



# Unusual pattern of skipped or shortened moulting of flight feathers in late-breeding Common Shelducks

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Received: 31 January 2022 / Revised: 21 April 2022 / Accepted: 23 April 2022 / Published online: 23 June 2022  
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## Abstract

Experimental studies have shown that individual wildfowl can shorten or skip moulting if the time between breeding and wintering is short; however, studies in wild birds are scarce. We tracked nine Common Shelducks *Tadorna tadorna* during the breeding and moulting seasons and determined the flightless time during moulting based on typical movement patterns. We found different movement patterns for two late-breeding females, suggesting that they skipped or shortened the moult of their flight feathers. These results provide a link between previous experimental studies and the situation in wild birds, likely reflecting an individual trade-off between the times allocated to moulting and breeding, respectively.

**Keywords** *Tadorna tadorna* · Flight feathers · Annual cycle · Wildfowl · Breeding season · Water bird

## Zusammenfassung

### Ungewöhnliches Muster einer übersprungenen oder verkürzten Mauser des Fluggefieders bei spät brütenden Brandgänsen

Experimentelle Studien haben gezeigt, dass die Mauser bei einzelnen Entenvögeln verkürzt oder übersprungen werden kann, wenn nur wenig Zeit zwischen der Brutzeit und dem Winter liegt. Studien an wildlebenden Vögeln sind jedoch selten. Wir haben neun Brandgänse *Tadorna tadorna* während der Brut- und Mauserzeit mit Satellitensendern verfolgt und ihre flugunfähige Zeit während der Mauser anhand typischer Bewegungsmuster für diesen Zeitraum bestimmt. Bei zwei spät brütenden Weibchen fanden wir ungewöhnliche Bewegungsmuster, die vermuten lassen, dass sie die Mauser des Fluggefieders übersprungen oder verkürzt haben. Diese Ergebnisse liefern eine Verbindung zwischen früheren experimentellen Studien und wildlebenden Vögeln. Wahrscheinlich spiegeln sie eine notwendige Abwägung zwischen der Zeit wider, welche individuelle Vögel für die Mauser und die Brutzeit zur Verfügung haben.

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Communicated by F. Bairlein.

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This paper is dedicated to the memory of Hermann Hötker who sadly died on July 24, 2019. We miss his inspiring thoughts, his expertise, and his distinctive humour.

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## Introduction

Birds need to moult and replace worn flight feathers to retain good flight capability. Most water birds moult all their flight feathers simultaneously once a year, resulting in a period of flightlessness (Jenni and Winkler 2020). The start, duration, and end of moult is controlled hormonally and linked to breeding and the photoperiod (Dawson 2008; Jenni and Winkler 2020). Prolactin levels peak at the end of the breeding period, and their subsequent decrease may affect the onset of moult (Dawson 2008). Moult starts shortly after breeding, while breeding can in turn delay the onset of moult (reviewed in Jenni and Winkler 2020). However, moulting of flight feathers must be completed before environmental conditions deteriorate in autumn (Düttmann et al. 1999; Jenni and Winkler 2020). The application of experimental

testosterone implants to artificially prolong the breeding stage interrupted or prevented moulting, suggesting that moult needs to start within a fixed time (Dawson 2008). Some species skipped breeding after a successful breeding season to catch up with moulting (Jenni and Winkler 2020), suggesting a trade-off between time allocated to breeding and moulting, respectively. Although partial and skipped moulting of flight feathers have been described in wildfowl including Whooper Swans (*Cygnus cygnus*; Campbell and Ogilvie 1982), Flying Steamer Ducks (*Tachyeres patachonicus*; Wilson et al. 2007), Lesser Magellan Geese (*Chloephaga picta picta*; Summers and Martin 1985), and Greater Magellan Geese (*C. picta leucoptera*; Summers 1983), these could not be linked to breeding activity. Difficulties in following non-breeding birds mean that skipped breeding as a result of moulting and skipped moulting as a result of late breeding, are likely to be more common than previously thought (Jenni and Winkler 2020).

Düttmann et al. (1999) used testosterone implants to simulate prolonged breeding stage in captive Common Shelducks (*Tadorna tadorna*; hereafter ‘Shelducks’); the later in the season they removed the implant, the more likely the individuals were to moult only part of their flight feathers or not moult at all. Shelducks from most of Europe migrate to a moulting area in the German part of the Wadden Sea after breeding to moult their flight feathers (Hoogerheide and Hoogerheide 1958). Based on these results and observations of wild species (see above), we carried out satellite telemetry of Shelducks during the breeding and post-breeding moulting periods. We first aimed to identify periods during which individuals were flightless as a result of moulting of their flight feathers. We also aimed to investigate if there was temporal constraint between breeding and moulting of flight feathers in wild Shelducks, and if late breeding might lead to shortened or skipped moulting of flight feathers.

## Methods

Shelducks were captured in breeding areas close to the moulting site in the Elbe estuary, Germany (distance: 25–60 km). Shelducks incubate from late April until mid-June (reviewed in Patterson 1982). We caught three late-breeding incubating females on 14th, 21st, and 22nd June 2011, using a small mist net (mesh size 3 cm) at the entrance of their burrow. One stopped breeding after being caught. We also caught six males from 20th May to 4th June 2012–2013 using a whoosh net (10×5 m, mesh size 4 cm; Pete Reid, UK). The birds’ body conditions were normal (mean females: 965 g; mean males: 1178 g; compare Patterson 1982). We equipped the birds with solar GPS transmitters (30 g each; Microwave Telemetry, MD, USA). Devices using ARGOS satellites ( $n = 7$ ) located individuals

four times per day during the breeding season (May to June) and hourly otherwise; devices using GSM satellites ( $n = 2$ ) located individuals depending on a battery charge, up to once a minute. The devices were attached using a 3-g Teflon-backpack harness following Roshier and Asmus (2009). The devices, including the harness, accounted for means of 3.4% of female and 2.8% of male body weights.

We conducted spatial analyses using QGIS (version 3.10.7; QGIS Development Team 2020). We measured the distances covered by individuals within 1 h during the moulting period (June–October; compare Kempf and Eskildsen 2000; Oelke 1969) and the distances to tidal channels, i.e. to permanent water bodies, at daytime low tide. Tidal channels were identified using bathymetry maps from 2011 to 2013 (Milbradt et al. 2015) and aerial photographs taken during low tide in 2008 (Google Earth Pro, version 7.3.3; Google LLC.2020) and 2013 (Folmer et al. 2014). Channels  $\geq 2$  m below sea level (NN) and with a diameter  $\geq 50$  m were classified as ‘major tidal channels’. In many places in the area, ebb tide usually drops about 1.57 m below sea level, and shallow water bodies with permanent water were not identifiable in the 2-m-scaled bathymetry maps. We therefore further analysed areas 0–2 m below sea level using aerial images. Channels with a diameter of 5–50 m were classified as ‘shallow tidal channels’. Low tide was classified as 1 h before until 1 h after minimal low tide. Tidal data were obtained from federal administration services (WSV, Tönning). The moulting area was defined following Kempf and Eskildsen (2000). We also noted when individuals crossed barriers, such as dikes and islands at low tide, likely by flying.

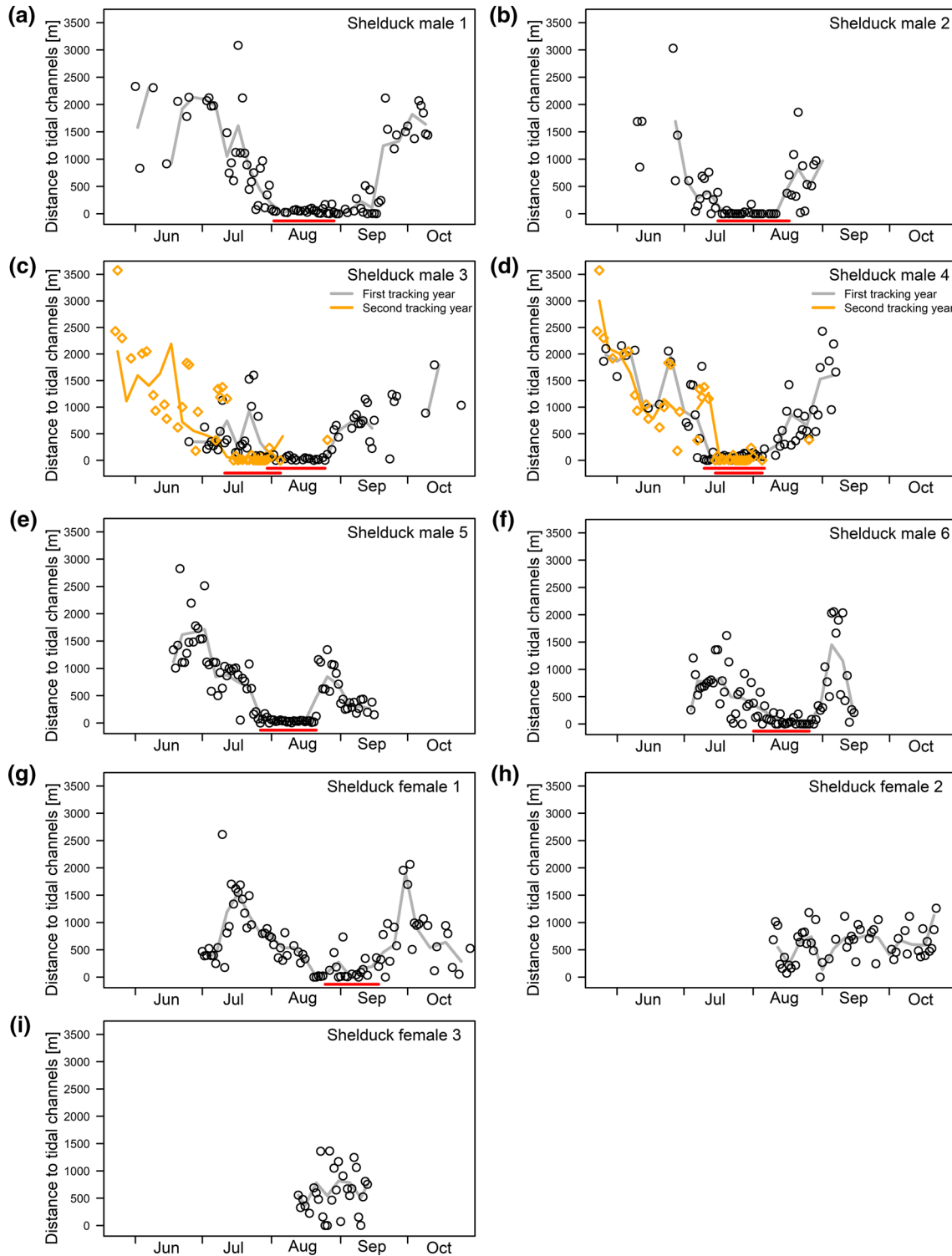
We compared the distance to tidal channels in the moulting area during and outside the moulting period using a generalized linear mixed model (GLMM, package *mgcv*) in R (version 3.6.2; R Core Team 2019), with individuals as random factors. We calculated several models and chose the one with the smallest Akaike Information Criterion, which was a Gaussian error distribution. We tested violations of the model assumptions visually using appropriate plots. We included a correlation structure (corARMA) to account for temporal autocorrelation (5th order). Slight heterogeneity of variances was accounted for by including the varIdent variance structure. We found slight aberrance from normality but assumed only a small bias because the AIC was smallest for the model with normally distributed errors.

## Results

During the moulting season, the mean distance to tidal channels at daytime low tide for all individuals combined was 602 m (interquartile range [IQR] = 66.5–921.9 m range = 0–3576.2 m). All six males and the female that

stopped breeding after being caught showed a 24–35 days period (mean = 28.4 days) with frequent locations close to tidal channels (Fig. 1) at daytime low tide (mean = 72.5 m;

IQR = 0.8–88.9 m; range = 0–733.6 m; Fig. 1). Most locations were close to major tidal channels (90.1%) compared with shallow tidal channels (9.9%). This was



**Fig. 1** Distances of individuals in the mouling area from tidal channels during daytime low tide. Circles show mean distance per day; line displays mean distance per pentad; gaps indicate periods in

which individuals had left the mouling area; red bottom line indicates periods classified as mouling

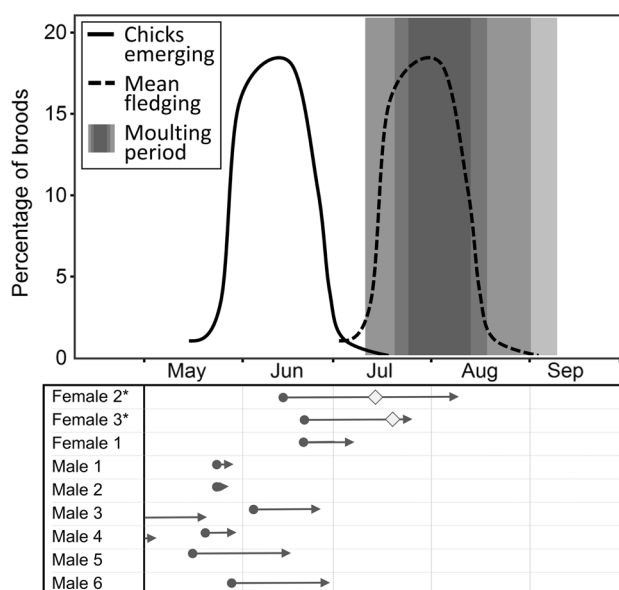
significantly different compared with the periods before and after (mean distance = 878.7 m; IQR = 363.7–1209.9 m; range = 0–3576.2 m; GLMM, estimate = 611.02, confidence interval [CI] = 519.2–702.8,  $p < 0.001$ ; Fig. 1). During the periods spent close to tidal channels, individuals did not cover long distances (Supplementary Appendix, Fig. A1) or cross any barriers (Supplementary Appendix, Fig. A2). Towards the end of those periods, individuals increasingly spent high tide within, rather than at the edges of salt-marshes, as before.

Two females showed different movement behaviours during the moulting season. One (Fig. 1h) left the breeding area on 9th August and moved to the moulting area. Six days later, she spent daytime low tide near a small tidal creek for 5 days (Fig. 1i). She once moved to a tidal flat 7 km away, in accord with the direction of water flow. This period was followed by frequent flights (movements against the tidal flow and covering large distances in a short time; Fig. 1h and appendix Fig. A1h). Another female left the breeding area on 25th July and was first located in the moulting area on 6th August (Fig. 1i). She was located near tidal creeks at daytime low tide on single days (Fig. 1i) and performed many long-distance movements against the tidal flow, either each day or  $\leq 6$  days apart (Supplementary Appendix, Fig. A1i).

## Discussion

Our results suggest that the period when Shelducks were located close to tidal channels during daytime low tide represented the period when they were flightless, due to moulting of their flight feathers. Previous studies showed that Shelducks usually frequented the rims of tidal channels during daytime low tides (i.e. close to permanent water bodies), when they were flightless during moulting, probably to allow them to escape from predators more easily (Oelke 1969). This was supported by our finding that during that the birds crossed no barriers and did not cover any long distances in a short time during this period.

However, this period of behaviour was not evident for two late-breeding female Shelducks, suggesting that they skipped moult or moulted incompletely. One showed typical patterns of moulting, including flightlessness, for 5 days compared with the scheduled 25–32 days (Hoogerheide and Hoogerheide 1958), suggesting that this individual did not perform a complete moult. The other female showed no period with typical flightless behaviour. Both females left their breeding area late (Fig. 2), and at least one was first located in the moulting area when the number of moulting Shelducks was already declining (Fig. 2), indicating that most had already finished or almost finished moulting, suggesting that both females faced a temporal constraint between breeding and moulting (reviewed in Patterson 1982, Fig. 2). Chicks from



**Fig. 2** Overview of Shelduck phenology based on satellite-tracked individuals. Solid curve: percentage of broods with emerging chicks (redrawn from Patterson 1982); dashed curve: percentage of fledging assuming a mean fledging time of 53 days (reviewed in Patterson 1982); shaded area: moulting period (darker colours indicate more moulting Shelducks in the moulting area in the Elbe estuary; redrawn from Kempf and Eskildsen 2000). \*Females with different moulting behaviour. Solid circles: date of catching and equipping with GPS devices (females during incubation); diamonds: end of incubation (females); arrowheads: leaving the breeding area. Note that males 3 and 4 were tracked during successive moulting periods

different broods mix in crèches, accompanied by the parents of one brood (reviewed in Patterson 1982), with around 58% percent of broods mixed in crèches, up to late July (Williams 1974). This coincides with an increase in moulting Shelducks in the moulting area (Fig. 2), suggesting that crèches enable adults to participate in moulting flocks. However, few adults remain in the breeding areas until September (Patterson 1982), leaving little time for moulting in adults that attend late-hatching chicks (Fig. 2). Speeding up moult seems unlikely, because shedding the wing and tail feathers simultaneously already minimizes moult duration, and although increasing the feather-growth rate might reduce the moult duration by a few days, it would also reduce feather quality, likely reducing survival and lowering breeding success in subsequent seasons (reviewed in Jenni and Winkler 2020). Kempf (1993) and Oelke (1969) found that late-moulting Shelducks were less likely to survive the following year, but no quantitative analyses were provided.

The present and previous results suggest that late-breeding Shelducks face temporal limitations in their annual cycle and face a trade-off situation, sometimes resulting in only partial or no moulting of their flight feathers. Our results thus provide a link between experimental endocrine and classical ecological studies in Shelducks. The study also

demonstrates the suitability of long-term GPS telemetry as a powerful tool to study moulting and identify rare moult-behaviour patterns.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10336-022-01989-y>.

**Acknowledgements** Most of the GPS devices were funded by Naturschutzbund Deutschland e.V. (NABU) via its ‘NABU Club’. The German Federal Environmental Foundation (Deutsche Bundesstiftung Umwelt) supported the research with their Scholarship Programme (AZ 20011/118) and funded one GPS device. We thank the Wasserstraßen- und Schifffahrtsamt (WSV) Tönning for providing tidal data, the Bundesamt für Seeschifffahrt und Hydrographie (BSH) for bathymetry data, and the National Park Administration Schleswig-Holstein for providing aerial photographs. Thanks to Dominic V. Cimiotti for support in the field, helpful discussions, and comments on a previous version of this manuscript. Moritz Mercker gave helpful advice on the statistics. Thanks to Hans-Heiner Bergmann, Wolfgang Fiedler, Bendikt Gießing, Klaus Günther, Kristian Lilje, and Andreas Schmidt for helpful advice on fieldwork. Thanks to Holger A. Bruns, Brigitte Kliner-Hötke<sup>†</sup>, Bernd Schaarschmidt and all other fieldwork helpers. Thanks to Hans Oelke<sup>†</sup> and Norbert Kempf for helpful discussions. Thanks to Susan Furness for language editing.

**Author contributions** Conceptualization: DSC (main), HH (support), SG (support); Methodology: DSC (main), Hermann Hötke (support), SG (support); Formal analysis and investigation: DSC (main), HH (support), SG (support); Writing – original draft preparation: DSC; Writing – review and editing: SG; Funding acquisition: DSC (main / equal), HH (main / equal), SG (support); Resources: SG (main), HH (support); Supervision: SG (main), HH (support).

**Funding** Open Access funding enabled and organized by Projekt DEAL.

**Data availability statement** The tracking data are archived at Movebank (<https://www.movebank.org>), and are available on request.

## Declarations

**Conflict of interests** The authors declare that no competing interests exist.

**Ethics statement** All institutional and national guidelines for the equipment and handling of birds were followed. Permissions were given by the Ministry of Energy, Agriculture, the Environment, Nature and Digitalization of the Federal State of Schleswig-Holstein (file number V 312–72241.123–34 (22–2/11)).

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