



Rapid flight feathers moult and fat stores in the Common Snipe *Gallinago gallinago* in the early stage of autumn migration

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Abstract

We analysed primary and secondary feather moult and fat reserves in 539 Common Snipes captured in the middle Pripyat River Valley, an important stopover site for waders in Central Europe, between 2002 and 2022. The average daily rate of feather growth was 1.89% in primaries and 2.27% in secondaries, being one of the highest documented in waders. The estimated duration of growth for a single flight feather varied from 11 to 21 days in primaries and from 8 to 11 days in secondaries. Moreover, multiple flight feathers (up to 14) were replaced simultaneously. As a result, the wing moult in Common Snipes was rapid with the mean primary moult duration estimated at 53 days (28 June–20 August) according to the Underhill–Zucchini model, and only 20 days in secondaries (31 July–20 August) based on moult estimates of individual secondaries. Hence, although secondary feathers began to grow when primary moult was already advanced, moulting of both flight feather groups was completed in most birds at almost the same time. Our study shows that Common Snipe in the middle Pripyat River Valley exhibit very rapid wing moult with large wing gaps. Fat reserves and thus body mass of Common Snipes were the lowest when the wing gap was greatest, compensating for their reduced wing area. Late and slow movement towards wintering grounds, allows them to moult rapidly at the early stage of autumn migration, which is likely to occur only in sites with abundant food resources.

Keywords Waders · Moult migration · Primary moult · Secondary moult · Wing gap · Fat score

Zusammenfassung

Schnelle Schwungfedermauser und Fettreserven bei der Bekassine *Gallinago gallinago* zu Beginn des Herbstzuges

Wir analysierten die Mauser der primären und sekundären Schwungfedern sowie die Fettreserven von 539 Bekassinen, die zwischen 2002 und 2022 im mittleren Tal des Flusses Pripjat gefangen wurden, einem wichtigem Rastgebiet für Watvögel in Mitteleuropa. Die durchschnittliche tägliche Wachstumsrate der primären Schwungfedern betrug 1,89% und die der sekundären Schwungfedern 2,27%, eine der höchsten Wachstumsraten, die bei Watvögeln bisher dokumentiert wurden. Die geschätzte Wachstumsdauer für einzelne primäre Schwungfedern variierten zwischen elf und 21 Tagen und für sekundäre Schwungfedern zwischen acht und elf Tagen. Außerdem wurden mehrere Schwungfedern (bis zu 14) gleichzeitig erneuert. Nach dem Underhill-Zucchini-Modell verlief die Flügelmauser bei den Bekassinen also sehr schnell, mit einer geschätzten durchschnittlichen Mauserdauer von 53 Tagen (28. Juni bis 20. August) für primäre Schwungfedern und nur 20 Tagen (31. Juli bis 20. August) für sekundäre Schwungfedern. Obwohl die sekundären Schwungfedern erst zu wachsen begannen, als die Mauser der primären Schwungfedern bereits weit fortgeschritten war, wurde die Mauser der beiden Flugfedergruppen bei den meisten Individuen fast gleichzeitig abgeschlossen. Unsere Studie zeigt, dass Bekassinen im mittleren Tal des Flusses

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Pripjat eine schnelle Flügelmauser mit großen Lücken in den Flügeln vollziehen. Die Fettreserven und damit die Körpermasse der Bekassinen waren am geringsten, als die Lücken im Flügel am größten waren, um die verringerte Flügelfläche zu kompensieren. Späte und langsame Zugbewegungen in Richtung der Überwinterungsgebiete ermöglichen es den Bekassinen, zu Beginn des Herbstzuges schnell zu mausern, was wahrscheinlich nur dort geschieht, wo es reichliche Nahrungsressourcen gibt.

Introduction

The wing moult is an important stage in migrants' annual cycle. The loss of wing area due to missing and/or not fully grown primaries and secondaries increases wing loading and may impair flight performance (Rayner 1988; Swaddle and Witter 1997; Hedenström 2003). Therefore, the timing of the flight feather replacement rarely coincides with such an energy-demanding stage of the annual cycle as migration (Kjellén 1994). Even though birds may compensate for increased wing loading by reducing their body mass (Holmgren et al. 1993; Swaddle and Witter 1997; Lind and Jakobsson 2001), migrants need to accumulate energy reserves (mainly fat) for non-stop migratory flights (Berthold 1993). Hence, there is a trade-off between the necessity to increase body mass before migratory flight and reduced wing area during feather moult. In waders, for example, active primary feather moult during migration was recorded mainly in short- and medium-distance migratory species (i.e., Snow and Snow 1976; Meissner and Huzarski 2006, but see Holmgren et al. 1993). Whereas trans-equatorial migrants complete flight feathers replacement in wintering grounds, and adjust it to the abundance of food (Remisiewicz et al. 2009; Barshep et al. 2013) or prior migratory flight (Holmes 1966; Owen and Krohn 1973). The primary feather moult may also start on the breeding grounds, later may be suspended for migration, and resumed after the arrival to wintering grounds (Serra et al. 2006). Hence, waders display a wide variety of flight feather moult strategies (Remisiewicz 2011; Jackson and Underhill 2022), with the duration of moult being the key factor determining feather durability. Flight feathers that grow slowly are of better quality and last longer than feathers that are grown rapidly (Dawson et al. 2000; Serra 2001). Another moult strategy recorded in many waterfowl (i.e., Panek and Majewski 1990; Köhler and von Krosigk 2006; Fox et al. 2014) is the so-called moult migration, in which flight feather replacement starts and is at least partially completed on a staging area, after a post-breeding migratory movement. The moult migration has been found also in some waders (Hoffmann 1957; Jehl Jr 1987; OAG Münster 1991; Barbaree et al. 2016). However, unlike waterfowl, waders retain the ability to fly during flight feathers moult but may exhibit reduced flight performance due to the presence of a gap in the wing area, which makes them more vulnerable to predation (Swaddle and Witter 1997; Swaddle et al. 1999).

Primaries and secondaries have different functions in a bird's wing. The lift is generally produced by the inner wing by creating the airfoil shape of the bird's wing, as air moves over the surfaces of the secondaries, whereas thrust is produced by the primaries of the outer wing mostly generated on the downstroke of flapping flight (Azuma 1992; Dvořák 2016). However, our knowledge of the moult pattern of secondaries in waders is sparse as they are usually omitted in moult studies that mostly focus on the primary replacement (but see: Henriksen 1985; Summers et al. 2004).

The Common Snipe *Gallinago gallinago* is a migratory wader that breeds throughout northern Eurasia and migrates in large numbers toward wintering grounds in southwestern Europe and northwestern Africa (Glutz von Blotzheim et al. 1977; Minias et al. 2010). This species adopts the B-strategy of migration (sensu Alerstam and Högstedt 1982), i.e., faces strong interspecific competition on their wintering grounds, their autumn migration starts late and is strongly influenced by worsening weather conditions (Alerstam and Högstedt 1982; Włodarczyk et al. 2007), with adults and juveniles migrating at the same time (Pinchuk et al. 2007). The flight feather replacement in the Common Snipe starts at the breeding ground or at the onset of migration, with birds arriving at wintering grounds after completing the flight feathers' and body feathers' moult (Glutz von Blotzheim et al. 1977). The most comprehensive analysis of flight feather replacement in this species has been provided by the OAG Münster (1975). However, due to the lack of modern statistical methods that study is only descriptive.

This study aims to estimate the start, duration, and variation in the start date of primary and secondary moult using advanced methods based on the Underhill–Zucchini model (Underhill and Zucchini 1988; Underhill et al. 1990) in Common Snipe staging in the Middle Pripjat Valley in Central Europe. The application of this model enables a far more detailed insight into the flight feathers' moult, its progress over time, and variation in the moult rate of individual feathers. As the accumulation of fat reserves is crucial for the beginning of the migratory flight and the gap in the wing area increases the energetic cost of flight (Hedenström 2003), we also focus on the influence of the wing gap size on the amount of fat stores accumulated by Common Snipe at this early stage of their migration.

Methods

Study area

Studies were conducted in the floodplain meadows of the Pripjat River near Turov, Gomel Region, Belarus (N 52° 04', E 27° 44') (Fig. 1). This is an important stopover site for waders during spring and autumn migrations (Meissner et al. 2011; Pinchuk and Karlionova 2011; Pinchuk et al. 2016). The Common Snipe breeds there in low densities, i.e., between 0.5 and 3.7 pairs/km² ha, where grass communities are predominant (Mongin 2002; authors' unpublished data). From mid-June, the number of Common Snipe in the floodplain meadows increases rapidly, reaching a daily maximum of up to 400–500 individuals in the trapping area, i.e., a small peninsula of about 0.6–0.7 km² formed by the Pripjat River and a small tributary (authors' unpublished data).

Field study

The field study was conducted over 11 consecutive seasons, from 2002 to 2022. Birds were captured at different times

and with different intensities from mid-June to mid-October. To maximise the number of captured snipes different catching methods were used. Walk-in traps were located on riverine islands and wet meadows during the whole study period. In some years, playback calls were used through the night to attract Common Snipe to the catching site. Birds staying there were flushed to mist nets every hour (Pinchuk and Karlionova 2006). Birds were aged according to plumage characteristics, and only adult snipes were considered, as juveniles do not moult flight feathers during autumn migration (Włodarczyk et al. 2008). Three individuals with suspended primary moult and uninitiated secondary moult were excluded from the analysis. In total, 539 individuals were used in the analyses. In two birds, a moult of secondaries was not recorded (Table 1).

Table 1 The number of Common Snipe in three different stages of primary and secondary moult

Flight feathers	Not started moult	In moult	Finished moult	Total
Primaries	6	381	152	539
Secondaries	185	197	155	537

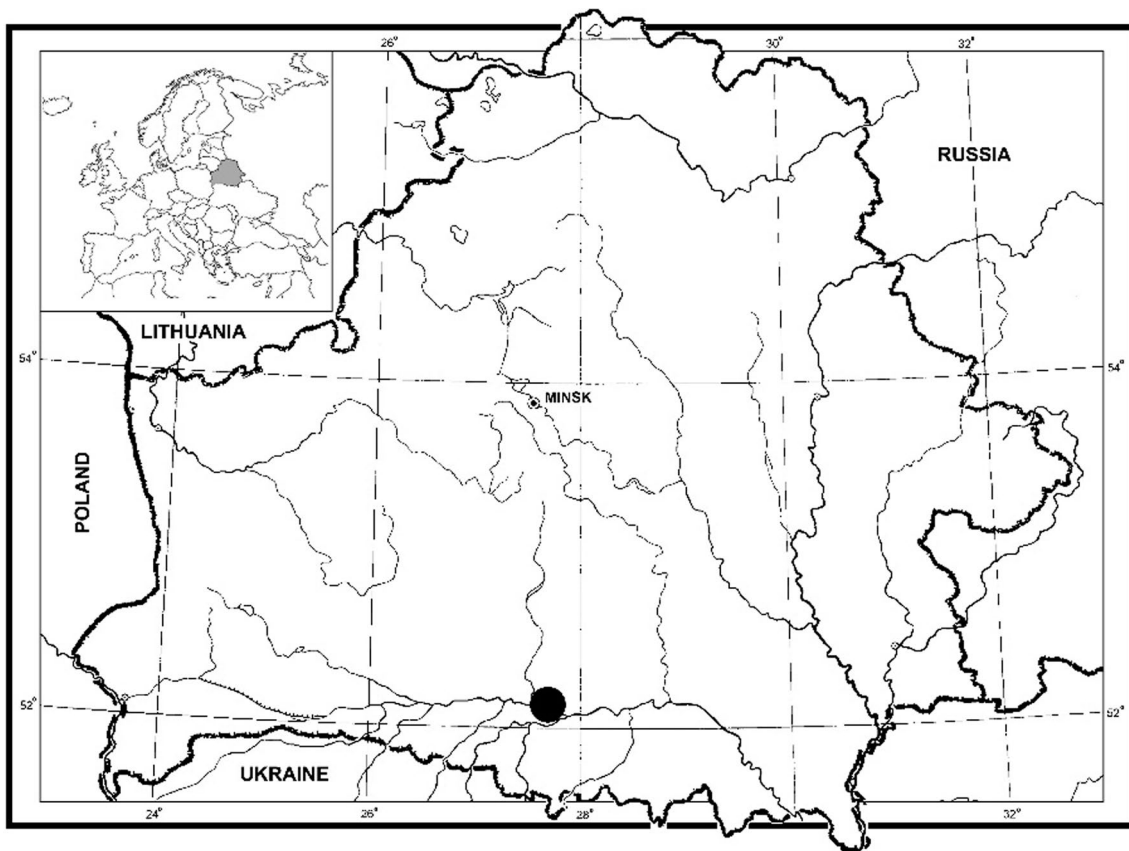


Fig. 1 Location of the study area in the middle Pripjat River Valley near Turov (black dot)

The amount of subcutaneous fat was assessed according to an eight-point scale developed for waders (Meissner 2009). Every year, the accuracy and repeatability of measurements taken by different ringers were checked as described by Busse and Meissner (2015).

Moult analysis

As primaries and secondaries have different functions during the flight, in this study, their moult pattern has been analysed separately, with the results of the two analyses compared. We used the standard moult formula, where the moult stage of each of the ten primaries and ten secondaries was recorded as a score between 0 (old feather) and 5 (new full-grown feather) (Ashmole 1962). Because the outer primaries are heavier than the inner ones and the distribution of their moult scores is not linear (Summers 1980), the moult scores were converted to Percentage of Primary Feather Mass Grown (PPFMG), where feathers that had moult scores of 1, 2, 3, 4 and 5 were given a corresponding moult index of 0.125, 0.375, 0.625, 0.875 and 1, respectively (Underhill and Zucchini 1988). The mean percentage mass for each primary of the studied species needed for this transformation was taken from Meissner et al. (2018). Consequently, the same procedure was applied to secondaries, despite small differences in their masses (Table 2). Secondaries were collected from three birds found dead, dried to constant mass in a convection oven at 60 °C, and then weighed, as rapidly as possible after drying, to an accuracy of 0.1 mg using an electronic balance as described by Meissner et al. (2018). The moult scores of secondaries were converted to the Percentage of Secondary Feather Mass Grown (PSFMG) same as in primaries.

The proportion of individuals that had completed primary moult (PPMFG = 1) and not initiated moulting (PPFMG = 0) was unequal (Table 1). Therefore, some Common Snipe began replacing their primary flight feathers before arriving at the study area. Hence, the Type 4 moult model for birds in active moult and those that have completed their moult was applied (Underhill and Zucchini 1988; Underhill et al. 1990). The moult parameters of secondaries were estimated using the Type 2 moult model because individuals in all three moult stages were present in the collected sample, i.e., not yet moulting their secondaries, in active secondary

moult, and birds, which have completed their secondary moult (Table 1). Consistently, when estimating the moult parameters for individual primaries and secondaries, the moult model Type 4 was applied to the two innermost primaries and the moult model Type 2 to the remaining primaries and secondaries. To compare the growth rate of primaries and secondaries, we calculated the daily rate of feather material growth (FMG/day) by dividing the relative mass of all primaries or secondaries by the estimated duration of moult.

The ratio of the relative mass of each flight feather to its estimated duration of moult provided an estimate of its daily growth rate expressed as a percent of PPFMG and PSFMG per day (Serra 2000; Underhill 2003). Using estimated starting and ending dates of moult for each flight feather with their daily growth rate, we plotted their cumulative growth during the moult, assuming that daily growth values are constant (Underhill and Zucchini 1988).

We estimated the Proportion of Flight Feather Mass Missing (PFFMM), where feathers with moult scores of 1, 2, 3 and 4 are assumed to represent 0.875, 0.625, 0.375 and 0.125 of the relative feather mass missing, respectively, i.e., the missing relative mass of each of the primary and secondary flight feather. After summing up these values, we obtained an assessment of the amount of missing wing area due to moult, i.e., wing gap (Ward et al. 2007; Barshep et al. 2013).

Similar to Podlaszczuk et al. (2016), we used a fat score as an index of body condition because the lean body mass of birds during the moult may change considerably (Murphy and King 1992; Lind et al. 2004), including the ratio of pectoral muscle size to body mass (Lind and Jakobsson 2001). Whereas visible subcutaneous fat reflects an approximately linear increase in fat mass in waders (Meissner 2009). Division of the year into 5-day periods followed Berthold (1973).

Our study sample included birds caught with walk-in traps during the day and mist-nets with playback calls during the night, which may lead to a mix of birds in different body condition, i.e., those that have stopped in the study area and active migrants lured to land (Figuerola and Gustamante 1995). A Generalized Linear Model (GLM) (McCullagh and Nelder 1989) was applied to check for the differences in fat score, primary and secondary moult advancement (continuous, response variables) between birds caught during the day and birds caught at night with playback calls (categorical, explanatory variable) in the following 5-day periods

Table 2 Absolute and relative masses of the Common Snipe secondaries ($N=3$)

	Secondary number									
	Outer									Inner
	1	2	3	4	5	6	7	8	9	10
Mean mass (mg)	66.5	68.8	68.3	68.0	67.5	68.0	68.5	69.5	70.3	71.0
Relative mass (%)	9.7	10.1	9.9	9.9	9.8	9.9	10.1	10.1	10.2	10.3

(continuous, explanatory variable). The latter was the only statistically significant variable influencing fat score, PFMG, and SFMG, while the capture method was insignificant in all three models (Table S1). Hence, data on birds captured with playback calls and without luring were combined in further analyses.

Results

At the beginning of the field study period, in June, the majority (83%) of Common Snipe that were captured had growing primaries. The first individual with a completed moult of primaries was caught on 28th July, and the bird with all primaries and secondaries moulted was observed on 1st August. The time of primary and secondary moult largely overlap (Fig. 2). The mean primary moult duration was estimated at 53 days, lasting from 28th June to 20th August, while the mean moult duration for secondaries was 44 days, nine days shorter, starting on 29th July and ending on 11th September (Fig. 2, Table 3). As a result, secondaries had a higher daily rate of feather material growth than

primaries (Table 3). In contrast to PPFMG, the distribution of PSFMG values over time deviates from a linear with a group of high values in birds captured in July (Fig. 2B). Consequently, the variance in moult duration according to the standard deviation parameter of Underhill and Zucchini (1988) model was about 6 days larger for secondaries than for primaries (Table 3). This means that in the case of secondaries, the UZ moult model cannot estimate moult parameters well and the presented average values for the start date, duration, and end date (Table 3) should be regarded as a very approximate. However, the distribution of PSFMG values over time with great daily rate of the feather material growth clearly indicated a very high feather replacement rate.

The primaries were shed sequentially from innermost to outermost, and the number of growing flight feathers gradually increased till P5, then slightly decreased when primaries from sixth to eighth have been shed (Fig. 3). When the innermost secondary was shed, the number of growing flight feathers was still low and later distinctly increased with the fall of two subsequent secondaries (Fig. 3). Just after the start of the secondary moult, the median number of simultaneously growing flight feathers reached 12 (with the

Fig. 2 Temporal distribution of the Proportion of Primary Feather Mass Grown (PPFMG) (A) and Proportion of Secondary Feather Mass Grown (PSFMG) (B) for Common Snipe. Solid lines—the mean course of the primary and secondary moult, dashed lines—95% confidence intervals

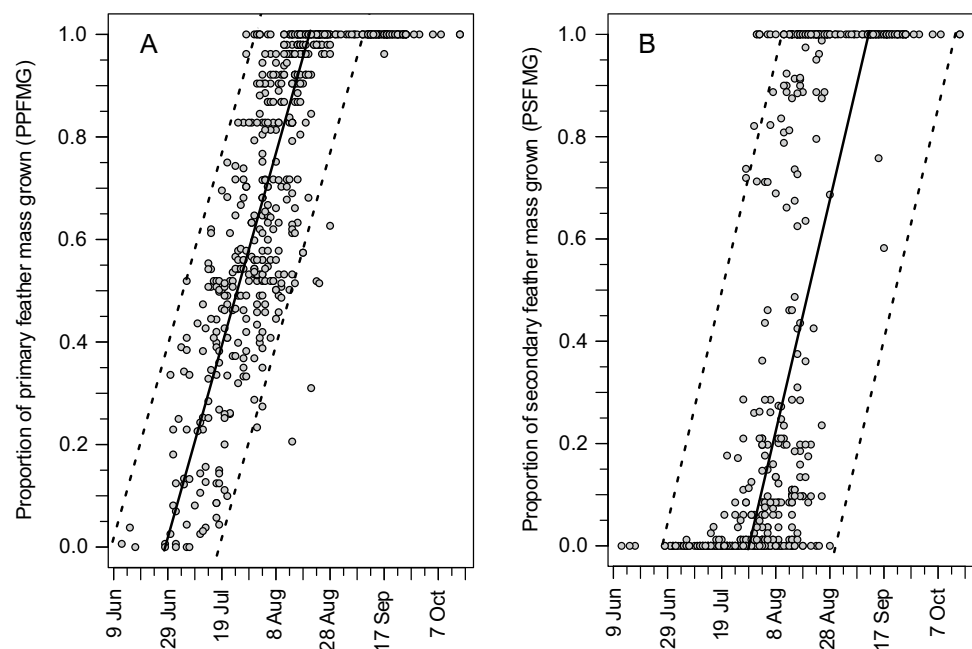
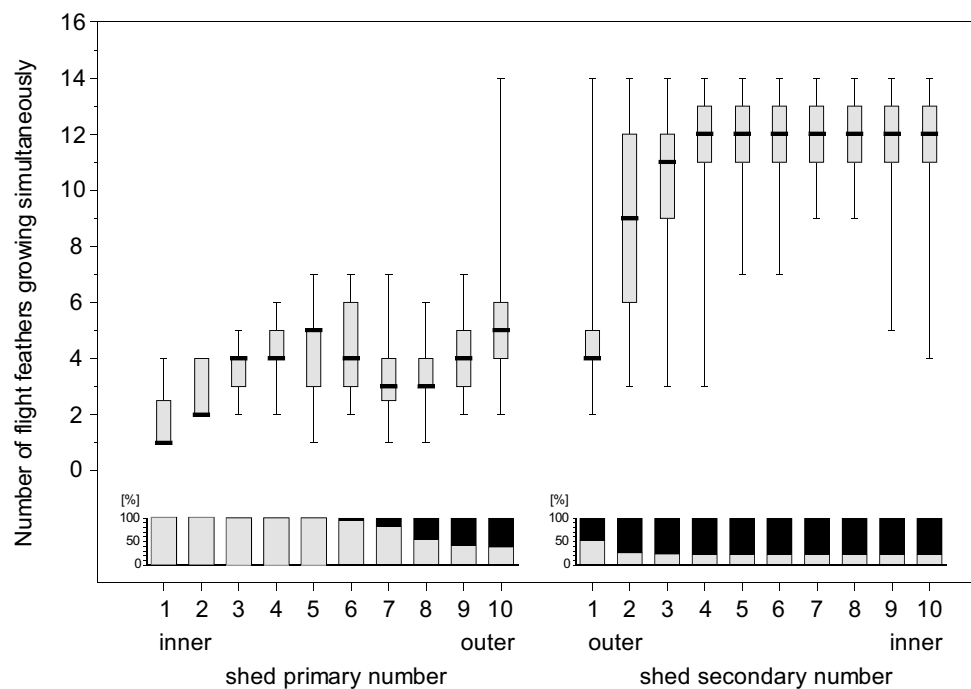


Table 3 Parameters of the primary and secondary moult estimated for Common Snipe with the UZ moult models, and the estimated daily rate of the feather material growth (FMG/day), calculated from the moult durations

Flight feathers	Mean start date (SE)	Duration in days (SE)	Mean end date (SE)	SD of the start date (SE)	FMG/day (%)
Primaries	28 Jun (1.6)	53 (2.1)	20 Aug (1.4)	10.2 (0.4)	1.89
Secondaries ^a	29 Jul (1.1)	44 (1.8)	11 Sep (1.5)	16.4 (0.8)	2.27

^aSecondary moult parameters should be considered very approximate due to the non-linearity of PSFMG values over time (Fig. 2B)

Fig. 3 The number of flight feathers growing simultaneously while each of 10 primaries and 10 secondaries was shed (moult score = 1) with bar graphs showing the percentage of growing primaries (grey) and secondaries (black). Horizontal bold line—median, grey rectangle—interquartile range, vertical line—range



maximum value being 14), due to most secondaries being shed at once and growing at the same time when primary moult was close to being completed (Fig. 3).

The earliest start of the secondary moult was recorded when PPFMG was 0.40, but it intensified when PPFMG reached 0.50, and from that moment the mass of new secondaries grew rapidly (Fig. 4). In most cases, the primary moult was completed before the secondary replacement was finished, but the time of completing the replacement of both groups of flight feathers varied greatly between individuals. The primary moult was completed when PSFMG was in a wide range between 0.1 and 1.0, with few individuals finishing the secondary moult just before the end of the primary moult (Fig. 4).

The estimated duration of growth for each of the primaries varied from 11 to 21 days, while for secondaries from 8 to 11 days (Fig. 5, Table S2). The daily growth rates of primaries revealed a progressive increase from innermost to outermost feather shown by the steeper growth lines for the outer primaries than those for the inner primaries (Fig. 5, Table S2). As a result, growth rates of individual primaries largely varied, being about two times higher in outermost compared to innermost ones. The daily growth rates of secondaries except for two outermost were similar and varied between 1.10 and 1.24 PSFMG/day. Secondaries grew 1.3–2.7 faster than primaries (Table S2) with multiple feathers replaced simultaneously (Fig. 5). Estimated starting date of S1 and moult end date of S10 were 31 July and 20 August, respectively, suggesting an overall secondary moult duration of only 20 days (Table S2), which is 24 days shorter

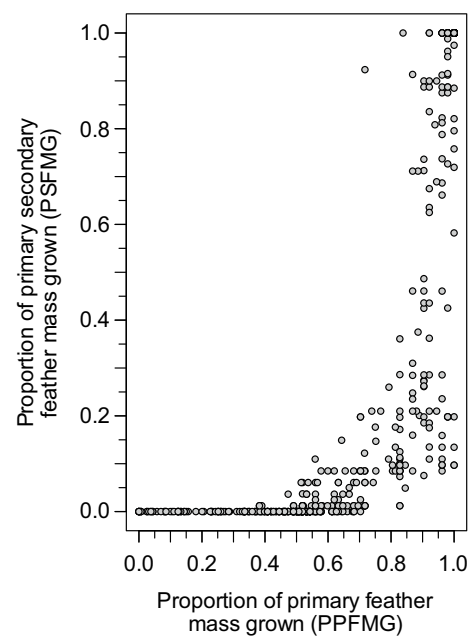
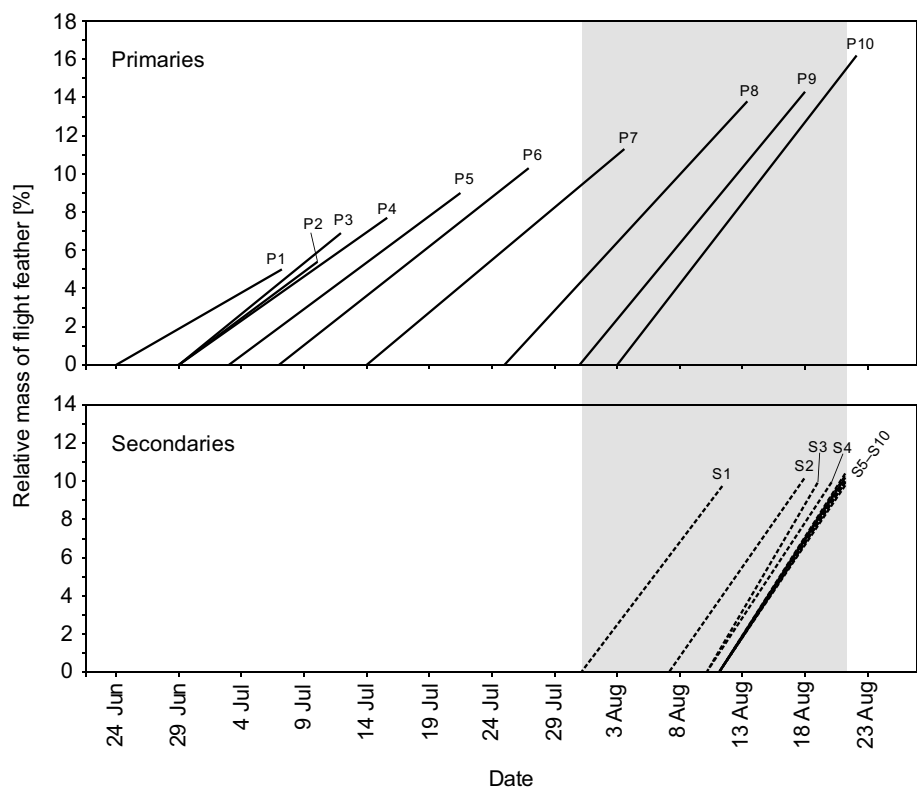


Fig. 4 The scatterplot of proportions of primary and secondary feather mass grown in Common Snipe

than duration given by PPFMG (Table 3). This discrepancy is less pronounced in primary feathers, where the mismatch is 5 days only (Table 3, Table S2).

The size of the wing gap was negatively correlated with the fat score ($r = -0.31$, $P < 0.001$). The greatest gap in wing area with a median PPFMM larger than 0.48 was noted in

Fig. 5 Dates of the start and end of moult of individual primaries (P1–P10, solid lines) and secondaries (S1–S10, dashed lines) moulted by Common Snipe in the middle Pripyat River Valley. The endpoints of lines are at the relative mass of each flight feather. The grey area shows the range of average replacement times for all secondaries



birds with fat scores between 0 and 2, whereas in those with fat scores 3 and higher, the median PFFMM distinctly decreased (Fig. 6).

Discussion

Common snipes staging in the study area originate from the vast breeding grounds of western Russia. Whereas those originating from northwestern Russia are much less numerous, as shown by the distribution of ringing recoveries (Baumanis 1985; Minias et al. 2010). Thus, we assume that obtained parameters of primary and secondary moult are representative of Common Snipe breeding in the vast area of western Russia, which pass numerously through southern Belarus and winter in Western Europe. A similar approach was applied in the analysis of the development of breeding plumage in the Black-headed Gull *Chroicocephalus ridibundus*, that winter in vast area of central and northwestern Europe (Meissner et al. 2024).

In many Common Snipe, the primary moult begins on the breeding grounds (Glutz von Blotzheim et al. 1977) and that is why only about 1% of individuals that were captured at the study site had no indication of moult (i.e., all old flight feathers present). The mean growth rate of flight feathers in the Common Snipe moulted in the middle Pripyat River Valley is one of the highest documented in waders (Table S3).

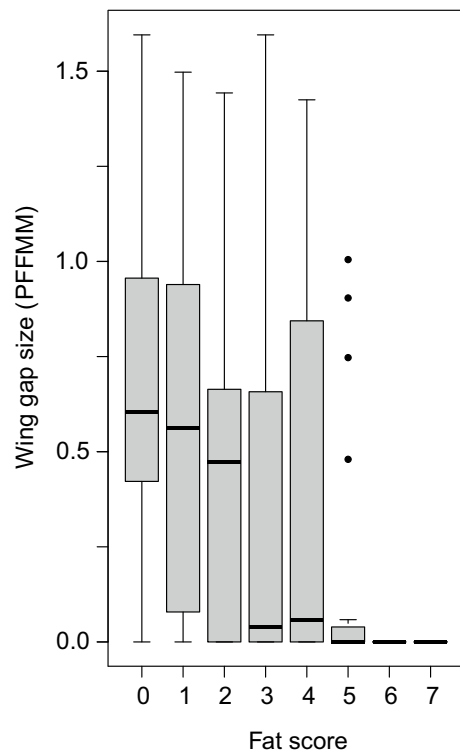


Fig. 6 Wing gap size expressed as a proportion of flight feather mass missing (PFFMM) in Common Snipes with different fat scores. Horizontal line—median, rectangle—interquartile range, vertical line—range, dots—outliers

This rapid feather growth and many flight feathers growing simultaneously (especially secondary feathers) result in a very short time duration of the wing moult lasting only about 50 days. This minimises the time of reduced flight ability when birds are exposed to increased predation pressure. In addition, when the wing gap is the largest, Common Snipe reduce fat stores, thus lowering their wing load. During wing moult, flight performance is often seriously impaired (Hedenström and Sunada 1999; Swaddle et al. 1999) and birds commonly reduce their body mass to maintain good flight performance (i.e., Holmgren et al. 1993; Serra et al. 1999; Lind and Jakobsson 2001; Galindo-Espinosa et al. 2013). Birds moulting their flight feathers appear to compensate for the aerodynamic effect of the wing gap by remoulding the flight muscle and reducing their body mass, thereby effectively increasing the flight-muscle ratio (Lind and Jakobsson 2001). Moreover, in the Common Snipe, the moult of greater upper wing coverts is finished before the secondaries are shed and underwing coverts stay unmoulted before the moult of secondaries has been completed. It has been suggested that greater coverts aid flight ability to some extent by reducing the size of the wing gap (OAG Münster 1975). A similar rapid moult of flight feathers was found in the Long-billed Dowitcher *Limnodromus scolopaceus* exhibiting the moult migration on its staging area in the Great Basin (Barbaree et al. 2016). The process of rapid moult requires extra food available, in the amount above the needs of daily maintenance (Murphy and King 1992; Lindström et al. 1993; Bairlein 2017). The middle Pripyat River Valley provides snipes with abundant invertebrates in wet riverine meadows (Hajdamowicz et al. 2015; Witkowska et al. 2022).

The pattern of secondary moult in the Common Snipe resembles that found in species that moult all flight feathers simultaneously, temporarily losing the ability to fly (Panek and Majewski 1990; Fox et al. 2014). The extraordinary rapid replacement of secondaries in the Common Snipe has been described previously (OAG Münster 1975) where in most cases, as in our study, shortly before or after the outermost secondary had finished growing nearly all other secondaries were shed at the same time. Failure to meet the assumptions concerning the linearity of the moult model has consequences in significant difference, i.e., 24 days, in the moult duration of secondaries calculated in the analysis of individual feathers' moult (Fig. 5) and PSFMG (Table 3). This discrepancy is distinctly lower in the moult of primary feathers, where the mismatch is 5 days only. Difference in the moult duration estimated by these two methods was as high as 38 days in a study of curlew sandpipers *Calidris ferruginea* moulting primaries in India (Barshep et al. 2013), where also the assumption of model linearity was not fully met (see Fig. 1 in this publication). Therefore, when the increase in the proportion of feather mass over time is not linear, it is better to use the parameters of UZ moult model

calculated for individual feathers to estimate the duration of replacement of a given feather tract.

In the Purple Sandpiper, *Calidris maritima* secondaries are also shed rapidly, but sequentially from the outermost to innermost feather (Summers et al. 2004). Among all wader species that moult studied with the UZ moult models, this species is the only one to show higher mean growth rates of primaries than the Common Snipe (Table S3). The wing moult of the Purple Sandpiper, especially in the Norwegian wintering population, seems to occur under time pressure, as these birds finish primary replacement in early November when weather conditions become increasingly bad. Completion of wing moult in Common Snipe in the middle Pripyat River Valley coincides with a rapid decrease in bird numbers at the beginning of September (authors' unpublished data). A drop in the number of Common Snipe in stopover sites in Poland was reported at a similar time (Bocheński et al. 2006; Grzywaczewski et al. 2009; Meissner et al. 2009; Kaczorowski and Czyż 2013). In Western Europe, this decrease is noted somewhat later, in October (Kraus and Kraus 1972; OAG Münster 1975; Winkler und Herzig-Straschil 1981; Thies 1996; Laber 2003), which is in line with the south-west and west directions of autumn movement of this species across Europe (Baumanis 1985; Minias et al. 2010). Common snipes complete the post-breeding migration to the wintering grounds in NW Europe by November/December (Glutz von Blotzheim et al. 1977), hence, this rapid wing moult enables them to start to move toward wintering grounds with new flight feathers. The new feathers provide better flight performance increasing escape flight speed and energy gain per wingbeat compared to old feathers (Williams and Swaddle 2003; Hedenström 2003). Yet, the distance from the study area to the Common Snipe wintering grounds is not very large (Minias et al. 2010) and the benefits of having a set of new flight feathers are unlikely to be significant here. Rapid feather replacement requires abundant food resources, and this is probably the main reason for the very high number of Common Snipe staging in the Middle Pripyat Valley and the very rapid process of flight feathers replacement.

The size of the wing gap is reduced when subsequent primaries from innermost to outermost are in moult (Holmgren et al. 1993; Remisiewicz et al. 2009), which was found also in this study. This is an adaptation to minimize the size of the wing gap during primary moult because reduced wing area within outer primaries compromises flight efficiency by decreasing wing thrust. Whereas during secondary moult, the gap is much larger due to many feathers shed simultaneously. Secondaries are mainly responsible for creating the lift during flying, and at a time of limited flight capability, a quick take-off seems to be more important for escaping a predator than the additional energy cost linked to impairment of a flapping flight, by missing many secondaries. This is probably the reason for the lower variability in the progress of primary moult compared to secondary moult.

The strategy of overlapping moult with migration or breeding seems to be a complex trade-off between environmental conditions and the time constraints imposed by the time window for migratory movements (Remisiewicz 2011). As a result, waders exhibit different moult strategies depending on migration distance (Holmgren et al. 2001; Meissner and Huzarski 2006), age (Meissner 2007; Summers et al. 2010), sex (OAG Münster 1991; Summers et al. 2004), and food availability at the moulting site (Remisiewicz et al. 2009; Barshep et al. 2013). Our study shows that Common Snipe in the middle Pripyat River Valley exhibit rapid flight feather moult with large wing gap and low fat scores, which may suggest that this species employs moult migration and gather in suitable sites to undergo the whole process of wing moult before the movement to wintering grounds. Moreover, at that time, Common Snipe also renewed their wing coverts, rectrices, tertials, and most body feathers (OAG Münster 1975). The moult migration is quite common in ducks (Salomonsen 1968; Jehl Jr 1990), but there are only few wader species that combine elements of moult migration and staging at a single locality (Jehl Jr 1990). In our study, only 17 individuals (3.2%) were caught more than once during the season despite the high number of Common Snipe staging in the study area. The low number of recaptures may be because birds often avoid areas where they have been captured previously (Keyes and Grue 1982; Muraoka and Wichmann 2007). Yet, it may also indicate that large concentrations of moulting Common Snipe are only short-term and that the birds move between the sites where food abundance is high, like moulting Wood Sandpipers *Tringa glareola* in South African inland (Remisiewicz et al. 2009). Hence, it remains unknown whether moult migration regularly occurs in this species, but it seems that B-strategy with late and slow movement towards wintering grounds, allows Common Snipe to moult rapidly at the early stage of autumn migration and continue migratory flight with new flight feathers. Large summer and autumn aggregations of this species in the middle Pripyat River Valley are exceptional (Glutz von Blotzheim et al. 1977). Such concentrations of thousands of snipes have been recorded only in the areas abundant in food, such as sewage farms and fishponds or dam reservoirs with periodically released water (Kraus and Kraus 1972; OAG Münster 1975; Kunysz and Hordowski 1992; Janiszewski et al. 1998). Rapid flight feather replacement requires high food abundance (Wilson and Morrison 1981; Remisiewicz 2011) and perhaps this is why the large concentrations of the Common Snipe are not often observed. Hence, the described moult process may apply only to such unique conditions with large bird concentrations while individuals migrating in small flocks staging in lower quality sites may moult differently.

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Author contributions PP conceived the idea, and organized and performed the field study. WM analysed the data and wrote the manuscript. All read and approved the final draft of the manuscript.

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Data and code availability The data and code are available upon request to the corresponding author.

Declarations

Conflict of interest The authors declare there is no conflict of interest.

Ethical approval All conducted procedures followed Belarussian law.

Consent to participate Not applicable.

Consent for publication Not applicable.

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