

Primary moult of Eurasian Spoonbills *Platalea l. leucorodia* in the Wadden Sea in relation to age, breeding and migration

Arjen P. de Boer^{1,2,*}, Wouter M.G. Vansteelant^{1,2,3} & Theunis Piersma^{1,2,4}

de Boer A.P., Vansteelant W.M.G. & Piersma T. 2024. Primary moult of Eurasian Spoonbills *Platalea l. leucorodia* in the Wadden Sea in relation to age, breeding and migration. *Ardea* 112: 217–227. doi:10.5253/arde.2023.a19



Despite major implications, moult remains understudied compared with other major annual cycle phenomena such as breeding and migration. This is certainly true for Eurasian Spoonbills *Platalea l. leucorodia* for which even the primary moult has remained poorly described. Using digital photography, we studied primary moult of Spoonbills in the eastern Dutch Wadden Sea from July to October 2021. From the images that were sufficiently clear to quantify primary moult we obtained a total of 168 observations for immatures and 790 for adults. We aged spoonbills by the extent of black on the primary tips and scored their abdominal profile as an index of body mass. Progression of the descendent moult showed a distinct sigmoid pattern, implicating population turnover at the start and end of the study period. Also, few individuals completed moult in the study area. Therefore, we applied Underhill-Zucchini models to actively moulting individuals. As expected, immatures were estimated to initiate moult over a month earlier (11 June) than adults (20 July). Surprisingly, immature spoonbills moulted at a higher rate, which would allow immatures to complete primary moult in 131 days without suspension compared with 170 days in adults. As a fast moult may reduce feather quality, we speculate that the black wing tips of immature spoonbills may compensate for lower feather quality. Birds with low abdominal profile scores were observed only in July and August, but fat birds were seen throughout the study period. The incidence of suspended moult sharply increased through September in both age groups. By late September 30–40% of birds had suspended moult and abdominal profile scores peaked. This means that immature and adult spoonbills appear to synchronize the suspension of moult before migration, despite marked age differences in the onset and rate of primary moult. Spoonbills may benefit from synchronized migration by improving navigational accuracy and flight efficiency through collective decision-making and formation flights.

Key words: feathers, abdominal profile, annual cycles, migration, keratin, photography, waterbirds

¹BirdEyes, Centre for Global Ecological Change at the Faculties of Science & Engineering and Campus Fryslân, University of Groningen, Zaailand 110, 8911 BN Leeuwarden, The Netherlands;

²Rudi Drent Chair in Global Flyway Ecology, Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences, University of Groningen, P.O. Box 11103, Groningen, 9700 CC, The Netherlands;

³Theoretical and Computational Ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, The Netherlands;

⁴NIOZ Royal Netherlands Institute for Sea Research, Department of Coastal Systems, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands;

*corresponding author (arjenpdeboer@hotmail.com)

Feathers made of keratin are structures that are subject to wear and tear. As proper performance lasts less than a year for most feather types, birds replace them regu-

larly, often once or twice a year, a body maintenance process called moult (Payne 1972, Jenni & Winkler 2020). The growth of feathers is a resource-demanding

process (Murphy 1996, review in Jenni & Winkler 2020) and as birds with actively growing feathers may suffer functional handicaps with respect to insulation, ornamentation or flight (review in Jenni & Winkler 2020), the timing of moult of various feather tracts should be tightly integrated with other annual cycle challenges such as breeding and migration (e.g. Kjellén 1994, Buehler & Piersma 2008, Dietz *et al.* 2013). For example, migrants tend to separate moult, even of their body feathers, from long-distance migratory flights (Piersma & Jukema 1990, Zwarts *et al.* 1990, Jenni & Winkler 2020). In large species this poses problems because chick rearing time is long, and their large feathers require a disproportionately long time to grow (Hedenström 2006, Rohwer *et al.* 2009). As the length of a year is fixed, moult may be suspended before migration and resumed afterwards (Ginn & Melville 1983, review in Jenni & Winkler 2020). In such suspended moult, some feathers are completely replaced while others are left for later renewal, resulting in fully-grown wings consisting of two (and sometimes more) feather generations.

As discussed by Rohwer *et al.* (2009) and Jenni & Winkler (2020), larger birds have a hard time to fit even a single (and possibly suspended) descendent moult into an annual cycle. Such species may solve the problem by simultaneous or synchronous primary moult (in grebes Podicipedidae, flamingos Phoenicopteridae, waterfowl Anseriformes and cranes Gruidae; e.g. Piersma 1988, Jehl 1990), or breaking the primary moult up into stages, where moult is suspended at some point and resumed to complete it either within a year, or in multiple years. Rohwer *et al.* (2009: Figure 1C) showed that only three of c. 23 reviewed species heavier than 1500 g managed to complete primary moult without losing the capacity to fly.

More than 50 years ago, in their grand review of moult, Stresemann & Stresemann (1966) stated that Eurasian Spoonbills *Platalea l. leucorodia* (henceforth called 'spoonbills'), birds weighing up to 2 kg, would replace their outer flight feathers, the primaries, in a descendent way, i.e. that the primaries would be replaced from the innermost out, leaving a gap in the wing where new primaries are growing. Nevertheless, Stresemann & Stresemann (1966) added a question mark to the statement and it remains unclear on which data their inference is based. Bauer & Glutz von Blotzheim (1966) summarized the moult of spoonbills as follows: "Altvögel scheinen sowohl in Spätsommer und Früherbst als auch von Januar bis März im Winterquartier das Gesamte Gefieder zu wechseln, also im Laufe eines Jahr zwei Vollmausern durchzumachen.

Eingehendere Untersuchung der Mauser ist dringend erwünscht". ("Old birds seem to change their entire plumage in late summer and early autumn as well as from January to March in the winter quarters, i.e. they go through two complete moults in the course of a year. A more detailed study of the moult is urgently desired.") Thirty years later, Cramp & Simmons (1997) added some detail: "Wing moult starts with inner primaries in August–September; probably stops [i.e. is suspended] during migration, and is finished in winter quarters". Primary moult patterns of other species of spoonbill such as the Yellow-billed Spoonbill *Platalea flavipes* and the Roseate Spoonbill *Platalea ajaja*, remain largely undescribed as well (Dumas 2020, Matheu *et al.* 2020). Furthermore, age-related differences in moult patterns of spoonbills are not described at all.

We examined the primary moult of spoonbills in the eastern Dutch Wadden Sea from July to October 2021, using photos collected on Schiermonnikoog where spoonbills breed and from Lutjewad, on the mainland coast of the province of Groningen, a site where large numbers of Schiermonnikoog-breeders are joined by other spoonbills after the breeding season. Lutjewad is used as a staging site prior to the southward migration towards wintering grounds ranging from France to Senegal (Piersma *et al.* 2022). We aim to verify and expand the limited knowledge of the primary moult of spoonbills in quantitative ways using digital photography. Of particular interest are age differences in the onset and speed of primary moult, as well as the suspension of primary moult and its overlap with fuelling prior to southward migration. Assuming that the onset of moult is constrained by breeding activities, we expect non-breeding immatures to initiate moult several weeks before adults (Boere 1976). However, due to their greater experience and knowledge of resources in the Wadden Sea, adults may be able to moult faster, and achieve similar moult scores as immatures prior to migration.

METHODS

The study area in the eastern part of the Dutch Wadden Sea consisted of the system of intertidal flats and gullies bordered by the barrier island Schiermonnikoog in the north and the dike of the Dutch mainland, including the embanked Lauwersmeer in the south (Figure 1). Throughout summer, this entire area is used by spoonbills breeding on Schiermonnikoog (e.g. Lok *et al.* 2023). After the fledging of young, spoonbills

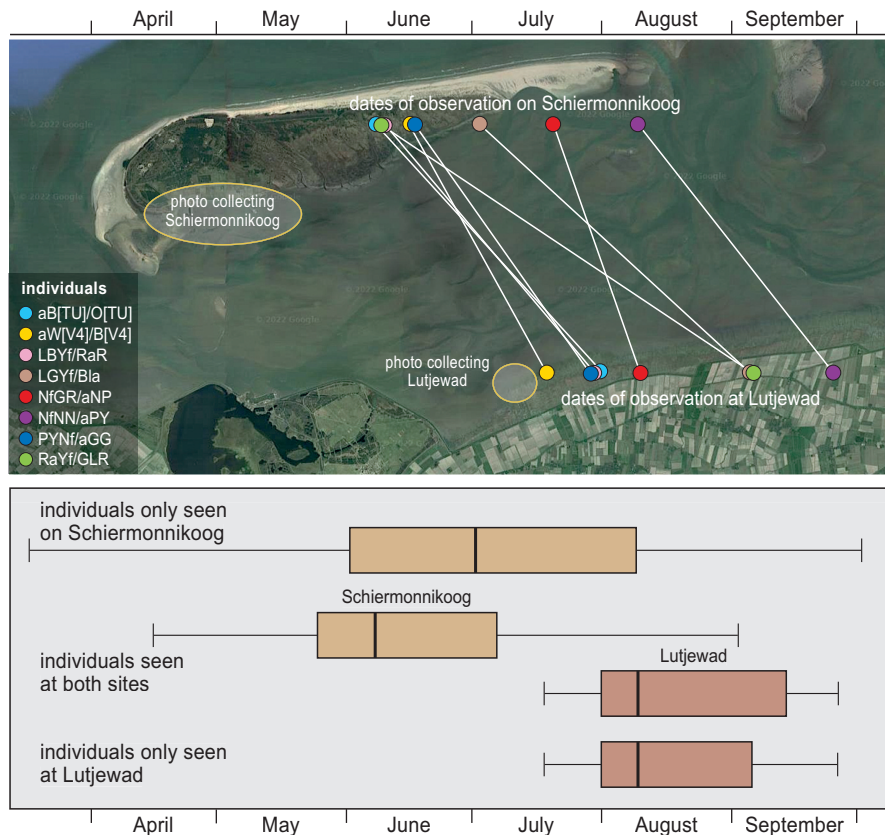


Figure 1. Study area of Schiermonnikoog and Lutjewad in the eastern Dutch Wadden Sea, along with examples of shifts of individually colour-ringed Eurasian Spoonbills from Schiermonnikoog to Lutjewad during July–September 2021 (top panel), and the distribution of observation dates of individually colour-ringed spoonbills at Schiermonnikoog and Lutjewad depending on whether they were seen at one or both study sites. The boxes enclose 50% of the data points, the vertical lines show the median date and the horizontal lines show the range of observation dates. Note that at Lutjewad observations only started in mid-July.

gradually leave the island for the mainland coast and the Lutjewad area in the province of Groningen appears to be of particular significance (Figure 1; Piersma *et al.* 2022). Accounting for these individual movements, to best ‘capture’ the entire primary moult cycle, observations were collected both at Schiermonnikoog and at the Groningen coast (Figure 1).

At Schiermonnikoog (53°28'N, 06°10'E) photographic sampling of spoonbills passing by in flight, at close or medium range, was performed every few days from 27 June to 1 October 2021. Most photos were taken as birds were flying in and out of a small lake, the Westerplas, and across the marina area in the southwest of Schiermonnikoog. On the Groningen coast off Hornhuizen (53°24'N, 06°20'E), just south of the low tide feeding grounds of Lutjewad (Piersma *et al.* 2022), 11 full field days were spent from 17 July to 27 September. Here, next to a high tide roost for waterbirds, we set up a hide four hours prior to high tide to avoid disturbance to the roosting birds. Roughly four

hours after high tide, after all spoonbills and other waterbirds had left on their own accord, the hide was dismantled and the study area left. At Schiermonnikoog a Nikon D500 body with a 300-mm f/4.0 lens was used, while at Lutjewad we used a Canon 7D Mark ii body with a 400-mm f/5.6 L lens.

Over 17,000 images were processed and examined using Adobe Photoshop Lightroom Classic CC. Minor contrast and lighting adjustments were occasionally applied to enhance visibility of primary feathers or growing primary pins. A total of 1471 usable images, each one representing a single data point, were obtained, 535 of which were collected on Schiermonnikoog and 936 on Lutjewad. 513 of these images were of juveniles hatched earlier that summer, recognizable by their light and fleshy coloured bills of relatively small size, and none of them showed any traces of primary moult. After excluding these images, a total of 958 images of non-juvenile spoonbills were used in the analysis.

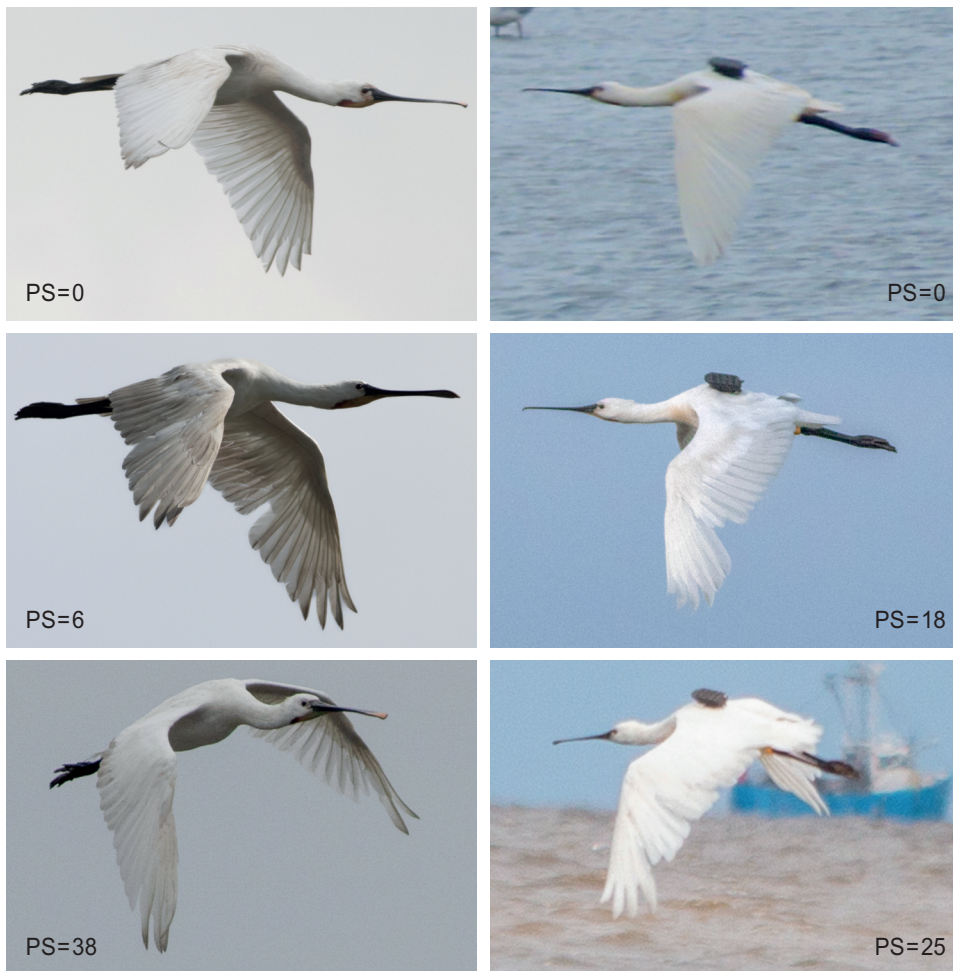


Figure 2. Typical field images used to score primary moult of Eurasian Spoonbills. On the left are three example images of anonymous individuals (photos by A.P. de Boer), on the right three images showing progression of moult in Sinagote (photos top to bottom by M. Muller, A.P. de Boer and S.K. de Vries), a female breeding on Vlieland and moving for moult to Lutjewad (see Piersma *et al.* 2022). PS = Primary Score.

Birds in flight were aged as ‘immature’ on the basis of black-coloured tips of especially the outermost primary flight feathers (Figure 3; for a review of this and other ageing criteria, see A. Hellquist at <http://surfbirds.com/mb/Features/spoonbill/ageing-spoonbill-0402.html>). Birds in their 2nd and 3rd calendar-year which are unlikely to have been breeding are called ‘immatures’. Birds with slightly mottled or completely white outer primaries were considered ‘adults’ (Figure 3).

High-quality photos, i.e. photos that were sharp and clearly showed all 10 primaries of at least one wing (Figure 2), were selected for scoring, for which we used the system widely used for birds in the hand (Ginn & Melville 1983). Here, each of the 10 primary feathers

received a score ranging from 0 to 5. Old feathers (showing wear or discoloration, score 0), a missing/shed feather (score 1), up to a third grown (score 2), up to two-thirds grown (score 3), up to completely grown (score 4) or completely grown (score 5). The resulting primary score was the sum of all primary feather scores, ranging from 0 to 50. As the scores 1–4 indicate growing feathers, moult suspension occurred when we observed primaries with scores of 0 and 5 in the same wing.

Jenni & Winkler (2020), on the basis of an in-depth review, conclude that the shedding intervals of primaries are such that a constant rate of feather material production is achieved. This results in the outer primaries of spoonbills, which are longer than the inner



Figure 3. Black wing tips of Eurasian Spoonbills. The extent of black on the tips of the outer primaries decreases with age and are approximated to calendar year (CY) as follows: (A) Juvenile, (B) 2CY, (C) 3CY, (D) 4CY, (E) Adult (photos by A.P. de Boer).

primaries, taking more time to fully regrow. To linearize the process of moult progression, we determined the proportions of feather mass grown (PFMG), ranging from 0 to 1 (Underhill & Joubert 1995). A set of slightly worn primaries was obtained from a deceased spoonbill and the dry mass of each primary weighed up to the nearest mg; the following averages of three measurements were used: P1 = 0.441 g, P2 = 0.473 g, P3 = 0.515 g, P4 = 0.591 g, P5 = 0.665 g, P6 = 0.793 g, P7 = 0.928 g, P8 = 0.925 g, P9 = 0.897 g and P10 = 0.757 g. The proportion of the feather mass grown in relation to the total mass of all primary feathers was calculated using the function ‘ms2pfmg’ from the R-package ‘moult’ (Erni *et al.* 2013).



Figure 4. The scoring of the abdomens of Eurasian Spoonbills in flight, from 1 (lean) to 5 (fat), inspired by methods routinely used in studies of geese (Owen 1981) and shorebirds (Wiersma & Piersma 1995; photos by A.P. de Boer).

To assess the body condition of spoonbills we used a 5-score abdominal profile index, as developed by Owen (1981) for the study of geese, and also applied to much smaller shorebirds (Wiersma & Piersma 1995). The abdominal profile of standing and walking spoonbills appeared impossible to score sensibly, possibly due to the often fluffed belly feathers. However, in flight the belly feathers seem to be held rather tightly to the body, and we therefore scored the abdominal profile (ranging from 1 = lean to 5 = fat) for birds in flight (Figure 4). Of the 958 images, 880 were suitable for abdominal profile scoring.

The number of repeat observations in our dataset is unknown, but not negligible. Although a substantial portion of birds using the area were colour-ringed, the colour ring combinations were not always completely

legible on images of birds in flight. 36 colour ring combinations of adults and immatures were read on the photographs, of which six were observed more than once a single day, and 11 of which were observed more than once throughout the observation period. A more easily recognizable individual in our images was ‘Sinagote’, a female with a rich history of observation (Piersma *et al.* 2022) carrying a black tracker on her back (Figure 2). From her tracking data we know that Sinagote was present at Lutjewad from 21 July to 14 September. During this period we had eight field days at Lutjewad and photographed Sinagote on four of these days. This suggests a substantial portion of repeat observations in our dataset.

All analyses were conducted in statistical software R v. 4.0.2 (R Core Team 2020). All graphs were produced

using the ‘ggplot2’ package (Wickham 2016). We first explored the general pattern of moult progression visually, by comparing running averages of moult scores with a loess-smoothing procedure in ggplot2. This revealed a sigmoidal trend, indicating population turnover at the start and end of our study period. Moreover, our data indicate that our study period did not cover the beginning of the moult period, especially for immatures, and the completion of moult (in both age groups). Therefore, to estimate the start dates and rate of moult of different age cohorts we used type 3 Underhill-Zucchini models (Underhill & Zucchini 1988), which are implemented by the function ‘moult’ of the R-package ‘moult’ (Erni *et al.* 2013). The type 3 model uses only actively moulting individuals (i.e. PFMG score > 0 and < 1).

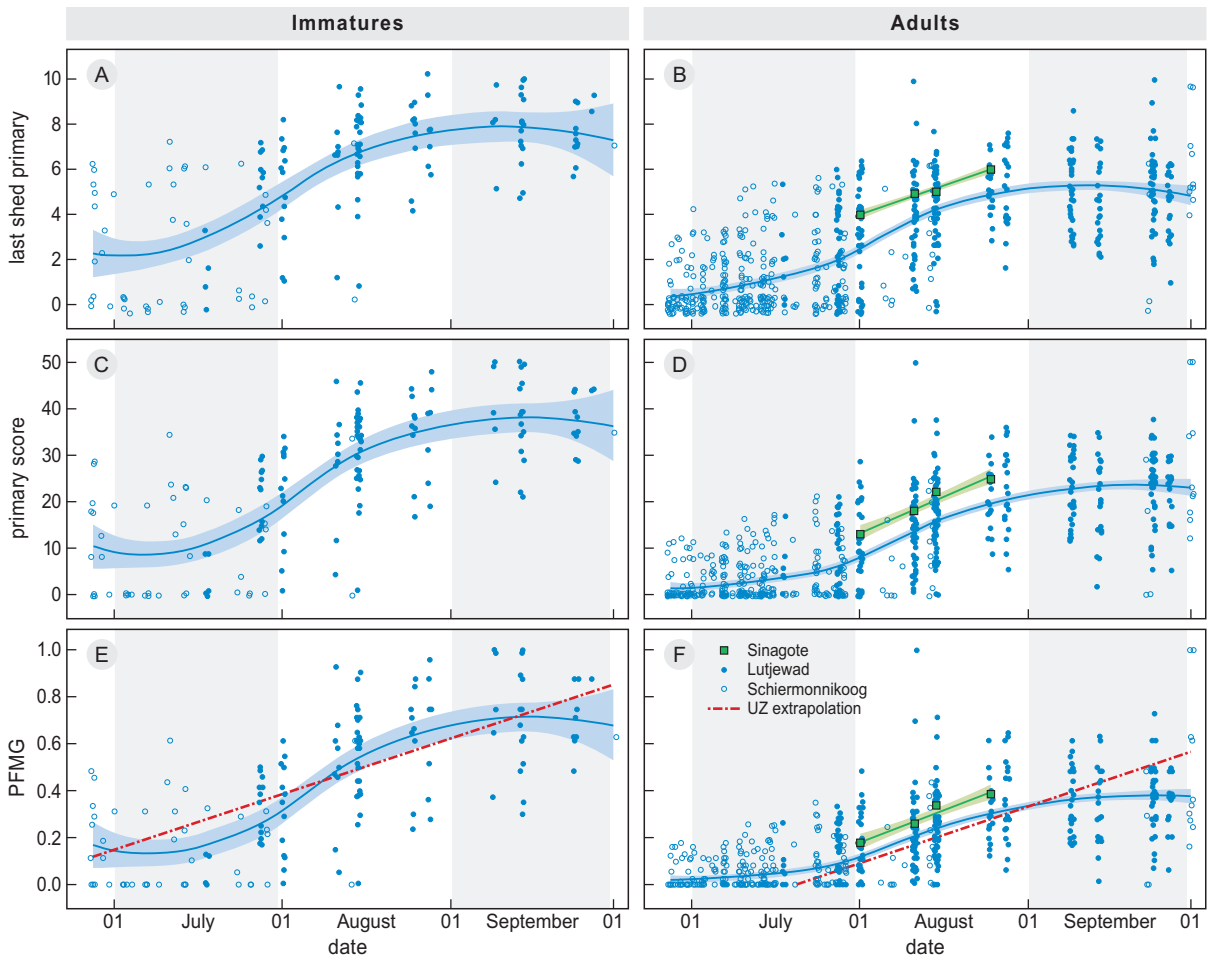


Figure 5. Seasonal progress of primary moult of immature (left) and adult (right) Eurasian Spoonbills expressed as: (A,B) the number of the last shed primary, (C,D) the primary moult score and (E,F) the Proportion Feather Mass Grown (PFMG). The data points for the individual called ‘Sinagote’ are marked in green. The blue curves are running averages with a 95% confidence interval to describe seasonal patterns. The extrapolations from the UZ models are shown as red lines (E&F).

RESULTS

The primary scores of spoonbills from the eastern Dutch Wadden Sea increased over time, with some immatures achieving scores of 20–30 (i.e. 4–6 newly grown primaries), and some adult scores up to 10–12 (i.e. 2 newly grown primaries) in late June (Figure 5). Few individuals completed primary moult in our study area.

As anticipated on the basis of individuals moving from Schiermonnikoog to Lutjewad in the course of the study period (Figure 1), the overlapping data distributions from the two sites are consistent with the idea that we were sampling the same population at both locations. The progress in primary moult scores was not linear over time, regardless of whether it was measured in terms of the last shed primary, primary score, or PFMG (Figure 5). Running averages computed over our full dataset (including birds that did not yet start moult

and those that completed moult), showed clear sigmoidal trends. By contrast, the steady, linear progress of primary moult of the repeatedly photographed individual Sinagote nicely paralleled the steepest slope of the running average during the middle of our study period (Figure 5B, D, F). According to type-3 Underhill-Zucchini models (Table 1), immatures would need 131 days to grow all primaries (starting on 11 June) whereas adults would require 170 days (starting on 20 July), without any suspension. We cannot estimate the real end date of moult, because this would depend on how long it is suspended during and after migration.

The proportion of scored spoonbills with suspended primary moult in Lutjewad and on Schiermonnikoog was rather low, rising sharply only from September onwards to 35% of immatures and 40% of adults by late September (Figure 6A). Only three immatures out of 168 samples were scored as having completed primary moult and only one out of 790 samples for

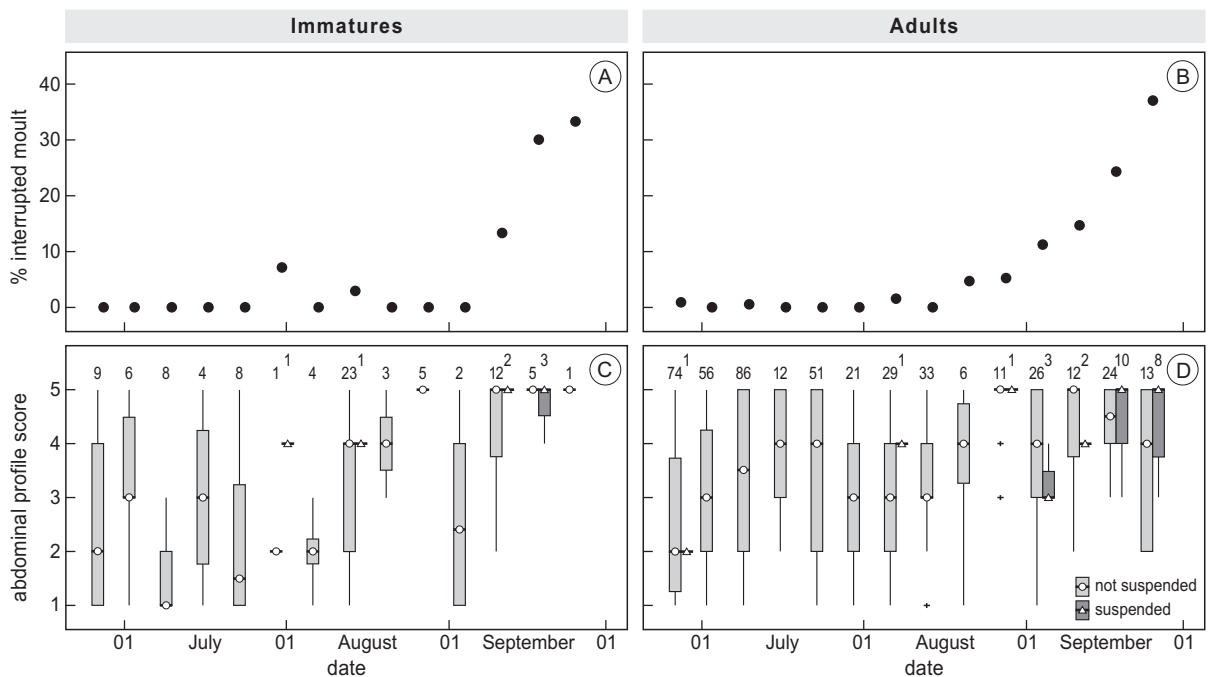


Figure 6. Seasonal change, at weekly intervals from 27 June, in the incidence of the suspended moult in immatures (left) and adult (right) Eurasian Spoonbills (top row) and the distributions of their abdominal scores (bottom row).

Table 1. Moult parameters for immature and adult Eurasian Spoonbills according to the Underhill-Zucchini method.

Subset	Start date (SE)	SD (SE) (days)	Moult duration (SE) (days)
Immatures	11 June (13)	30 (5)	131 (25)
Adults	20 July (5)	27 (2)	170 (16)

adults. Lean birds were only found until September, but fat birds were seen throughout the study period (Figure 6B), with immature birds slightly lagging behind adults (Figure 6C). As such, spoonbills' abdominal profiles increased well before they suspended their moult.

DISCUSSION

The observations reported here confirm the inferences by both Stresemann & Stresemann (1966) and Bauer & Glutz von Blotzheim (1966) that Eurasian Spoonbills show a descendent primary moult. Very few birds, however, completed primary moult in the Wadden Sea and only 35–40% of birds observed in September suspended primary moult before migrating. We suspect that most Spoonbills leave their moulting area as soon as moult is suspended and are therefore underrepresented in our sample. In addition, based on post-breeding movements of GPS-tracked Spoonbills (unpublished data), it seems likely that at least some of the birds that initiated moult at our study site moved to other nearby staging sites before suspending moult and initiating migration. Moult suspension is consistent with the suggestion in Cramp & Simmons (1997) that primary moult stops (i.e. is suspended) during southward migration, so that spoonbills would have to complete the moult in their winter quarters. Thus, we have been able to empirically underpin the sparse existing descriptions of spoonbill primary moult.

Furthermore, adults started primary moult about five weeks later than immatures. This was expected based on the idea that breeding and moult will be separated in time in most species (Boere 1976). This is certainly the case for Sinagote, a female who, after having tended chicks, was photographed on Vlieland on 13 July without any signs of moult. She was later photographed at Lutjewad, c. 90 km to the ENE, on 1 August with a primary score of 13 and P4 being the last shed primary and on 25 August with a primary score of 25 and P6 being the last shed primary.

Our results also confirm that moult is separated in time from migration in spoonbills. Indeed, the incidence of suspended moult sharply increased among birds of both age groups before they all left the summer range by late September. We also demonstrated that fuelling for southward migration completely overlapped with the moult of the inner half of the primaries in both age groups. Spoonbills thus avoided migrating with large gaps in the wing and seem to synchronize the suspension of post-breeding moult and fuelling between age groups.

Did we discover anything new? We may have, by showing that immatures not only start primary moult earlier, but also moult faster than adults according to the Underhill-Zucchini models. This allowed non-breeding immatures to replace 2–3 additional primaries (Figure 5) compared to adults, before the onset of migration. If continued without suspension, primary moult would be 39 days shorter in immatures than in adult birds; 131 days (a little over four months) as opposed to 170 days (five and a half months). On the basis of the scaling relationship presented by Hedenström (2006): $T_{\text{moult}} \text{ (d)} = 34.4 \times \text{body mass}^{0.19} \text{ (g)}$, the primary moult duration of a 1850-g spoonbill would be predicted at 144 days, which is considerably shorter than our estimate for adults and slightly longer than we estimated for immatures. This discrepancy could be due in part to imperfections in our study design, such as population turn-over during our study period. However, our estimates correspond strongly with a recent review by Scott & Underhill (2024, see Figures 9 and 10), as well as with the moult speed of Sinagote, which paralleled the steepest slope of the running average for adults in the middle of our study period, suggesting the discrepancy is due to other reasons.

The reviews of Dietz *et al.* (2015) and Jackson & Underhill (2022) suggest that if spoonbills moult like shorebirds, moult rates at more southerly latitudes might well be lower than in the Wadden Sea. Documenting differences in moult speed between sites would provide an interesting case of it being a function of location rather than of taxon only. The pattern of the suspended primary moult suggested in our study differs from the complete descendent moult shown by most shorebirds in the Wadden Sea including Red Knots *Calidris canutus* and Bar-tailed Godwits *Limosa lapponica* (Boere 1976, Dietz *et al.* 2013). Instead, the suspended primary moult, such as that of spoonbills, is characteristic of at least two inland shorebirds, i.e. Black-tailed Godwits *Limosa l. limosa* (van Dijk 1980) and Ruff *Calidris pugnax* (Koopman 1986).

As adults have less time to replace the primaries (between breeding and migration) than young non-breeders, it may come as a surprise that the moult speed of experienced adults is slower than that of immatures. Then again, slower feather growth tends to result in higher quality feathers (Dawson *et al.* 2000, Hera *et al.* 2009); according to Scott & Underhill (2024), a moult duration of 170 days would lead to 'good quality' feathers for a bird the size of a Spoonbill, while 131 days would be placed in the 'poor quality' category. This means that the faster moult of immatures likely results in feathers of lower quality, which



may shed a new light on the fact that immature spoonbills grow their outermost primaries with a black tip and all primaries with a black rachis, a physical trait common to all spoonbill species (del Hoyo 1992). Black keratin is stronger than white keratin (Jenni & Winkler 2020). Thus, black-tipped primaries of juveniles and immatures may represent a compensatory investment in feather strength. Such a ‘protective cap’ may also help young spoonbills to cover longer periods with a single set of primaries compared to adults. After all, juvenile feathers grown in May–July will need to last at least until June–Sept of the next year, i.e. 14 months. Some outermost primaries need to last even longer until after the second southbound migration in Sept–Oct of their second calendar year, i.e. 15–16 months or more. The ‘operational time’ of flight feathers will ultimately decrease to roughly 12 months in adult spoonbills.

In spoonbills photographed in flight during southward migration, e.g. during their crossing from Spain to Morocco (Piersma *et al.* 2020), we were unable to find birds with moult gaps. This means that we now need to know where and when the spoonbills that started primary moult in the Wadden Sea complete it. If they would resume moult upon arrival on their individual wintering grounds (Lok *et al.* 2011), we expect to find spoonbills actively moulting primaries in October–November from Atlantic France in the north to

Senegal in the south. Alternatively, if they resemble the closely related ibises (Threskiornithinae), spoonbills may resume moult only in the latter stages of the non-breeding period before spring migration (Davis & Kricher 2020). Either way, we expect Eurasian Spoonbills to complete their descendent moult within a single non-breeding period.

All considered, we think our most significant finding is that immature and adult spoonbills synchronize the suspension of moult ahead of migration, regardless of marked age differences in the onset and rate of primary moult, with more new primaries in place in immatures than in adults. For immatures and adults with prior migratory experience this synchronization is probably not essential for learning viable routes and non-breeding destinations (Mueller *et al.* 2013, Aikens *et al.* 2022, Lok *et al.* in prep). However, there is ample evidence to suggest that synchronizing (pre-)migratory activities may also allow experienced spoonbills to achieve safer and more efficient long-distance flights, e.g. through collective navigation (Guttal & Couzin 2010, Berdahl *et al.* 2018) and formation flight (Weimerskirch *et al.* 2001, Portugal *et al.* 2014). The next vanguard question is how they achieve this synchronization. The recent discovery of frequent vocal communication at post-breeding and stop-over sites certainly suggests that spoonbills actively deliberate migratory departures (Lagarde & Piersma 2021).

ACKNOWLEDGEMENTS

First of all, we like to thank Folkert Abma and Marjolein Leenknecht for taking the time to photograph spoonbills in flight on Schiermonnikoog and making their material available. We thank Michiel Muller for his photos of Sinagote and other spoonbills from Vlieland. We also thank Petra de Goeij for helping set up field work at Lutjewad and Suzanne de Vries for filling in for Arjen de Boer on two field days. Tamar Lok curates the colour-ring resighting database of Werkgroep Lepelaar and shared the relevant data to summarize movements of individuals from Schiermonnikoog and Lutjewad in 2021. Lukas Jenni kindly discussed issues and two anonymous reviewers gave helpful feedback.

REFERENCES

- Baikens E.O., Bontekoe I.D., Blumenstiel L., Schlicksupp A. & Flack A. 2022. Viewing animal migration through a social lens. *Trends Ecol. Evol.* 37: 985–996.
- Bauer K.M. & Glutz von Blotzheim U.N. 1966. *Handbuch der Vögel Mitteleuropas*: Band 1. Akademische Verlagsgesellschaft, Frankfurt am Main.
- Berdahl A.M., Kao A.B., Flack A., Westley P.A.H., Codling E.A., Couzin I.D., Dell A.I. & Biro D. 2018. Collective animal navigation and migratory culture: from theoretical models to empirical evidence. *Phil. Trans. R. Soc. Lond. B* 373: 20170009.
- Boere G.C. 1976. The significance of the Dutch Waddensee in the annual life cycle of Arctic, subarctic and boreal waders. Part 1. The function as a moulting area. *Ardea* 64: 210–291.
- Buehler D.M. & Piersma T. 2008. Travelling on a budget: predictions and ecological evidence for bottlenecks in the annual cycle of long-distance migrants. *Phil. Trans. R. Soc. B* 363: 247–266.
- Cramp S. & Simmons K.E.L. (eds) 1997. *Handbook of the birds of the Western Palearctic*. Vol. 1. Oxford University Press, Oxford.
- Davis Jr. W.E. & Kricher J.C. 2020. Glossy Ibis (*Plegadis falcinellus*). In: Billerman S.M. (ed.) *Birds of the world*, v. 1.0. Cornell Lab of Ornithology, Ithaca, NY, USA.
- Dawson A., Hinsley S.A., Ferns P.N., Bonser R.H.C. & Eccleston L. 2000. Rate of moult affects feather quality: A mechanism linking current reproductive effort to future survival. *Proc. R. Soc. B* 267: 2093–2098.
- del Hoyo J., Elliot A. & Sargatal J. 1992. *Handbook of the birds of the world*. Vol 1. Lynx Edicions, Barcelona.
- Dietz M.W., Rogers K.G. & Piersma T. 2013. When the seasons don't fit: Speedy molt as a routine carry-over cost of reproduction. *PLoS ONE* 8: e53890.
- Dietz M.W., Rogers K.G., Gutiérrez J.S. & Piersma T. 2015. Body mass and latitude both correlate with primary moult duration in shorebirds. *Ibis* 157: 147–153.
- Dumas J.V. 2020. Roseate Spoonbill (*Platalea ajaja*). In: Poole A.F. & Gill F.B. (eds) *Birds of the world*, v. 1.0. Cornell Lab of Ornithology, Ithaca, NY, USA.
- Erni B., Bonnevie B.T., Oschadleus H.D., Altwegg R. & Underhill L.G. 2013. Moulting: An R package to analyze moult in birds. *J. Stat. Softw.* 52: 1–23.
- Ginn H.B. & Melville D.S. 1983. *Moult in birds*. British Trust for Ornithology, Tring.
- Guttal V., Couzin I.D. 2010. Social interactions, information use, and the evolution of collective migration. *PNAS* 107: 16172–16177.
- Hedenström A. 2006. Scaling of migration and the annual cycle of birds. *Ardea* 94: 399–408.
- Hera I. de la, Pérez-Tris J. & Tellería J.L. 2009. Migratory behaviour affects the trade-off between feather growth rate and feather quality in a passerine bird. *Biol. J. Linn. Soc.* 97: 98–105.
- Jackson C.H.W. & Underhill L.G. 2022. Primary moult strategies in adult migrant waders (Charadrii). *Wader Study* 129: 126–137.
- Jehl J.R. Jr 1990. Aspects of molt migration. In: Gwinner E. (ed.) *Bird migration: Physiology and ecophysiology*. Springer-Verlag, Berlin, pp. 102–113.
- Jenni L. & Winkler R. 2020. *The biology of moult in birds*. Helm, London.
- Kjellén N. 1994. Moulting in relation to migration in birds - a review. *Ornis Svec.* 4: 1–24.
- Koopman K. 1986. Primary moult and weight changes of Ruffs in The Netherlands in relation to migration. *Ardea* 74: 69–77.
- Lagarde F. & Piersma T. 2021. Vocal signalling by Eurasian Spoonbills *Platalea leucorodia* in flocks before migratory departure. *Ardea* 109: 243–250.
- Lok T., Overdijk O., Tinbergen J.M. & Piersma T. 2011. The paradox of spoonbill migration: most birds travel to where survival rates are lowest. *Anim. Behav.* 82: 837–844.
- Lok T., van der Geest M., Bom R.A., de Goeij P., Piersma T. & Bouten W. 2023. Prey ingestion rates revealed by back-mounted accelerometers in Eurasian Spoonbills. *Anim. Biotelem.* 11: 5.
- Matheu E., del Hoyo J., Garcia E.F.J. & Boesman P.F.D. 2020. Yellow-billed Spoonbill (*Platalea flavipes*). In: del Hoyo J., Elliott A., Sargatal J., Christie D.A. & de Juana E. (eds) *Birds of the world*, v. 1.0. Cornell Lab of Ornithology, Ithaca, NY, USA.
- Mueller T., O'Hara R.B., Converse S.J., Urbanek R.P. & Fagan W.F. 2013. Social learning of migratory performance. *Science* 341: 999–1002.
- Murphy M.E. 1996. Energetics and nutrition of molt. In: Carey C. (ed.) *Avian energetics and nutritional ecology*. Chapman & Hall, New York, pp. 158–198.
- Owen M. 1981. Abdominal profile - a condition index for wild geese in the field. *J. Wildl. Manage.* 45: 227–230.
- Payne R.B. 1972. Mechanisms and control of molt. In: Farner D.S. & King J.R. (eds) *Avian biology*, vol. 2. Academic Press, New York, pp. 103–155.
- Piersma T. 1988. The annual moult cycle of Great Crested Grebes. *Ardea* 76: 82–95.
- Piersma T. & Jukema J. 1990. Budgeting the flight of a long-distance migrant: changes in nutrient reserve levels of Bar-tailed Godwits at successive spring staging sites. *Ardea* 78: 315–337.
- Piersma T., de Goeij P., Bouten W. & Zuhorn C. 2022. Sinagote, the biography of a spoonbill. Lynx Edicions, Barcelona.
- Portugal S.J., Hubel T.Y., Fritz J., Heese S., Trobe D., Voelkl B., Hailes S., Wilson A.M. & Usherwood J.R. 2014. Upwash exploitation and downwash avoidance by flap phasing in ibis formation flight. *Nature* 505: 399–402.
- R Core Team 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

- Rohwer S., Ricklefs R.E., Rohwer V.G. & Copple M.M. 2009. Allometry of the duration of flight feather molt in birds. *PLoS Biol.* 7: e1000132.
- Stresemann E. & Stresemann V. 1966. Die Mauser der Vögel. *J. Ornithol.* 107: 1–448.
- Scott T. & Underhill L.G. 2024. Global review of quantitative studies of primary moult of birds using the Underhill-Zucchini moult model. *Front. Bird. Sci.* 3.
- Underhill L.G. & Joubert A. 1995. Relative masses of primary feathers. *Ring. & Migr.* 16: 109–116.
- Underhill L.G. & Zucchini W. 1988. A model for avian primary moult. *Ibis* 130: 358–372.
- van Dijk A.J. 1980. Waarnemingen aan de rui van de Grutto, *Limosa limosa*. *Limosa* 53: 49–57.
- Weimerskirch H., Martin J., Clerquin Y., Alexandre P. & Jiraskova S. 2001. Energy saving in flight formation. *Nature* 413: 697–698.
- Wickham H. 2016. *ggplot2: Elegant graphics for data analysis*. Springer-Verlag, New York.
- Wiersma P. & Piersma T. 1995. Scoring abdominal profiles to characterize migratory cohorts of shorebirds: An example with Red Knots. *J. Ornithol.* 66: 88–98.
- Zwarts L., Ens B.J., Kersten M. & Piersma T. 1990. Molt, mass and flight range of waders ready to take off for long-distance migrations. *Ardea* 78: 339–364.

SAMENVATTING

De rui is een belangrijk aspect in het vogelleven, maar relatief weinig onderzocht vergeleken met andere belangrijke onderwerpen, zoals het broedgedrag en de vogeltrek. Dit geldt ook voor de Europese Lepelaar *Platalea l. leucorodia*, waarvan de slagpenrui slechts marginaal is beschreven. Wij onderzochten van juli tot oktober 2021 in het oosten van de Nederlandse Waddenzee aan de hand van foto's de slagpenrui van Lepelaars.

Beeldmateriaal waarop de slagpenrui duidelijk te zien was, leverde in totaal 168 waarnemingen van jonge en 790 waarnemingen van volwassen Lepelaars op. De leeftijd werd bepaald aan de hand van de grootte van de zwarte vleugeltoppen, het lichaamsgewicht werd gescoord aan de hand van de ronding van de buik. De voortgang van de rui verliep volgens een duidelijk sigmoïd patroon, wat een indicatie is voor een sterke turnover van vogels aan het begin en het einde van de onderzoeksperiode. Slechts weinig individuen maakten de gehele slagpenrui binnen het onderzoeksgebied door. Om het begin en de snelheid van de rui te schatten aan de hand van een Underhill-Zucchini-model hebben we alleen gegevens van actief ruiende vogels gebruikt. Zoals verwacht, lag de geschatte startdatum voor jonge Lepelaars meer dan een maand eerder (11 juni) dan die van volwassenen vogels (20 juli). Jonge Lepelaars ruiden, met een geschatte ruiduur van 131 dagen (mits geen onderbreking), sneller dan volwassen vogels (170 dagen). Een snelle rui gaat ten koste van de kwaliteit van de veren, en we veronderstellen dat de zwarte toppen van de slagpenen van jonge Lepelaars daarvoor compenseren. Lepelaars met een laag lichaamsgewicht werden alleen waargenomen in juli en augustus, terwijl dikke Lepelaars gedurende de gehele periode werden waargenomen. Het aantal Lepelaars dat de rui onderbrak, nam in september snel toe, ongeacht de leeftijdscategorie. Aan het eind van deze maand was het lichaamsgewicht het zwaarst en had 30-40% van de Lepelaars hun slagpenrui onderbroken. Hieruit leiden we af dat jonge en volwassen Lepelaars het onderbreken van de rui synchroniseren nog voordat de wegtrek begint, ondanks de grote leeftijdsgebonden verschillen in start en duur van rui. Lepelaars kunnen voordeel onderkennen van gesynchroniseerd trekken met soortgenoten als gevolg van hun gezamenlijke route en formatievluchten.

Corresponding editor: Maja Bradarić

Received 19 April 2023; accepted 6 November 2023

SUPPLEMENTARY MATERIAL

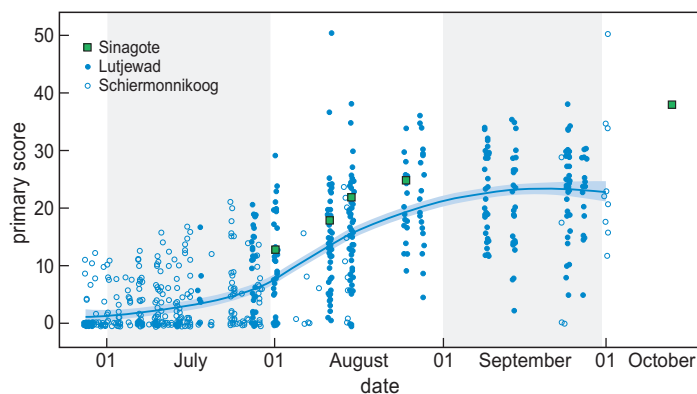


Figure S1. Footage of Sinagote flying over her wintering grounds in France on 13 October 2021, yielded one additional data point. She was filmed with a primary score of 38, with P8 being the most recently shed primary, over two-thirds grown.