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Brief Report

Tracking Moulting Patterns in Atlantic puffins (*Fratercula arctica*): A Seven-Year Study at Oceanário de Lisboa

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Abstract: Moulting is a crucial yet challenging life-history trait to study in seabirds, particularly in the wild. Public aquariums offer valuable opportunities to collect detailed data, which, although not directly transferable to wild populations, provide important insights. At Oceanário de Lisboa, six *Fratercula arctica* individuals were monitored over seven years to document moulting patterns. The start and end of each moult were consistently recorded around the spring and autumn equinoxes. Pre-alternate moults lasted between 17 and 73 days, while pre-basic moults ranged from 11 to 48 days, with primary moults occurring between the two. This study is the first to document an asynchrony between the primary and the pre-alternate moults in *F. arctica*, highlighting a previously unreported aspect of the species' moulting process. This seven-year time series and its findings prompt a call for action for further studies in controlled conditions, to investigate this pattern under different conditions and across puffins' life stages. Such data could be crucial for developing more effective conservation strategies for this vulnerable species. These findings emphasize the importance of continued monitoring and research on ex situ puffin populations to expand our understanding of their moulting behaviour and its implications for wild populations.

Keywords: puffins; pre-alternate moult; pre-basic moult; ex situ setting; equinox; conservation

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1. Introduction

The Atlantic puffin (*Fratercula arctica*, Linnaeus, 1758) is classified as "Vulnerable" by the International Union for Conservation of Nature [1] due to a severe decline in breeding populations, following similar trends of other northeast Atlantic seabirds [2]. Alongside threats like overfishing and habitat loss [3], limited knowledge of this species' key life-history traits hampers effective conservation. Moulting, a critical phase, is poorly understood but known to increase mortality risk [4].

While the timing and process of moulting have been previously documented in some seabirds [4–7], it remains difficult to pinpoint for some species such as the Atlantic puffins [4,8,9], which spend most of the year at sea [10]. Recent studies using geolocators [11] and stable isotope analysis [12] have helped identify moulting periods, but more data are needed.

Ex situ studies of puffins, while not fully reflective of wild conditions [13], provide valuable insights into moulting patterns. These studies allow for the close monitoring of individuals and colonies in controlled environments, offering data otherwise unattainable in the wild.

After fledging at approximately 50 days post-hatch, puffins spend winters offshore [14]. Adults reach maturity at three years but typically breed from age five [8,15]. After breeding, they undergo a complete moult (neck, face, and wings). During this period, puffins shed their flight feathers in a catastrophic moulting pattern, where birds lose all or most of their primary flight feathers simultaneously, rendering them temporarily flightless, and vulnerable to predators, storms, and reduced foraging efficiency [4,12]. Compared with other alcids in the North Atlantic, puffins' moult, particularly of primary feathers, is often unsynchronised within populations and varies between individuals and colonies [4,16].

This study tracked the moulting patterns of Atlantic puffins kept in stable conditions for over two decades, providing valuable insights through controlled, long-term monitoring. Our findings help address significant knowledge gaps in this species' life history. Given the scarcity of moulting data in wild populations [11], particularly concerning timing, environmental influences, and the impact on individual health, controlled ex situ research is a crucial tool for advancing our understanding of puffin moulting behaviour.

2. Methods

2.1. Colony and Environmental Conditions

In 1997, 23 six-week-old Atlantic puffins were collected from the wild in Iceland and introduced to the Northern Atlantic Habitat at Oceanário de Lisboa in 1998. Each bird was fitted with coloured leg bands for long-term identification. Since then, food consumption and behavioural patterns have been qualitatively assessed, with empirical feather moult monitoring starting in 1998. A structured moult recording system was implemented in 2017. The puffins share their habitat with a 12-member *Uria aalge* (Pontoppidan, 1763) colony and a large collection of teleosts, elasmobranchs, and invertebrates.

The Northern Atlantic enclosure replicates rocky coastal habitats with a two-level design. The lower level features a 389 m^3, five-metre-deep saltwater aquarium with a 50-minute filtration turnover, complemented by waterfalls. The upper level is vegetated with Northern Atlantic flora such as *Cedrus atlantica glauca* and *Juniperus* sp. In the puffins' breeding season, nesting areas and cedar leaves are provided for environmental enrichment.

Water parameters are daily controlled: temperature at 13 °C, pH 8.10–8.15, salinity 31–32 ppt, dissolved oxygen at 99%, and other nutrient levels carefully managed. Air temperature ranges from 10 °C to 26 °C. Natural light illuminates the exhibit through an all-glass ceiling skylight. During autumn and winter, an artificial lighting system (20 × 400 W metal iodide spotlights) lights up the enclosure whenever the daily exterior medium luminance is below 12.500 Luxes from 10:00 to 20:30.

To keep handling stress to a minimum, each puffin was weighed once or twice a year. Throughout the study, the recorded weight data (n = 40) ranged from 340 g to 565 g, averaging 436.7 ± 58.3 g. As the puffins share their habitat with common murres and are fed simultaneously, individual food consumption or an evident change in appetite and body weight was not possible to quantify for the period of this study.

Puffins are hand-fed twice daily with fish species like sprat and capelin, with individual feeding records maintained. It is not possible to quantify the amount of food consumed by each puffin, as the remaining food (ad libitum) is provided to the entire colony after each hand-feeding session. Total food quantity is adjusted to minimize waste, ensuring adequate nutrition. Puffins' physical condition is tracked through daily observations, periodic weighing, and annual welfare assessments.

2.2. Data Collection and Analysis

From 2017 to 2024, six *Fratercula arctica* individuals (five from 2023) were closely monitored to determine their moult stages, with the start and end dates of each moult carefully recorded. Various terms exist to describe bird moults [7,17,18]. In this study, we used the terms pre-alternate moult (PAM) and pre-basic moult (PBM) [sensu 7] to refer to the summer, or breeding season, moult and the winter, or non-breeding season, moult, respectively. To minimise potential observer errors and given the subtle plumage changes (particularly in the face and neck) that signal the onset of each moult, all records were conducted by a single person, the primary aquarist responsible for that enclosure. While there were occasional days when this aquarist was unavailable, other trained aquarists documented any changes with notes and photographs for validation. Every moulting date was ultimately confirmed by the primary aquarist, minimising any potential bias in the dataset. For consistency, the following criteria for determining the onset and completion of the PAM was defined as follows: The onset of the PAM, or summer/breeding season moult, was identified by the initial appearance of small light grey or nearly white spots, which represent emerging feathers. The first day on which these new feathers become visibly detectable to the naked eye was recorded as the beginning of the moult period. The completion of the moult was defined as the point at which no further colour changes are observed on the birds' facial region. This was confirmed when all facial and neck feathers reached their final colouration, and the boundaries between light grey facial feathers and the darker feathers on the crown and neck were distinct and well-defined. Similarly, the criteria for the PBM moult were the following: The onset of the PBM, or winter moult, was identified by the appearance of small dark spots, indicating new feather growth on the puffin's face. The first visible appearance of these new dark feathers was recorded as the beginning date of the PBM. The completion of the PBM was marked when no further changes in feather colour were observed, and the face exhibits a uniformly dark appearance. This endpoint was more challenging to determine than that of the PAM, as the tonal differences in facial feathers were less distinct. Additionally, during this moult period, the puffins undergo a partial beak moult, with sections of the beak shell shedding at variable times. This beak moult was not associated with a specific phase of feather moult and could occur unnoticed, as it lacked a predictable timing or visual signal. This approach was also applied to the primary moult, where differences are more pronounced as all flight feathers are shed almost simultaneously. The moulting process was documented with images, capturing the birds both with and without their primary feathers, as well as in their breeding and winter plumages. For the primary moult, we used the term primary moult (PM), following Harris et al. (2014) [4], to define the period from the first day when all the primaries have shed until they have all fully regrown. Spearman's rank correlation was applied to investigate individuals' moult duration across years. PAM and PBM duration within individuals were analysed and compared with the yearly average moult duration. We further investigated the displacement of each moult's onset (PAM and PBM) to the spring and autumn equinoxes.

3. Results

3.1. Seven Years of PAM and PBM

The PAM and PBM duration of each puffin from 2017 to 2024 is presented in Table 1, with the annual average plus standard deviation for each moult type. The beginning and end dates of moulting for each bird in the mentioned years can be consulted in Supplementary Material, Table S1. The PAM duration ranged from 17 to 73 days, with an average of 30.8 ± 12.0 days for the seven years studied (n = 45). The analysis of mean PAM durations revealed that the fastest moulting occurred in 2020, with an average duration of 22.1 ± 3.3 days. Conversely, the longest PAM moulting period was observed in 2024, averaging 35.8 ± 19.9 days. For PBM, the fastest moulting for this time series was completed in 11 days, while the slowest took 48 days (average of 27.2 ± 7.5 days, n = 39). Comparing the yearly means, 2018 had the shortest average moulting duration of 22.6 ± 14.5 days, whereas 2023 had the longest, averaging 30.2 ± 8.6 days. No correlation was found in the PAM and PBM duration between the individuals along the analysed period ($p > 0.01$ for all Spearman Tests).

During the non-breeding season, puffins exhibit winter plumage, marked by darker feathers on the neck and head. In contrast, the breeding season is characterized by lighter feathers in these same regions. These seasonal variations in plumage can be observed in the same individual (P71), with the bird displaying darker pre-basic plumage (PB) and lacking primary feathers in January (Figure 1), while in July, it shows lighter pre-alternate plumage (PA) accompanied by new primary feathers (Figure 2).

Table 1. Moult type, pre-alternate moult (PAM), pre-basic moult (PMB), and primary moult (PM) average duration (days) of six *Fratercula arctica* (P18, P24, P25, P33, P43, P71) at Oceanário de Lisboa from 2017 to 2024. Annual average duration plus standard deviation is presented. Up-pointing and down-pointing arrows, respectively, indicate moult duration above or under the total average, for PAM (30.8 ± 12.0, n = 45) and PBM (27.2 ± 7.7, n = 39). The "na" stands for non-available data.

Year	Moults\PuffinID	P18		P24		P25		P33		P43		P71		Annual Average Moult Duration (Days) ± SD
2017	PAM	↓	20	↑	41	na		↑	33	↑	34	↑	32	32.0+/−7.5
	PBM	↑	34	↓	27	na		↓	25	↑	31	↑	34	30.2+/−4.0
2018	PAM	↓	30	↑	44	↓	25	↑	33	↑	31	↓	28	31.8+/−6.5
	PBM	↓	23	↓	11	na		↑	38	↑	31	↑	33	27.2+/−10.5
2019	PAM	↑	36	↓	30	↑	73	↓	22	↑	36	↓	17	35.6+/−19.8
	PBM	↑	35	↓	14	↑	39	↑	29	↑	31	↑	29	29.5+/−8.5
2020	PAM	↓	20	↓	23	↓	26	↓	23	↓	20	↓	21	22.1+/−2.3
	PBM	↑	29	↓	20	↓	19	↓	22	↓	20	↑	28	23.0+/−4.3
2021	PAM	↑	33	↓	20	↑	33	↓	21	↓	22	↑	31	26.6+/−6.2
	PBM	↓	25	↓	21	↑	48	↓	22	↓	19	↑	34	28.1+/−11.0
2022	PAM	↓	21	↓	29	↑	45	↓	26	↑	64	↓	21	34.3+/−17.0
	PBM	↑	30	↓	24	↓	21	↓	19	↓	24	↓	21	23.1+/−3.8
2023	PAM	↑	35	↓	20	na		↑	36	↑	31	↓	24	29.2+/−6.9
	PBM	↓	23	↓	20	na		↑	35	↑	41	↑	32	30.2+/−8.6
2024	PM		31		33	na			30		37		29	32.0+/−3.1
	PAM	↑	34	↓	23	na		↑	65	↑	32	↓	25	35.8+/−16.9

Figure 1. *Fratercula arctica* "P71" in January 2024 without primary feathers and displaying the characteristic pre-basic plumage (PB). Image credits: Rui Calado, 2024.

Figure 2. *Fratercula arctica* "P71" in July 2024, with new primary feathers and the pre-alternate plumage (PA). Image credits: Rui Calado, 2024.

Although the setting was controlled, environmental factors varied throughout the year. Water and air temperatures were considered when comparing the start and end dates of the puffins' moult. Between 2018 and the end of the study, the water temperature remained stable at approximately 13 °C due to husbandry restrictions for new animals in the exhibit. Before 2018, water temperatures ranged from 12.5 °C in winter to 15.5 °C in summer. The air temperature within the enclosure consistently ranged from a mean minimum of 13.6 ± 1.4 °C in winter to a mean maximum of 16.6 ± 1.8 °C in summer. The lowest recorded air temperature during the study was 9.4 °C, while the highest reached 26.6 °C. Yearly variation was very consistent throughout the years. In parallel, Lisbon's daily light hours, at 38°43′0.01″ N, 9°7′59.99″ W, and representing the daily hours of natural light that illuminates the puffin's exhibit, were measured. Light hours varied from 9.4 in Winter to 14.8 hours in the summer (average 12.2 ± 1.87 h, n = 2769 days).

Oceanário's daily light hours were calculated considering the artificial lighting system that lights up whenever the daily exterior medium luminance drops below 12.500 Luxes. This resulted in an increment up to 2.0 h (average 12.9 ± 1.1 h, n = 2769 days) as the daily natural light hours decreased and the automated lighting system compensated. Lighting adjustments occurred as the national legal hour is changed twice yearly around the spring and autumn equinoxes, frequently on the last weekend of March and October, respectively. No statistics were applied to test these reduced and yearly stabled environmental variations on the moults' beginnings or durations. A visual representation of these seven-year time series' parameters can be found in the preprint (DOI: 10.13140/RG.2.2.36807.30883).

The relation between the moults' beginnings and the autumn and spring equinoxes was investigated. Evidence that the start of each moult is very close to these environmental events is possible to notice in the PAM start with the spring equinox (Figure 3) and even more evident for the PBM start with the autumn equinox (Figure 4).

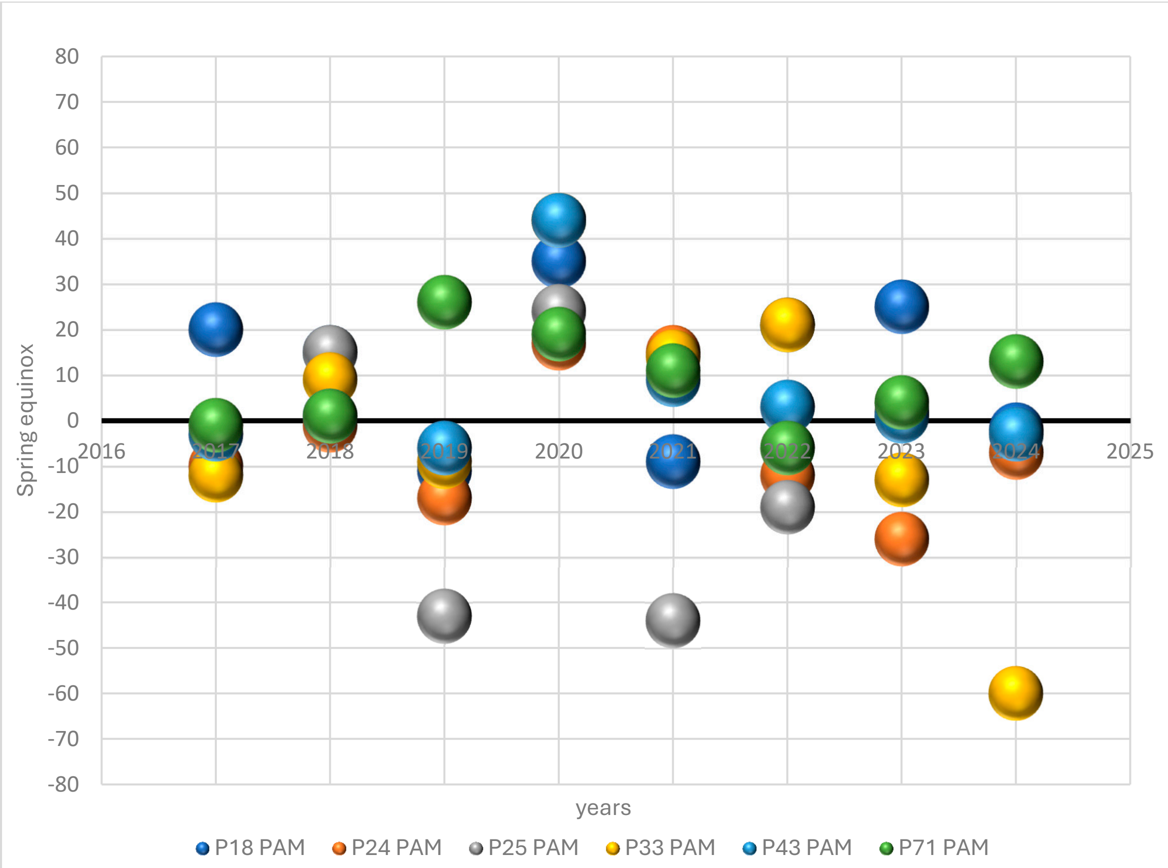

Figure 3. Difference in days between the beginning of each individual (P18, P24, P25, P33, P43, P71) pre-alternate moult (PAM) and the spring equinox (21/03) between 2017 and 2024.

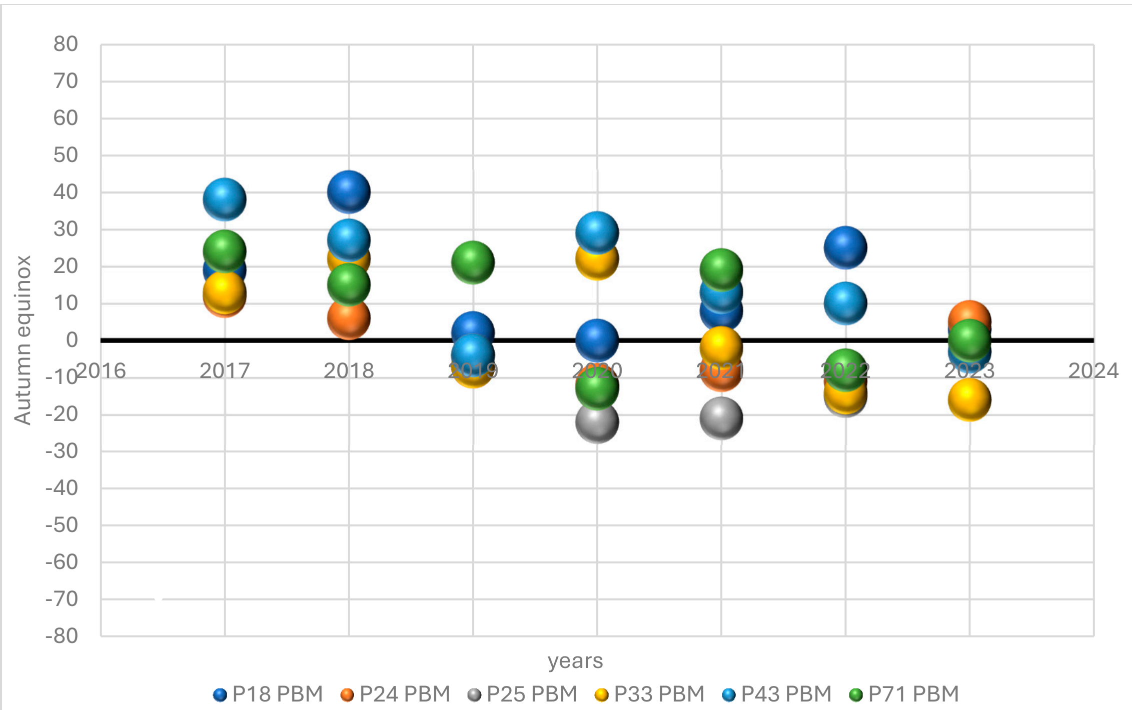

Figure 4. Difference in days between the beginning of each individual (P18, P24, P25, P33, P43, P71) pre-basic moult (PBM) and the autumn equinox (23/09) between 2017 and 2023.

3.2. Primary Moult Data

At the Oceanário de Lisboa, the primary moult of the five birds in the colony was recorded in January 2024. All individuals began shedding their primaries between January 8 and January 31, except for P18, who started on 1 February. This moult had an average duration of 32 days, with the fastest bird (P71) completing it in 29 days and the slowest (P43) taking 37 days. In 2024, each bird's primary moult (PM) occurred close to their pre-alternate moult (PAM), with the primary feathers being shed 15 to 30 days before the onset of each individual's PAM. Although primary moult is documented only for January 2024 in this study, similar observations in previous years prompted our decision to formally investigate and record this process.

4. Discussion

Moulting is a critical process for many seabird species, characterised by high variability and complexity, particularly as it often occurs at sea [11,12]. Several unresolved questions can be effectively and affordably studied in ex situ birds [19]. This study documents seven years of Atlantic puffins' moults, where PAM lasted between 17 and 73 days, averaging 30.8 $\pm$ 12.0 days (n = 45). PBM ranged from 11 to 48 days, with an average of 27.2 $\pm$ 7.5 days (n = 39). We observed the pre-alternate moult, characterised by the shedding of head and neck feathers, occurring in early spring, as previously reported by Pyle (2009). After this moult, the birds display their summer or breeding plumage. The pre-basic moult was observed from September to October, with one exception: P18 in 2018, which began moulting in early November (Table S1). During this phase, all body feathers except the primaries were shed. This finding is consistent with Pyle's (2009) suggested timing for total body feather moult, which occurs from August to October. PBM onset dates were more clustered around the equinox, showing less variation across individuals and years.

Moulting is typically triggered by changes in day length [13], suggesting that the colony's moults were likely influenced by seasonal daylight variations during the spring and autumn equinoxes. While artificial lighting in the Oceanário's enclosure may have caused slight shifts in moult timing, the birds still began moulting near the equinoxes. Despite living in an artificial environment for over two decades, these birds appear to follow similar timings of PAM and PBM to those seen in their wild counterparts. Bridge (2004) similarly observed natural moulting patterns in seabirds at SeaWorld San Diego, despite altered photoperiods. At this latitude (32°44′ N, 117°10′ W), summer daylight hours were extended to match conditions at 60° N, though winter daylight shortening was not possible, similar to Oceanário. The moulting durations of tufted puffins and common guillemots in that study were within the reported range. For Atlantic puffins, no moult duration data were available at that time, though it was stated that *F. arctica* shed secondary feathers only after the primaries emerged [5]. Various factors are expected to influence moulting in birds, including diet, temperature, photoperiod, and stressors like predators, affecting the timing, rate, and extent of moult, as well as plumage colour [20,21]. However, this study found no significant differences in moult durations across years, or a noticeable trend within individuals which, given the reasonably stable environmental conditions and small sample size, limited the need for further investigation into potential relationships between environmental factors and moult patterns in these ex situ puffins.

Moulting requires significant energetic and nutritional resources for feather growth [9,11,13]. Although an increased appetite was observed in hand-fed Oceanário puffins before moulting, we could not quantify changes in food intake or body weight. Primary feather moult is especially critical as puffins are flightless and vulnerable during this period at sea. The exact timings and durations of PM remain unclear [9,11,22]. Previous studies show variations in timing, with PM occurring between September and March [4,11], and sometimes after the breeding season [23]. However, the Anker-Nilssen et al. (2017) study suggests a different timing. In these authors' sample, over 200 puffin carcasses were analysed after a severe storm and most adults were close to finishing or had recently completed moult by the time of death, indicating a reduction in flight and diving ability [24]. This study provides evidence that, for most of the adult birds, primary moult completion and associated flightlessness occurred in January. Our findings support this timing, showing PM occurring in January, 15 to 30 days before the PAM and the breeding season. While our study only documents PM for 2024, previous identical empirical observations motivated this research. The duration of the primary moult we observed (29 to 37 days) aligns with the flightless period associated with the catastrophic moult in alcids, typically reported to last 19 to 40 days [12,19,25,26]. Additionally, it lines up with the late winter suggested by Pyle (2009). As this catastrophic moulting pattern likely evolved in alcids to shorten the moult duration and minimise the flightless period [13,15], it is noteworthy that the timing remains consistent even in managed environments, where food availability and foraging ranges are stable, and predation risk is minimal or absent. An observation not previously documented in the literature is the presence of a brief time gap between the end of these ex situ puffins' primary moult (when all new primaries have grown) and the onset of the PAM.

Further studies across institutions that keep Atlantic puffins are needed to collect more significant data (with larger samples) on moult triggers and the patterns of birds at different latitudes while defining criteria to support the moults' beginning and end dates. Comparing PAM, PBM, and PM timings will help to determine whether moults are tied to the equinoxes and other environmental factors. Future research should also aim to document moult patterns by age. Juvenile puffins, for instance, could moult their primaries twice a year, while adults do so once [11]. It could be further investigated if the PM and PAM overlap under different conditions, if ageing influences moult timing, or if abundant food and predator absence extend moult duration.

While our sample of puffins is limited, the findings provide valuable insights into *F. arctica*'s moulting patterns, contributing to a broader understanding, critical for improving species management and conservation in the wild while expanding knowledge of ex situ populations.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/jzbg5040049/s1, Table S1 The beginning, end dates, and duration of pre-alternate moult, and pre-basic moult of six *Fratercula arctica* at Oceanário de Lisboa, from 2017 to 2024; preprint dataset for the study (DOI: 10.13140/RG.2.2.36807.30883).

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Institutional Review Board Statement: All research procedures followed the ethical guidelines outlined by Oceanário de Lisboa and adhered to the legal requirements of the country in which the study was conducted. This study involved non-invasive observations of animals. Occasional weighing sessions were performed keeping restrain time and interference with the subjects to a minimum. The study design and protocol are under the European Union Directive 2010/63/EU. Every effort was made to minimize disturbance and ensure the welfare of the animals during the observational period.

Data Availability Statement: All data are available in the Supplementary Materials.

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