Moult in Common Whitethroat in a confined breeding population in relation to date, sex, breeding history and weight

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(*Med et dansk resumé: Tornsangerens fældning i en afgrænset ynglebestand i forhold til dato, køn, ynglehistorik og vægt*)

Abstract The moulting process of Common Whitethroat *Curruca communis* has been widely reported but not previously for a confined and well documented breeding population. This study demonstrates that the onset, progress, and termination of the cycle of moulting of remiges (flight feathers) and rectrices (tail feathers) differ significantly according to sex, breeding performance and weight. The relationship between post-nuptial moulting and autumn migration departure is also described. The fieldwork was carried out in the 1976 breeding season on the isle of Hjelm, Denmark. Birds raising one clutch began their moult earlier than birds producing two clutches, and males started moulting earlier than females. In pairs with only one clutch, both sexes moulted at the same rate and following parallel lines. However, in pairs with two clutches, females moulted at a significantly slower rate than males and exhibited a higher degree of suspended moulting. In fact, the renewal of secondaries was incomplete in 72% of the whole population and with females on the lead. Both sexes achieved a significant increase in weight (males 23.8% and females 17.8%) during the moult. Thus, food scarcity can hardly have been of any importance up to the start of autumn migration, which generally began when renewal of primaries and tail feathers was completed, or even a day or two before, and without waiting for moulting of secondaries to be completed. The results underline that an appropriate start of autumn migration is mandatory but on the other hand the benefits of a completed moult should not be disregarded. An early start may be crucial to facilitate the circumvention or crossing of the Sahara Desert, while fresh remiges could play a role in overall survival on the 5000 km journey to Africa.

Introduction

Common Whitethroats *Curruca communis* of the nominate race are long-distance migrants breeding in the west, north and central parts of continental Europe and in the British Isles, and wintering in bush savannah to the south of the Sahel zone in Africa at approximately 12-18° N (Moreau 1972, Cramp & Brooks 1992, Zwarts *et al.* 2023).

Before leaving the breeding grounds, Whitethroats exhibit a wide array of different moulting strategies with respect to remiges and rectrices. The moulting procedure of Whitethroats is well described from several European studies undertaken at bird observatories (Williamson 1968, Pimm 1973, Hall & Fransson 2001, Remisiewicz *et al.* 2019, Jenni & Winkler 2020). However, the process within a confined breeding community of known identity has previously not been published. Bird observatories handle migrating birds from larger but rarely well-defined geographical areas where significant temporal and geographical differences in moulting patterns can occur. To some degree the same uncertainty must characterize analyses of moult cards from nationwide programs (Snow 1965, Haukioja 1971, Ginn & Melville 1983, de la Hera *et al.* 2009).

A full understanding of the moulting cycle of migrating passerines requires a deep knowledge of individual life histories. The absence of population studies with known individual life stories leads to ignorance of sex and breeding performance as determinants of initiation, performance and completion of the moulting cycle, and hence erroneous conclusions.

The onset of moulting in passerines such as Whitethroat occurs in response to a mixture of hormonal changes caused by environmental variables such as photoperiod and temperature but also by an endogenous annual rhythmicity (Gwinner 1977). Again, these variables have not yet been tested against sex and life history of Whitethroats.

Whitethroats stay at their breeding grounds in Northern Europe for less than 140 days, with the moulting period spanning 59 days (Shirihai *et al.* 2001, own obs.). This leaves only about 80 days for breeding activities. A full breeding cycle of two clutches, with nest building and mating, egg laying, incubation and rearing of young, requires 10+5+10+25 = 50 days for the first clutch and slightly less at 40 days for the second clutch (no mating games needed) (Hansen 2023). This very tight timetable exerts a great deal of pressure on the individual bird and necessitates compromises between rearing the last or late clutches and starting moulting. Birds that raise two clutches or just breed late run the risk of having too little time for a complete moult at the breeding grounds before departure and may react with several shortcuts compared to the full moulting process.

Offsetting moulting of several flight feathers before traveling to Africa may be necessary to comply with the timetable. On the other hand, the success of the approximately 5000 km journey, which includes circumvention of or flying over the Sahel region, may depend on fresh plumage, especially in terms of perfect remiges and rectrices. But the advantage of a fully renewed plumage may be lost if the price is a delayed departure from the breeding grounds. A modest but quite consistent difference in the sex ratio of spring populations of breeding warblers may perhaps be attributed to these differences in moulting success and thus their effects on the evolutionary survival of the two sexes. The question about when and where moulting is completed in birds with suspended moulting still needs to be addressed.

Study site

Situated in the Kattegat 6 km off the mainland of Jutland, the island Hjelm (56°8′0″N; 10°48′10″E) consists of a moraine hill of 25 ha reaching up to 45 m above sea level and surrounded by a 37 ha flat marine foreshore with dry open grasslands and beaches. In 1975-1976, when the present study took place, the hilly plateau was a very suitable breeding ground for Whitethroat, while the bare lowlands were unsuitable as nesting habitat.

The isolation of the island has prevented random intrusions of breeding birds from neighbouring areas, and the study area of 25 ha supported a sufficiently large population (165 birds forming 72 breeding pairs) to offer enough data for statistical analyses. Furthermore, the study area was not too large to be carefully examined every day so that all breeding pairs and their nests were under permanent monitoring.

The island no longer had any human inhabitants, so there were no disturbing or destructive activities – except for our own research activities. After 125 years of farming, the plough was parked in 1965, and the farmer departed for the mainland. Since then, wild flora and fauna had spread across the 15 ha of former fields. In 1975-1976 regrowth was still in an early phase, generating perfect habitats for a very large population of Whitethroats. Since then, regrowth has continued, and the hilly plateau became covered by dense tree growth which to-day is unsuitable as a breeding habitat for Whitethroat (Hansen 2021).

Lack of predators meant that the breeding population on Hjelm during 1975-1976 was characterized by stability, site fidelity and firm relationships between males and females in solid breeding pairs, in stark contrast to other descriptions of Whitethroat communities (Siefke 1962, Diesselhorst 1968, Emmrich 1971, Payevsky 1999). During the 1976 season only two individuals and one egg clutch were lost to some avian predators. This contrasts sharply with predation as the main cause behind 51.8% failed breeding attempts in British Whitethroats in a study based on 3176 mapped nests (Mason 1976). The total absence of any four-legged predators on the island may explain this marked difference.

Methods

The present study took place during the full breeding season 24 April - 17 September 1976 and was based on two main methods of data collection:

1. 10 hours daily systematic netting of passerines for ringing and identifying all breeding individuals and collecting morphometric data, changes in weight and state of moulting.

2. Daily identification rounds for mapping colour ringed Whitethroats in the field and actively searching for their nests.

The most important prerequisites for a successful in-depth field study of population dynamics were created following 1970 when standardized ringing of migratory (and breeding) birds, especially in the spring months, was established. The ringing effort was consistent and systematic, with two to three experienced bird ringers working 10 hours daily catching birds using 30-35 stationary mist nets evenly distributed over the 25 ha morainic hill, including the former fields (15 ha) and the overgrown slopes (10 ha). Only inclement weather was allowed to disrupt this routine.

Most local breeding birds were tagged during spring with coloured plastic rings with unique codes, and over the years a unique insight was obtained into the population's age and sex distribution, site fidelity and territoriality. Due to the constant ringing effort all breeding birds could be identified and all nests found in 1976 (Hansen 2023) so that it could be documented that Hjelm supported an extraordinarily dense breeding population of Whitethroats.

During the period 1 July to 17 September 1976 all adult Whitethroats caught were examined for state of moulting. The same scheme and the same scoring system as originally designed by the British Trust for Ornithology (Snow 1965, 1967) were used with the exception that we focused on remiges and rectrices and only made notes of other features. In addition to collecting these data we weighed the birds each time they were netted, and notes were taken on their general condition.

Materials

The material includes all Whitethroat individuals from a confined local breeding population, where sex, breeding history and weight of all individuals were known.

Sexing during handling of mist-netted birds was carried out in accordance with the criteria of Svensson (1975) and in females was confirmed largely by the presence or not of incubation patches in different stages (only females develop this). Sex was also repeatedly verified by the daily field observations of birds singing (only males sing), nest-building, brooding, and feeding.

In total, 149 moult cards were completed comprising 63 cards of local adult males plus one foreign adult male and 85 cards of local adult females. Since some individuals were recaptured and analysed more than once, the material includes only 40 individual males and 53 individual females, i.e. 93 individuals from the breeding population, which during the 1976 season included 165 ringed and colour marked individuals, of which just over half (57%) were examined for state of moulting.

All data are given in detail in Appendix 1 (and appear from Fig. 2).

Throughout this paper, the terms primary score, secondary score and tail score are used for the state of moulting of remiges and rectrices. The scores were obtained as the sums of the individual feather points with each feather being scored as follows: 0 points for an old feather; 1 point for a missing feather or one in pin; 2, 3, 4 points for feathers 1/3, 2/3 and 3/3 of their normal length, and 5 points for a new feather, once its waxy sheath had been lost. This means that the maximum score is 50 for primaries, 30 for secondaries, and 30 for tail feathers plus 15 points for the three innermost secondaries, also called tertials; all these maximum scores when combined add up to a sum of 125 points for a completed moult.

When the 149 moult cards from the period 1 July - 17 September are distributed on a 6-step scale, where each step covers 20 points (note, however, that group 6 includes 25 points), the overview of the total material given in Tab. 1 is obtained. As the table shows, the frequency of recaptures throughout the moulting period changed quite drastically when the moult scores began increasing rapidly. Three reasons can be given for the sharp drop in recaptures after the first group and the increase in recaptures again from the fifth group.

Reason #1: As soon as a bird sheds the first innermost primary, its ability to fly is significantly reduced. This results in low mobility and thus a lower chance of being netted and examined in the stationary mist nets (Haukioja 1971).

Tab. 1. Distribution of the 149 moult cards according to moult score. See explanations in the text.
Fordelingen af de 149 fældeskemaer i forhold til fældningsgrad. Se forklaringer i teksten.

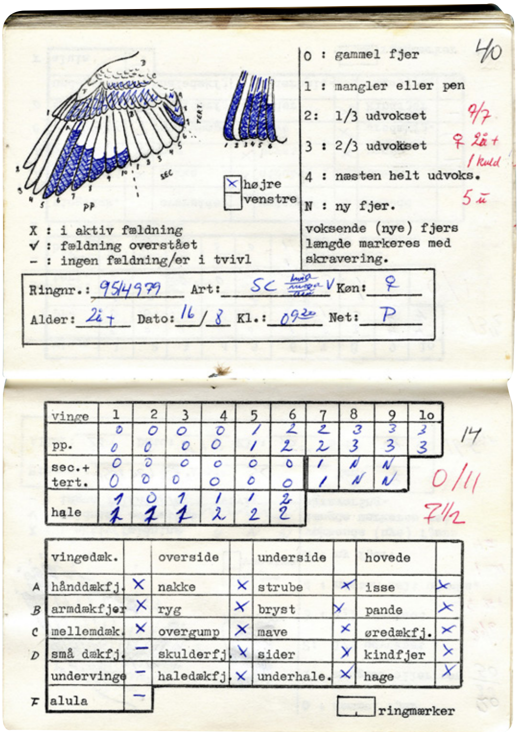
Group	Moult score	Number of moult cards
1	1-19	61*
2	20-39	15
3	40-59	7
4	60-79	3
5	80-99	11
6	100-125	8

* 44 analyses with 0 points are omitted

For example, female ZM 9514979, analysed on 16 August, was barely able to fly with a score of only 14 out of 50 points for the primaries, which constitute critical feather loss, and with a total score of 32.5 points out of a possible 125. On the other hand, all secondaries were still old, while the rectrices were severely reduced with a score of just 7.5. As seen from Fig. 1, which shows this individual's score card, the bird only had four functional primaries out of 10. Even with all old secondaries intact, this did not mean that the bird avoided being recorded by the ringer as "almost unable to fly due to advanced moulting". In all other regards, the bird was in excellent condition weighing a healthy 15.3 g.

Reason #2: When the breeding season is over, the activity of the adult breeding birds decreases, because they no longer must provide food for 3-6 begging youngsters but just support themselves. This behaviour change reduces the chances of being trapped and scored. For the breeding population, feeding of offspring culminated on 2 July (Hansen 2023), when half of all young had left their nests. After 15 days of dependence on the parent birds, the juveniles were self-sufficient.

Reason #3: The third factor could be migration away from the island before moulting is completed. Checking several Hjelm-birds with clearly suspended moulting suggests that this occurs regularly. As can be seen from Appendix 2 Tab. A1, the majority (72%) of the examined individuals stopped moulting before it was completed. Adult migrants apparently did not occur on the island in 1976 until the first and only adult Whitethroat of foreign origin was caught as late as 14 September. This individual was a male with a moulting score of 118 points: on both wings the third inner secondary had not been renewed, while the two innermost secondaries were only almost fully grown. Hence, this foreign bird had started out for Africa in a state of suspended moult.



40

0 : gammel fjer
1 : mangler eller pen
2: 1/3 udvokset 9/7
3 : 2/3 udvokset ♀ 2år+
1 kuld
4 : næsten helt udvoks.
N : ny fjer. 5 u

☒ højre
☐ venstre

X : i aktiv fældning
√ : fældning overstået
- : ingen fældning/er i tvivl

voksende (nye) fjers længde markeres med skravering.

Ringnr.: 9514979 Art: SC [illegible] V Køn: ♀
Alder: 2i+ Dato: 16/8 Kl.: 09²⁰ Net: P

vinge	1	2	3	4	5	6	7	8	9	1o	
pp.	0 0	0 0	0 0	0 0	1 1	2 2	2 2	3 3	3 3	3 3	14
sec.+ tert.	0 0	0 0	0 0	0 0	0 0	0 0	1 1	N N	N N		0/11
hale	1 1	0 1	1 1	1 2	1 2	2 2					7½

	vingedæk.		overside		underside		hovede	
A	hånddækfj.	X	nakke	X	strube	X	isse	X
B	armdækfjer	X	ryg	X	bryst	X	pande	X
C	mellemdæk.	X	overgump	X	mave	X	øredækfj.	X
D	små dækfj.	–	skulderfj.	X	sider	X	kindfjer	X
	undervinge	–	haledækfj.	X	underhale.	X	hage	X
F	alula	–						

☐ ringmærker

Fig. 1. Moult chart where the progress of moulting for remiges and rectrices is described on a point scale from 0 to 5 for each feather with 0-50 points for primaries, 0-45 points for secondaries and tertiaries, and 0-30 points for the tail (Snow 1967). The total score for a complete renewal of these vital parts of the plumage adds up to 125 points.
Fældningsskema, hvor fældningen af hånd- og armsvingfjer beskrives på en punktskala fra 0 til 5 for hver fjer med samlet 0-50 point for håndsvingfjer, 0-45 point for armsvingfjer og tertialer og 0-30 point for halen. Den samlede score for en fuldstændig fornyelse af disse vitale dele af fjerdragten giver 125 points.

For the sake of easy overview and comparability, a time code is used that covers the general period of the Whitethroat's stay in Denmark. Instead of ordinary dates, day 1 means 1 May and so on. However, where deemed helpful, this time code is translated to the real date.

When all data from Hjelm 1976 are presented graphically, the figure resembles the traditional picture of the moulting process (Fig. 2), where measurements have been collected from migratory birds with

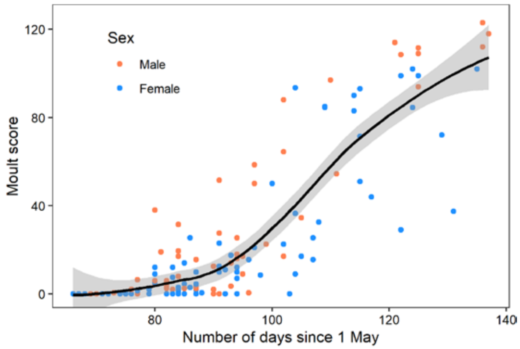


Fig. 2. All records of Whitethroats during the moulting period with moult score plotted against number of days since 1 May. N = 149.
Alle analyser af Tornsangere i fældningsperioden med fældepoint plottet mod antal døgn siden 1. maj.

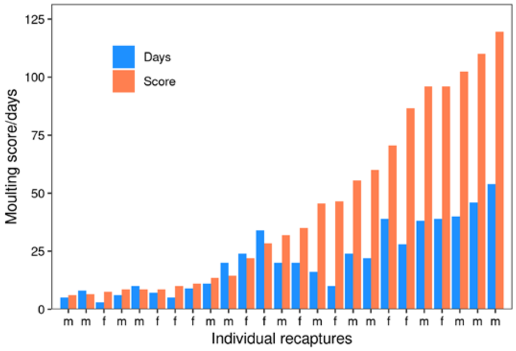


Fig. 3. The individual moulting process of 14 males (m) and 11 females (f) which in 22 cases were caught twice in active moult and in three cases were caught three times. Some of these data allow the true moulting period to be extrapolated with greater accuracy than previously.
Den individuelle fældningsproces for 14 hanner (m) og 11 hunner (f), som i 22 tilfælde blev fanget to gange i aktiv fældning og i tre tilfælde tre gange. Nogle af disse data gør det muligt at ekstrapolere den sande fældningsperiode med større nøjagtighed end tidligere.

an unknown life story and arriving from an unknown geographical area (e.g., Fig. 6 in Williamson 1968). This is how virtually all researchers so far have described the process, but with no breeding history established the result is a blurred picture of the rather flexible moulting strategies used by most Whitethroats.

Results with comments

The first Whitethroat from the local population in active moulting was captured on 12 July (day 73). It was an unpaired male that had shed the innermost primary feather on the right wing, resulting in a score of 0.5 points. The last individual bird from the breeding population was caught and analysed on 13 September (day 136), i.e. 62 days later. It was also a male but with a score of 123 out of 125 possible points. Its primary feathers lacked just one point, while secondary feathers and tail feathers still lacked 0.5 points each.

Moulting in the breeding population as such began around 14 July (day 75) and was completed around 11 September (day 134, Fig. 2), and thus extended over 59 days. Fig. 2 also shows that no individuals from the breeding population were recaptured with a fully completed moult, suggesting that the birds leave the island immediately or even before all their flight feathers have been renewed.

Fig. 2 contains no statistical analysis as such, but simply demonstrates the 'average' progress for the population (the black line) with 95% confidence intervals around the black line (the grey field). The sigmoid curve thus represents the trend for all data points over time. The method for representing this average progress is a LOESS smother (locally estimated scatterplot smoothing).

As an example of possible extrapolation of the time consumption of the moult, the almost completely moulted male (far right in Fig. 3) had spent 54 days renewing its flight feathers from a score of 3.5 points to 119.5 points out of the possible 125. A simple extrapolation shows that the total time consumption of this individual for a complete moult would be 57 days. When you consider the five individuals to the far right as a group and calculate their individual time consumption in the same way as above, the result is 49-57 days with an average of 52 days.

Moving further to the left, the variation between individuals immediately increases and makes simple calculations unreliable. This is partly because moulting as a biological process only rarely follows straight lines, and partly because the strategy of not renewing all flight feathers (suspended moult) makes it impossible to calculate the overall time consumption of a full moulting circle when individuals are still in the early stages.

Differences in the moulting process between males and females

The first striking result of our analyses is that males

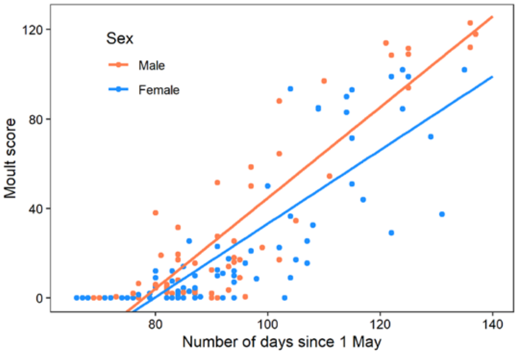


Fig. 4. Moulting rates of males and females, respectively. N = 149.
Fældningshastigheden for hhv. hanner og hunner.

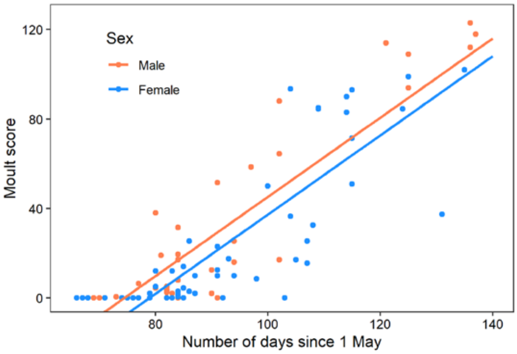


Fig. 5. One-clutch males (40) and females (54) moult at the same rate, but females moult a few days later than males.
Hanner (40) og hunner (54) med et kuld fælder i samme hastighed men med nogle døgns forskydning.

generally began moulting four days earlier than females and completed a full renewal 18 days faster, as shown in Fig. 4. There is a significant effect of both time ($P < 0.0001$), sex ($P = 0.0138$) and of the interaction between time and sex ($P = 0.0173$), implying that moulting rate does differ between sexes. The total number of observations was 149, divided into 63 males and 85 females from the breeding stock (plus one foreign male), although with several repeated catches. The statistical model is therefore a linear mixed effect model with bird ID as a random effect to account for the fact that some individuals had been measured more than once. This model also accounts for individuals with particularly high or low moulting rates due to factors other than time.

The formula, where y is the moulting score and x is the date, for the males is $y = 2.03 * x +/- 158.04$, which gives a start of moulting on 17 July (day 78) and completion on 16 September (day 139), i.e., a total time span of 61 days. For females, the formula is $y = 1.64 * x +/- 131.11$, resulting in start of moulting on 19 July (day 80) and with a 'theoretical' end date as late as 3 October (day 156), resulting in a total 'theoretical' time span of 79 days.

The use of the label 'theoretical' signals that the real progress is less than what the mathematical calculation dictates because some males and a larger proportion of females do not complete a full moult before starting out on autumn migration.

Our data includes measurements from three unpaired males. However, no tendency towards an earlier start of moulting was seen in these idlers. All three individuals followed the average course.

Differences between males and females with one or two clutches

A simple linear regression test of moulting as a function of time and sex shows a significant effect of both time ($P < 0.0001$) and sex ($P = 0.040$), whereas the interaction between the sexes is not significant ($P = 0.088$) as shown by the parallel lines in Fig. 5.

Males with one clutch began moulting significantly earlier (four days) than females with one clutch, and females also completed later (five days), while the moulting rate (time consumption) was largely the same for both sexes. The number of measurements was 94 (40 males and 54 females), and the formulas for the two lines for males are $y = 1.77 * x +/- 131.71$, which gives a start on 14 July (day 75) and completion on 22 September (day 145), a total moulting period of 70 days. The equation for the females is $y = 1.77 * x +/- 139.62$ and gives a starting date on 18 July (day 79) and completion date on 27 September (day 150), i.e. a total moulting periode of 71 days.

Both processes are obviously influenced by different degrees of suspended moult. See also the overview in Appendix 2 Tab. A2.

Two-clutch males and females showed significant differences in moult scores with females lagging far behind males when moulting was tested as a function of time and sex using a simple linear regression (Fig. 6). We obtained a significant effect of time ($P < 0.0001$) but not of sex alone ($P = 0.12$), whereas the interaction between time and sex was significant ($P = 0.005$).

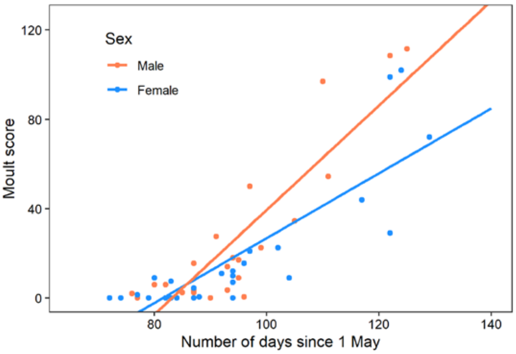


Fig. 6. Two-clutch males (24) and females (31) moult at different rates.
Hanner (24) og hunner (31) med to kuld fælder med forskellig hastighed.

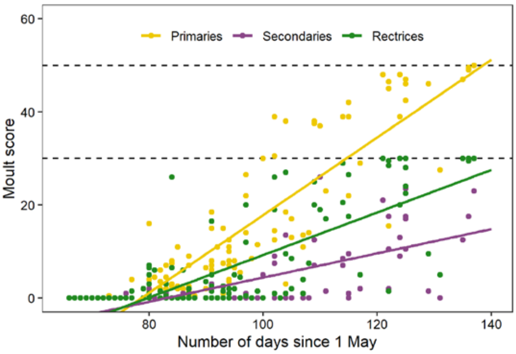


Fig. 7. Completion of moulting of the three groups of remiges. The two dashed horizontal lines indicate the full moult score of 30 for secondaries and 50 for primaries. N = 149.
Fældehastighed for de tre forskellige fjergrupper. De stiplede vandrette linjer angiver den fulde fældningsscore på 30 for armsvingfjer og 50 for håndsvingfjer.

The moulting rates were significantly different between the sexes (with males moulting faster than females). Note that due to the interaction, it may be difficult to tell whether there was a difference in moulting score (but not rate) between the sexes when interaction is present.

The total number of measurements includes 24 males and 31 females with two clutches. The formula for the regression line for males is y = 2.34 * x +/- 194.27 and gives the starting date as 22 July (day 83) with completion on 14 September (day 137), i.e., a total moulting period of 54 days. The formula for females is y = 1.45 * x +/- 118.26 and gives the starting date as 21 July (day 82), i.e., nearly the same date as the males but with 'theoretical' completion as late as day 168 (15 October), i.e., after 86 days.

Moult score of remiges and rectrices versus time

Among passerines it is a widespread principle that adult birds carry out a complete moult on the breeding grounds before autumn migration (Jenni & Winkler 2020), and that moulting begins with the renewal of the 10 primaries from inside and out. Moulting of the tail feathers begin when 3-5 primaries are actively being renewed, and the secondaries will follow when 4-7 primaries are moulting (Svensson 1975). When all remiges and rectrices are renewed, autumn migration can begin. While this may be the general pattern of passerines, it is, however, only exceptionally followed by Whitethroats (Pimm 1973, Hall & Fransson 2001, Jenni & Winkler 2020), a deviation also confirmed by the present study.

First, differences in moulting rate (time) and moulting scores (points) for the three different groups of flight feathers in the entire population as a function of time were tested (Fig. 7). The model is a linear mixed effect model with bird ID as random effect, which takes into consideration that some individuals have been measured more than once. This model also accounts for individuals with particularly high or low moulting rates due to factors other than time. There is a significant effect of time (P < 0.001), group of feathers (P < 0.001) and interaction between group of feathers and time (P < 0.001). This means that the moulting rate (score over time) differs for primaries, secondaries and rectrices.

The formula for primaries is y = 0.83 * x +/- 65.66, which gives a starting date 19 July (day 80) with completion 16 September (day 139). The renewal of the 10 primaries of both wings thus with few deviations took place for the population in 58 days.

The regression line for secondaries has the formula y = 0.26 * x +/- 21.58. This gave a significantly later starting date as 24 July (day 85) and a 'theoretical' completion as late as 14 November (day 198). This adds up to a moulting period of 113 days, which is obviously nonsense. However, the explanation is that all six secondaries are very often not renewed before the autumn migration.

Moulting of tail feathers followed the formula y = 0.46 * x +/- 36.42 and began at the time when the first primaries were dropped on 19 July (day 80). In

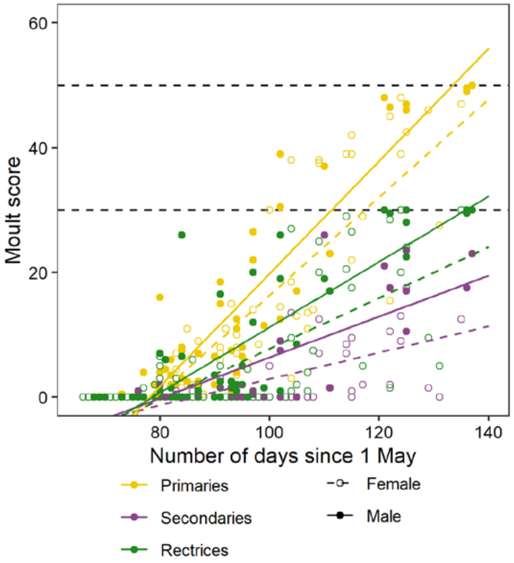


Fig. 8. Moult scores of all remiges separated between males (solid lines) and females (dashed lines) based on the same data as Fig. 7. The two dashed horizontal lines indicate the full moult score of 30 for secondaries and 50 for primaries.
Fældehastighed for alle fjergrupper fordelt mellem hanner (fuldt optrukne linjer) og hunner (stiplede linjer) baseret på de samme data som i Fig. 7. Fældehastighed for de tre forskellige fjergrupper. De stiplede vandrette linjer angiver den fulde fældningsscore på 30 for armsvingfjer og 50 for håndsvingfjer.

contrast to secondaries, renewal of all tail feathers took place within almost 100% of the population and was completed on 21 September (day 144). The full renewal took 64 days.

The conclusion is that primaries and rectrices are replaced almost completely and within almost the same period. In contrast, the moulting of secondaries is generally incomplete and begins significantly later than primaries and rectrices and in most individuals is interrupted before all feathers have been renewed.

Moulting score for all remiges in relation to sex and date
Comparison of all three groups of remiges in terms of sex (Fig. 8) shows that females (dashed lines) lag behind males when it comes to finishing but not with regard to starting date of the moult. There is a significant effect of time ($P < 0.0001$), of feather groups (primary, secondary, rectrices; $P < 0.0001$), sex ($P = 0.0104$), interaction between time and group ($P < 0.0001$), and interaction between time and sex ($P = 0.0004$). Thus, there is a significant difference in rate of moulting for primary, secondary and rectrices (interaction between time and group) and in the rate of moulting for the two sexes (interaction between time and sex).

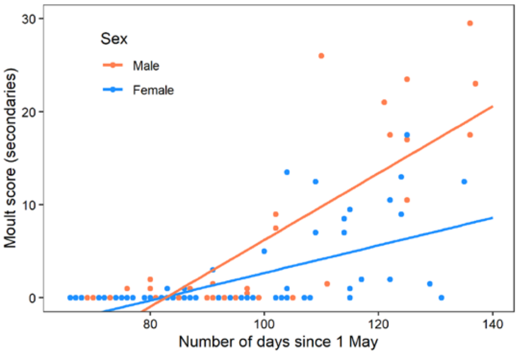


Fig. 9. The rate of suspended moult in the whole population. N = 149.
Forekomsten af individer med afbrudt fældning i hele bestanden.

At first sight, the analysis indicates that both males and females renewed primaries and rectrices in a parallel progress, however, with females starting one day later for primaries, on the same day for secondaries, and three days later for rectrices. On the other hand, the differences in rate of moulting of wzsecondaries were very large. Here, the two sexes showed significant deviations in moult score, especially for the females, with some individuals having an asymmetric moult of secondaries where one wing was lagging behind the other in score of points (Appendix 2 Tab. A2).

The rate of suspended moult in the whole population
Females showed a significantly higher incidence of suspended moult than males when the 25 birds with suspended moult on Hjelm was examined (Fig. 9). All these individuals were in such a state of advanced moulting of the primaries (scoring at least 30 points out of the possible 50) that the possible occurrence of suspended moult could be assessed with great certainty (all data in Appendix 1). Out of the 25 individuals, 17 (71%) had suspended moult with one or more feathers involved. This group consisted of six males (5 with 1 clutch and 1 with 2 clutches) versus 11 females (7 with 1 clutch and 4 with 2 clutches). The difference between the small numbers was not significant (Chi Square test with Yate's correction for small values gave 8/8.5) but do seem to show a trend.

The distribution of these 17 individuals between one and two clutches results in 12 against five (42%), which corresponds exactly with the distribution of the two types of clutches in the population in 1976 (Hansen 2023).

Both sexes appeared to use the strategy 'suspended moult', where one or more or even all secondaries were not renewed. This strategy must be seen as an adaptation to the tight timetable which applies especially to Africa-migrating birds that are raising two clutches (Jenni & Winkler 2020, Hansen 2023). The strategy of suspended moult makes it possible to leave 'on time' for the autumn migration and appears to be used to a much greater extent by females than males.

The formulas for the two lines in Fig. 9 are the same as presented in Fig. 8 and they emphasize the marked difference between the sexes. The moulting of secondaries for males started on day 82 and ended theoretically on day 171 (18 October), while the females started on day 89 but ended theoretically as late as day 230 (16 December).

Two individuals present strikingly low moulting scores compared to the general trends among the other birds and therefore should be highlighted. Both were females and were performing the latest breeding attempts of the season.

The first (ZM 9515234) was a female breeder with two successful clutches but with different males, where the last pulli hatched on 13 July and only became independent in early August. On 30 August (day 122), this female showed a rather poor moulting score of 15.5 points, pointing to a quite serious moulting delay. On the other hand, weighing 17.3 g documented that the female was in generally fine condition. However, with a primary score of only 15.5 out of 50 on day 122 and needing a total of 59 days for a complete primary moult, this individual would have to spend another 41 days on the island before she could fly south if renewal of all primaries was a 'must', and therefore this female would theoretically leave on day 163 at the earliest, i.e., 10 October.

The second individual was also a female (ZM 9589670) which had only produced one clutch at Hjelm but nevertheless appeared to be a very late breeder. The clutch consisted of three eggs, with the first egg laid 13 July and two more in the following two days. The clutch was supposed to hatch on 25 July but was abandoned before then. The first contact with this bird was made as late as 12 July, when it was captured and ringed in a state of egg laying with a highly swollen and vascularized brood patch and weighing a rather heavy 18.2 g. Next day it delivered the first of three eggs. It is unlikely that this bird had stayed on the island since spring without making a breeding attempt, or being observed or captured, suggesting that this female was a failed breeder from some mainland location. Such wandering behaviour after breeding failures has already been described as typical by Diesselhorst (1968).

This female was captured again and analysed on 8 September but was in quite an atypical condition with all six secondaries on both wings old and worn, but with primaries in advanced moult (27.5 points) and with six primaries renewed. However, the tail still consisted of old feathers except for a single new one on both sides. The weight was okay, although not strikingly so at 15.9 gram. With primaries scoring only 27.5 points out of a possible 50 on day 131 and with a total spell of 59 days needed for a complete moult of primaries, this individual would need another 32 days before she could fly south with all primaries renewed. Theoretically this female would therefore only leave on day 163 at the earliest, i.e., 10 October. These calculations naturally assume that all ten primaries must be renewed before departure, which is unlikely to have happened in this case. One or more primaries will have to be suspended to keep up with the timetable.

At first glance, it may seem striking that both females theoretically needed the same number of days to finish a complete moult, i.e., finishing 10 October, but this can only be explained as a sheer coincidence.

The moulting of primaries and rectrices, which are both important for flight ability, occurred quite synchronously for the two sexes, but with males starting 1-3 days earlier, whereas secondaries of both sexes were moulted with irregularity and with females deviating most significantly with a high occurrence of suspended moult.

The frequency of suspended moult in the Hjelm population

When the term 'theoretical' is used to signify the end date of moult completion for several females, it is to indicate that most of these individuals cannot have completed moulting in the breeding area before the onset of autumn migration. If this were the case, the

0 : gammel fjer
1 : mangler eller pen
2: 1/3 udvokset
3 : 2/3 udvokset
4 : næsten helt udvoks.
N : ny fjer.
voksende (nye) fjers længde markeres med skravering.

☐ højre
☐ venstre

X : i aktiv fældning
✓ : fældning overstået
– : ingen fældning/er i tvivl

20
30
50

28/6
♀ 2å+
1 kuld
4 u

Ringnr.: 9558569 ✓ Art: SC Køn: ♀
Alder: 2å+ Dato: 17/8 Kl.: 15 Net: V7 16.5gr

vinge	1	2	3	4	5	6	7	8	9	1o
pp.	1	2	3	3	4	N	N	N	N	N
sec.+ tert.	4 4	2 0	0 0	0 0	1 1	1 1	N N	N N	N N	
hale	3	4	4	4	N	N	✓			
	3	4	4	4	N	N	H			

38
7/15
25

Fig. 10. An illustrative example of an individual with suspended moult. Photo: KH.
Et illustrativt eksempel på et individ i afbrudt fældning.

full cycle of all females would not end before day 156 (3 October) and for females with two clutches, not until day 168 (15 October), as demonstrated earlier, but at that date the birds are on the Iberian Peninsula or well down in southern Europe (Pimm 1973, Mead & Watmough 2009).

The strategy is known as 'suspended moult' and can include both primaries and secondaries. It was described early in the literature (Pimm 1973) but never elucidated in relation either to sex or breeding history. On Gotland, Hall & Fransson (2001) investigated the relationship between moulting and departure time for the autumn migration of local Whitethroats, but again without regard to sex and breeding history. However, Hall & Fransson found that 77% of the individuals studied failed to renew one or more flight feathers, presumably to keep up with the migration timetable. Hall & Fransson formulated criteria for identifying those individuals with suspended moult as follows:

"We consider moult to have been interrupted if the shortest growing feather reached half of its full length without any of the remaining old feathers being shed. This means that it is possible to recognize a completed moult earlier in the moult circle than an interrupted moult. The frequency of interrupted moult estimated in this study may, therefore, be seen as a minimum value."

Based on this definition, moulting was assessed for 61 birds from Gotland, and the result was that 43 individuals (70.5%) had interrupted the moult of the secondaries and four (6.6%) had interrupted the moult of the primaries, together adding up to 77% of all birds examined. Four individuals exhibited simultaneously interrupted moult of both primaries and secondaries.

Based on the same definition, I have assessed those 25 birds on Hjelm which were in such a state of advanced moulting of primaries (at least 30 points out of the possible 50) that the extent of interrupted moult of the wing feathers could be assessed with great certainty (all data in Fig. 3). Out of the 25 individuals, 17 (71%) had suspended moult with one or more secondaries remaining. The result has already been communicated in detail in Fig. 9.

Female ZM 9558569 was checked on 17 August and represents an example of suspended moult, with a score of 38 points for primaries but only eight points for secondaries, which is also confirmed by the photo (Fig. 10) where the two old secondaries can be identified due to the light outer web. This female had delivered a clutch of four chicks, with the first egg laid on 15 June. At the check-up, she was in good condition, weighing 16.5 g.

Tests of weight as a function of time and sex for the entire period 1 July - 17 September were performed

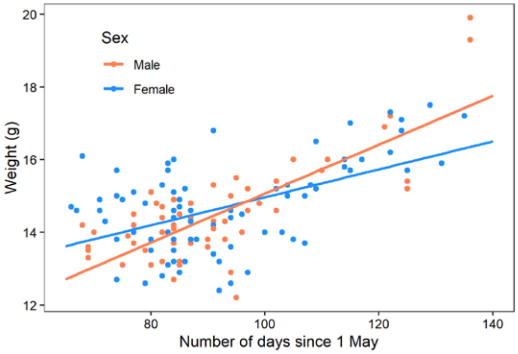


Fig. 11. Weight change as a function of number of days and sex. Moulting starts around day 73. N = 149.
Vægtændringer som funktion af døgn og køn. Fældningen begynder omkring dag 73.

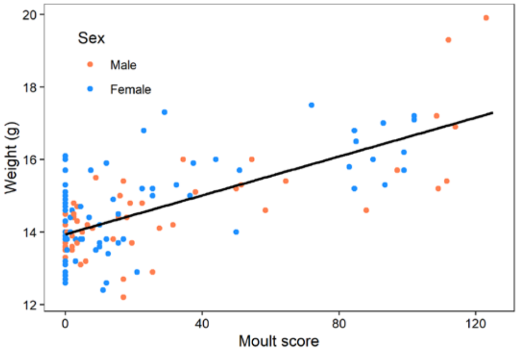


Fig. 12. The relationship between weight and moult score. N = 138.
Forholdet mellem vægt og fælderate.

using a linear mixed effect model with bird ID as random effect to account for the fact that some individuals have been measured more than once (Fig. 11). This model also accounts for individuals with particularly high or low weight changes due to factors other than time, which therefore do not affect the analysis. Start of moulting is defined as the date when the individual scores 0.5 moulting points.

Pimm (1973) believed that the frequency of suspended moult "is an adaptation to an unpredictable food supply". Murphy & King (1992) established the obvious fact that "renewal of flight feathers is an energy- and protein demanding process", as quoted by Waldenström & Ottosson (2002), who added on their own account that "variation in the extent of moult clearly implies that there seems to be a cost associated with the primary and secondary moult".

However, none of the cited researchers have provided data for either food supply or the birds' condition to substantiate their claims. The reason for not doing this is probably lack of any knowledge of the breeding history of their birds. Our data show that access to food hardly plays any limiting role because during the moulting period our birds achieved quite a significant increase in weight alongside the moulting process. Furthermore, Hall & Fransson (2001) provides a very telling example of rapid fuelling before departure, as an individual Whitethroat increased its body weight during the period 29 August to 3 September from about 17 g to 21.7 g at the same time as completing its moult.

In the period 1 July - 17 September males achieved an average weight increase (Fig. 11) of 4.3 g (23.8 %), raising from 13.8 g at the start of the moulting period to 18.1 g at the end. Females increased their weight in the same period by 3.1 g (17.8 %) from 14.3 g at the start to 17.4 g at the end. There is a significant effect of time ($P < 0.0001$) but not of sex alone ($P = 0.46$), and a significant interaction between time and sex ($P = 0.0043$).

This means that weight gain over time is different for males and females (higher for males than for females). The result will be the same even if the zero values for moulting are omitted. The number of observations is 138, with 58 males and 80 females. The formula for males is:

$y = 0.07 * x + 8.34$. Day 78 weight: 13.8; day 139 weight: 18.1; increase: 4.3 g (23.8%)

and for females:

$y = 0.04 * x + 11.12$. Day 80 weight: 14.3; day 156 weight: 17.4; increase: 3.1 g (17.8%)

The relationship between weight and moult score is the same for males as well as for females when we tested weight as a function of total moult score and sex (Fig. 12). The model is a linear mixed effect model with bird ID as random effect, to account for some individuals having been measured more than twice. This model also accounts for individuals with particularly high or low moulting rates due to factors other than time, so these factors do not affect the analysis.

There is no difference between the sexes when it comes to gaining weight before migration, but this depends on the chosen test because as the p-value is only just above 0.05. I have therefore chosen the simplest model without an effect of sex, and here there is only a significant, positive effect of moulting ($P < 0.0001$, $N = 138$) on weight. This means that any difference between females and males is not real. Even if zero measurements for moult scores are excluded, the result does not change. There is the same significant, positive effect of moulting on weight for both sexes. As time goes by weight goes up.

The formula for the graph is $y = 0.03 * x + 13.94$. At the onset of moulting (moult score 0.5) the average weight is 14.0 g, while at the end (moult score 125) the weight will be 17.7 g. So, alongside the completion of moulting, the population as such is increasing the weight of its individuals on average by 3.7 g (26%). Food availability seems hardly to be a regulating, let alone limiting, factor for moulting.

The explanation for the sex differences in weight as a function of time (Fig. 11) but not as a function of moult score (Fig. 12) is probably to be sought in the fact that heavier starting weights of still breeding females contribute quite large fluctuations of the data because egg production continued during all of July.

General discussion

As a result of the fieldwork at Hjelm during the 1976 breeding season, significant differences in the moulting process and strategies of Common Whitethroat between males and females and between individuals with one or two clutches were demonstrated. The breeding success of the population is of course defined by the number of juveniles fledged per pair, which is assumed to have a knock-on but not necessarily positive effect on the choice of moulting strategy. Indeed, many late-breeding individuals were forced to refrain from a complete moult, with a consequent deterioration in physical condition, while in extreme cases the entire clutch was abandoned with the loss of all offspring. Two examples are reported in detail in Appendix 2 Text A3.

The likely reasons for these significant differences in moulting processes and strategies, as well as the effects of these, are discussed in the following.

When the population was divided according to breeding history it was seen that males with only one clutch started moulting four days earlier than females with one clutch, and similarly that the males finished moulting five days earlier, so that males and females with one clutch largely moulted within the same timeframe (Fig. 5). The pattern for birds with two clutches was quite different. The two sexes began moulting at roughly the same time, but males completed their moult in 54 days, while females theoretically moulted over 86 days (Fig. 6). 'Theoretically' is used because many females relied on the suspended moult strategy, which significantly shortens the moulting period, although old feathers to some extent may impair their ability to fly and thus lower their chances for survival (Møller & Nielsen 2018). With this strategy, the late females can take a shortcut to a timely start of the autumn migration, though they may be in a non-perfect plumage.

Couples with only one clutch generally had plenty of time to complete the care of the fledglings before preparing for moulting, but the males nevertheless initiated the moult earlier than females. This may be interpreted as the result of a generally weaker breeding drive of males. However, some individuals with only one clutch initiated the moult late in the breeding season, so that they performed it in parallel with the ordinary two-clutch birds. The three clutches that were lost as described in Appendix 2 Text A3 all were first clutches that had been started late.

When males and females with two clutches began moulting at the same time, this is likely to be the result of the increasing time pressure that late breeders with two clutches will nearly always be exposed to. Males with two clutches in our study therefore withdraw earlier from parental duties to begin a complete moult in accordance with the endogenously determined start date (Gwinner 1977), whereas females probably with a stronger breeding drive must continue to feed the fledglings to a greater extent while at the same time beginning to moult the first feathers. However, because of having to obtain food for both the continued growth of the young and their own need to renew remiges and build up fat deposits, the females must moult at a slower pace (Fig. 6) and often arrest their moult before it is completed. Thus, significantly more females than males make use of the suspended moult strategy (Fig. 9).

To understand the reasons for these different strategies, it is useful to recognize just how compressed is the Whitethroat's annual visit to Denmark. The stay is governed by a particularly strict schedule with several waypoints that must be met at the right time

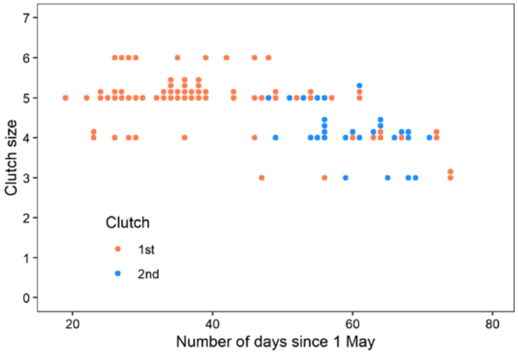


Fig. 13. The temporal distribution of clutch size in 1st and 2nd clutches by date of first egg.
Den tidsmæssige fordeling af antal æg i 1. og 2. kuld efter dato for 1. æg.

to ensure the individual's and thus the population's maximum breeding success. The decisive waypoints include the date of arrival, the date of the first egg in the first clutch and in the second clutch, the start date of the moulting cycle and the final departure date for Africa. The maximum annual visit extends over 140 days from early May to mid-September, of which the 59 days of the moulting period take up 42% of the length of stay.

Any shift in a bird's timely arrival at these waypoints may have cascading effects on breeding success, mortality, and timing of later life history stages as demonstrated by Tøttrup *et al.* (2012) and may therefore be of decisive importance for the trajectories of the population. From season to season, most of these waypoints are determined by exogenous influences such as temperature and precipitation in the winter quarters (Zwarts *et al.* 2023) and during migration regarding arrival date (Sondell 2000, Tøttrup *et al.* 2012), and on the breeding grounds regarding date of first egg (own observations). Contributing to defining the other waypoints and especially the start of moulting are the endogenous rhythms of the species (Gwinner 1977), which apparently block a significant advance of the start of migration in autumn (Tøttrup *et al.* 2006a).

The explanation may be that the start of the moulting cycle is defined predominantly endogenously and that there is only little individual plasticity. Søderdahl & Tøttrup (2024) examined ringing data from 2003-2021 for five long distance migrants at Blåvand Bird Observatory and found that Eurasian Blackcap *Sylvia atricapilla*, Pied Flycatcher *Ficedula hypoleuca* and Willow Warbler *Phylloscopus trochilus* all showed a significant delayed departure in autumn, whereas Garden Warbler *Sylvia borin* showed none and Common Whitethroat only tendencies for delayed median and late population departure. Whitethroat results were 0.28 days per year and 0.51 days per year, respectively, but both are non-significant.

Our data includes measurements from three unpaired males. However, no tendency towards an earlier start of moulting was seen in these idlers. All three individuals followed the average course. So even though these males could have started moulting significantly earlier than the breeders, this did not happen. This observation emphasizes the importance of hormonal changes brought about by seasonal changes (Gwinner 1977, Helbig *et al.* 1989) as an initiator of moulting, with day length being the most likely 'starter'. So, starting is not a question of having time but of the right time (Fig. 4).

Climate changes over the past half century has advanced the median spring passage of Whitethroats in North Europe by 3-4 days (Tøttrup *et al.* 2006b, Karlsson & Ehnbom 2021) and thus opened the possibility of an increasing proportion of pairs with two clutches and therefore higher productivity (Hansen 2023). This successful adaptation may partly be the reason for the documented geographical expansion of the species in Denmark during the past decades to become Denmark's currently most widespread bird species (Vikstrøm & Moshøj 2020), although the Danish population index for the species has been stable for 50 years (Vikstrøm *et al.* 2023).

Generally, breeding activities and moulting are thought to be mutually exclusive and are normally separated quite sharply in time (Jenni & Winkler 2020). When moulting overlaps with breeding to some degree, a trade-off between adult body maintenance (feather renewal) and parental care is to be expected. Two cases of late clutches with pulli being abandoned as already described (Appendix 2 Text A3) testify to this trade-off, which has also been demonstrated experimentally by Svensson & Nilsson (1997) who investigated the consequences of moult/breeding overlap by removing first clutches of Blue Tit *Cyanistes caeruleus*, thereby inducing late repeat clutches. Among the delayed pairs, a high proportion of males and some females started their moult as early as during incubation or feeding of nestlings.

The schedule of wing- and tailfeather moult in Common Whitethroat in late summer is dependent on both sex and breeding efforts including suspended moult in late birds. Photo: Mogens Hansen.
Forløbet af fældningen af sving- og halefjer hos Tornsanger er forskelligt mellem hanner og hunner og afhænger tillige af de enkelte individers ynglestatus. Især sent ynglende hunner afbrød ofte fældningen og påbegyndte trækket med en eller flere 'gamle' sving- og halefjer.

Moulting Blue Tit males also fed their nestlings to a lesser extent than non-moulting ones, and nestling mortality increased as a direct result of the early onset of male moult. A case of moult/breeding overlap has also been reported for Common Redstart *Phoenicurus phoenicurus* (Porkert & Hromádko 2012).

When Whitethroats bet on a late second clutch, this must be seen as an evolutionary choice in the eternal struggle to contribute to the gene pool, but this choice is not without risks because the individual is 'punished' quite severely when late clutches must be abandoned. In 1976, 72 first clutches produced an average of 4.82 eggs, while 28 second clutches produced an average of 3.31 eggs (Fig. 13) which contributed to some 31% of the total annual production (Hansen 2023). But individuals going for a second clutch lose all the energy that was invested in the production of a lost second clutch, and in addition, the unlucky females must start the autumn migration in a poorer condition due to suspended moult.

The described differences between males and females in relation to moulting history place a generally higher physical load on the females, especially when they must produce two rounds of eggs and then fly 5000 km to Africa in non-perfect plumage. Post-breeding females must therefore be assumed to stand a poorer chance of survival than males, an assumption that may help us explain the skewed distribution of sexes in the spring population of many long-distance migratory passerines (Donald 2007).

In 1976, the breeding population of Whitethroats on Hjelm included a total of 87 males (53 %) and 78 females (47 %) (Hansen 2023). At Christiansø Biological Field Station north-east of Bornholm in the Baltic Sea, 440 primarily staging Whitethroats were ringed and sexed in the period 1992-97 (from a total of 895) of which 54.3 % (239) were males (Lausten & Lyngs 2004). Figures from Gedser Bird Observatory at the southernmost tip of Denmark also show a clear predominance of males in spring and a later departure date for females than males in autumn. Hence, in the springs of 2007-2022, 489 Whitethroats were ringed and sexed as males (55 %) and 399 as females (45 %), but another 740 birds were not sexed (Kayser 2018, B. Kayser pers. comm. 2023). As it is not known how the sexed birds were sampled from the total population, these results should be treated with some caution.

The age distribution of the Whitethroat breeding population in 1976 on Hjelm could be calculated to consist of 79 2cy birds and 77 3cy+ birds, a percentage distribution close so fifty-fifty (Hansen 2023). Delving further into the age and sex question, we found 45 2cy-males and 43 2cy-females. However, nine 2cy males did not breed successfully, so the breeding population consisted of 36 2cy males (35 natives) and 43 2cy females (13 natives). Among older birds (3cy+), 42 were males and only 35 were females (Hansen 2023). If this is a general feature of Whitethroat populations, the excess of males in spring could be the result of older females having higher mortality due to the greater physical strain of their breeding activities and less efficient moulting the year before.

On the one hand, climate change means that the breeding season for Whitethroats in Denmark has been extended because the birds are able to arrive earlier. More time increases the frequency of pairs with two clutches, and then the population may grow. On the other hand, a higher frequency of two clutches means that pressure on females increases both physically and in relation to the moulting cycle, but so far obviously not to an extent that has prevented the population's wellbeing in recent decades (Meltofte *et al.* 2021).

Acknowledgements

Above all, the five ringers who participated in the 1976 season deserve my greatest recognition for their diligent and tireless efforts. Not until today has it been clear to me how hard they toiled to securely record all data. They were Ebbe Arnfeldt Hansen, John Frikke, Erik Hørning, Ole Nøhr and Lene Sørensen. The latter participated throughout the whole season as both ringer and being responsible for the demanding work of recording the daily catch numbers and observations. My sincere thanks. Next, Professor Kaj Sand-Jensen deserves my warmest recognition for good advice and enriching sparring about the manuscript. Sand-Jensen has read and commented on several drafts of the script. Kenneth Thorø Martinsen performed the statistical analyses and prepared the graphic figures with great accuracy and patience. The colour ringing of the Whitethroats was carried out in full understanding with the management of the ringing department of the Zoological Museum, who also supported the project with copious amounts of traditional aluminium rings. Ulf Ottoson and one anonymous reviewer provided me with valuable comments and suggestions for improving the manuscript. The editors Jon Fjeldså and Hans Meltofte also deserve thanks for great patience and pedagogical efforts finalizing the manuscript, and finally my thanks go to Nick Quist Nathaniels for an eminent check on the translation of it into English. Finally, a hearty thanks shall go to the family that owns Hjelm, for their generous acceptance of our long-term stays.

Resumé

Tornsangerens fældning i en afgrænset ynglebestand i forhold til dato, køn, ynglehistorik og vægt

Forløbet af Tornsangerens fældning er blevet rapporteret hyppigt, men ikke tidligere på baggrund af en afgrænset og veldokumenteret ynglebestand. I denne undersøgelse demonstreres, hvordan start, forløb og afslutning af fældningscyklus for svingfjer og halefjer adskiller sig væsentligt i forhold til køn, ynglehistorik og vægt. Også sammenhængen mellem afslutningen af fældningen og starten på efterårstrækket beskrives. Feltarbejdet blev udført i ynglesæsonen 1976 på øen Hjelm i Kattegat.

Tornsangere, der producerer et kuld, begynder at fælde tidligere end fugle, der producerer to kuld, såvel som at hanner starter tidligere end hunner (Fig. 4). I par med kun et kuld fælder begge køn med samme hastighed og i parallelle forløb (Fig. 5). Derimod i par med to kuld fælder hunner med en betydelig langsommere hastighed end hanner (Fig. 6), hvilket fører til en markant højere grad af afbrudt fældning (Fig. 7), hvor flere hunner ikke formår at forny alle svingfjer før trækstart.

Tornsangere, der producerer to kuld eller yngler sent, risikerer at have for lidt tid til en komplet fældning af alle svingfjer, før efterårstrækket skal påbegyndes, og disse sene ynglefugle reagerer på tidspresset ved at skyde forskellige genveje i forhold til en komplet fældning. De suspenderer fældningen af især flere armsvingfjer for at vinde tid (Fig. 8). Faktisk er fornyelsen af armsvingfjer ufuldstændig hos flertallet af individer og forekommer hos omkring 72 % af hele populationen og med hunnerne i front (Fig. 9).

Begge køn opnår en signifikant stigning i vægt (hanner 23,8 % og hunner 17,8 %) under fældningen (Fig. 11). Fødeknaphed kan således næppe være vigtig op til starten af efterårstrækket, som generelt begynder, når fornyelsen af håndsvingfjer og halefjer er fuldendt, eller endda en dag eller to før.

Starten på fældningscyklus anses for at være styret af miljøvariabler som daglængde og temperatur, men også af en endogen årsrytme. Derfor udgør startdatoen et solidt waypoint på en fast rejseplan, som fuglene skal følge med kun beskeden plads til afvigelser. De kan endda tvinges til at opgive både æg og redeunger. Afrejsens waypoint er ikke blevet flyttet af klimaændringerne, i modsætning til ankomstdatoen om foråret, som er fremskyndet med 3-4 dage.

I overensstemmelse med andre undersøgelser indikerer resultaterne, at en rettidig start på efterårstrækket er af afgørende betydning, men på den anden side bør fordelene ved en komplet fældning ikke negligeres. En tidlig trækstart kan være afgørende for at lette omgåelsen eller overflyvningen af Sahara-ørkenen, men fornyede svingfjer må også formodes at spille en vigtig rolle for den samlede overlevelse på den 5000 km lange rejse til Afrika.

Hanner, der fælder både tidligere og mere fuldstændigt end hunner, kan antages at have bedre chancer for overlevelse, da de har flere nye fjer. Denne forskel kan forklare den skæve fordeling af kønnene i ynglebestanden på Hjelm i 1976 med 54 % hanner sammenlignet med 46 % hunner, et

træk som også understøttes af andre skandinaviske data fra Christiansøs Naturvidenskabelige Feltstation og fra Gedser Fuglestation. Da det ikke er anført, hvordan de kønsbestemte fugle blev udtaget fra den samlede population, bør disse resultater dog behandles med nogen forsigtighed.

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Appendix 1: https://pub.dof.dk/link/2024/2.appendix1
Appendix 2: https://pub.dof.dk/link/2024/2.appendix2

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