

1 **Breeding status influences timing but not duration of moult in the Northern**
2 **Fulmar *Fulmarus glacialis***

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Seabirds are key marine top predator species that are often used as indicators of the environmental quality of the oceans. Their breeding phenology has been studied extensively, but their pelagic habits mean less is known about the phenology of other events during the non-breeding period. Here, we used miniaturised saltwater immersion light-based geolocators (GLS) to investigate moult phenology in individuals with known breeding histories in a population of Northern Fulmar *Fulmarus glacialis* in Orkney, Scotland. As seabirds spend more time on the water during moult, moulting periods can be identified from patterns of variation in the amount of time that birds are in contact with saltwater. Estimates of daily variation in this behaviour during the non-breeding period were based upon wet/dry sensors and then modelled to characterise the timing of the moult. Light-based geolocation provided information on the areas used by each individual during its moult period. Inter-individual variability in moult timing was investigated in relation to sex and breeding success in the previous summer. We found a sex difference in the location of the moult, but not in its timing. However, the timing of moult did differ between individuals that had succeeded or failed in their previous breeding attempt, with successful breeders moulting the latest. In contrast, the duration of moult did not depend on prior reproductive success, but there was evidence of inter-annual variation in moult duration. GLS studies have provided a step change in our understanding of the at-sea distribution of pelagic seabirds. Our work highlights how activity data from these devices can add value to such studies by identifying key phases of the annual cycle, and locations at these times, when seabirds may be at particular risk. Furthermore, our findings indicate that individual and inter-annual variation in breeding success may influence phenological patterns in other phases of their annual cycle.

Keywords: phenology, moulting, non-breeding, Procellariiformes, light-based geolocation

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Avian moult is an energetically demanding process (Cherel *et al.* 1994, Murphy 1996) which can also incur indirect costs by impairing flight (Swaddle & Witter 1997, Guillemette *et al.* 2007, Gutowsky *et al.* 2014). Temporary periods of flightlessness, or lower flight performance, increase vulnerability to predators and can limit access to resources (Green *et al.* 2004, Guillemette *et al.* 2007). Together, these direct and indirect costs of moult can result in trade-offs between the timing of moult and the two other major avian life-history events: breeding and migration (Bridge 2011). Most work on these trade-offs has focused on passerines, which moult after breeding and prior to migration; thus allowing the moult process to be observed directly (Hemborg & Lundberg 1998). There have been extensive studies of breeding phenology in many seabirds (e.g. Keogan *et al.* 2018). However, moult generally takes place once birds have dispersed from breeding grounds, constraining direct observations of pelagic seabirds. Information on the timing of their moult has therefore been dependent upon *ad hoc* observations at sea or analyses of carcasses (e.g. Brown 1988, Edwards & Rohwer 2005, Bugoni *et al.* 2015). As a consequence, there is limited information on the timing of moult in many pelagic seabirds (Bridge 2006, Gutowsky *et al.* 2014, Cherel *et al.* 2016) and the key areas that these birds may be using at this time (e.g. Harris *et al.* 2014). Given that reduced flight performance may increase their vulnerability to various natural and anthropogenic stressors (Green *et al.* 2004), better information on moult patterns is also required to support effort to manage high seas areas to protect pelagic seabirds.

In the past, moulting strategies amongst Procellariiformes have been particularly difficult to characterize. Some studies have suggested that moult and reproduction are more likely to overlap in this order (Bridge 2006). However, this can be difficult to assess unless studies of moult are conducted on birds of known reproductive status (Allard *et al.* 2008). Recent development of geolocation loggers has allowed investigation of the non-breeding period of seabirds at unprecedented temporal and spatial scales (Croxall *et al.* 2005). Most commonly, geolocation loggers have been used to describe migratory pathways and wintering grounds (e.g. Frederiksen *et al.* 2012, Dias *et al.* 2013, Fayet *et al.* 2017). However, most geolocation devices also have salt water immersion sensors that can be used to test whether moulting seabirds have quasi-flightless periods where most time is spent on the water (Mackley *et al.* 2011, Gutowsky *et al.* 2014, Cherel *et al.* 2016). Gutowsky *et al.* (2014) pioneered the use of wet-dry logger data to identify the moult period in North Pacific

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albatrosses, and obtained a clear signal that underpinned the 'quasi-flightless stage hypothesis'. Cherel *et al.* (2016) subsequently verified this by demonstrating that immersion data could be used to characterize the timing and location of moult in three smaller subantarctic petrel species. They firstly characterized moult in the Blue Petrel *Halobaena caerulea*, a reference species that is known to renew its plumage in autumn, and identified a strong peak in daily time spent sitting on water during the expected moult period. They then used this peak as a proxy to characterize the contrasting moult strategies of two other petrel species. This approach now opens up new opportunities for understanding moult strategies in a range of pelagic species by integrating biologging data with individual based demographic studies; thereby permitting assessments of variation in the timing of moult in relation to known reproductive performance.

In this study, we used data available from geolocation loggers with wet/dry sensors to characterize the timing and location of moult in a well-studied colony of Northern Fulmars *Fulmarus glacialis* in Scotland. Existing information on moult patterns in this species has been based either upon observations of birds around breeding colonies (Carrick & Dunnet 1954, Allard *et al.* 2008) or analysis of beached or by-caught individuals (Quinn *et al.* 2016). These techniques have shown that the moult occurs post-breeding, but they cannot be used to explore variation in moult duration or links between moult timing and reproductive success. Here, our primary objectives were to explore whether the timing or duration of moult varied between birds that bred unsuccessfully or successfully in the preceding breeding season, and birds of different sex. In addition, we aimed to identify the areas used by Northern Fulmars from this population during their moult, to assess whether there are discrete areas where they may be more vulnerable to anthropogenic stressors.

METHODS

Study site and logger deployment

Fieldwork was conducted on Eynhallow, Orkney (59°8'N; 3°8'W) where individual based studies of breeding Northern Fulmars have been ongoing since the 1950s (Dunnet 1991).

Individuals have been marked using unique colour ring combinations, and information on their reproductive status has subsequently been based upon observations made during three

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standardized visits to the colony in each breeding season; during the incubation, hatching and fledging periods (for details see Lewis *et al.* 2009, Cordes *et al.* 2015).

Since 2006, these studies have been developed to include assessments of the foraging distribution of known breeders (Edwards *et al.* 2016, Quinn *et al.* 2016). These have been based upon the deployment of miniature Global Location Sensing (GLS) loggers on adult breeders at the colony. Several different GLS models were used during the study, primarily MK 3 and MK 5 loggers produced by British Antarctic Survey (Cambridge, CB3 0ET, UK), MK3006 loggers produced by Biotrack (Wareham BH20 4PL, UK) and C250 loggers produced by Migrate Technology Ltd. (Cambridge, CB1 0QY, UK). Loggers weighed between 1 g and 2.5 g, and were fixed to one of the darvic leg rings using cable ties, giving a maximum total device weight of 4 g (< 0.5% of the lightest individual's body weight).

Devices were recovered 1-3 years later, generally at the nest but occasionally after birds were captured in flight. Annual attendance of breeding adults at this colony varied considerably, and can be as low as 50% in some years (Thompson & Ollason 2001). This, in turn, affected the likelihood of recovering loggers, resulting in an average recovery rate of 46% over one year to 76% after two or more years.

All devices recorded light level and saltwater immersion every 3 seconds, and stored the maximum light levels and the number of wet samples in every 5- or 10-minute period. After recovery, data were downloaded and extracted using either the BASTrak software (British Antarctic Survey) or IntigeoIF (Migrate Technology Ltd.)

Moult characterisation and individual variability in the timing of moult

The key purpose of this study was to investigate the individual timing and location of the moult in relation to the previous breeding attempt. Northern Fulmars at this colony typically lay their eggs during the last two weeks of May, and the first annual colony census of incubating birds occurs as close as possible to the 1st of June (Dunnet 1991). We therefore defined the annual cycle as the period between June 1st of one year and May 31st of the following year.

Due to occasional logger failure or limited memory capacity on multi-year deployments, activity data were not always available throughout complete deployments. Previous studies of carcasses indicate that moult in Northern Fulmars occurs after the end of

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the breeding season and is completed by the end of December (Carrick & Dunnet 1954, Allard *et al.* 2008, Quinn *et al.* 2016) when birds start to attend the colony periodically until the next breeding season (Coulson & Horobin 1972, Macdonald 1980, Slater 1990). For these analyses, we therefore selected only those birds and years in which activity data were available throughout the entire mid-August to mid-December period. Furthermore, we only used data from years in which there were activity records from at least 10 birds, and birds for which sex and breeding status in the previous breeding season were known. This resulted in a dataset that included 139 moult cycles (82 individuals; 44 males and 38 females; see Supporting Information Table S2 for detailed sample sizes per season).

Following Cherel *et al.* (2016), we used daily variation in the proportion of time spent sitting on the water to define the moult period at both population and individual levels. Immersion data from the different logger models were used to first classify each bird's activity within the 5- or 10-minute sample periods (depending upon the logger model used). Given that the logger is placed on a leg ring and is fully submerged when birds spend their time sitting on the water, we used the daily accumulated time that the logger had been fully submerged in saltwater (i.e. total time spent fully submerged in a 24 hour period; midnight UTM to midnight UTM) as a proxy for this behaviour. Sampling periods where the logger was only partly submerged (i.e. a mix of wet and dry records on a sample period) or fully dry were therefore used to characterise other behaviours (e.g. foraging and in flight or on land, respectively) and excluded from this data analyses. Purpose written R script was used to obtain the daily proportion of time in which each bird was sitting on the water throughout each deployment (available in Supporting Information Appendix S1).

To characterise variation at the population level, we calculated a mean value for the proportion of the day which birds spent on the water throughout the annual cycle. Individual-based estimates of the timing of moult were then based upon a Generalized Additive Model (GAM) that was fitted to the 'wet' data for each bird's annual cycle using the approach developed by Cherel *et al.* (2016). Following Cherel *et al.* (2016), the core moult period was defined as the time window (consecutive days) when the predicted 'wet' variable exceeded 75% of the value of the peak in the daily proportion of time wet (see Supporting Information Fig. S1 for an example GAM). These GAM results also provided estimates of the date of the peak of wetness, and start, median, end dates, and duration of the moult for each individual.

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95% CI around the fitted GAM were used to provide an estimate of variability around each individual estimate of moult duration.

Influence of breeding status on the timing of moult

Data on an individual's moult phenology were then integrated with data from colony observations to explore how moult characteristics were influenced by an individual's previous breeding success. Variability in moult characteristics were investigated using a linear mixed model fitted with maximum likelihood in the *lme4* package (Bates *et al.* 2015). The bird's ID was incorporated in the model as a random effect to prevent pseudo-replication due to the presence of data from several different annual cycles for some birds. We used start date, median date and duration of the moult as response variables. The end date of the moult was highly correlated to start date and duration, so was not included as a response variable. We included the following explanatory variables: sex of the individual, year and previous breeding success. Visits were made to the study colony on three occasions in each breeding season: in late May to identify which birds were on eggs; in mid July to estimate hatching success; and in mid August to record the presence of chicks prior to fledging (see Lewis *et al.* 2009). Breeding success was therefore classified into four categories: 1) Not recorded breeding at the colony in that year, 2) Failed on an egg, 3) Failed on a chick, 4) Successfully fledged a chick. An interaction between sex and reproductive success was also incorporated in the model to explore whether males and females responded in the same way to a successful or failed reproductive attempt. The significance of each explanatory variable was tested with the 'Anova' function using type III Wald Chi-square tests from the *car* package (Fox & Weisberg 2011). Model selection was carried out by removing every non-significant factor, and confirming the better fit of the model using Akaike Information Criterion, correcting for small sample size, with the function 'AICc' from the *MuMIn* package (Bartoń 2016). Models with $\Delta AICc \leq 2$ were considered the best of the set of candidate models. Following this analysis, multiple comparison post-hoc Tukey tests were performed to assess specific differences within significant variables, using the 'glht' function from the *multcomp* package (Bretz & Westfall 2008). Assumptions of homoscedasticity and normal distribution of the model's residuals were verified for every candidate model.

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All analyses were carried out with R version 3.1.3 (R Core Team 2015) and statistical significance was taken to be $P < 0.05$.

Spatial distribution of individuals during their quasi-flightless moult period

Geolocation data were then used to characterise the distribution of individual fulmars during their core moult period. Twilight events were determined from where light curves intersected with a selected threshold of 9 for MK 3, 5 and 3006 geolocators and 11 for C250 geolocators, using the BASTrack (British Antarctic Survey; Fox 2010) or IntiProc software from Migrate Technology Ltd (Coton, Cambridge, UK; Fox, 2015), respectively. Twilight events were checked visually to remove data from days with constant light or dark, or where shading events occurred. If a light curve clearly suggested a more correct placement of a sun event, events were moved. On average, 6 % of resulting twilight events were moved.

The light data were further processed following procedures in Hanssen *et al.* (2016). Sun elevation angles were determined individually for each geocator (ranging from -1° to -4.5°) by combining in-habitat calibrations, using the breeding colony as a reference point, with visually inspecting latitude vs. date plots (Hanssen *et al.* 2016, Supporting Information Fig. S2). A smoothing process was applied twice to positional data to reduce location errors (Hanssen *et al.* 2016, but see Phillips *et al.* 2004 and Fox, 2015). Following this procedure, 75% individuals had daily locations for $> 95\%$ of their moult period (Supporting Information Table S1). In those few ($< 5\%$) cases where daily locations were available for $< 70\%$ of days during the moult cycle, this was typically because birds were using high Arctic areas at this time of year.

Information on the start and end date for each individual's moult (as defined by the GAM) was used to filter the resulting geolocation data and estimate the great circle distance between each of the bird's twice-daily locations and the breeding colony. To visualise differences between individuals, we estimated the geographic mid-point of locations obtained for each bird during their respective moult periods, excluding locations during the equinox, using the function 'geomean' in the *geosphere* package (Hijmans 2016). We used the distribution of distances to the colony to provide an estimate of variability and comparison of male and female locations during the moult period. For many individuals, the moult period included part of the autumn equinox (8th September – 20th October). To explore whether this

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biased estimates of the geographic mid-point, we also calculated a second geographic mid-point for each bird that included data from the equinox by using observed values of longitude and proxy values for latitude that were based upon that individual's moult locations from outwith the equinox.

The distance between the geographic mid-point of male and female moult locations and the breeding colony was also compared using linear mixed models fitted with maximum likelihood in the *lme4* package (Bates *et al.* 2015), with bird ID as a random effect and sex of the bird as the explanatory variable. Significance of the explanatory variable was tested with the 'Anova' function as above.

RESULTS

Moult characterisation and individual variability in the timing of moult

At the population level, there was a clear increase in the daily proportion of time spent on the water in the period between July and December (Fig. 1). The same pattern was observed by plotting the raw data for each of the 139 annual cycles, and individual patterns were successfully quantified by plotting a GAM for each cycle. Overall, the earliest moult start date was July 6th, and the latest end date was December 23rd. However, there was marked variability in the timing of the moult within this time-window (Fig. 2). For the start date of moult, the median was 18th of August (interquartile range: 7th - 29th August). The median date of the moult was 21st September (interquartile range: 8th - 30th September), whilst the median end date for the moult was 23rd October (interquartile range: 13th October - 4th November). The median duration of the moult was 68 days (interquartile range: 57 -78 days; Supporting Information Table S1 provides the detail of these estimates for each individual bird).

Influence of life-history traits and annual variation on individual variability

Inter individual variability in the timing of the moult was explained by different explanatory variables for each of the three moult characteristics we chose to model (i.e. start date, median date and duration; see Table 1). For start date, the best model contained only the previous breeding status as an explanatory variable (Table 2). Birds of differing breeding status

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exhibited significant differences in the start date of their subsequent moult (LMM, $\chi^2 = 248.50$, $P < 0.001$; Fig. 3). Non-breeders and birds that failed on an egg started their next moult at a similar time (Tukey, $P > 0.05$, $z = 0.5$): 26th July ± 2.8 days (mean \pm SE) for non-breeders and 27th July ± 2.3 days for birds who failed on an egg. Birds that failed on a chick started their moult significantly later than both other groups, around the 13th August ± 2.3 days (Tukey, $P < 0.05$, $z = 5.6$ and 5.8 , respectively). Finally, successful breeders moulted latest (Tukey, $P < 0.05$, $z = 11.3$, 12.4 and 7.4 compared to non-breeders, and birds that failed on an egg or a chick groups, respectively). On average, these successful birds started their moult on 27th August ± 0.9 days, one month after birds which failed on eggs or were not recorded breeding (Fig. 3). There were slight annual differences in the start of moult, but these were not significant (see Table 3).

Differences in the median date of the moult were less clear (Table 2). There was slightly more support for the model containing both sex and breeding status than the model containing only breeding status ($\Delta AICc = 1.4$). However, the difference in median date between the sexes was slight (LMM, $\chi^2 = 3.67$, $P = 0.055$; Males: 21st September ± 1.8 days; Females: 18th September ± 1.9 days). On the other hand, the difference in median date of moult for individuals of differing breeding status was highly significant (LMM, $\chi^2 = 204.53$, $P < 0.001$) and showed a similar pattern to that seen in start dates. Non-breeders and birds that failed on an egg had similar median dates (2nd September ± 2.1 and 1st September ± 2.2 days; Tukey, $P > 0.05$, $z = -0.228$), median date for birds that failed on a chick was later (16th September ± 2.1 days, Tukey, $P < 0.05$, $z = 4.33$, and 5.24 , respectively) and that for successful birds was latest (30th September ± 1.1 days, Tukey, $P < 0.05$, $z = 9.73$, 11.63 and 7.08 , respectively). Similarly, there was a slight but not significant annual difference in median date of the moult.

AICc differences were even smaller for models using duration as a response variable (see Table 2). Based on the same process, we selected the model with the smallest AICc, which contained only the cycle year as an explanatory variable. Annual variation was significant (LMM, $\chi^2 = 17.806$, $P = 0.003$), with durations in 2008/09 being up to 2 weeks longer than in 2009/10 and 2010/11, and with intermediate values for the remaining years (Table 3).

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Location during the moult

Combining the activity data with geolocation data, we found that moulting Northern Fulmars from the Eynhallow colony were located across a broad geographical range from the mid-Atlantic to the Barents Sea (Fig. 4). One cluster of individuals was found over the North Sea and continental shelf. Smaller clusters of moulting individuals occurred in the mid-Atlantic and along the Norwegian Shelf and into Arctic waters of the Barents Sea. A similar pattern was observed when using additional longitudinal information from the equinox, suggesting that there was no east-west bias as a result of excluding all locations from the equinox (Supporting Information Fig. S2). Females tended to predominate in areas further from the colony (i.e. mid-Atlantic and Arctic locations) and males were more common over the North Sea. This sex difference in the distance between the geographic mid-point of moulting locations and breeding colony was highly significant (LMM, $\chi^2 = 23.03$, $P < 0.001$; Fig. 5).

DISCUSSION

This study suggests that the method developed by Cherel *et al.* (2016) to characterise the timing of the moult in small petrels can be extended to other Procellariiformes. In applying this method, we assume that observed changes in the proportion of time that birds spent wet result from a change in flight performance, as originally suggested by Gutowsky *et al.* (2014). In previous studies using wet-dry sensors on Procellariiformes, foraging activity has typically been characterised by 5- or 10-minute periods containing a mixture of both wet and dry samples (Mattern *et al.* 2015). An increase in sample periods in which birds remain on the water could potentially represent an alternative surface foraging behaviour. However, whilst proxies of diet indicate that foraging characteristics of Northern Fulmars can change between late winter and the breeding season (Owen *et al.* 2013), the marked increase in daily time spent on the water occurred much earlier in the non-breeding period (Fig. 1). This change in wet-dry activity also coincides with previous estimates of the timing of primary moult based upon analyses of dead fulmars (Quinn *et al.* 2016). We therefore suggest that the activity data from this population indicate that all individuals had started their moult in July or August, and had finished moulting by late December.

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The use of activity data from known individuals provided additional information on moult phenology that offers new insights for broader comparative studies (Bridge 2011). First, variations in the amount of time that birds spent on the water provided estimates of the duration of an individual's moult, which was typically around two months (Fig. 2). Existing estimates of moult duration in seabirds are based on approximate dates for moult initiation and completion, potentially leading to overestimation of an individual's moult pattern (Bridge 2006). Activity based techniques can therefore provide finer-scale individual level measures which can be used to compare the duration of moult both between and within species. Second, by combining these data with information on known reproductive histories, we were able to explore the relationship between the timing of breeding and moult at the individual level. Individual-based studies linking variation in moult patterns to reproductive success are rare amongst seabirds, and were previously based only upon moult characteristics obtained from observations of known breeders at the colony (Barbraud & Chastel 1998, Rohwer *et al.* 2011). Detailed colony-based studies can now use these techniques to explore interactions between key life-history events both at the colony (breeding success) and at sea (migration schedules (e.g. Catry *et al.* 2013) and moult patterns).

Our analyses revealed that inter-individual variability in the timing of the moult was related to success during the previous breeding attempt, with non-breeders or birds that failed early in the season starting their moult around one month earlier than successful breeders (Fig. 3). These data are in accordance with a recent experimental study on Cory's Shearwater *Colony nectris borealis*, which used a combination of tracking and stable-isotope analysis to demonstrate that birds that were induced to fail moulted earlier compared to successful breeders (Ramos *et al.* 2018). Colony observations of albatrosses have also shown that breeding success can influence subsequent moult in those larger species that have a complex biennial moult (Furness 1988, Prince *et al.* 1993, Rohwer *et al.* 2011). In those cases, failed breeders increased the number of primary flight feathers that they moulted, which could result from an earlier initiation and/or longer moult duration. Detailed mechanisms controlling prebasic moult remain unclear, but our observations are in line with the suggestion that higher levels of sex-steroid hormones delay the onset of moult in active breeders (Hahn *et al.* 1992). In passerines, delays in moult initiation typically require a faster moult to maintain migration schedules (Hahn *et al.* 1992). However, our data suggest that breeding success did not

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influence the duration of the moult, meaning that the pattern observed for the start date of moult (Fig. 3) was retained in the median and end dates of moult. Experiments on European Starlings *Sturnus vulgaris* demonstrated that shorter moult duration led to the production of lower quality feathers (Dawson *et al.* 2000), which could compromise future reproductive success in seabirds that make long foraging trips during chick rearing (Rohwer *et al.* 2011). In the absence of a fixed migration schedule, individual moult durations in Northern Fulmars may be less variable in order to maximise feather quality although, as discussed below, inter-annual variation in duration suggest moult duration may be affected by external environmental conditions.

These findings also provide new insights into previous studies that used traditional techniques to assess the extent to which moult and breeding overlap. Northern Fulmars that breed successfully are constrained to central place foraging from the colony until their chicks fledge in late August or September. Whilst non-breeders and early failures may leave the colony earlier, observations of marked birds indicate that not all do so (Anderson 1962, P. Thompson unpubl. data). This can result in an overlap between observations of breeding and moulting birds at the population level, but these results demonstrate that events do not necessarily overlap at the individual level. No evidence of active breeders moulting flight feathers was found at our study site (Carrick & Dunnet 1954, this study) or at a Canadian Arctic colony (Allard *et al.* 2008). Allard *et al.* (2008) suggested that their observed temporal overlap of breeding and moulting individuals resulted from large scale movements and overlapping ranges of birds from different colonies, with moult occurring earlier in colonies characterised by earlier egg-laying. However, our results suggest that Allard *et al.*'s (2008) observations could simply result from within colony variation in reproductive success, as failed breeders that remain around the colony could initiate moult up to a month earlier than the active breeders. Nevertheless, we made only low intensity colony visits in the last few weeks of chick rearing, when very few adults were observed. Thus, some evidence of moult could have been missed.

Rohwer *et al.* (2011) highlight the potential for extending colony-based studies to explore trade-offs between moult and reproduction. Estimates of moult phenology from activity loggers provide additional opportunities to extend such studies by following birds after dispersal from the colony, thus exploring unresolved questions about timing and

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duration of seabird moult arising from analyses of carcasses (Bridge 2011). Atlantic Puffins *Fratercula arctica* for example have a protracted period of moult with bi-modal peaks in both October and March, suggesting they may moult twice during the non-breeding season (Harris *et al.* 2014). Individual based data are required to test such hypotheses, and explore how these patterns relate to previous reproductive histories. However, interpretation of individual bouts of at-sea behaviour in auks are more complicated because they may withdraw one leg into the plumage while sitting on the water (Linnebjerg *et al.* 2014). Nevertheless, modelling longer-term variations in behaviour using the approach developed by Cherel *et al.* (2016) may provide opportunities to use existing datasets (e.g. Fayet *et al.* 2017) to compare putative moult patterns in individuals of known reproductive status over multiple years and from different colonies.

As reported by Allard *et al.* (2008), we found no sex differences in the timing of moult. There was, however, a tendency for females to moult at more distant locations from the colony, in line with sex-differences in the foraging areas used by these birds during the winter (Quinn 2014) and pre-laying exodus (Edwards *et al.* 2016). GLS studies of non-breeding distribution are already providing new insights into potential moulting areas (e.g. Harris *et al.* 2015). The use of activity data to refine estimates of birds' locations during critical moult periods can further support risk assessment and conservation planning (Croxall *et al.* 2012). Unlike many other waterbird species (Kirby 1995) Northern Fulmars from this single colony were dispersed over a wide geographical area rather than congregating at specific locations during their moult. Current conservation activity often focuses on identifying Important Bird Areas, where seabirds may aggregate to feed or engage in other key behaviours such as moulting (Lascelles *et al.* 2016, Krüger *et al.* 2017). Our data highlight that focused area-based conservation interventions may be less easily applied to highly dispersed and wide-ranging species such as Northern Fulmars. Observed levels of dispersion during the moult suggests that the viability of individual colonies should be buffered against localized impacts such as oil spills, which could adversely affect breeding populations aggregating in common wintering areas (Fauchald *et al.* 2002). At a finer-scale, however, it remains possible that birds from this single colony do still aggregate during the moult, potentially associating with individuals from a broad range of colonies around the North Atlantic. Further tracking work at multiple sites could assess overlap between colonies

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and the ecological and conservation importance of these interactions. In particular, it would be valuable to explore the extent to which males and females may be differentially exposed to threats such as fisheries by-catch or contaminants during this vulnerable phase of the annual cycle (Fauchald *et al.* 2002, Anderson *et al.* 2011, Van Franeker *et al.* 2011).

Annual variation in environmental conditions and prey availability are recognised to have profound consequences for breeding phenology (Frederiksen *et al.* 2004, Wanless *et al.* 2009), and may similarly affect the timing or duration of moult. For example, experimental studies on passerines suggest that feeding resources during the non-breeding season could influence the timing of pre-alternate moult initiation in wild birds (Danner *et al.* 2015). We found no evidence of interannual variation in moult initiation in the years we studied, but the duration of moult did vary between years (Tables 2 & 3). However, our estimates of moult duration did vary markedly, with some individuals undergoing moults of up to 120 days (Fig. 2; Supporting Information Table S1). This, together with small sample sizes in some years constrained a more detailed assessment of these patterns, but these results highlight the potential for using individual-based activity data to explore the importance of intrinsic and extrinsic drivers of such variation. Studies of beached Northern Fulmars during winters with unusually high mortality indicate that feather renewal had slowed down or fully arrested in many of these birds, resulting in highly degraded flight feathers and poor down plumage (Van Franeker 2011). Future work could link activity based estimates of moult patterns and flight behaviour with direct measures of feather quality at subsequent capture (e.g. Dawson *et al.* 2000), or indirect measures of over-winter stress from measures of feather cortisol (e.g. Ramos *et al.* 2018). Integration of these approaches with long-term deployments of tri-axial accelerometer loggers (Williams *et al.* 2017) would be particularly valuable for understanding the energetic consequences of observed differences in moult patterns. In contrast to Northern Fulmars, Southern Fulmars *Fulmarus glacialis* exhibit extensive overlap between moult and breeding, with a high level of primary moult even during late incubation (Barbraud & Chastel 1998). These two species are otherwise similar in many aspects of their ecology and biology, and this overlap may result from food availability being very high but restricted to a short Antarctic summer (Barbraud & Chastel 1998). Others have suggested that the duration of moult may also vary in different environments. For example, Murphy and King (1992) proposed that wintering areas used for moult could influence timing at the species or even

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population level, with birds experiencing a shorter moult at higher latitudes. Here again, there is potential to use the analyses developed by Gutowsky *et al.* (2014) and Cherel *et al.* (2016) to test this hypothesis upon widely distributed species by integrating geolocation and activity data collected from high and low latitude colonies.

In conclusion, these results demonstrate that the breeding performance of Northern Fulmars subsequently influences other life-cycle events such as moult during the non-breeding season. One important question arising from this is the extent to which this variation may lead to longer-term carry-over effects. In a multi-colony study of carry-over effects in Black-legged Kittiwakes *Rissa tridactyla*, Bogdanova *et al.* (2017) detected links between the timing of migration and subsequent breeding events, but annual variations in environmental conditions weakened the strength of these effects. Carry-over effects could arise directly through energetic constraints, or because the renewal of plumage provides a signal of body condition in many species (Lantz & Karubian 2016), meaning moult could influence breeding performance through mate choice. Further work with additional multi-year data from known breeders could explore how the patterns we observed in Northern Fulmars interact with environmental variation, and whether moult phenology influences subsequent breeding attempts as seen in some larger species with more complex biennial moult patterns (Rohwer *et al.* 2011).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. R code to calculate daily activity summaries

Figure S1. Example of fitted GAM model, with 95% CI.

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748 **Figure S2.** Location of the moulting Northern Fulmars breeding at Eynhallow,
749 including data from during the equinox (in contrast to Figure 4 in the main paper).

750 **Table S1.** Summary data on the moult characteristic of all individuals

751 **Table S2.** Detailed sample sizes per cycle year.

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TABLES & FIGURES

Response variable	Significant explanatory variable(s)	P-value	Wald Chisq	Random effect variance
Start date	Breeding status	< 0.0001	248.50	3.30
Median date	Breeding status	< 0.0001	204.53	5,06
	Sex	0.055	3.67	
Duration	Cycle year	0.003	17.81	23.56

Table 1. Results of the significance of different explanatory variables for each response variable used with the linear mixed model including bird number as a random effect.

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~ sex + breeding status + cycle year + sex : breeding status				ΔAICc	wAICc
Start date				11.524	0
		***		5.159	0.06
		***		4.134	0.1
		***		0	0.83
				135.142	0
Median date				9.128	0.01
	*	***	.	2.168	0.18
	.	***		0	0.54
		***		1.404	0.27
				117.889	0
Duration				9.956	0
		*		5.52	0.03
		**		0.028	0.47
		**		0	0.47
				5.544	0.03

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Table 2. Model selection based on AICc, for the three response variables (start date of moult, median date of moult and duration of moult), using linear mixed models including bird number as a random effect. Explanatory variables used in each model are highlighted in grey. Significance of each explanatory variables used is represented as follows: · ($P < 0.1$); * ($P < 0.05$); ** ($P < 0.01$); *** ($P < 0.001$). The best-fitting model is represented between the dotted lines.

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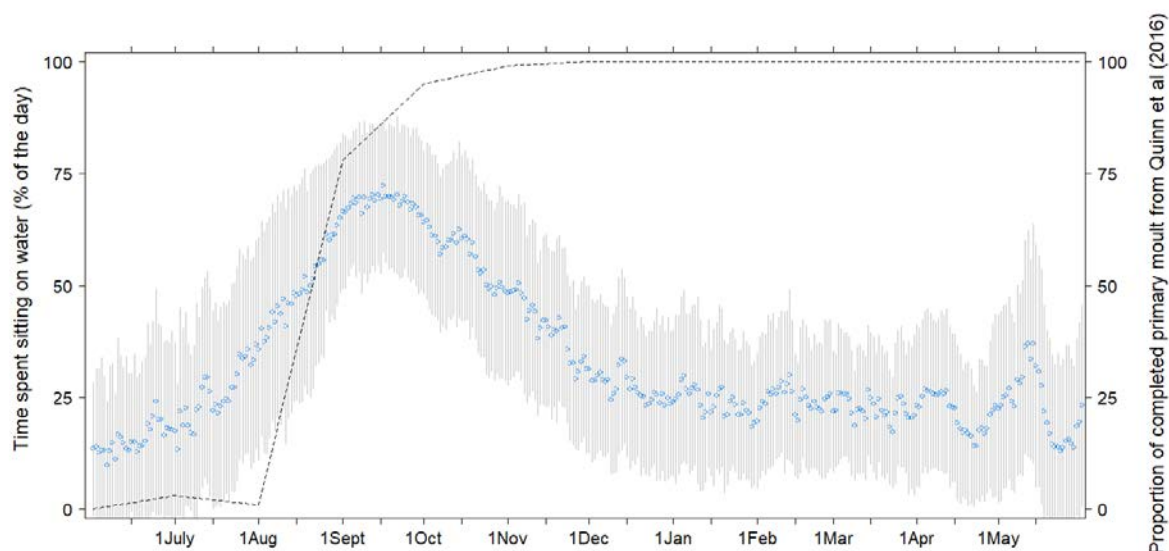
Breeding status	N	Start date	Median date	End date	Duration
Not recorded breeding	13	26 July (± 2.8) ^a	2 September (± 2.1) ^a	9 October (± 3.1)	75.3 (± 4.2) ^a
Failed on an egg	19	27 July (± 2.3) ^a	1 September (± 2.2) ^a	6 October (± 2.9)	70.4 (± 2.8) ^a
Failed on a chick	33	13 August (± 2.3) ^b	16 September (± 2.1) ^b	20 October (± 2.5)	68.3 (± 2.2) ^a
Successfully fledged	74	27 August (± 0.9) ^c	30 September (± 1.1) ^c	2 November (± 1.9)	66.7 (± 1.9) ^a
Cycle year					
2008/2009	15	20 August (± 2.5) ^a	28 September (± 2.7) ^a	6 November (± 3.6)	78.5 (± 3.1) ^a
2009/2010	24	18 August (± 2.5) ^a	19 September (± 2.3) ^a	20 October (± 2.7)	63.5 (± 2.7) ^b
2010/2011	35	22 August (± 2.1) ^a	23 September (± 2.4) ^a	25 October (± 3.1)	64.6 (± 2.4) ^b
2011/2012	14	28 July (± 3.4) ^a	3 September (± 2.8) ^a	11 October (± 3.5)	75.6 (± 3.9) ^{a,b}
2014/2015	28	22 August (± 3.4) ^a	25 September (± 3.2) ^a	28 October (± 3.8)	67.0 (± 3.2) ^{a,b}
2015/2016	23	11 August (± 3.6) ^a	15 September (± 3.4) ^a	20 October (± 3.9)	70.1 (± 3.3) ^{a,b}
Sex					
Males	77	17 August (± 1.8) ^a	21 September (± 1.8) ^a	26 October (± 2.1)	69.6 (± 1.6) ^a
Females	62	16 August (± 2.1) ^a	18 September (± 1.9) ^a	22 October (± 2.2)	66.9 (± 2.1) ^a

Table 3. Timing of the moult by biotic and abiotic factors. Values are mean dates (± SE). Results from the post hoc Tukey tests are presented (values not sharing the same superscript letter are significantly different at $P < 0.05$). As we chose not to use end date as a response variable in our model because of its high correlation to start date and duration, no post hoc results are available.

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Figure 1. Variation in the mean daily percentage of time spent on water (\pm SD) for 139 annual cycles from 82 individual Northern Fulmars tracked between 2007 and 2016 (left axis). For comparison, the dashed line represents the cumulative proportion of birds that had completed their primary moult in the dataset from beached and by-caught North Sea Northern Fulmars (from Quinn *et al.* 2016, right axis).



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Figure 2. Variability in the timing of the moult. Distribution of the characteristics of the moult extracted from the activity data using GAM. The boxes depict interquartile range, with median as a bold line. Whiskers indicate variability outside the upper and lower quartiles. Outliers are plotted as circles. (A: Start date; B: Median date; C: End date; D: Duration).

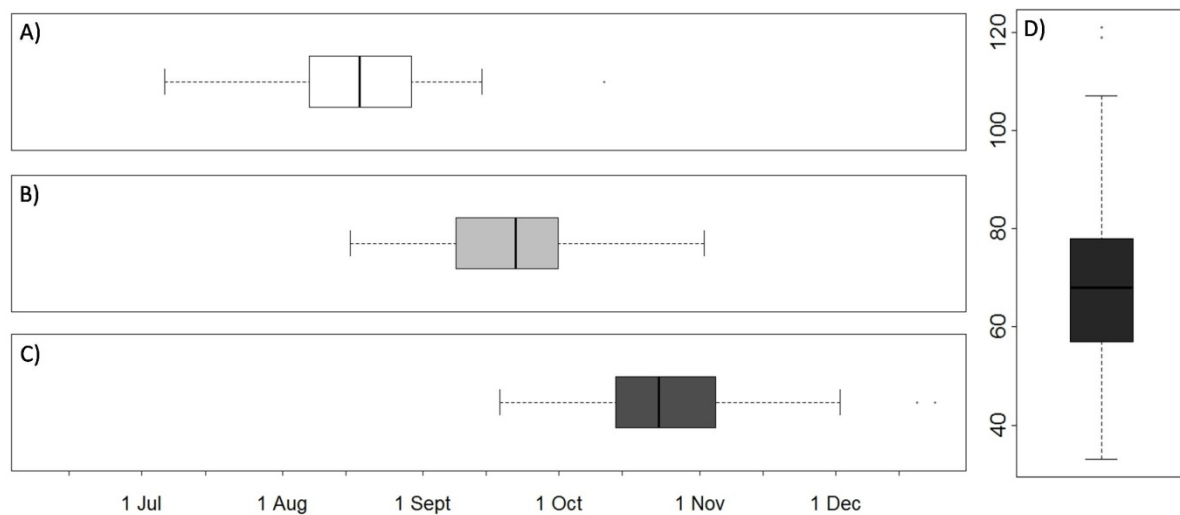


Figure 3. Differences in the starting date of the moult explained by breeding status. The boxes depict interquartile range, with median as a bold line. Whiskers indicate variability outside the upper and lower quartiles. Outliers are plotted as circles.

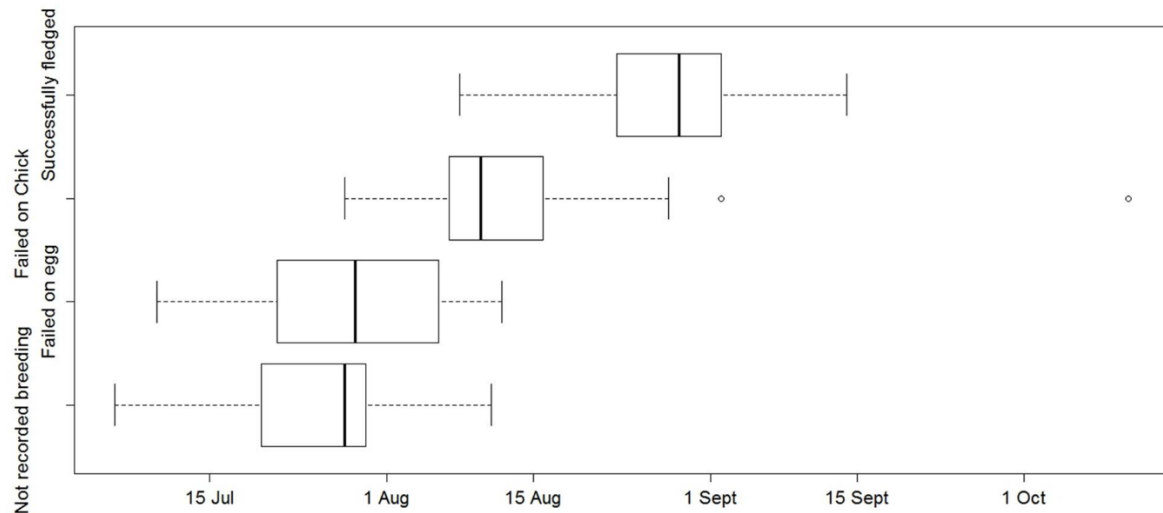
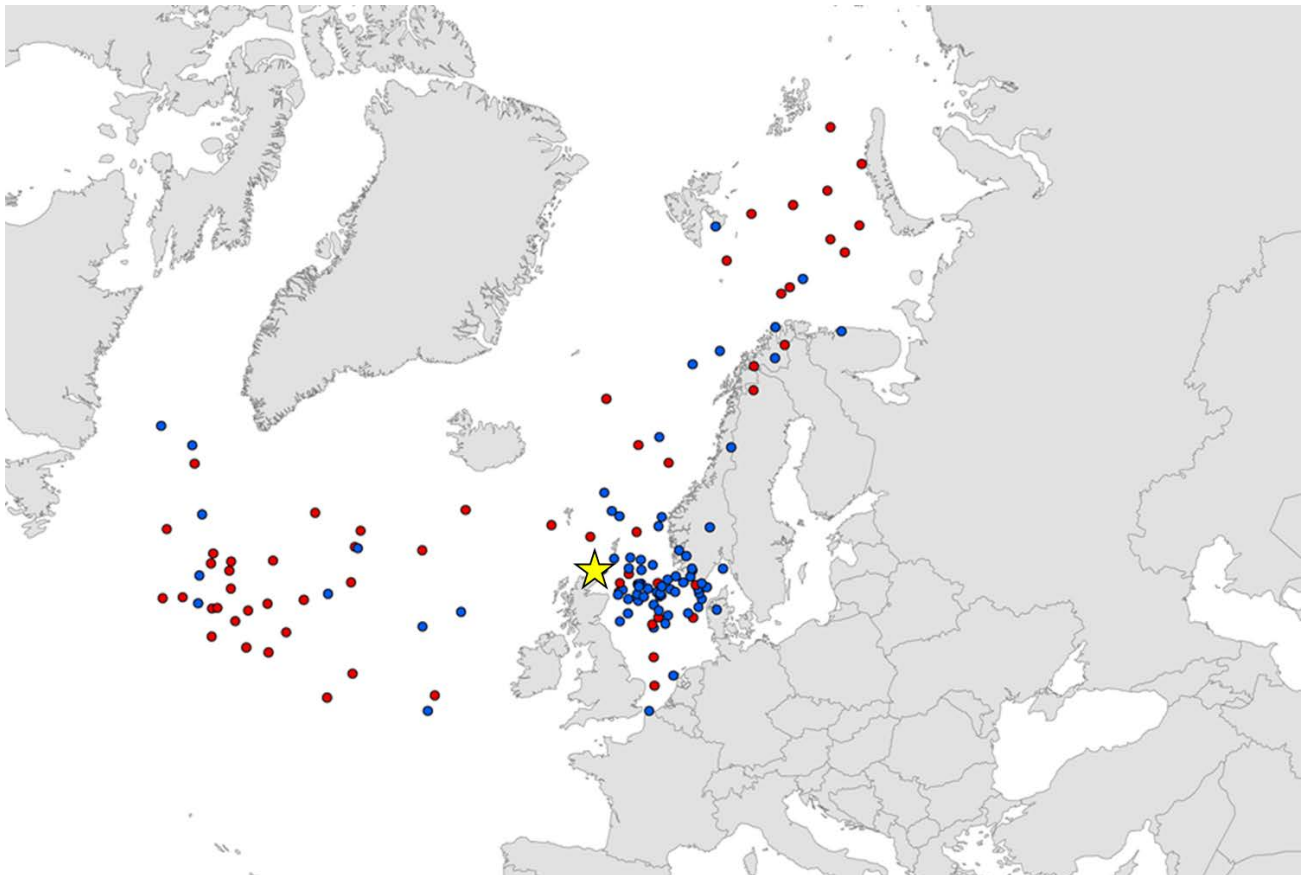
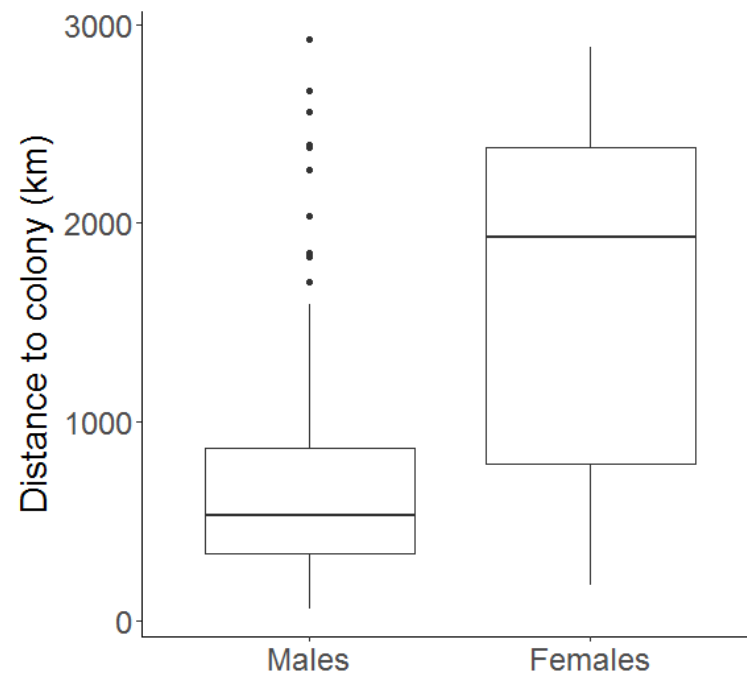


Figure 4. Location of the moulting Northern Fulmars breeding at Eynhallow (colony represented by the yellow star). Points represent the geographic mean moulting location calculated from the locations between the start and end dates of each individual's moult, excluding locations from within the autumn equinox. Males are represented by blue points and females by red points ($n = 135$, as mean locations were not calculated for the four individuals where locations could not be determined for $> 75\%$ of days during the moult; see Table S1).



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Figure 5. Boxplot showing the sex difference in the distance between an individual's geographic mid-point during the moult and the breeding colony. The boxes depict interquartile range, with median as a bold line. Whiskers indicate variability outside the upper and lower quartiles. Outliers are plotted as circles.



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