44	62	106	162	174	65	16	6	159	205	145	108	85	103
%	51.3	85.7	21.9	0.0	0.4	0.4	1.1	3.9	5.0	10.0	15.8	22.2	38.0	58.1	62.4	23.3	5.7	2.2	57.0	73.5	52.0	38.7	30.5	36.9

always located between P1 and P6 (Table 3). Both primary moult extent and flight feather moult extent were closely correlated to primary moult focus: the more proximal the focus, the higher the moult extent ($r_s = 0.87$, $P < 0.001$ for primaries and $r_s = 0.80$, $P < 0.001$ for flight feathers; $n = 48$; the bird with moult focus on P9 was not included). The birds that replaced some primaries ($n = 49$) had nearly always renewed all their tertials (98 % of the cases), as well as all (74 % of cases) or most rectrices. Among birds without replaced primaries, complete tertial moult was also the rule (29 of 34 birds), although all rectrices were replaced only rarely (4 of 34). Nearly half the birds (48 %) moulted the whole of their tails. Five out of six birds with only one renewed rectrix moulted R1; of birds with 2–5 rectrices renewed ($n = 34$), 7 birds replaced R1–2, 1 R1–3 and 26 (76.5 %) moulted some of their innermost and outermost feathers.

Approximately 92–97 % of the flight feathers, remiges, primaries and rectrices were replaced according to the expected order of moult priorities (Tables 2, 4). The percentage of errors observed in these groups of feathers was significantly different from zero (confidence limits do not include zero; Fig. 2) and in all cases, figures were very low and differed significantly from what would be expected by chance.

Moult sequence

Nearly all birds replaced tertials following the sequence S8 > S9 > S7 and in only one case was S8 found to be nodal (Fig. 3). Although in no case was S7 found to have moulted before S9, the opposite was recorded in 127 birds. Data from birds studied after moult completion indicate that moult of secondaries can proceed either from two moult foci (from S1 and from either S5 or more frequently S6) or from only one (generally from S6). Birds trapped in active moult in September, however, were only found to initiate moult from S1 or more rarely S2 and often continued inwards (Fig. 3). In 10 of the 14 cases in which the moult started from S1 (only in 2 of the 6 cases when moult began from S2), P1 had also been replaced. However, in only 3 of the 8 cases in which S6 was replaced was P1 also renewed.

Primary moult was initiated from a variable but almost always single moult focus located between P1 and P6, and nearly always proceeded descendantly (Fig. 3). Only 4 out of 110 birds had more than one primary moult focus. Rectrices usually began to moult from R2 (rarely R3) and then proceed in two different waves, inwards towards R1 and outwards towards R6 (Fig. 3). In a number of birds (21 out of 145), the moult proceeded from two different moult foci, inwards from R2 and outwards from one of the outermost rectrices or just R6. Birds starting from R1 either

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Table 2 Number of birds with some feathers replaced, total number of feathers replaced and number of errors observed and expected by chance in the different groups of feathers in Goldfinches studied during moult ($n = 273$) and after moult completion ($n = 83$)

	Flight feathers	Remiges	Tertials	Secondaries	Primaries	Rectrices
After moult completion						
Birds with some feathers replaced (% of total)	83 (100.0)	83 (100.0)	83 (100.0)	10 (12.0)	49 (59.0)	80 (96.4)
Total number of feathers replaced (mean)	792 (9.5)	438 (5.3)	239 (2.9)	19 (1.9)	180 (3.7)	354 (4.4)
Errors observed (% of total of feathers replaced)	68 (8.1)	28 (6.4)	0 (0.0)	3 (15.8)	14 (7.8)	10 (2.8)
Errors expected (% of total of feathers replaced)	317 (40.0)	134 (30.6)	4 (1.7)	6 (31.6)	61 (33.9)	83 (23.4)
During moult						
Birds with some feathers replaced (% of total)	254 (91.0)	247 (88.5)	240 (86.0)	20 (7.2)	187 (67.0)	228 (81.7)
Total number of feathers replaced (mean)	1,941 (7.6)	1,136 (4.6)	443 (1.8)	30 (1.5)	663 (3.5)	805 (3.5)
Errors observed (% of total of feathers replaced)	946 (48.7)	510 (44.9)	2 (0.5)	30 (100.0)	168 (25.3)	214 (26.6)

Table 3 Frequency with which each primary was the moult focus in Goldfinches studied after moult completion ($n = 49$)

Primary	Frequency
1	6
2	1
3	5
4	13
5	18
6	5
9	1

A descendant moult sequence is assumed

replaced only this feather or more rarely also moulted R2 or some of the outermost feathers (usually only R6). Birds without any signs of primary moult tended to start rectrix moult from R1 (instead of R2) much more frequently (13 out of 34 cases) than those moulting primaries (four out of 66). Except for the tertials, the percentage number of errors observed in birds trapped during moult was similar or even higher than would be expected to occur by chance and distinctly higher than in birds studied after moult completion (Fig. 2; Table 2).

In birds replacing primaries, the relationship between primary moult progression and both tertial and rectrix moult progression varied markedly according to the emplacement of the primary moult focus (Figs. 4, 5): the more distal the primary moult focus, the more delayed was the start of primary moult with respect to the initiation of tertial and rectrix moults (ANCOVA $F_{5,178} = 213.16$, $P < 0.001$ for rectrices; $F_{5,201} = 177.15$, $P < 0.001$ for tertials; in both cases, primary moult progression was set as the dependant variable and tertial and rectrix moult progressions as covariates). The more proximal the primary moult focus, the more the relationship resembled that found in adults. The relationship between tertial and rectrix moult progression was fairly constant and similar to that observed in adults, and did not vary according to the primary moult focus (ANCOVA $F_{5,174} = 0.72$, $P > 0.05$; rectrix moult progression was set as the dependant variable and tertial moult progression as a covariate).

Discussion

The moult patterns observed after moult completion indicate that postjuvenile moult in the Goldfinch is characterized by a fairly strict order of moult priorities. Given the individual variability in moult extent that is typical of partial moults, as well as the different states, values and relevance of each feather at any given time (Jenni and Winkler 1994), the existence of a certain order of moult priorities is probably an essential requirement of partial moults. In the Goldfinch, feathers placed higher up the list of priorities tend to be those that are more exposed to wear and tear and those that may have more important signalling roles (Mester and Prünte 1982). This is especially obvious in rectrices, where the central and outermost feathers have higher moult priorities, and in primaries, where P5 and P6 and to a lesser extent P4 and P7 (the most exposed feathers when the wing is folded), are top of the list of priorities. It is remarkable, nevertheless, that birds tend to prefer to replace P9 (which is only exposed from below) instead of P8 (which is not exposed), since this implies having to moult primaries through two different foci (present results; unpublished data). This has also been found to occur in the Linnet *Carduelis cannabina* and Greenfinch *Carduelis chloris*, species with similar wing structures (Gargallo and Clarabuch 1995, and unpublished data).

The sequence of postjuvenile moult in the Goldfinch differs markedly from the order of moult priorities. Primaries are nearly always replaced descendantly from a moult focus that moves further inwards as the number of primaries to be replaced increases, as suggested also by previous studies (Mester and Prünte 1982; Jenni and

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Table 4 Frequency of moult and expected order of moult priorities in the different groups of feathers as estimated from a sample of 83 Goldfinches studied after postjuvenile moult completion

Feather	Moult frequency	Order of moult priorities					
		Flight feathers	Remiges	Tertials	Secondaries	Primaries	Rectrices
S9	79	2	2	2			
S8	83	1	1	1			
S7	77	3	3	3			
S6	8	15	10		1		
S5	4	18	13		2		
S4	2	19	14		3		
S3	1	20	15		4		
S2	2	19	14		3		
S1	2	19	14		3		
P1	6	17	12			8	
P2	7	16	11			7	
P3	12	13	8			5	
P4	25	12	7			4	
P5	42	10	5			2	
P6	45	8	4			1	
P7	27	11	6			3	
P8	7	16	11			7	
P9	9	14	9			6	
R1	79	2					1
R2	69	4					2
R3	43	9					6
R4	46	7					5
R5	51	6					4
R6	66	5					3

Feathers with the same frequency are given the same order of moult priority

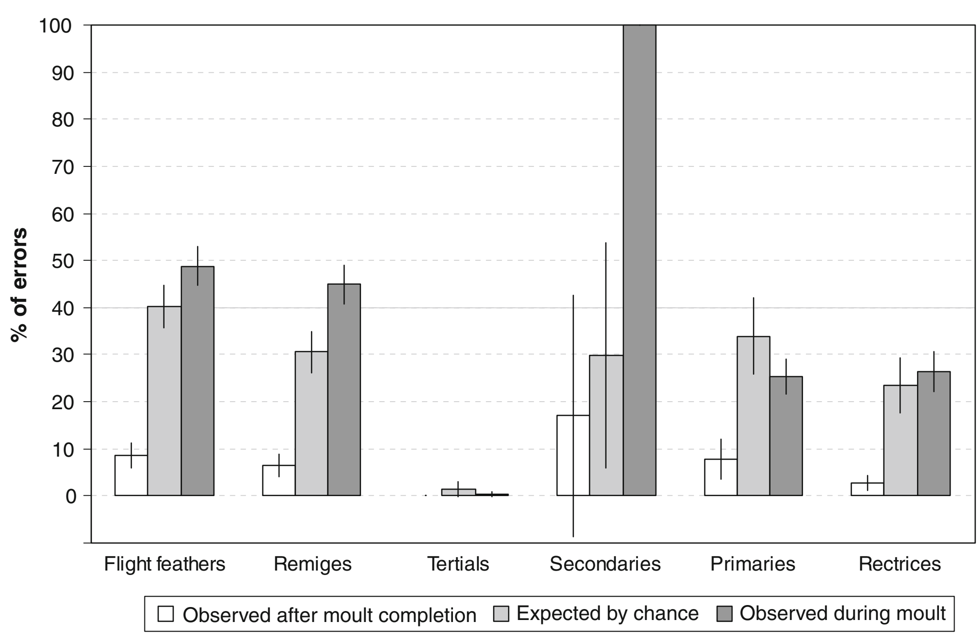

Fig. 2 Percentage of errors observed and expected to occur by chance in Goldfinches *Carduelis carduelis* studied after moult completion and the percentage of errors observed during moult (±95 % confidence intervals). Only birds with some replaced feathers were included in the analysis of each group of feathers (see Table 2 for sample sizes)

Winkler 1994; Gargallo and Clarabuch 1995). Accordingly, the more extensive the postjuvenile moult, the closer the moult sequence is to that of the adults. The sequence of the rectrix moult also differs largely from the order of moult priorities and varies according to the number of feathers to be replaced. The birds that end up replacing

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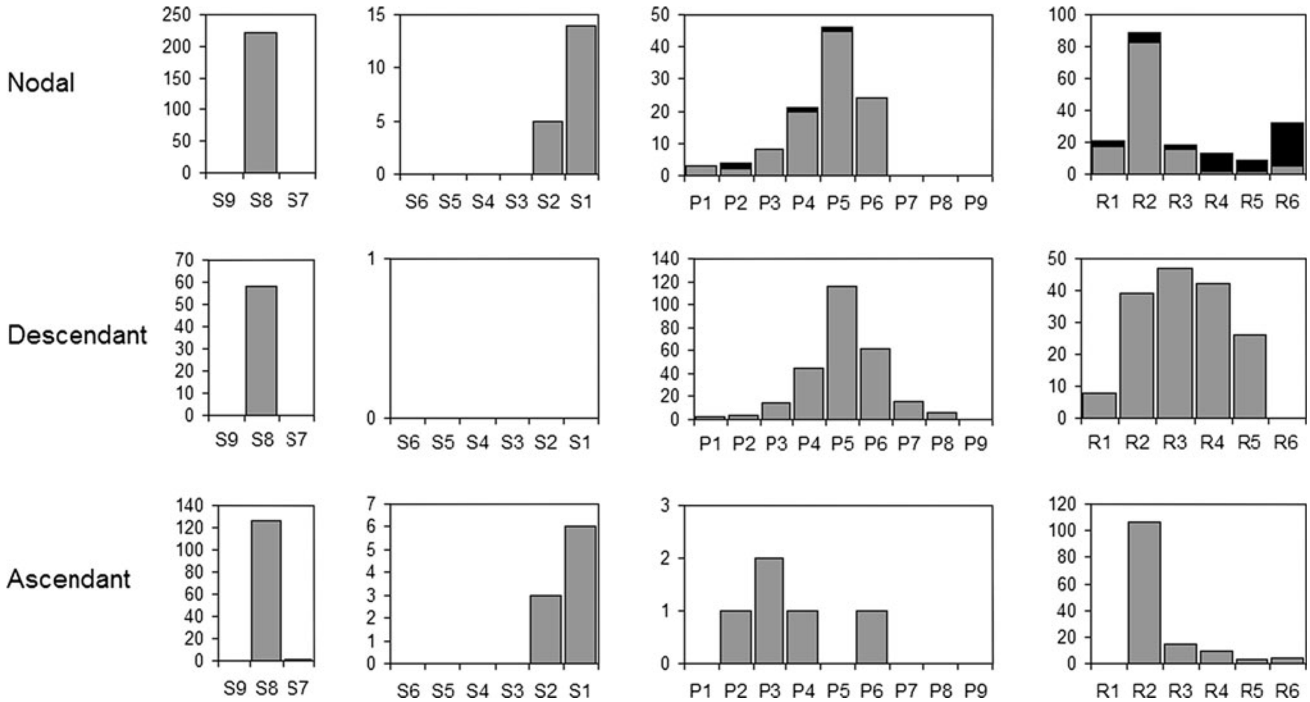

Fig. 3 Frequency with which each flight feather was classified as nodal (*upper row*; *grey* those classified as primary nodes), descendant (*middle row*) or ascendant (*bottom row*) in Goldfinches studied during moult

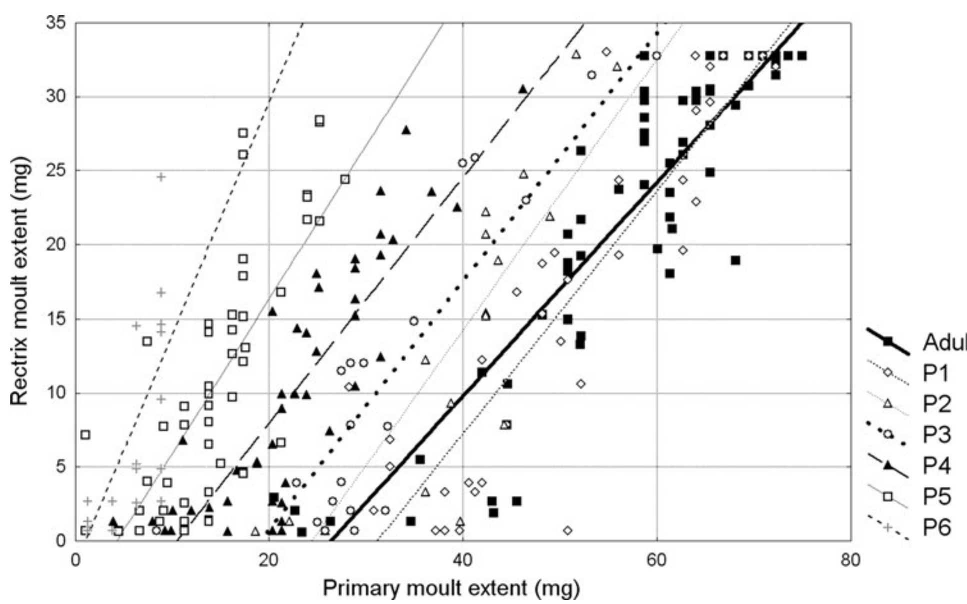

Fig. 4 Relationship between the progression of primary and rectrix moult according to the primary moult focus in Goldfinches trapped during postjuvenile moult (moult focus *P1–P6*) and postnuptial moult (*Adult*). Data on adults are provided for comparison

most or all rectrices (birds that moult primaries) tend to start their rectrix moult from R2 and match the sequence found in adult Goldfinches; that is, a divergent sequence initiated at R2 (present results; Middleton 1969). On the other hand, the higher tendency observed in birds not replacing primaries to initiate moult from R1 seems to be due largely to birds that renew very few rectrices (usually only R1 or R1 and R6). Moult of secondaries only seems to proceed ascendantly from S1 in birds that moult very extensively (birds moulting from P1). By contrast, birds that only renew their innermost secondaries tend to moult less extensively. In agreement with Mester and Prünte (1982), no active moult of innermost secondaries was detected in birds trapped in active moult in September, indicating that their replacement occurs during the final stages of moult.

The dependence of the moult sequence on the final moult extent becomes evident when examining the

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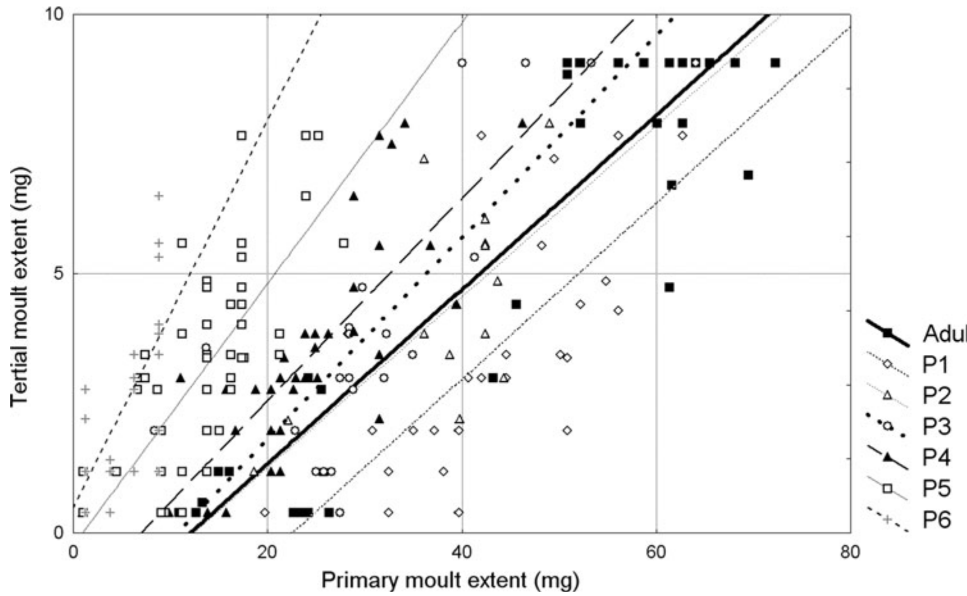

Fig. 5 Relationship between the progression of primary and tertial moult according to the primary moult focus in Goldfinches trapped during postjuvenile moult (moult focus *P1–P6*) and postnuptial moult (*Adult*). Data on adults are provided for comparison

relationship in the moult progression between different feather tracts. Birds adjust their moult sequences so that the greater the extent of the partial moult (i.e. the more inward the moult focus in the primaries), the more they delay the initiation of rectrix and tertial moult in relation to the start of primary moult. As with primary, rectrix and secondary moults, the greater the final moult extent, the more the moult sequence coincides with that of adults. By adjusting the moult sequence according to the final moult extent (and therefore the final moult pattern) rather than the order of moult priorities, birds may optimise energetic costs and flight performance. If the moult sequence matched the order of moult priorities, primary moult would finish much later than tertial and rectrix moults. However, as is shown here, Goldfinches extend moult progression across the different tracts quite evenly. This is characteristic of the basic moult sequence (Jenni and Winkler 1994) and therefore could respond to important functional adaptations. Furthermore, by ensuring that the moult does not match the order of moult priorities, birds reduce the number of gaps in primaries and rectrices, thereby benefiting their flight performance (cf. Swaddle et al. 1999; Williams and Swaddle 2003; Hedenström 2003). In addition, the adoption of a quite strict descendant primary moult may provide better protection during flight for growing primaries (Noordhuis 1989).

The fact that the moult sequence differs markedly from the order of moult priorities and varies to a large extent in terms of the final moult extent indicates that Goldfinches fix with precision, either before the moult starts or at the very beginning of the moult, which feathers will be replaced. Since the moult sequence is established in terms of the final moult extent, birds are obliged to fix this parameter prior to moult initiation. This becomes particularly clear when observing the moult sequence in birds replacing primaries. By the time these birds start moulting by shedding one of their primaries, almost no other feathers have been renewed (cf. Figs. 4, 5); however, with a low margin of error (cf. Fig. 2), they will end up replacing all their tertials and all or nearly all rectrices, as well as a variable number of secondaries and primaries (i.e. all those with a higher moult priority than the primary with which the moult began). To the best of my knowledge, this is the first time that it has been formally demonstrated that the extent of a partial moult is mostly determined in advance. This finding may have important implications for interpreting partial or incomplete moult patterns and for our understanding of the underlying factors controlling these moults.

Since the moult extent is largely established prior to or at the beginning of the moult, by this point Goldfinches must already have accumulated enough information to be able to fix this parameter with sufficient confidence. There is evidence in this species and many others that moult timing and extent is closely regulated by the photoperiod (Dolnik and Gavrilov 1980; Berthold and Querner 1982; Gwinner et al. 1983; Gwinner and Neusser 1985; Gwinner 1986; Noskov and Rymkevich 1985; Rymkevich and Bojarinova 1996; Bojarinova et al. 1999; Helm and Gwinner 1999; Dixit and Singh 2011), which is the only clue that can precisely predict the time available for moulting (the main factor limiting postjuvenile moult extent in European passerines; Rymkevich 1990; Jenni and Winkler 1994; Gargallo and Clarabuch 1995). Therefore, the photoperiod could be the key factor determining moult extent in the Goldfinch, although birds could somewhat alter this

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parameter in terms of their physical state and/or signalling requirements at the beginning of the moult period, or according to the time they had available to prepare for moult (i.e. the time lapse between fledging and the start of the postjuvenile moult; Gosler 1991; Senar et al. 1998; Senar 2006).

Goldfinches select the extent of their partial moult in advance and invariably seem to end up attaining this extent after moult completion. If Goldfinches could arrest their moults before completion (i.e. before reaching the predetermined moult extent), the resulting moult patterns would be distinctly aberrant (as moult sequences mostly differ from the order of moult priorities). However, the low number of errors observed after moult completion clearly demonstrates that there is little room left for such a possibility. This indicates that Goldfinches undertaking a partial moult are not necessarily more prone to interrupting their moults than those that are moulting completely. Plumage replacement is such an important part of the annual avian cycle that, as has been shown, once a complete moult is initiated, even starving birds are unable to halt it (Murphy et al. 1988). Partial moults, particularly those that include the first major replacement of juvenile feathers, produce vital improvements in plumage quality and performance and often represent some of the most significant changes in the appearance of birds (Jenni and Winkler 1994; Pap et al. 2007). Therefore, birds undertaking partial moults may also be very reluctant or unable to interrupt these moults unless this possibility is already predetermined (as occurs in species undertaking true moult interruptions; Berthold and Querner 1982; Jenni and Winkler 1994). Given the length of the breeding season in the Goldfinch, particularly in southern Europe (Cramp and Perrins 1994), when postjuvenile moult begins, the juvenile flight feathers of birds born early in the year are already several months old and the most exposed feathers are the most worn. Therefore, the earlier birds are born, the greater is the need to replace more plumage and the greater the time available for moulting. Under this scenario, Goldfinches may benefit from fixing a predetermined level of plumage replacement that will depend on the time available and possibly also on their physical state, and will then replace feathers following the best-fitting moult sequence given the feathers that have to be renewed (Fig. 6).

Being incomplete by definition, it is intrinsically difficult to discern whether a given partial moult has or has not been interrupted before completion. However, the findings presented here for the Goldfinch show that the use of the terms 'interrupted' or 'arrested' to describe partial moults for which it is unknown whether they were going to proceed any further (e.g. Gosler 1991; Pyle 1997) is meaningless. This could also apply to moult patterns, usually interpreted as suspended or arrested complete moults (e.g. Pied Flycatcher *Ficedula hypoleuca*, Willow Warbler *Phylloscopus trochilus*, Bonelli's Warbler *Phylloscopus bonelli* and various *Sylvia* warblers; Norman 1991; Cramp 1992), which can reflect extensive partial moults that form part of interlaced, seasonally divided moult strategies (Jenni and Winkler 1994; Shirihai et al. 2001). We still need further and better descriptions of the patterns and sequences of partial and incomplete moults before their true biological significance can be fully determined.

Taking into account the fact that Goldfinches determine the extent of their postjuvenile moult prior to moult initiation, the mechanisms governing the moult sequence might be simpler than the large variability of moult patterns actually suggests. Similarities with the adult moult sequence (e.g. tertial moult, the descendant replacement of primaries and the divergent moult of rectrices in many first-year birds), as well as the fact that similarities tend to increase with moult extent, indicate that this sequence could be based largely on that of the complete moult. In fact, to a large extent, the patterns of feather replacement described here could be explained by the existence of a main underlying moult sequence (i.e. that of the adult complete moult) that generates different 'observed' patterns of feather replacement when feathers that will be retained are, consequently, omitted from the sequence (Fig. 6). This would also explain why the progression of the tertial moult in relation to that of the rectrices is similar to the pattern observed in adults, irrespective of the number of primaries that are to be replaced.

The fact that the most extensive partial moults in Goldfinches closely resemble a complete moult raises the question of exactly where the true limit between these two types of moults lies. It is important to bear in mind that some first-year birds are known to undertake a complete adult-like moult, while others replace all their plumage except for a few primary coverts (Gargallo and Clarabuch 1995). Generally, Goldfinches undertaking a partial postjuvenile moult involving all their flight feathers can be separated from those undertaking a complete moult by the sequence of replacement of the primary coverts (apparently only replaced simultaneously with their corresponding primary in complete moults; Jenni and Winkler 1994; Gargallo and Clarabuch 1995). However, given the findings reported here, this sequence of replacement of the primary coverts may also reflect a further approach to the complete adult moult sequence in birds undertaking still more extensive partial moults. Therefore, the question whether the complete postjuvenile moult in the Goldfinch is simply the end of a continuum of possible moult patterns or whether it represents a qualitatively distinct moult process remains unanswered.

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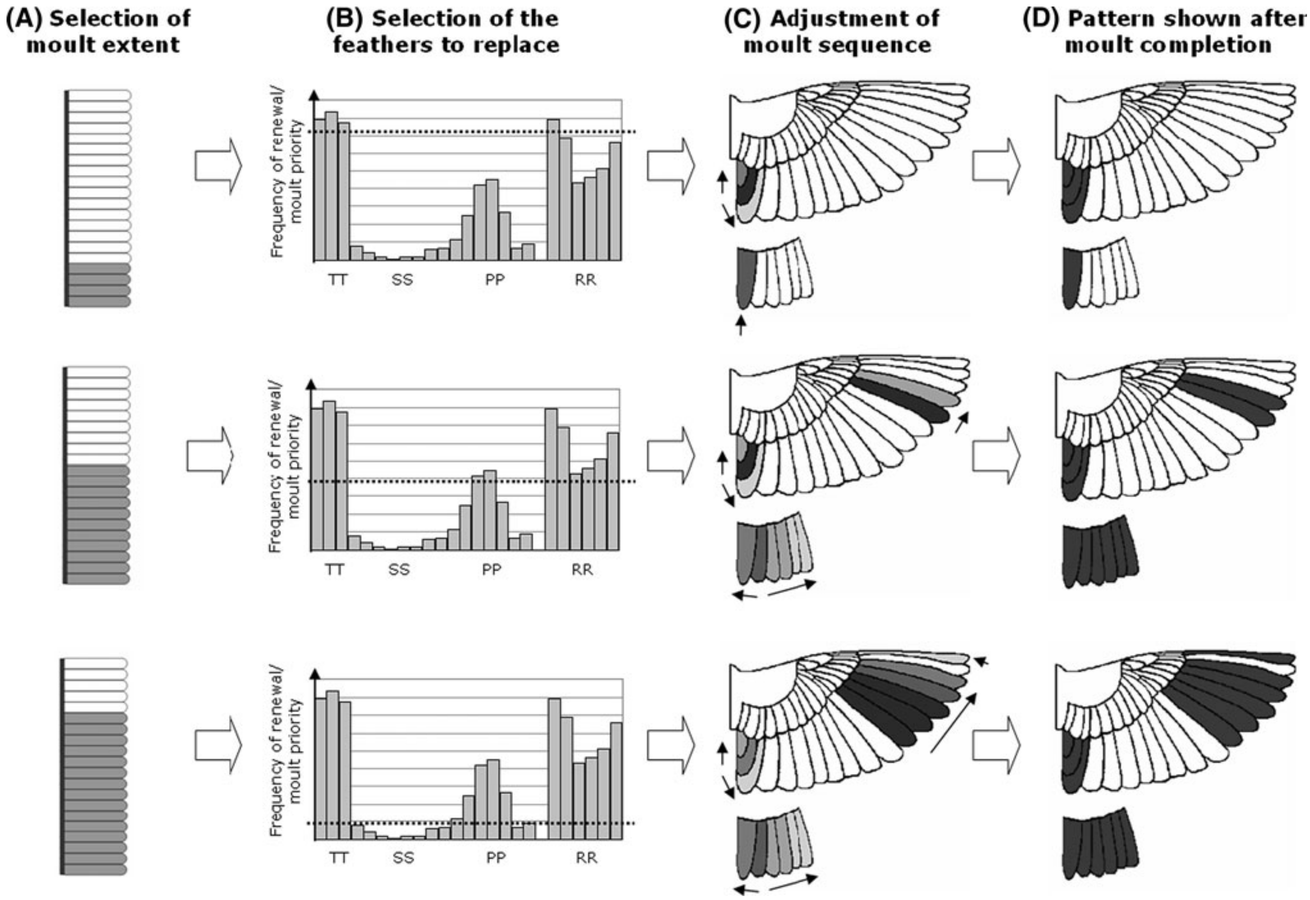

Fig. 6 Schema of the system of feather selection and replacement followed by first-year Goldfinches (three different hypothetical birds moulting to different extents are shown). Prior to or at the beginning of moult, birds fix the extent to which they will moult (*vertical line*; **a**). Birds select which particular feathers will be replaced according to an order of moult priorities: the higher the moult extent to be undertaken, the greater number of feathers from the list of priorities that are added to the selection (**b**; note that the higher the renewal frequency of a feather, the higher is its position in the order of moult priorities). Birds moult following a sequence that is adjusted to the number and particular feathers selected to be replaced (**c**; *arrows* show moult focus and waves; feather darkness reflects the relative time of shedding: darker feathers are shed earlier). After moult completion, moult patterns (**d**) match those expected to occur according to the order of moult priorities even if this order (**b**) differs markedly from the order in which feathers are actively replaced (**c**)

The system of feather selection and replacement described here in the postjuvenile moult of the Goldfinch (Fig. 6) could also be applicable to other species undertaking extensive partial moults. A descendant primary moult with a variable focus that moves inwards as more primaries are replaced has also been suggested for the partial first prenuptial moult in the Woodchat Shrike *Lanius senator* (Bensh et al. 1991) and the Eastern Orphean Warbler *Sylvia* [*h.*] *cassirostris* (Shirihai et al. 2001), as well as for the postjuvenile moult of the Greenfinch, the Siskin *Carduelis spinus*, the Linnet and the Crossbill *Loxia curvirostra* (unpublished data; Jenni and Winkler 1994). Moreover, a descendant primary moult seems to be the norm in the majority of species undertaking extensive partial moults (cf. Miller 1928; Michener and Michener 1940; Williamson 1968; Gauci and Sultana 1979; Gwinner and Biebach 1977; Rohwer 1986; Bensh et al. 1991; Cramp 1992; Jenni and Winkler 1994; Shirihai et al. 2001). However, it still remains to be seen to what extent the findings detailed here for the Goldfinch also apply to the partial moults of much more limited extent.

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References

Bensch S, Hasselquist D, Hedenström A, Ottosson U (1991) Rapid moult among palaearctic passerines in West Africa—an adaptation to the oncoming dry season? Ibis 133:47–52

Berthold P, Querner U (1982) On the control of suspended moult in an European trans-Saharan migrant, the orphean warbler. J Yamashina Inst Ornithol 14:157–165

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Bojarinova JG, Lehikoinen E, Eeva T (1999) Dependence of postjuvenile moult on hatching date, condition and sex in the great tit. J Avian Biol 30:437–446

Cramp S (ed) (1992) The birds of the western Palearctic, vol 6. Oxford University Press, London

Cramp S, Perrins CM (eds) (1994) The birds of the western Palearctic, vol 8. Oxford University Press, London

de la Cruz F, de Lope F, Sanchez JM (1992) Postjuvenile moult in the azure-winged magpie *Cyanopica cyanea cooki*. Ringing Migr 13:27–35

Dixit AS, Singh NS (2011) Photoperiod as a proximate factor in control of seasonality in the subtropical male tree sparrow, *Passer montanus*. Front Zool 8:1. doi:10.1186/1742-9994-8-1

Dolnik VR, Gavrilov VM (1980) Photoperiodic control of the molt cycle in the chaffinch (*Fringilla coelebs*). Auk 97:50–62

Dwight KL (1900) The sequence of plumages and molts of the passerine birds of New York. Ann NY Acad Sci 13:73–360

Flinks H (1999) Muster, Intensität und zeitliche Aspekte der postjuvenilen Mauser beim Schwarzkehlchen (*Saxicola rubetra*). Vogelwarte 40:11–27

Gargallo G (1995) Further evidence for additional pre-nuptial moult in melodious warblers (*Hippolais polyglotta*). Die Vogelwarte 38:96–99

Gargallo G (1996) Evidence for partial prenuptial moult in adult and first-year penduline tits *Remiz pendulinus*. Bird Study 43:157–163

Gargallo G (1997) Ageing Cetti's warbler *Cettia cetti* by means of plumage characteristics. Ringing Migr 18:14–17

Gargallo G, Clarabuch O (1995) Extensive moult and ageing in six species of passerines. Ringing Migr 16:178–189

Gauci C, Sultana J (1979) Moult of the sardinian warbler. Il-Meril 20:1–13

Ginn HB, Melville DS (1983) Moult in birds. BTO guide 19. BTO, Tring

Gosler AG (1991) On the use of greater covert moult and pectoral muscle as measures of condition in passerines with data for the great tit *Parus major*. Bird Study 38:1–9

Gwinner E (1986) Circannual rhythms. Springer, Berlin

Gwinner E, Biebach H (1977) Endogene Kontrolle der Mauser und Zugdisposition bei südfinnischen und südfranzösischen Neuntötern *Lanius collurio*. Vogelwarte 29:56–63

Gwinner E, Neusser V (1985) Die Jungendmauser europäischer und afrikanischer Schwarzkehlchen *Saxicola torquata rubicola* and *auxillaris* sowie von F_1-Hybriden. J Ornithol 126:219–220

Gwinner E, Dittami J, Gwinner H (1983) Postjuvenile molt in East African and Central European stonechats *Saxicola torquata axillaris*, *S. t. rubicola* and its modification by photoperiod. Oecologia 60:66–70

Hedenström A (2003) Flying with holey wings. J Avian Biol 34:324–327

Helm B, Gwinner E (1999) Timing of postjuvenal molt in African (*Saxicola torquata axillaris*) and European (*Saxicola torquata rubicola*) stonechats: effects of genetic and environmental factors. Auk 116:589–603

Herremans M (1988) Postjuvenile moult, phenology and biometry of grey wagtails *Motacilla cinerea* migrating over central Belgium. Ringing Migr 9:103–116

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

Mester H, Prünte W (1982) Die "sektorale" postjuvenile Handschwingenmauser der Carduelinen in Südeuropa. J Ornithol 123:381–399

Michener H, Michener JR (1940) The moult of house finches of the Pasadena region. Condor 42:140–153

Middleton ALA (1969) The moult of the European goldfinch near Melbourne Victoria. Emu 69:145–154

Miller AH (1928) The molts of the loggerhead shrike *Lanius ludovicianus* Linnaeus. Univ Calif Publ Zool 30:393–417

Murphy ME, King JR, Lu J (1988) Malnutrition during the postnuptial molt of white-crowned sparrows: feather growth and quality. Can J Zool 6:1403–1413

Newton I (1964) The moult of the bullfinch *Pyrrhula pyrrhula*. Ibis 108:41–67

Noordhuis R (1989) Pratonen in slagpenrui: ecofysiologische aanpassinngen. Limosa 62:35–45

Norman SC (1991) Suspended split-moult systems—an alternative explanation for some species of Palearctic migrants. Ringing Migr 12:135–138

Noskov GA, Rymkevich TA (1985) Photoperiodic control of postjuvenile and postnuptial molts in passeriformes. Int Ornithol Congr 18:930–934

Pap PL, Barta Z, Tökölyi J, Vágási CI (2007) Increase of feather quality during moult: a possible implication of feather deformities in the evolution of partial moult in the great tit *Parus major*. J Avian Biol 38:471–478

Payne RB (1972) Mechanisms and control of molt. In: King JR, Farner DS (eds) Avian biology, vol 2. Academic, New York, pp 104–155

Pilastro A, Tasinazzo S, Guzzon C (1996) Extension of post-juvenile moult and ageing of the Cetti's warbler *Cettia cetti* in Northern Italy. Avocetta 20:107–112

Pyle P (1997) Identification guide to North American birds. Part I. Slate Creek, Bolinas

Richter A (1972) Zum Umfang der Jungendmauser am Flügel der Amsel *Turdus merula*. Ornithol Beob 69:1–16

Rohwer S (1986) A previously unknown plumage of first-year indigo buntings and theories of delayed plumage maturation. Auk 103:281–292

Rohwer S (2008) A primer on summarizing molt data for flight feathers. Condor 110:799–806

Rohwer S, Ricklefs RE, Rohwer VG, Copple MM (2009) Allometry of the duration of flight feather molt in birds. PLoS Biol 7:e10000132. doi:10.1371/journal.pbio.1000132

Rymkevich TA (1990) Moult of passerines of northwestern USSR. Izd-vo Leningradskogo Universiteta, Leningrad (in Russian)

Rymkevich TA, Bojarinova JG (1996) Variation in the extent of postjuvenile moult in the great tit near Lake Lagoda (Russia). Bird Study 43:47–59

Senar JC (2006) Bird colors as intrasexual signals of aggression and dominance. In: Hill GE, McGraw KJ (eds) Bird coloration, volume 2: function and evolution. Harvard University Press, Cambridge, pp 87–136

Senar JC, Copete JL, Martín AJ (1998) Behavioural and morphological correlates of variation in the extent of post-juvenile moult in the siskin *Carduelis spinus*. Ibis 140:661–669

Shirihai H, Gargallo G, Helbig AJ (2001) Sylvia warblers. Identification, taxonomy and phylogeny of the genus *Sylvia*. Black, London

Sokal RR, Rohlf FJ (1995) Biometry, 3rd edn. Freeman, San Francisco

Swaddle JP, Williams EV, Rayner MV (1999) The effect of simulated flight feather moult on escape take-off performance in starlings. J Avian Biol 30:351–358

Underhill LG, Zucchini W (1988) A model for avian primary moult. Ibis 130:358–372

Williams EV, Swaddle JP (2003) Moult, flight performance and wingbeat kinematics during take-off in European starlings *Sturnus vulgaris*. J Avian Biol 34:371–378

Williamson K (1968) Identification for ringers. The genus *Sylvia.* BTO field guide 9, 2nd edn. BTO, Tring

Yuri T, Rohwer S (1997) Molt and migration in the northern rough-winged swallow. Auk 114:249–262