

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

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

37

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

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39 Avian moult is an energetically demanding process (Cherel *et al.* 1994, Murphy 1996) which
40 can also incur indirect costs by impairing flight (Swaddle & Witter 1997, Guillemette *et al.*
41 2007, Gutowsky *et al.* 2014). Temporary periods of flightlessness, or lower flight
42 performance, increase vulnerability to predators and can limit access to resources (Green *et al.*
43 2004, Guillemette *et al.* 2007). Together, these direct and indirect costs of moult can result in
44 trade-offs between the timing of moult and the two other major avian life-history events:
45 breeding and migration (Bridge 2011). Most work on these trade-offs has focused on
46 passerines, which moult after breeding and prior to migration; thus allowing the moult process
47 to be observed directly (Hemborg & Lundberg 1998). There have been extensive studies of
48 breeding phenology in many seabirds (e.g. Keogan *et al.* 2018). However, moult generally
49 takes place once birds have dispersed from breeding grounds, constraining direct observations
50 of pelagic seabirds. Information on the timing of their moult has therefore been dependent
51 upon *ad hoc* observations at sea or analyses of carcasses (e.g. Brown 1988, Edwards &
52 Rohwer 2005, Bugoni *et al.* 2015). As a consequence, there is limited information on the
53 timing of moult in many pelagic seabirds (Bridge 2006, Gutowsky *et al.* 2014, Cherel *et al.*
54 2016) and the key areas that these birds may be using at this time (e.g. Harris *et al.* 2014).
55 Given that reduced flight performance may increase their vulnerability to various natural and
56 anthropogenic stressors (Green *et al.* 2004), better information on moult patterns is also
57 required to support effort to manage high seas areas to protect pelagic seabirds.

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

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72 data could be used to characterize the timing and location of moult in three smaller
73 subantarctic petrel species. They firstly characterized moult in the Blue Petrel *Halobaena*
74 *caerulea*, a reference species that is known to renew its plumage in autumn, and identified a
75 strong peak in daily time spent sitting on water during the expected moult period. They then
76 used this peak as a proxy to characterize the contrasting moult strategies of two other petrel
77 species. This approach now opens up new opportunities for understanding moult strategies in
78 a range of pelagic species by integrating biologging data with individual based demographic
79 studies; thereby permitting assessments of variation in the timing of moult in relation to
80 known reproductive performance.

81 In this study, we used data available from geolocation loggers with wet/dry sensors to
82 characterize the timing and location of moult in a well-studied colony of Northern Fulmars
83 *Fulmarus glacialis* in Scotland. Existing information on moult patterns in this species has
84 been based either upon observations of birds around breeding colonies (Carrick & Dunnet
85 1954, Allard *et al.* 2008) or analysis of beached or by-caught individuals (Quinn *et al.* 2016).
86 These techniques have shown that the moult occurs post-breeding, but they cannot be used to
87 explore variation in moult duration or links between moult timing and reproductive success.
88 Here, our primary objectives were to explore whether the timing or duration of moult varied
89 between birds that bred unsuccessfully or successfully in the preceding breeding season, and
90 birds of different sex. In addition, we aimed to identify the areas used by Northern Fulmars
91 from this population during their moult, to assess whether there are discrete areas where they
92 may be more vulnerable to anthropogenic stressors.

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95 **METHODS**

96

97 **Study site and logger deployment**

98 Fieldwork was conducted on Eynhallow, Orkney (59°8'N; 3°8'W) where individual based
99 studies of breeding Northern Fulmars have been ongoing since the 1950s (Dunnet 1991).
100 Individuals have been marked using unique colour ring combinations, and information on
101 their reproductive status has subsequently been based upon observations made during three
102 standardized visits to the colony in each breeding season; during the incubation, hatching and
103 fledging periods (for details see Lewis *et al.* 2009, Cordes *et al.* 2015).

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

113 Devices were recovered 1-3 years later, generally at the nest but occasionally after
114 birds were captured in flight. Annual attendance of breeding adults at this colony varied
115 considerably, and can be as low as 50% in some years (Thompson & Ollason 2001). This, in
116 turn, affected the likelihood of recovering loggers, resulting in an average recovery rate of
117 46% over one year to 76% after two or more years.

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

122

123 **Moult characterisation and individual variability in the timing of moult**

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

130 Due to occasional logger failure or limited memory capacity on multi-year
131 deployments, activity data were not always available throughout complete deployments.
132 Previous studies of carcasses indicate that moult in Northern Fulmars occurs after the end of
133 the breeding season and is completed by the end of December (Carrick & Dunnet 1954,
134 Allard *et al.* 2008, Quinn *et al.* 2016) when birds start to attend the colony periodically until
135 the next breeding season (Coulson & Horobin 1972, Macdonald 1980, Slater 1990). For these
136 analyses, we therefore selected only those birds and years in which activity data were

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137 available throughout the entire mid-August to mid-December period. Furthermore, we only
138 used data from years in which there were activity records from at least 10 birds, and birds for
139 which sex and breeding status in the previous breeding season were known. This resulted in a
140 dataset that included 139 moult cycles (82 individuals; 44 males and 38 females; see
141 Supporting Information Table S2 for detailed sample sizes per season).

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

155 To characterise variation at the population level, we calculated a mean value for the
156 proportion of the day which birds spent on the water throughout the annual cycle. Individual-
157 based estimates of the timing of moult were then based upon a Generalized Additive Model
158 (GAM) that was fitted to the 'wet' data for each bird's annual cycle using the approach
159 developed by Cherel *et al.* (2016). Following Cherel *et al.* (2016), the core moult period was
160 defined as the time window (consecutive days) when the predicted 'wet' variable exceeded
161 75% of the value of the peak in the daily proportion of time wet (see Supporting Information
162 Fig. S1 for an example GAM). These GAM results also provided estimates of the date of the
163 peak of wetness, and start, median, end dates, and duration of the moult for each individual.
164 95% CI around the fitted GAM were used to provide an estimate of variability around each
165 individual estimate of moult duration.

166

167 **Influence of breeding status on the timing of moult**

168 Data on an individual's moult phenology were then integrated with data from colony
169 observations to explore how moult characteristics were influenced by an individual's previous

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170 breeding success. Variability in moult characteristics were investigated using a linear mixed
171 model fitted with maximum likelihood in the *lme4* package (Bates *et al.* 2015). The bird's ID
172 was incorporated in the model as a random effect to prevent pseudo-replication due to the
173 presence of data from several different annual cycles for some birds. We used start date,
174 median date and duration of the moult as response variables. The end date of the moult was
175 highly correlated to start date and duration, so was not included as a response variable. We
176 included the following explanatory variables: sex of the individual, year and previous
177 breeding success. Visits were made to the study colony on three occasions in each breeding
178 season: in late May to identify which birds were on eggs; in mid July to estimate hatching
179 success; and in mid August to record the presence of chicks prior to fledging (see Lewis *et al.*
180 2009). Breeding success was therefore classified into four categories: 1) Not recorded
181 breeding at the colony in that year, 2) Failed on an egg, 3) Failed on a chick, 4) Successfully
182 fledged a chick. An interaction between sex and reproductive success was also incorporated in
183 the model to explore whether males and females responded in the same way to a successful or
184 failed reproductive attempt. The significance of each explanatory variable was tested with the
185 'Anova' function using type III Wald Chi-square tests from the *car* package (Fox & Weisberg
186 2011). Model selection was carried out by removing every non-significant factor, and
187 confirming the better fit of the model using Akaike Information Criterion, correcting for small
188 sample size, with the function 'AICc' from the *MuMIn* package (Bartoń 2016). Models with
189 $\Delta\text{AICc} \leq 2$ were considered the best of the set of candidate models. Following this analysis,
190 multiple comparison post-hoc Tukey tests were performed to assess specific differences
191 within significant variables, using the 'glht' function from the *multcomp* package (Bretz &
192 Westfall 2008). Assumptions of homoscedasticity and normal distribution of the model's
193 residuals were verified for every candidate model.

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

196

197 **Spatial distribution of individuals during their quasi-flightless moult period**

198 Geolocation data were then used to characterise the distribution of individual fulmars during
199 their core moult period. Twilight events were determined from where light curves
200 intersected with a selected threshold of 9 for MK 3, 5 and 3006 geolocators and 11 for C250
201 geolocators, using the BASTrack (British Antarctic Survey; Fox 2010) or IntiProc software
202 from Migrate Technology Ltd (Coton, Cambridge, UK; Fox, 2015), respectively. Twilight

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203 events were checked visually to remove data from days with constant light or dark, or where
204 shading events occurred. If a light curve clearly suggested a more correct placement of a sun
205 event, events were moved. On average, 6 % of resulting twilight events were moved.

206 The light data were further processed following procedures in Hanssen *et al.* (2016).
207 Sun elevation angles were determined individually for each geolocator (ranging from -1° to -
208 4.5°) by combining in-habitat calibrations, using the breeding colony as a reference point,
209 with visually inspecting latitude vs. date plots (Hanssen *et al.* 2016, Supporting Information
210 Fig. S2). A smoothing process was applied twice to positional data to reduce location errors
211 (Hanssen *et al.* 2016, but see Phillips *et al.* 2004 and Fox, 2015). Following this procedure,
212 75% individuals had daily locations for > 95% of their moult period (Supporting Information
213 Table S1). In those few (< 5%) cases where daily locations were available for < 70% of days
214 during the moult cycle, this was typically because birds were using high Arctic areas at this
215 time of year.

216 Information on the start and end date for each individual's moult (as defined by the
217 GAM) was used to filter the resulting geolocation data and estimate the great circle distance
218 between each of the bird's twice-daily locations and the breeding colony. To visualise
219 differences between individuals, we estimated the geographic mid-point of locations
220 obtained for each bird during their respective moult periods, excluding locations during the
221 equinox, using the function 'geomean' in the *geosphere* package (Hijmans 2016). We used the
222 distribution of distances to the colony to provide an estimate of variability and comparison of
223 male and female locations during the moult period. For many individuals, the moult period
224 included part of the autumn equinox (8th September – 20th October). To explore whether this
225 biased estimates of the geographic mid-point, we also calculated a second geographic mid-
226 point for each bird that included data from the equinox by using observed values of longitude
227 and proxy values for latitude that were based upon that individual's moult locations from
228 outwith the equinox.

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

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236 RESULTS

237

238 Moulting characterisation and individual variability in the timing of moult

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

250

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

252 Inter individual variability in the timing of the moult was explained by different explanatory
253 variables for each of the three moult characteristics we chose to model (i.e. start date, median
254 date and duration; see Table 1). For start date, the best model contained only the previous
255 breeding status as an explanatory variable (Table 2). Birds of differing breeding status
256 exhibited significant differences in the start date of their subsequent moult (LMM, $\chi^2 =$
257 248.50, $P < 0.001$; Fig. 3). Non-breeders and birds that failed on an egg started their next
258 moult at a similar time (Tukey, $P > 0.05$, $z = 0.5$): 26th July \pm 2.8 days (mean \pm SE) for non-
259 breeders and 27th July \pm 2.3 days for birds who failed on an egg. Birds that failed on a chick
260 started their moult significantly later than both other groups, around the 13th August \pm 2.3
261 days (Tukey, $P < 0.05$, $z = 5.6$ and 5.8 , respectively). Finally, successful breeders moulted
262 latest (Tukey, $P < 0.05$, $z = 11.3$, 12.4 and 7.4 compared to non-breeders, and birds that failed
263 on an egg or a chick groups, respectively). On average, these successful birds started their
264 moult on 27th August \pm 0.9 days, one month after birds which failed on eggs or were not
265 recorded breeding (Fig. 3). There were slight annual differences in the start of moult, but
266 these were not significant (see Table 3).

267 Differences in the median date of the moult were less clear (Table 2). There was
268 slightly more support for the model containing both sex and breeding status than the model

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269 containing only breeding status ($\Delta\text{AICc} = 1.4$). However, the difference in median date
270 between the sexes was slight (LMM, $\chi^2 = 3.67$, $P = 0.055$; Males: 21st September ± 1.8 days;
271 Females: 18th September ± 1.9 days). On the other hand, the difference in median date of
272 moult for individuals of differing breeding status was highly significant (LMM, $\chi^2 = 204.53$, P
273 < 0.001) and showed a similar pattern to that seen in start dates. Non-breeders and birds that
274 failed on an egg had similar median dates (2nd September ± 2.1 and 1st September ± 2.2 days;
275 Tukey, $P > 0.05$, $z = -0.228$), median date for birds that failed on a chick was later (16th
276 September ± 2.1 days, Tukey, $P < 0.05$, $z = 4.33$, and 5.24, respectively) and that for
277 successful birds was latest (30th September ± 1.1 days, Tukey, $P < 0.05$, $z = 9.73$, 11.63 and
278 7.08, respectively). Similarly, there was a slight but not significant annual difference in
279 median date of the moult.

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

286

287 **Location during the moult**

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

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301 **DISCUSSION**

302

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

318 The use of activity data from known individuals provided additional information on
319 moult that offers new insights for broader comparative studies (Bridge 2011). First, variations
320 in the amount of time that birds spent on the water provided estimates of the duration of an
321 individual's moult, which was typically around two months (Fig. 2). Existing estimates of
322 moult duration in seabirds are based on approximate dates for moult initiation and
323 completion, potentially leading to overestimation of an individual's moult pattern (Bridge
324 2006). Activity based techniques can therefore provide finer-scale individual level measures
325 which can be used to compare the duration of moult both between and within species. Second,
326 by combining these data with information on known reproductive histories, we were able to
327 explore the relationship between the timing of breeding and moult at the individual level.
328 Individual-based studies linking variation in moult patterns to reproductive success are rare
329 amongst seabirds, and were previously based only upon moult characteristics obtained from
330 observations of known breeders at the colony (Barbraud & Chastel 1998, Rohwer *et al.* 2011).
331 Detailed colony-based studies can now use these techniques to explore interactions between
332 key life-history events both at the colony (breeding success) and at sea (migration schedules
333 (e.g. Catry *et al.* 2013) and moult patterns).

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334 Our analyses revealed that inter-individual variability in the timing of the moult was
335 related to success during the previous breeding attempt, with non-breeders or birds that failed
336 early in the season starting their moult around one month earlier than successful breeders
337 (Fig. 3). These data are in accordance with a recent experimental study on Cory's Shearwater
338 *Colonectris borealis*, which used a combination of tracking and stable-isotope analysis to
339 demonstrate that birds that were induced to fail moulted earlier compared to successful
340 breeders (Ramos *et al.* 2018). Colony observations of albatrosses have also shown that
341 breeding success can influence subsequent moult in those larger species that have a complex
342 biennial moult (Furness 1988, Prince *et al.* 1993, Rohwer *et al.* 2011). In those cases, failed
343 breeders increased the number of primary flight feathers that they moulted, which could result
344 from an earlier initiation and/or longer moult duration. Detailed mechanisms controlling
345 prebasic moult remain unclear, but our observations are in line with the suggestion that higher
346 levels of sex-steroid hormones delay the onset of moult in active breeders (Hahn *et al.* 1992).
347 In passerines, delays in moult initiation typically require a faster moult to maintain migration
348 schedules (Hahn *et al.* 1992). However, our data suggest that breeding success did not
349 influence the duration of the moult, meaning that the pattern observed for the start date of
350 moult (Fig. 3) was retained in the median and end dates of moult. Experiments on European
351 Starlings *Sturnus vulgaris* demonstrated that shorter moult duration led to the production of
352 lower quality feathers (Dawson *et al.* 2000), which could compromise future reproductive
353 success in seabirds that make long foraging trips during chick rearing (Rohwer *et al.* 2011). In
354 the absence of a fixed migration schedule, individual moult durations in Northern Fulmars
355 may be less variable in order to maximise feather quality although, as discussed below, inter-
356 annual variation in duration suggest moult duration may be affected by external
357 environmental conditions.

358 These findings also provide new insights into previous studies that used traditional
359 techniques to assess the extent to which moult and breeding overlap. Northern Fulmars that
360 breed successfully are constrained to central place foraging from the colony until their chicks
361 fledge in late August or September. Whilst non-breeders and early failures may leave the
362 colony earlier, observations of marked birds indicate that not all do so (Anderson 1962, P.
363 Thompson unpubl. data). This can result in an overlap between observations of breeding and
364 moulting birds at the population level, but these results demonstrate that events do not
365 necessarily overlap at the individual level. No evidence of active breeders moulting flight
366 feathers was found at our study site (Carrick & Dunnet 1954, this study) or at a Canadian

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367 Arctic colony (Allard *et al.* 2008). Allard *et al.* (2008) suggested that their observed temporal
368 overlap of breeding and moulting individuals resulted from large scale movements and
369 overlapping ranges of birds from different colonies, with moult occurring earlier in colonies
370 characterised by earlier egg-laying. However, our results suggest that Allard *et al.*'s (2008)
371 observations could simply result from within colony variation in reproductive success, as
372 failed breeders that remain around the colony could initiate moult up to a month earlier than
373 the active breeders. Nevertheless, we made only low intensity colony visits in the last few
374 weeks of chick rearing, when very few adults were observed. Thus, some evidence of moult
375 could have been missed.

376 Rohwer *et al.* (2011) highlight the potential for extending colony-based studies to
377 explore trade-offs between moult and reproduction. Estimates of moult phenology from
378 activity loggers provide additional opportunities to extend such studies by following birds
379 after dispersal from the colony, thus exploring unresolved questions about timing and
380 duration of seabird moult arising from analyses of carcasses (Bridge 2011). Atlantic Puffins
381 *Fratercula arctica* for example have a protracted period of moult with bi-modal peaks in both
382 October and March, suggesting they may moult twice during the non-breeding season (Harris
383 *et al.* 2014). Individual based data are required to test such hypotheses, and explore how these
384 patterns relate to previous reproductive histories. However, interpretation of individual bouts
385 of at-sea behaviour in auks are more complicated because they may withdraw one leg into the
386 plumage while sitting on the water (Linnebjerg *et al.* 2014). Nevertheless, modelling longer-
387 term variations in behaviour using the approach developed by Cherel *et al.* (2016) may
388 provide opportunities to use existing datasets (e.g. Fayet *et al.* 2017) to compare putative
389 moult patterns in individuals of known reproductive status over multiple years and from
390 different colonies.

391 As reported by Allard *et al.* (2008), we found no sex differences in the timing of
392 moult. There was, however, a tendency for females to moult at more distant locations from
393 the colony, in line with sex-differences in the foraging areas used by these birds during the
394 winter (Quinn 2014) and pre-laying exodus (Edwards *et al.* 2016). GLS studies of non-
395 breeding distribution are already providing new insights into potential moulting areas (e.g.
396 Harris *et al.* 2015). The use of activity data to refine estimates of birds' locations during
397 critical moult periods can further support risk assessment and conservation planning (Croxall
398 *et al.* 2012). Unlike many other waterbird species (Kirby 1995) Northern Fulmars from this
399 single colony were dispersed over a wide geographical area rather than congregating at

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400 specific locations during their moult. Current conservation activity often focuses on
401 identifying Important Bird Areas, where seabirds may aggregate to feed or engage in other
402 key behaviours such as moulting (Lascelles *et al.* 2016, Krüger *et al.* 2017). Our data
403 highlight that focused area-based conservation interventions may be less easily applied to
404 highly dispersed and wide-ranging species such as Northern Fulmars. Observed levels of
405 dispersion during the moult suggests that the viability of individual colonies should be
406 buffered against localized impacts such as oil spills, which could adversely affect breeding
407 populations aggregating in common wintering areas (Fauchald *et al.* 2002). At a finer-scale,
408 however, it remains possible that birds from this single colony do still aggregate during the
409 moult, potentially associating with individuals from a broad range of colonies around the
410 North Atlantic. Further tracking work at multiple sites could assess overlap between colonies
411 and the ecological and conservation importance of these interactions. In particular, it would
412 be valuable to explore the extent to which males and females may be differentially exposed to
413 threats such as fisheries by-catch or contaminants during this vulnerable phase of the annual
414 cycle (Fauchald *et al.* 2002, Anderson *et al.* 2011, Van Franeker *et al.* 2011).

415 Annual variation in environmental conditions and prey availability are recognised to
416 have profound consequences for breeding phenology (Frederiksen *et al.* 2004, Wanless *et al.*
417 2009), and may similarly affect the timing or duration of moult. For example, experimental
418 studies on passerines suggest that feeding resources during the non-breeding season could
419 influence the timing of pre-alternate moult initiation in wild birds (Danner *et al.* 2015). We
420 found no evidence of interannual variation in moult initiation in the years we studied, but the
421 duration of moult did vary between years (Tables 2 & 3). However, our estimates of moult
422 duration did vary markedly, with some individuals undergoing moults of up to 120 days (Fig.
423 2; Supporting Information Table S1). This, together with small sample sizes in some years
424 constrained a more detailed assessment of these patterns, but these results highlight the
425 potential for using individual-based activity data to explore the importance of intrinsic and
426 extrinsic drivers of such variation. Studies of beached Northern Fulmars during winters with
427 unusually high mortality indicate that feather renewal had slowed down or fully arrested in
428 many of these birds, resulting in highly degraded flight feathers and poor down plumage (Van
429 Franeker 2011). Future work could link activity based estimates of moult patterns and flight
430 behaviour with direct measures of feather quality at subsequent capture (e.g. Dawson *et al.*
431 2000), or indirect measures of over-winter stress from measures of feather cortisol (e.g.
432 Ramos *et al.* 2018). Integration of these approaches with long-term deployments of tri-axial

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433 accelerometer loggers (Williams *et al.* 2017) would be particularly valuable for understanding
434 the energetic consequences of observed differences in moult patterns. In contrast to Northern
435 Fulmars, Southern Fulmars *Fulmarus glacialoides* exhibit extensive overlap between moult
436 and breeding, with a high level of primary moult even during late incubation (Barbraud &
437 Chastel 1998). These two species are otherwise similar in many aspects of their ecology and
438 biology, and this overlap may result from food availability being very high but restricted to a
439 short Antarctic summer (Barbraud & Chastel 1998). Others have suggested that the duration
440 of moult may also vary in different environments. For example, Murphy and King (1992)
441 proposed that wintering areas used for moult could influence timing at the species or even
442 population level, with birds experiencing a shorter moult at higher latitudes. Here again, there
443 is potential to use the analyses developed by Gutowsky *et al.* (2014) and Cherel *et al.* (2016)
444 to test this hypothesis upon widely distributed species by integrating geolocation and activity
445 data collected from high and low latitude colonies.

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

460
461 We thank Orkney Islands Council for access to Eynhallow and all the fieldworkers involved in deployment and
462 recovery of the GLS tags and colony monitoring. All ringing work was carried out under permit from the BTO.
463 We are grateful to James Fox of Migrate Technologies for recovering data from GLS loggers which would not
464 download, and Richard Phillips and Janet Silk of BAS for advice on GLS analysis. Lucy Quinn was supported
465 by a NERC Studentship and additional funding to support fieldwork was gratefully received from Talisman
466 Energy (UK) Ltd. Additional support for loggers and analysis was provided through the SEATRACK project,

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467 which is funded by the Norwegian Ministry of Climate and Environment, the Norwegian Ministry of Foreign
468 Affairs and the Norwegian Oil and Gas Association.

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744 **SUPPORTING INFORMATION**

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

746 **Appendix S1.** R code to calculate daily activity summaries

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

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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753 **TABLES & FIGURES**

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Response variable	Significant explanatory variable(s)	<i>P</i> -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

760

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

763



	~ sex	+ breeding status	+ cycle year	+ sex : breeding status	$\Delta AICc$	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

765

766 **Table 2.** Model selection based on AICc, for the three response variables (start date of moult,
767 median date of moult and duration of moult), using linear mixed models including bird
768 number as a random effect. Explanatory variables used in each model are highlighted in grey.
769 Significance of each explanatory variables used is represented as follows: · ($P < 0.1$); * ($P <$
770 0.05); ** ($P < 0.01$); *** ($P < 0.001$). The best-fitting model is represented between the
771 dotted lines.

772

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

774

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

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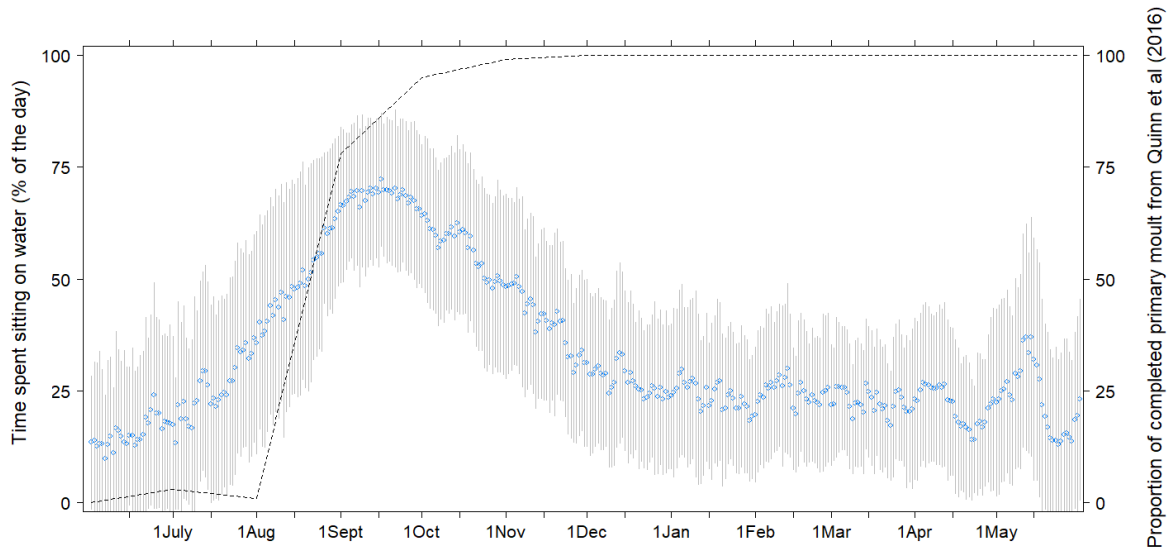
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788 **Figure 1.** Variation in the mean daily percentage of time spent on water (\pm SD) for 139 annual
789 cycles from 82 individual fulmars tracked between 2007 and 2016. For comparison, the dashed
790 line represents the cumulative proportion of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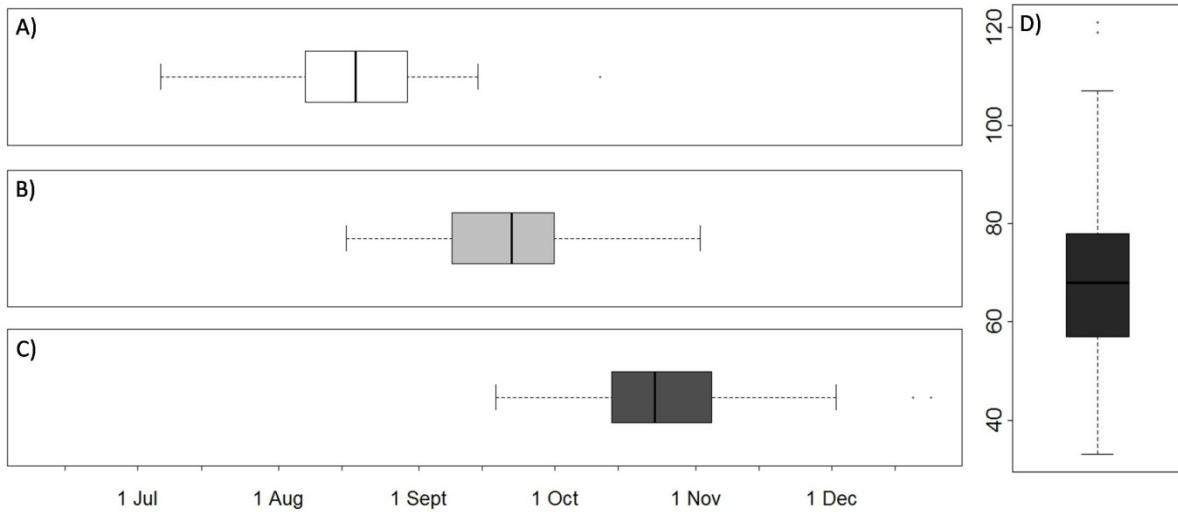


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797 **Figure 2.** Variability in the timing of the moult. Distribution of the characteristics of the moult
798 extracted from the activity data using GAM. The boxes depict Interquartile range, with median
799 as a bold line. Whiskers indicate variability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

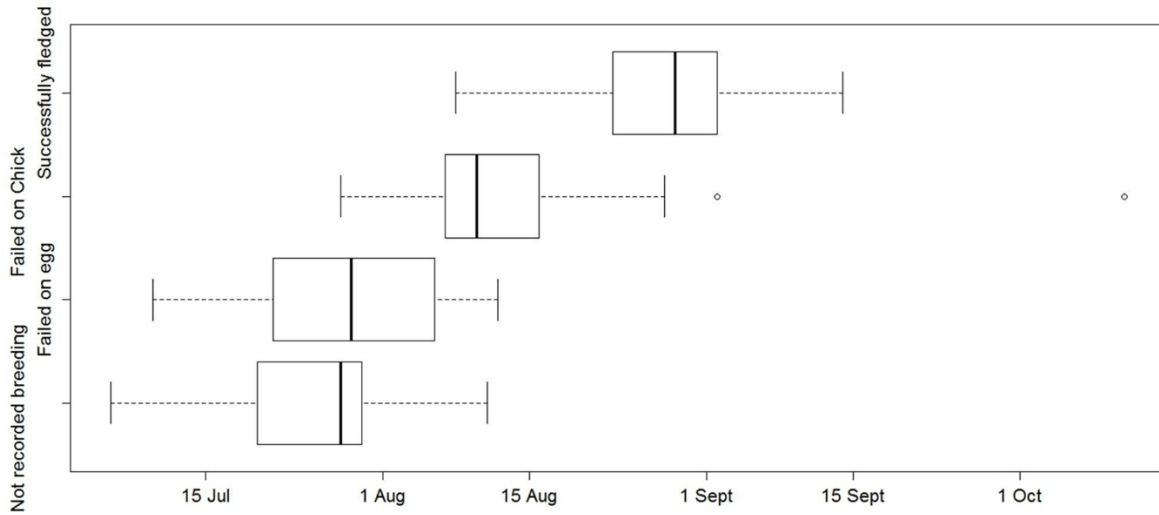
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808 **Figure 3.** Differences in the starting date of the moult explained by breeding status. The boxes
809 depict Interquartile range, with median as a bold line. Whiskers indicate variability outside the
810 upper and lower quartiles. Outliers are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

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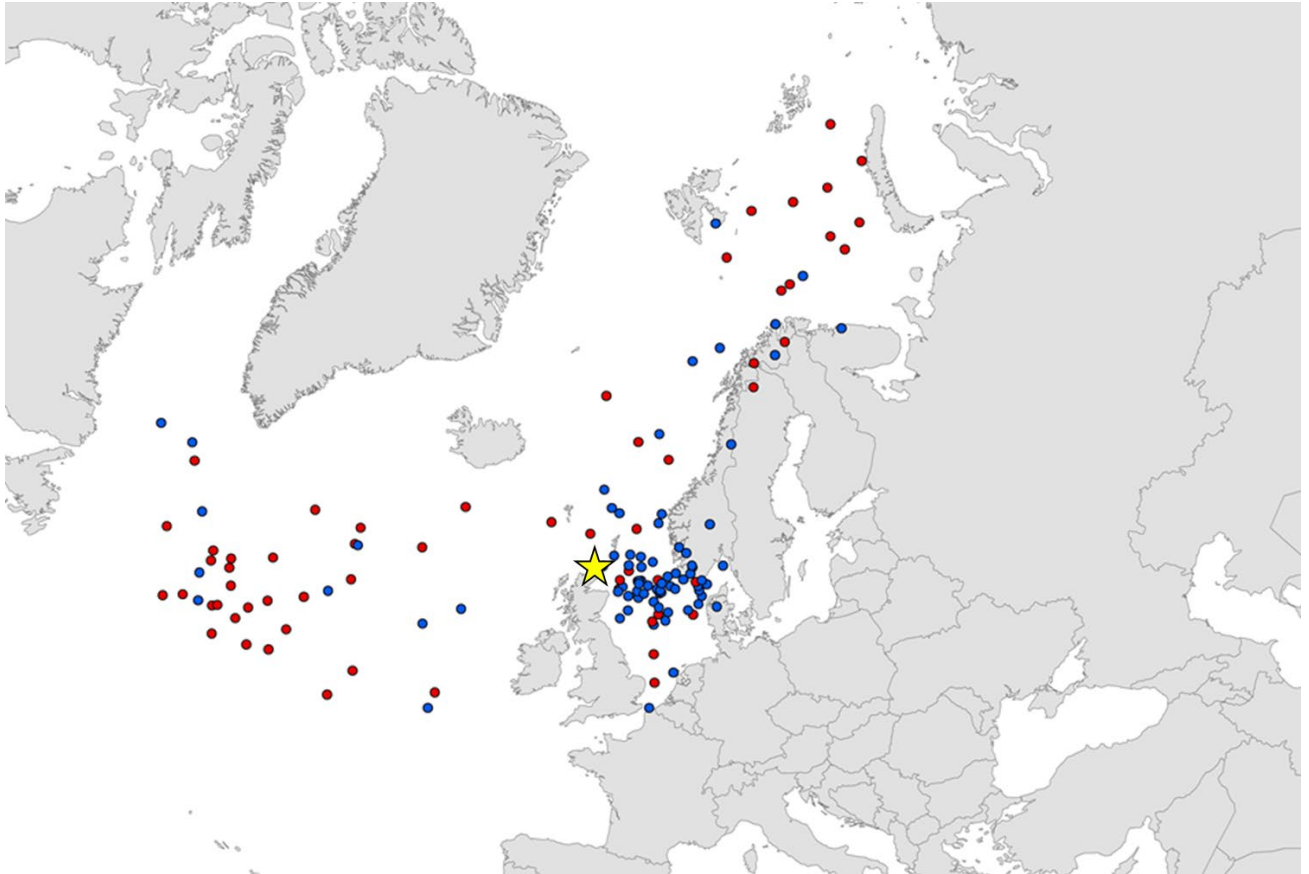
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817 **Figure 4.** Location of the moulting Northern Fulmars breeding at Eynhallow (colony
818 represented by the yellow star). Points represent the geographic mean moulting location
819 calculated from the locations between the start and end dates of each individual's moult,
820 excluding locations from within the autumn equinox. Males are represented by blue points
821 and females by red points ($n = 135$, as mean locations were not calculated for the four
822 individuals where locations could not be determined for $> 75\%$ of days during the moult; see
823 Table S1).
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829 **Figure 5.** Boxplot showing the sex difference in the distance between an individual's
830 geographic mid-point during the moult and the breeding colony. The boxes depict Interquartile
831 range, with median as a bold line. Whiskers indicate variability outside the upper and lower
832 quartiles. Outliers are plotted as circles.

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