New biologging approach reveals unique flightless moult strategies of Atlantic puffins

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Abstract

Animal-borne telemetry devices provide essential insights into the life-history strategies of far-ranging species and allow us to understand how they interact with their environment. Many species in the seabird family Alcidae undergo a synchronous moult of all primary flight feathers during the non-breeding season, making them flightless and more susceptible to environmental stressors, including severe storms and prey shortages. However, the timing and location of moult remains largely unknown, with most information coming from studies on birds killed by storms or shot at sea. Using light-level geolocators with saltwater immersion loggers, we develop a method for determining flightless periods in the context of the annual cycle. Four Atlantic puffins (Fratercula arctica) were equipped with geolocator/immersion loggers on each leg to attempt to overcome issues of leg-tucking in plumage while sitting on the water, which confounds the interpretation of logger data. Light level and saltwater immersion time-series data were combined to correct for this issue. This approach was adapted and applied to 40 puffins equipped with the standard practice deployments of geolocators on one leg only. Flightless periods consistent with moult were identified in the dual-equipped birds, whereas moult identification in single-equipped birds was less definitive and should be treated with caution. Within the dual-equipped sample, we present evidence for two flightless moult periods per non-breeding season in two puffins that undertook more extensive migrations (> 2000km), and were flightless for up to 76 days in a single non-breeding season. A biannual flight feather moult is highly unusual among non-passerine birds, and may be unique to birds that undergo catastrophic moult, i.e. become flightless when moulting. Though our conclusions are based on a small sample, we have established a freely available methodological framework for future investigation of the moult patterns of this and other seabird species.

Introduction

Biologging and telemetry studies have greatly advanced our knowledge of the behaviour and distribution of far-ranging animal species (e.g. Jouventin & Weimerskirch 1990, Kooyman 1966). They have also provided insights into their behaviour especially when direct observation is impossible or impractical (e.g. Wilson et al. 1991, Michel et al. 2022), which is often the case for the many marine species that spend prolonged

periods at sea far from land (e.g. Weimerskirch et al. 2006, Doyle et al. 2015, Bennison et al. 2019, Brooke 2018). Long-term device attachment allows us to explore distribution and behaviour over broad timescales, such as diel patterns of movement (Seyer et al. 2021), and describe life-history strategies, such as migration (Amélineau et al. 2021) or periodic moult (Grissot et al. 2018). By looking at the behaviour of an animal in relation to its spatial and temporal distribution, it is possible to identify key areas of conservation concern, and identify drivers of declines (Frederiksen et al. 2012, Fayet et al. 2021).

Many of the world's seabirds are threatened and declining (Dias et al. 2019, Paleczny et al. 2015), creating a pressing need to better understand vulnerable stages of their annual cycle. Seabirds tend to be highly susceptible to the impacts of climate change, including sea temperature rise and shifts in prey distribution and abundance (Durant et al. 2003, Sandvik et al. 2005), as well as extreme weather events (Clairbaux et al. 2021), with large wrecks recorded following severe winter storms at sea (Harris et al. 2014, Morley et al. 2017, Anker-Nilssen et al. 2018). Larger members of the seabird family *Alcidae* (hereafter alcids) moult all their primary flight feathers simultaneously (Peery et al. 2008) leading to a protracted flightless period, placing them at greater risk from such dynamic stressors. Alcids are often the most common species washed ashore in storm wrecks in the northern hemisphere (Morley et al. 2017). Obligatory flightless moult places them at greater risk from storm events, as they would not be able to fly to avoid the storm track. Their vulnerability to predation may be increased by their silhouette in downwelling light, which can provide a visual cue to underwater predators (Ulman et al. 2015, Doyle et al. 2015) that they may struggle to escape from when flightless. It may also increase their vulnerability to surface pollutants, because of the increased time spent on the water surface and the inability to escape expansive films of harmful substances such as petroleum oil (Robertson et al. 2012).

The Atlantic puffin (*Fratercula arctica*), hereafter puffin, is a seabird species that has undergone rapid population declines across most of their European breeding range during the 2000s (Harris & Wanless 2011), leading to their classification as Endangered in Europe by the European Red List Assessment in 2015 (BirdLife International, 2015). Puffins must carefully time and locate their moult to coincide with sufficient food availability, which can be patchily distributed at sea (Fauchald 2009, Jessopp et al. 2013). Clairbaux et al. (2021) calculated the fasting endurance of puffins as $6.5 (\pm 2.5)$ days in mid-autumn, and $4.6 (\pm 0.6)$ days in winter. Local depletion of food during moult therefore puts puffins at risk of starvation. Anker-Nilssen et al. (2018) found that most puffins washed ashore in a post-storm wreck in southwest Norway in early 2016 were in the late stage of primary moult, and almost all individuals were emaciated. Even though many would have been able to fly by the time they were washed ashore, moult may have prevented them from escaping the storm when they were flightless, during which they clearly struggled to find food, despite a highly varied diet (Baillie & Jones 2004), especially during the non-breeding season (Falk et al. 1992, Harris et al. 2015).

The duration, timing, and location of moult in puffins has proven difficult to determine, because it occurs during the non-breeding season when birds are away from their colonies. In other alcids, moult takes place shortly after the breeding season (Gaston & Jones 1998, Peery et al. 2008), facilitating observation of moulting individuals. Harris et al. (2014) assessed moult stage based on feather development of puffins either washed ashore during storm wrecks or shot at sea. They reported primary flight feather moult in puffins at any time from September to March, with peaks in October and March, which is considerably more variable than that of other alcid species that undergo flightless moult (Gaston & Jones 1998). Identifying the flightless period of surviving individuals using biologging studies has so far proven difficult. Leg-mounted saltwater immersion loggers are commonly used to classify seabird behaviour during the non-breeding season. Reduced time spent flying, during flight feather moult for instance, is usually reflected by an elevated proportion of time the leg and logger are wet (Grissot et al. 2019). Puffins, like other alcids, repeatedly tuck their legs into the plumage when on the water (Harris et al. 2010, Linnebjerg et al. 2014, I. Sempere, Oceanário de Lisboa, pers. comms, figure 1), confounding simple behaviour classification using these loggers.

This study uses light-level geolocators with integrated saltwater immersion switches deployed on puffins to identify patterns of behaviour thought to be consistent with flightless moult. By combining data from four individuals with a geolocator on each leg (dual-equipped birds), we developed a behavioural classification

method using raw light and saltwater immersion data. We show that we can use results from dual-equipped birds to quantify and correct for behaviours that would confound traditional methods, therefore identify flightless periods assumed to represent moult. We then adapt and validate this method for single-equipped birds, for which there are far more data. This approach may help us to identify overwintering strategies and areas of conservation concern for puffins and other alcids, whose highly restricted mobility during flightless moult may compound the negative impacts of environmental threats.

Methods

Deployment and recovery of geolocator devices

Geolocators (seven BAS Mk18-L, and one Mk14) were deployed on both legs of four adult puffins during the 2010 summer breeding season on Skomer Island, Wales (51.737N, 5.297W). Single geolocators (31 Biotrack (2012)/Lotek (2020) Mk4083 and 12 BAS Mk18 (2010)) were deployed on 40 adult puffins during the breeding season in 2010, 2012 and 2020 on Skellig Michael, Ireland (51.771N, 10.539W). Birds at both colonies were captured during chick-rearing either using purse nets at burrow entrances or by hand from the burrow, weighed and fitted with geolocators before being released back to their burrow. Capture and handling times were kept to a minimum. Geolocators were attached to a coloured plastic ring fitted around the tarsus, with total deployment weight (devices plus leg ring and cable tie attachment) always < 2% body mass, under 6g for dual-equipped loggers, and under 3g for single-equipped loggers. These devices measured light every minute in 6-bit units from 0 (light is below civil twilight, sun > 6 degrees below the horizon) to 64 (sun is well above the horizon) and saved the maximum light level sampled in 5-minute intervals, or 10-minute intervals for the single Mk14 logger used. Saltwater immersion data were sampled every 3 seconds as binary units of 0 (dry) or 1 (wet) and the number of wet samples in 10-minute intervals were saved as values between 0 (all dry) or 200 (all wet). Devices were recovered from birds during the subsequent breeding seasons. All work was carried out under licence from the British Trust for Ornithology (CO/6143, C/5311), with work in Ireland further licenced by the National Parks and Wildlife Service (06/2020, C41/2020, 26/2010, C051/2011, C116/2012, C039/2013, 11/2013). Attachment of dual-equipped geolocators was granted ethical approval by the British Trust for Ornithology Unconventional Methods Technical Panel, with ethical approval for handling and tagging in Ireland also approved by the University College Cork Animal Ethics Committee. All analyses were performed using R version 4.1.2 (R Core Team, 2021), and all code to run these analyses are available online (github.com/JamieHDarby/puffin_moult).

Location data

Positions were obtained from light-level data using a threshold method (supporting information) following established procedures (Lisovski et al. 2019). Areas of apparent residency were identified over the non-breeding season (August to March) using Lavielle segmentation, following methods from Amelineau et al. (2021), and mean distance to the colony of each area of residency was calculated. Migratory effort was described as the distance to the furthest point of residency from the colony.



Figure 1: Different puffin at-sea behaviours and the position of the tarsus during each. Loggers were mounted on the tarsus of study individuals. Puffins trail their tarsus in flight (a), which leaves the geolocator exposed to light and dry. Puffins sitting on the surface of the water may lower one or both legs for paddling and balance (b), which leaves the tarsus submerged and exposed to light. Puffins inactive on the water may also tuck one leg into their plumage (c), obscuring the tarsus from daylight and keeping it dry. Puffins hunting for prey underwater will have their tarsus submerged and exposed to light levels attenuated by water (d), though this is unlikely to reduce actual light readings, which are taken as a maximum over 5 or 10 minute intervals.

Accounting for leg-tucking behaviour

Puffins tend to tuck their legs into their plumage while resting on the water, usually just one at a time, but sometimes both (supporting information figure S1, pers. obs.), leaving the logger dry despite the puffin being on the water surface (figure 1). This means it can be difficult to distinguish between flight and rest from a geolocator immersion signal alone (Fayet et al. 2016). We developed a new method that identified and accounted for leg-tucking using concurrent light signals. This works on the basis that light levels recorded by the logger will be lower than expected for a given solar angle if the logger is obscured (supporting information), i.e. tucked into plumage (figure 1). Solar angles were calculated based on astronomical formulae using date, time, and location. These lower-than-expected light fixes were classified as tucking, and were appended to concurrent immersion data using a time series merge implemented using the *xts* package (Ryan & Ulrich 2020) to account for missing or delayed points in either data stream. The immersion data points associated with these fixes were adjusted to 100% wet, to reflect that they were assumed to be resting on water despite the logger reading fully or partially dry. This correction could only be applied to data occurring during daylight hours (solar angle > -6 degrees) and not during the hours of darkness.

Combining data from dual-equipped loggers

Immersion data from both leg tags were combined for each dual-equipped puffin, again using a time series merge implemented using the *xts* package. Proportions of time spent wet were compared pairwise for each fix interval and the higher value retained in a single data stream. This meant that even if one leg recorded dry and the other recorded wet for the same time interval, the "wet fix" was preferentially retained. If one leg was submerged, then the puffin must have been resting on the water, and the "dry fix" was an instance of leg-tucking not captured by methods described in the previous section.

Identifying moult periods in dual-equipped birds

We then assumed the corrected proportion of time spent dry per day was time in flight (prop_{flight}) and calculated the 5-day rolling average of this (prop_{flight-5}). Only values with a predicted solar angle of > -6 were used for this analysis, as some anomalous sustained dry periods were retained in nocturnal data points. Though these periods could in fact be due to sustained flight occurring at night, it is more likely due to puffins tucking both legs at once (Robertson et al. 2012, pers. obs.), or visits to the nest burrow approaching the breeding season. The tucking correction applied earlier will not have captured this on either leg's logger, as the expected light level at these low solar angles (< -6 degrees) is zero. An inferred flightless period of minimum 30 consecutive days was identified as a persistently low set of values of prop_{flight-5}, identified using an incrementing threshold. Put simply, days with prop_{flight-5} below this threshold value were defined as flightless. This value was iteratively increased from 0 by 0.0002 increments until a minimum sequence of 30 consecutive days were defined as flightless. This minimum duration was defined according to previous estimates of this species (Harris et al. 2010) and observations of captive puffins (D. Dial, National Aquarium USA, pers. comms). Moult was therefore defined as a continuous period of at least 30 days, during which little to no flight was inferred to have occurred by the processed immersion data. The same process was repeated, omitting any initially identified moult, to explore the possibility of a second flightless moult.

Testing single leg data in dual-equipped birds

A similar moult identification method was attempted using data from each dual-equipped logger in isolation. As before, the proportion of time spent wet was corrected for tucking behaviour using raw light signals. Any points with a solar angle below -3 degrees were omitted for this analysis, to ensure that leg-tucking was sufficiently captured using light data. Prop_{flight} and prop_{flight-5} were again calculated, and the same incrementing threshold method was used to identify putative moult periods of minimum 30 days duration. A maximum threshold value of 1% prop_{flight-5} was applied to restrict the likelihood of falsely identifying moult from noisy immersion time series. This meant that the 5-day rolling average of corrected flight, or prop_{flight-5}, had to remain below 1% for a period to be considered as moult. Independently derived inferred

moult periods were compared to combined data from dual-equipped loggers. Based on limited but good agreement (see results), the process was then applied to the geolocator data collected from 40 individuals equipped with single loggers from Skellig Michael, Ireland.

Observations from captive puffins

Several aquaria house captive puffins as part of displays. Aquarists from 3 of these facilities provided observations about moulting habits of their captive puffins to contextualise our results and test whether our conclusions were physiologically viable. We spoke to aquarists from Tierpark Bern, Switzerland, the National Aquarium, USA, and Oceanário de Lisboa, Portugal. All described variation in moulting behaviour, see details in supporting information. Further relevant observations are referenced as personal communications in the main text.

Results

Accounting for leg-tucking behaviour

Leg tucking was identified using raw light and immersion data streams from loggers from both single- and dual-equipped birds. Clear differences in raw immersion data can be seen from each leg of a single puffin, largely down to leg-tucking (figure 2A & 2B). Though we capture and account for much of the daylight leg-tucking using concurrent light data from the same logger (figure 2C), differences between corrected immersion time series from each leg suggests that not all leg-tucking is accounted for in this method (figure 2D & 2E). Data from both legs are therefore likely necessary to accurately identify flightless periods, i.e. primary feather moult (figure 2F). Using the dual-equipped loggers, we calculated that puffins spent 20.3% (SD = 18.9) of daylight hours tucking either or both legs, 10 times greater than the time spent in flight (1.9%, SD = 5.5). Puffins spent less than 1% of daylight hours in flight for 75% of days during the non-breeding period. Although the small sample size precluded detailed analysis, the proportion of time spent leg-tucking also varied with individual, time of year, and leg (supporting information).



Figure 2: Geolocator data process for a dual-equipped puffin (EJ47625) prior to moult identification, accounting for leg-tucking using raw light signals, and combining data from loggers on each leg. All data are displayed as a 2D rasterised time series. The x-axis represents calendar date, and the y-axis represents time in Universal Time Zone. A and B are the raw saltwater immersion signals from the puffin's left and right leg respectively. C highlights the data points inferred as leg-tucking using the raw light signals. D and E show the immersion data corrected for leg-tucking events shown in C, again for the puffin's left and right leg-mounted loggers, respectively. F shows the combined minimum of D and E, which represents the most accurate estimate of flight activity, given the data available. In F, data with a predicted solar angle of less than -6 are made semi-transparent to highlight the time series retained for moult detection. Consistent 0 values at night in F during April probably represent time spent in the burrow, i.e. neither leg wet.

Identifying moult periods from dual deployment birds

Table 1: Flightless moult periods identified in the four dual-equipped individuals. 1^{st} moult refers to the moult inferred by the first pass of the moult identification process, and 2^{nd} moult by the second pass of the same. A range of results are presented for each puffin, as results vary depending on which logger's time-series (left or right leg) is used as the basis for the combination of data.

ID	1^{st} moult start	1^{st} moult duration	2 nd moult start	2^{nd} moult duration
EJ47625	$8^{\rm th}$ - $16^{\rm th}$ Sep	35 - 45 days	$20^{\rm th}$ - $21^{\rm st}$ Feb	31 - 32 days
EL60569	$9^{\rm th}$ Sep	48 - 54 days	-	-
EL60573	17^{th} - 19^{th} Sep	33 - 35 days	$9^{\rm th}$ - $13^{\rm th}$ Feb	33 - 37 days
EL60648	$19^{\rm th} - 21^{\rm st} {\rm ~Sep}$	38 - 46 days	-	-

Each dual-equipped puffin had a moult period inferred to begin in September, while two had a second inferred moult period beginning in mid-February (table 1 & figure 3). There was some variation in the duration of moult, from 31 to 54 days. During inferred moult periods, the percentage of time spent dry according to raw immersion signals was 12.4%, while it was reduced to 4.2% when adjusted for leg tucking using data from a single leg. When data streams from both legs were corrected for tucking and combined, the proportion of time spent dry during inferred moult was 0.1%, compared to 2.4% for the rest of the non-breeding season. There was no marked increase in percentage of time spent leg tucking when undergoing moult (supporting information), consistent with observations of captive puffins (M. Huwiler, Tierpark Bern, pers. comm).



Figure 3: Inferred timing of flightless moult in four dual-equipped puffins. Immersion data were combined between two geolocators for each puffin. The green line represents time spent dry per day $(\text{prop}_{\text{fligth}})$ and the blue line is the 5-day rolling average of this $(\text{prop}_{\text{flight-5}})$. The blue bar underneath each plot represents moult inferred on the first pass of the moult identifiation process, the red bar represents a potential second

flightless moult identified by the second pass.

All moult periods occurred close to equinox periods, when the latitudinal accuracy of light level geolocation is greatly reduced. The average position of inferred moult was used to graphically represent moult location (figure 4), given that puffins are unlikely to move extensively when flightless, and most of the variation in location during moult is almost certainly due to error in location estimates. Both individuals with two inferred moult periods had more extensive migrations than those with one (table 2), with the autumn flightless moult occurring when they were furthest from their colony and the spring moult when much closer to the colony (figure 4).



Figure 4: Puffin tracks and associated moult periods. Each plot represents one individual and their mean moult locations, with a track derived from each logger. Geolocator positioning accuracy is reduced around the equinoxes, negatively affecting the latitudinal accuracy of moult locations, which were all inferred to occur around the equinoxes. The red dot corresponds to the colony location, Skomer, Wales. Note that portions of the track apparently crossing land are products of the inaccuracy of geolocator location estimates around the equinoxes, and associated smoothing.

Table 2: Metrics for each dual-equipped bird relating to migratory effort and moult periods. Residencies were described using Lavielle segmentation of net-squared displacement from the colony. Number of inferred moult periods and time spent in inferred moult altogether are also shown.

Bird ID	Most distant residency (dist / time)	Inferred moults	Total time in moult
EJ47625	$2054 {\rm km}$ / $49~{\rm days}$	2	76 days

Bird ID	Most distant residency (dist / time)	Inferred moults	Total time in moult
EL60569	728km / 41 days	1	54 days
EL60573	$3040 \mathrm{km} / 42 \mathrm{~days}$	2	66 days
EL60648	$1250 \mathrm{km}$ / 39 days	1	46 days

Identifying moult using single leg data

Using single logger data streams, only 1 moult period was identified from the 4 dual-equipped individuals, on the left leg of puffin EJ47625. The dates of this, 16th September to 30th October, exactly matched the moult period identified using data from both loggers. The percentage of time spent dry in this moult period was 0.4%. No second inferred moult period was detected on the second pass of the moult identification method.



Figure 5: Timing and location of inferred moult of Skellig Michael puffins. On the left, the proportion of time spent dry per day is graphed over the non-breeding season. The green line represents time spent dry per day (prop_{flight}) and the blue line is the 5-day rolling average of this ($prop_{flight-5}$). The blue bar underneath each plot represents putative moult inferred by the moult identifiation process. On the right, the corresponding inferred moult location is shown by a diamond shape, overlaid on the migratory path of the individual. The red dot represents Skellig Michael, their breeding colony. Note that portions of the track apparently crossing land are products of the inaccuracy of geolocator location estimates around the equinoxes, and associated smoothing.

Of the 40 single-equipped individuals from Skellig Michael, inferred moult periods were only apparent in 3

individuals. Periods of sufficiently reduced flight consistent with moult were not detected by our method in any of the other individuals (supporting information). These moult periods were 35, 52 and 72 days in duration and occurred in midwinter, starting in December or January, and took place either beyond the Irish Atlantic shelf margin (n = 2) or in the Mediterranean Sea (n = 1) (figure 5 & supporting information). Puffins from Skellig Michael showed reduced leg-tucking activity around midwinter, especially for puffins tagged in 2020, which corresponds with the moult periods inferred for this group (supporting information). This suggests that moult is more easily identifiable at this time of year due to an apparent reduction in legtucking behaviour, so the temporal distribution of moult inferred here is likely biased towards this period. These 3 individuals all moved approximately 2000 km from the colony to their furthest point of residency (supporting information), comparable to one of the Skomer birds that was inferred to have completed two moults.

Discussion

Methodology

To identify moult in puffins, we have developed a new method combining multiple data streams from geolocator loggers to more accurately identify year-round behaviours of seabirds. While this seems to work reasonably well for dual-equipped individuals, it also highlights some shortcomings of using standard singledeployment geolocators to identify fine-scale behaviours. Halpin et al. (2021) show how species' behaviour can unpredictably influence location estimates using light-level geolocators. Leg-tucking in alcids presents a similar problem for the interpretation of behaviours from saltwater immersion loggers on the same devices (Fayet et al. 2017, Linnebjerg et al. 2014). We provide a method to partially correct for this behavioural classification issue using concurrent light and immersion data. The limitations of this partial correction are reflected in the low success rate of moult inference in single-logger birds. Because puffins and some other alcids spend very little time in flight even when not undergoing moult (see results, Dunn et al. 2020), flightless moult is impossible to identify without relatively accurate behavioural data, and the few individuals for which moult periods were detected using a single logger are likely biased towards times of the year when leg tucking behaviour is less prevalent. Despite these constraints, our methods provide insights into the behaviour and life-history traits of a threatened species, and progresses our knowledge surrounding the timing and location of a highly vulnerable period in their annual cycle.

Over the last 10 - 15 years, hundreds of alcids have been tagged with a single geolocator throughout their biogeographic range (Fayet et al. 2017, Reiertsen et al. 2021), but our method does not have the power to identify moult in a sufficient proportion of individuals to robustly investigate population-wide patterns. More involved methods, for instance using machine learning to identify flightless stopovers (Guilford et al. 2009), usually require large amounts of pre-assigned training data to confidently infer behaviour, but may even then be liable to misclassification due to individual- or colony-level differences in behaviour (Bennison et al. 2018). Finer resolution data, such as from accelerometers, would allow us to identify flight with much more confidence (e.g. Patterson et al. 2019). GPS loggers would record far more accurate locations, potentially allowing us to identify imposed residency due to flightless moult. To date, none of these alternative devices are small or efficient enough for year-round deployment on puffins. Geolocators that record temperature can also be used to help correct for leg-tucking (Elliot & Gaston 2014, Dunn et al. 2020), though like the light-based corrections used in this study, temperature-based corrections do not fully capture all instances of leg-tucking. A ventrally mounted immersion switch would provide a truer representation of flight/nonflight behaviour, but despite being light enough for long-term deployment, techniques to mount devices long term on the body, as opposed to on a leg-ring, that do not affect the bird's performance, have not been developed (Lameris et al. 2018). For now, dual-equipped geolocators are probably the most viable method to investigate the flightless moult of puffins and other alcids. As technology improves and devices become smaller, the combined weight of two loggers will have less impact on an animal. Stable isotope analysis of moult feathers may also be used to coarsely gauge the location of the most recent primary moult (e.g. St. John Glew et al. 2018) and to validate geolocator based findings. To complement this, a relatively accurate geolocator-informed moult timing and location tells us where and when flight feathers were formed, allowing us to analyse the trophic position of food consumed during feather formation using stable isotope analysis (St. John Glew et al. 2019). It may also provide information on the prevalence of toxic chemicals in marine food webs at the time and location of moult by looking at chemical composition of feathers (Fort et al. 2016).

Biological findings

We have shown that the flightless moult strategy of breeding puffins varies markedly between individuals, and possibly colonies, despite usually being a fixed life-history trait within migratory bird species (Barta et al. 2008). We also found evidence that some individuals may undergo flightless moult twice in a non-breeding season, with this strategy possibly tied to more extensive migrations, though this relationship is based on a very small sample size. If this is the case, our results provide the first potential evidence for two flightless moult periods per year in a wild volant bird species (Beltran et al. 2018).

The exploration-refinement hypothesis (Guilford et al. 2011) suggests development over time of a fixed migration strategy that exploits predictable prey availability in space and time, leading to inter-individual variation (e.g. Harris et al. 2015). More extensive migration may allow puffins to exploit reliable food resources (Jessopp et al. 2013), especially during moult when their diving abilities are likely compromised (Bridge 2004). Prolonged flight during migratory phases may lead to accelerated feather wear and reduced flight efficiency for a bird with an already high wing-loading (Navarro & González-Solís, 2007, Greenewalt 1975), whose burrow nesting habits likely accelerate flight feather wear during the breeding season. Increased energy requirements for long-distance migrants also requires increased foraging effort and dive rates (Fayet et al. 2016), potentially further wearing wing feathers. This may result in two moults in one non-breeding season to maintain flight feather condition and retain flight efficiency (Barta et al. 2008). It may be that one or both moults are incomplete, allowing the puffins to remain partially volant. Small alcids in the genus Aethia forego synchronous moult, instead staging the replacement of primary flight feathers, allowing them to continue flying throughout moult (e.g. Bond et al. 2013). Some storm-wrecked puffins have shown evidence of a similar partial primary moult (M. Harris, unpublished data), though this has only been observed in a very small proportion of a very large sample of recovered birds, so is likely an anomaly or due to poor health. Biannual synchronous flightless moults have been observed in captive juvenile puffins (Swennen 1977, M. Huwiler, Tierpark Bern, pers. comm.), and while it is uncertain how these observations relate to wild breeding adults (Thompson & Kitaysky, 2004), it does highlight that this strategy is physiologically possible. In contrast, the two Skomer individuals that stayed closer to the colony (< 1500 km) during the non-breeding season clearly underwent a single flightless moult in autumn, not long after the summer breeding season. Flight feather moult is energetically demanding (Guillemette et al. 2007) and reduces foraging efficiency (Bridge 2004), so there are potential advantages in strategies that forego a second flight feather moult where possible. A trade-off likely exists between the energy required to undergo long-distance migration to highly productive areas, potentially necessitating two flightless moults, versus reduced migration effort and a single flightless moult, while also remaining in an area where feeding conditions may be poorer. Put simply, moult strategy in puffins could be dichotomous (biannual versus annual moult) associated with high versus low energy intake and expenditure, reflected in the activity budgets of long- and short-distance migrants (Fayet et al. 2017).

Previous studies, based on birds recovered dead rather than those from birds equipped with loggers that survived the non-breeding season, described an early/late bimodal distribution of puffin moult timings in the North Sea and around the Faroes Islands, with peaks in October and March (Harris et al. 2014). This timing largely agrees with our findings from Skomer individuals. It may be that dead birds identified as moulting in March were going through a second moult, though many more suitable tracking data, e.g. from dual-equipped puffins, would be required to suggest this with any confidence. The inferred moult of three Skellig Michael individuals occurred once, from December to February, with no evidence that this follows an earlier post-breeding flightless moult, although again, this is based on a small sample where moult could be resolved from single logger data streams. Similar moult timings were observed by Anker-Nilssen et al. (2018), who found that most puffins found following storm wrecks on the coast of Norway in February/March 2016, likely originating from colonies on the east coast of the UK, were in the latter stages of moult and had only recently become volant. Birds found dead are more likely to have been wintering relatively close to land, and so may not provide an unbiased sample of the wider population (Fayet et al. 2017). It is also possible that storms disproportionately affect moulting puffins that cannot fly to escape storm tracks, with reduced foraging efficiency during moult further compromised by storm conditions (Clairbaux et al. 2021). This does not seem to universally be the case, with a high proportion of moulting birds found in one wreck on the Norwegian coast (Anker-Nilssen et al. 2018) and a low proportion in another in the Bay of Biscay (Morley et al. 2017), despite both wrecks occurring at a similar time of year.

Conclusion

While limited to a small sample size, the results of this study markedly advance our understanding of a vulnerable period in the non-breeding season of a threatened species. We raise the intriguing possibility that puffins have a unique biannual flightless moult, leaving them flightless for 60-80 days over the course of a single non-breeding season, accounting for 20-30% of that total period. This highly unusual strategy may be tied to migration effort, though this is speculative due to our limited sample size. However, we have established a freely available workflow to further analyse dual-equipped seabirds to improve behaviour classification using geolocators. We hope this will promote further research on the flightless moult of puffins and other alcids, given that this life stage that leaves them are particularly vulnerable to antagonistic impacts from reduced prey availability, surface pollution and increased storm prevalence.

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Author contributions

MPH, SW, MJ, VBS, ALF, TH and JD created the concept. Data were collected by MJ, JD, JQ, ALF, TG and RF. JD led the analysis and writing of the manuscript, with strong contributions from all authors.

Data availability statement

Upon publication, data will be made freely available from Birdlife Seabird Tracking Database, and code is freely available at github.com/JamieHDarby/gls_puffin_moult.

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