

# 1 Earlier arrival despite constant breeding phenology

## 2 in two congeneric seabirds

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31 the manuscript.

32

33 Abstract

34 A global analysis recently showed that seabird breeding phenology (as timing of egg-laying and  
35 hatching) is surprisingly insensitive to changing climatic conditions and did not change over time [1].  
36 This group, the most threatened of all birds, is therefore prone to spatiotemporal mismatches with  
37 their food resources. Yet, other aspects of the breeding phenology may also have marked incidence  
38 on breeding success, such as the arrival date of adults at the breeding site following winter  
39 migration. Here we utilized a large tracking dataset of two congeneric seabirds breeding in 15  
40 colonies across 24° latitudes, to show that arrival date at the colony was highly variable between  
41 colonies and species (ranging 154 days) and advanced on average 1.5 days/year while timing of egg-  
42 laying remained unchanged, resulting in an increasing pre-laying duration between 2009 and 2018.  
43 Thus, we demonstrate that potentially not all components of seabird breeding phenology are  
44 insensitive to changing environmental conditions.

45

46 Keywords: pre-laying period, timing of egg-laying, *Uria aalge*, *Uria lomvia*, murre, guillemots

47

## 48 Introduction

49 Timing of life history events such as reproduction is predicted to have evolved to optimally utilize  
50 temporally favourable conditions in seasonal systems [2]. Breeding phenology is a key adaptation  
51 with direct consequences on reproductive success and population dynamics [3, 4]. Rapid climate  
52 change has led to an advancement of the annual cycle in many organisms in temperate and polar  
53 regions, while species that have not adjusted to climate change seem to be more prone to  
54 population declines [5, 6]. In seabirds, timing of egg-laying has been shown to be insensitive to  
55 changing climatic conditions globally, highlighting the vulnerability of this group to mismatches with  
56 lower-trophic-level resources [1]. Yet, spring arrival at the colony, and the pre-laying period – the  
57 time between arrival at the colony and egg-laying - are also important and rarely considered  
58 components affecting breeding success. This period allows birds to establish and defend nest sites  
59 [7], build up body condition [8, 9] and mate [10], which often starts months before egg-laying [11,  
60 12].

61 Here, we took advantage of a large tracking dataset, enabling us to determine arrival dates in two  
62 seabird species, across nine years (2009 - 2018) and 15 colonies across a large latitudinal gradient  
63 (56°N - 79°N), to test if arrival date also does not exhibit any trend across years, similar to timing of  
64 egg-laying [1]. This data was available for two colonial, congeneric species, the common (hereafter  
65 COGU, *Uria aalge*) and Brünnich's guillemot (hereafter BRGU, *Uria lomvia*). These species are long-  
66 distance migrants [13-15], have similar morphology and life history [16, 17], and exhibit no trend in  
67 breeding phenology ([1] +Descamps et al. in review GCB; Keogan et al. in review GCB), but  
68 contrasting population trends [18-20]. Their arrival date is hypothesized to be driven by timing of  
69 food availability in the vicinity of the colony [21, 22], which can be roughly approximated by latitude  
70 [23], or by colony size through increasing pressure on nest site defence displayed as longer pre-laying  
71 periods in larger colonies [11, 24, 25]. We tested the hypothesis that arrival date is without trend  
72 across years, same as egg-laying date. Further, we examined if arrival date is delayed with latitude,  
73 similar to timing of egg-laying [23], or determined by colony size due to pressure on nest site  
74 defence.

75

## 76 Material and Methods

### 77 *Data acquisition*

78 The date of first arrival at the colony for each colony and species was estimated using salt water  
79 immersion data recorded by light-level geolocators deployed on adult breeders. Arrival date was

80 here defined as the date when the pre-laying period commences. It was identified as the date when  
81 the majority of tracked individuals attended the colony for the first time after the non-breeding  
82 period, using the assumption that first arrival back at the colony is synchronized and independent of  
83 sex in guillemots [25-27] (details in SI). Using a colony-wide first arrival date rather than individual  
84 arrival dates resulted in more robust results due to limitations in logger data resolution and accuracy.  
85 Tracking data were available from 15 colonies (figure 1A), for one to eight years (in the period 2009 -  
86 2018). BRGU and COGU breed sympatrically at five of these colonies. Three instances of estimated  
87 arrival dates could be validated with available time-lapse camera data at two colonies (figure S1). To  
88 estimate pre-laying duration as well as temporal changes in phenology, we gathered annual  
89 measures of breeding timing which were available as population-level mean hatching dates at twelve  
90 colonies (details in SI) for one to seven years (in the period 2009 - 2018). To assess the potential  
91 consequences of variable arrival dates on reproductive success, we used annual breeding success for  
92 which data was available from five colonies (details in SI) for four to six years (in the period 2010 -  
93 2017).

#### 94 *Data analysis*

95 *Temporal trends in breeding phenology and their consequences* - Colony- and species-specific inter-  
96 annual variation in arrival dates was quantified as standard deviation (SD) from mean arrival timing.  
97 To test if arrival date changes with year we applied a linear mixed effect model (LME, package `lme4`)  
98 with standardized arrival dates (SD = 1, mean = 0) as response variable (n = 80), year as fixed effects  
99 and id (as combination of colony and species) as random intercept. The same model was applied on a  
100 subset of data for which mean hatching date data were available (n = 44). Using this subset of data,  
101 we applied the same fixed and random effects to standardized pre-laying duration as well as  
102 standardized mean hatching date as response variables in order to assess if guillemot hatching timing  
103 and pre-laying duration have changed over time. Most parsimonious models were selected using  
104 Akaike information criterion [28], resulting in all instances in a removal of species and its interaction  
105 with year as predictor variables. We calculated the percentage of variance explained by the fixed  
106 effects (marginal  $R^2$ ) and fixed and random effects (conditional  $R^2$ ; [29]). In order to assess if a large-  
107 scale factor is driving temporal trends in arrival date, we assessed temporal synchrony as mean  
108 correlation of standardized arrival dates between colonies using the `msynch` function (package `ncf`  
109 [30]). To test if potential temporal trends in arrival date had an effect on reproductive output, we  
110 applied a LME with standardized breeding success (SD = 1, mean = 0) as response variable,  
111 standardized arrival date as fixed effect and id as random intercept (n = 37).

112 *Effect of latitude and colony size on arrival date* - To test for the effect of latitude on arrival date at  
113 the colony, we applied a linear model with mean species- and colony-specific arrival date as the

114 response variable ( $n = 19$ ) and latitude and species and their interaction as predictors. Further, if  
115 latitude drives arrival date, we would expect that colonies close to each other would exhibit similar  
116 arrival timing. Hence, we used a Mantel-correlation test with 1000 permutations (package `ade4`) to  
117 test if spatial proximity can explain mean arrival date in either species. Alternatively, to test if arrival  
118 date and consequently pre-laying duration can be instead linked to colony size, we applied a linear  
119 model with mean species- and colony-specific pre-laying duration as the response variable ( $n = 15$ )  
120 and colony size on the log-scale and species as predictors. Population counts are taken from a similar  
121 time period to account for the contrasting population trends (table S1). To account for collinearity,  
122 we also tested latitude against colony size, but found no overall latitudinal trend (linear model,  
123  $\beta_{\text{latitude}} = -0.10$  with standard error (SE) = 0.10, adj.  $R^2 = <-0.01$ ). The Isle of May (the southernmost  
124 colony in the dataset) has been excluded from the above analyses as it constituted an outlier in both  
125 models. Observational data have previously shown that most breeding birds arrive back at the colony  
126 in the autumn and in at least some years birds attend the breeding sites throughout the winter [11,  
127 31]. Hence, an estimated arrival date in this colony is more uncertain than in all other colonies within  
128 the dataset. R (version 3.5.1, [32]) was used for all statistical analyses.

129

## 130 Results

### 131 *Timing of colony arrival*

132 Annual arrival dates varied between November 16 and April 18 with considerable variation across the  
133 Northeast Atlantic (figure 1B). Most of this variation is found between colonies (SD = 22.4 and 16.3  
134 days for COGU and BRGU, respectively, figure S1) and species (SD = 14.9 days across sympatric  
135 colonies), while colony- and species-specific inter-annual variation was significantly smaller (mean SD  
136 = 7.8 and 5.4 days for COGU and BRGU, respectively).

### 137 *Temporal variability in breeding phenology and its consequences*

138 Timing of hatching in guillemots showed no trend over time ( $\beta_{\text{year}} = -0.02$  with SE = 0.06, marg.  $R^2 =$   
139  $<0.01$ , cond.  $R^2 = <0.01$ ; figure 2C). In contrast, arrival date at colony advanced on average by 1.5  
140 days/year irrespective of species (range = 0.2 - 7.4 days/year; full dataset:  $\beta_{\text{year}} = -0.18$  with SE = 0.04,  
141 marg.  $R^2 = 0.23$ , cond.  $R^2 = 0.23$ ; subset with available mean hatching data:  $\beta_{\text{year}} = -0.21$  with SE =  
142 0.05, marg.  $R^2 = 0.33$ , cond.  $R^2 = 0.33$ ; figure 2A). This was also visible as prolonged pre-laying  
143 duration ( $\beta_{\text{year}} = 0.17$  with SE = 0.05, marg.  $R^2 = 0.20$ , cond.  $R^2 = 0.20$ ; figure 2B) as arrival date and  
144 pre-laying duration were highly and negatively correlated (-0.86). Colony arrival dates did not display  
145 synchrony among each other for either species (COGU: mean correlation = 0.20 with 95% confidence

146 interval (CI) = -0.21 - 0.74 and BRGU: 0.17 with CI = -0.43 - 0.93). And, no consequence of an  
147 advancing arrival date was detectable in exhibited breeding success for either species ( $\beta_{\text{std. arrival}} = 0.06$   
148 with SE = 0.17, marg.  $R^2 = <0.01$ , cond.  $R^2 = <0.01$ ; figure 2D).

149 *Does latitude or colony size predict arrival date?*

150 Mean arrival date at the colony could not be explained by latitude and the two species exhibited  
151 opposite trends ( $\beta_{\text{latitude BRGU}} = 1.63$  with SE = 1.24 and  $\beta_{\text{latitude * COGU}} = -2.73$  with SE = 2.19, adj.  $R^2 =$   
152 0.23, excluding Isle of May; figure 1B). Similarly, there was weak evidence for an effect of proximity  
153 on arrival dates for COGUs (Mantel correlation = 0.19,  $p = 0.14$ ), but somewhat stronger evidence in  
154 BRGUs (Mantel correlation = 0.29,  $p = 0.034$ ). Contrastingly, pre-laying duration showed substantial  
155 variability between colonies (mean = 75 days, SD = 19, range = 49 - 125) and was highly correlated  
156 with colony size ( $\beta_{\log(\text{size})} = 6.96$  with SE = 0.97, adj.  $R^2 = 0.82$ ; figure 1C).

157

## 158 Discussion

159 The main findings of our study are that timing of first arrival at the colony of both guillemot species  
160 and all colonies was highly variable and advanced through time despite no visible trend in mean  
161 hatching date. This advancement had apparently no effect on guillemot average breeding success.  
162 Further, the duration of the pre-laying period and hence timing of arrival is not determined by  
163 latitude, but is dependent on the size of the colony, being longer in large colonies, as well as timing  
164 of egg-laying, being later at higher latitudes [1, 23].

165 Theoretically, the minimum pre-laying duration required in guillemots is five days, as females  
166 undertake a four day long pre-laying exodus away from the colony [33]. Yolk formation (usually 14-15  
167 days [33]) could also occur away from the colony and fertilization occurs very soon after ovulation,  
168 which in turn occurs 24 hours before the egg is laid [10]. So, copulation right before the pre-laying  
169 exodus should be sufficient. Nonetheless, here we identified extensive pre-laying periods of more  
170 than one and up to several months with large variability between colonies and species. This may  
171 have costs and benefits associated with it. During this time period prospective breeders attend the  
172 colonies at regular intervals which restricts them to quasi central place foraging. This in turn limits  
173 their available prey options and could even lead to local depletion of food resources before spring  
174 bloom at large colonies [34], decreasing their body condition and potentially breeding probability  
175 prior to breeding. Alternatively, early return to the breeding sites might help secure nesting sites and  
176 mating partners [22], or it might be a response to unfavourable conditions experienced by these  
177 migrants during the end of their non-breeding period, resulting in an earlier return to the colony.

178 We showed that colony arrival date advanced in both the Brünnich's and common guillemot across  
179 the study area, while their timing of hatching did not display any trend as shown previously in  
180 seabirds globally [1] and for alcids in the Atlantic and Pacific (Descamps et al. in review GCB; Keogan  
181 et al. in review GCB). Contrary to these previous studies, concluding that breeding phenology is  
182 insensitive to climatic change, we identified a clear trend in arrival dates across both species studied.  
183 This advancement resulted in an increasing pre-laying duration as mean hatching date did not  
184 advance, suggesting that part of breeding in these seabirds is indeed sensitive to changing  
185 conditions, although we cannot derive conclusions regarding the process driving this phenomenon or  
186 if it is an adaptation to a changing environment. A potential explanation could be that the cue used to  
187 time arrival across the North Atlantic is changing as has been shown in some passerine species [35],  
188 but could not be demonstrated in others [36].

189 Although overall timing in both species exhibits the same trend, arrival time series were not  
190 synchronized between species and colonies. This indicates that short-term fluctuations in arrival date  
191 were not parallel through time among species and/or colonies, which suggests the interaction  
192 between large-scale environmental trends acting on the entire species combined with more local  
193 features. However, environmental conditions, although exhibiting the same trend, do not change  
194 homogeneously across the genus' range [37], which encompasses most of the North Atlantic for these  
195 species breeding within the study area ([13-15]+PAPER II). Hence, synchrony is not necessarily  
196 expected. As of now we could not detect any immediate consequences of advancing arrival dates on  
197 population-wide reproductive success. However, we cannot make any inference of the potential  
198 effect of advancing arrival dates on breeding propensity. Not all birds breed every year [38, 39] and  
199 the egg laying and hatching dates as well as the recorded breeding success may reflect only  
200 individuals with sufficient body condition, i.e. the ones that managed to get enough energy during  
201 the pre-laying period in order to breed [8].

202 Pre-laying duration and hence arrival timing at the colony could be linked with colony size [11, 24,  
203 25] rather than latitude. This suggests that arrival date might be driven by a combination of egg-  
204 laying date and colony size, which together determine pre-laying duration, and could explain the  
205 displayed large-scale variability in arrival timings between colonies as well as the lack of synchronicity  
206 between time series. Although guillemots typically show high nest site fidelity, site changes are  
207 documented which usually increase nest site quality for the usurper and decrease it for the usurped  
208 [40] underlining the importance of nest site defence as potential driver of arrival date. But, the  
209 influence of environmental conditions on arrival timing cannot be ruled out, as unfavourable weather  
210 has already been shown to affect pre-laying colony attendance in BRGU [26].

211 Our large-scale approach highlights the extent and importance of the pre-laying period in  
212 contributing to the challenges faced by colonial breeders in a changing environment. The advancing  
213 trend in arrival dates elucidates that not all parts of breeding phenology in seabirds are insensitive to  
214 change across years, although we cannot make inferences if this change is adaptive or not.

215

## 216 Acknowledgements

217 Funding for this study was provided by the Norwegian Ministry for Climate and the Environment, the  
218 Norwegian Ministry of Foreign Affairs and the Norwegian Oil and Gas Association through the  
219 SEATRACK project ([www.seapop.no/en/seatrack](http://www.seapop.no/en/seatrack)) as well as from the Research Council of Norway  
220 (project 216547), TOTAL E&P Norway and the TOTAL Foundation and the UK Natural Environment  
221 Research Council's National Capability. We would like to thank Børge Moe, Hálfván Helgi Helgason  
222 and Vegard Sandøy Bråthen for the logistical support within SEATRACK. This work would not have  
223 been possible without the combined effort and long term engagement of many researchers as well  
224 as numerous field assistants all across the Northeast Atlantic.

225

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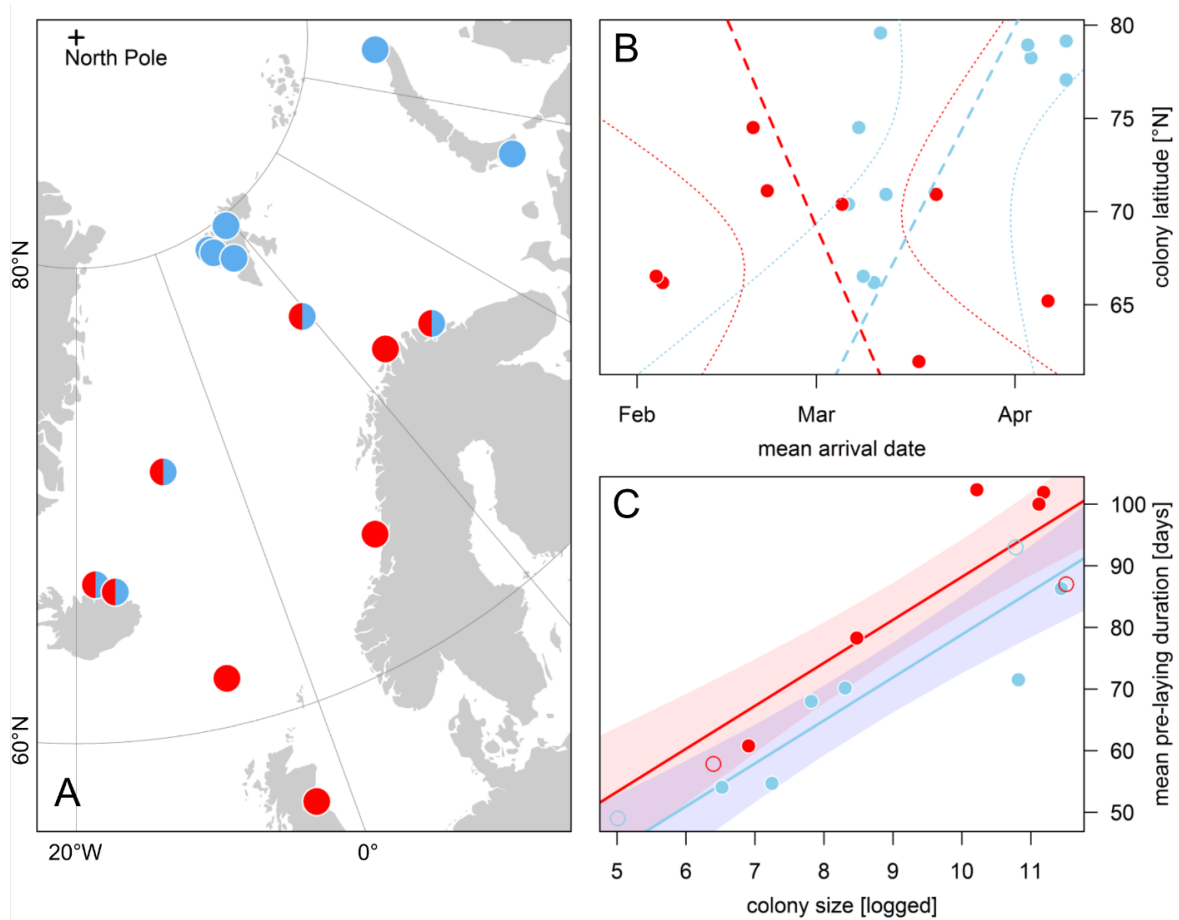
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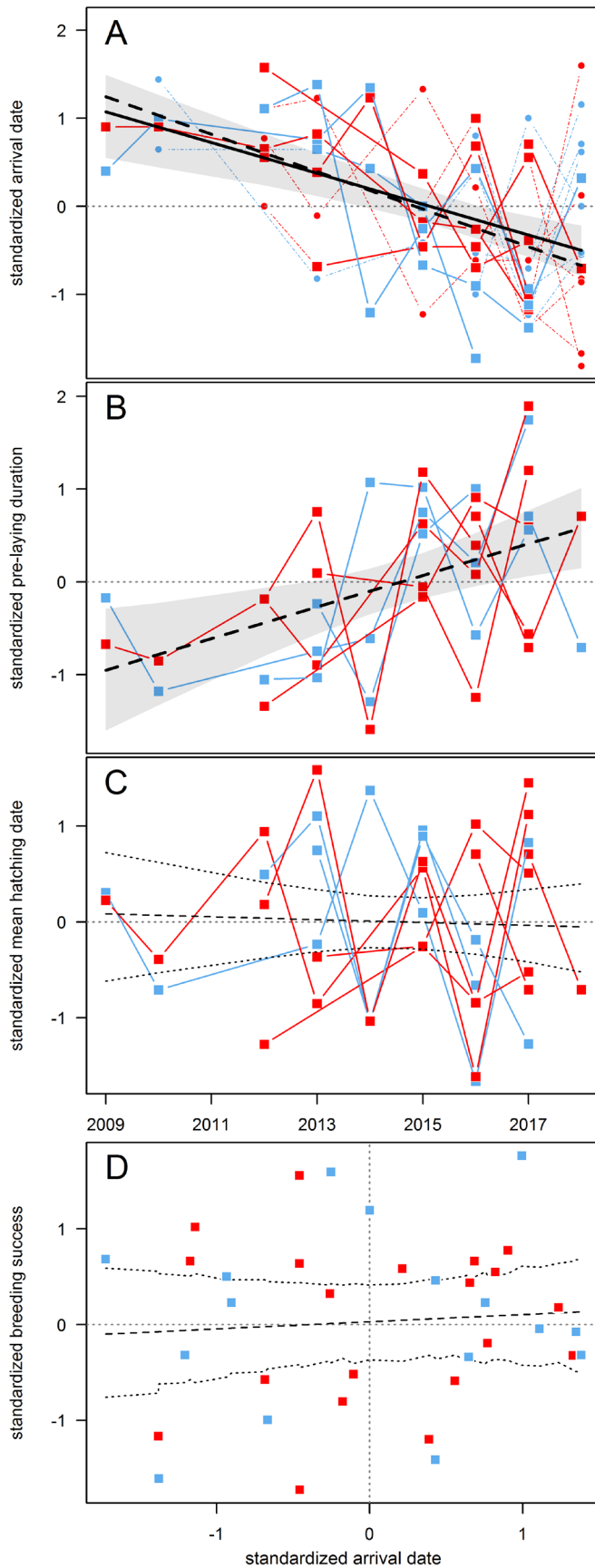
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327

328 **Figure 1.** Panel A displays the colony locations of common (red, COGU) and Brünnich's guillemots (blue, BRGU)  
 329 included in the study. Panel B illustrates the relationship between mean arrival date and latitude (excluding the  
 330 Isle of May), while panel C shows the correlation of mean pre-laying duration and colony size. Colonies with  
 331 less certain pre-laying duration estimates are indicated as open circles. Bands in panels B and C indicate  
 332 bootstrapped 95% confidence intervals for predicted values.



**Figure 2.** Temporal trends in arrival dates at the colony (Panel A), pre-laying duration (Panel B) and mean hatching date (Panel C). Dashed lines represent linear mixed effect model predictions for the subset of data for which hatching timing information was available (squares), while the solid line in panel A illustrates the same model prediction for arrival date using the entire dataset (squares and dots). Panel D shows the relationship between advancing arrival date and breeding success. Bands in all panels indicate bootstrapped 95% confidence intervals for predicted values calculated using the `bootMer` function with 1000 simulations (package `lme4`). Red and blue symbols represent common (COGU) and Brünnich's guillemots (BRGU), respectively.

## 1 Supplementary Material and Methods

2

### 3 *Estimation of arrival dates from logger data*

4 Annual first colony arrival dates for each colony and species were estimated using salt water  
5 immersion data recorded by light-level geolocators deployed on adult breeders (models: Mk15  
6 (British Antarctic Survey, Cambridge, UK), Mk3006 & Mk4083 (Biotrack, Wareham, UK), F100, C65,  
7 C250 & C330 (Migrate Technology, Cambridge, UK) or L250A (Lotek, St. John's, Newfoundland,  
8 Canada)). Sampling interval for Mk15, Mk3006 & Mk4083 was every 3 seconds, F100, C65, C250 &  
9 C330 sampled the state every 30 seconds and L250A loggers sampled salt water immersion every 5  
10 minutes. For comparability, we binned individual data into hourly bins for further analysis. Under the  
11 assumption that first arrival back at the colony is synchronized in guillemots [1, 2], we then defined  
12 annual first colony arrival dates as the first instance where the majority of the tracked breeding  
13 population attended the colony for at least two consecutive hours during daylight at the colony  
14 (defined as a solar angle above  $-6^\circ$ , i.e. civil twilight). Meaning that two consecutive hourly bins of  
15 salt water immersion data averaged over all tracked individuals from the considered colony, species  
16 and year needed to be more at least 50% dry during daylight at the colony (example in figure S1B).  
17 We considered five individuals a sufficient minimum sample size to estimate these dates as in this  
18 case at least three individuals needed to be present during these two hours to identify an arrival  
19 date. Mean logger sample size used to derive arrival date for each colony, species and year was 16  
20 individuals (standard deviation (SD) = 8; range = 5 – 38, table S1).

21

### 22 *Estimation of mean hatching dates*

23 Individual hatching dates were estimated by nest inspections at variable intervals during hatching or  
24 egg laying, while in the former case the incubation time was added (i.e. 33 days, [3]). These dates  
25 were then averaged to mean hatching dates with a mean sample size of 108 nests monitored (SD =  
26 218; range = 10 – 760, table S1). However, three instances of estimated mean hatching dates were  
27 only rough estimates based on observed hatching events during colony visits for recapture of logger-  
28 equipped individuals (table S1). These dates have been only used to estimate mean pre-laying  
29 duration and were not considered in other analyses. Mean pre-laying duration was defined as mean  
30 hatching date averaged across years of which we subtracted a 33 day incubation period as well as  
31 mean colony arrival date.

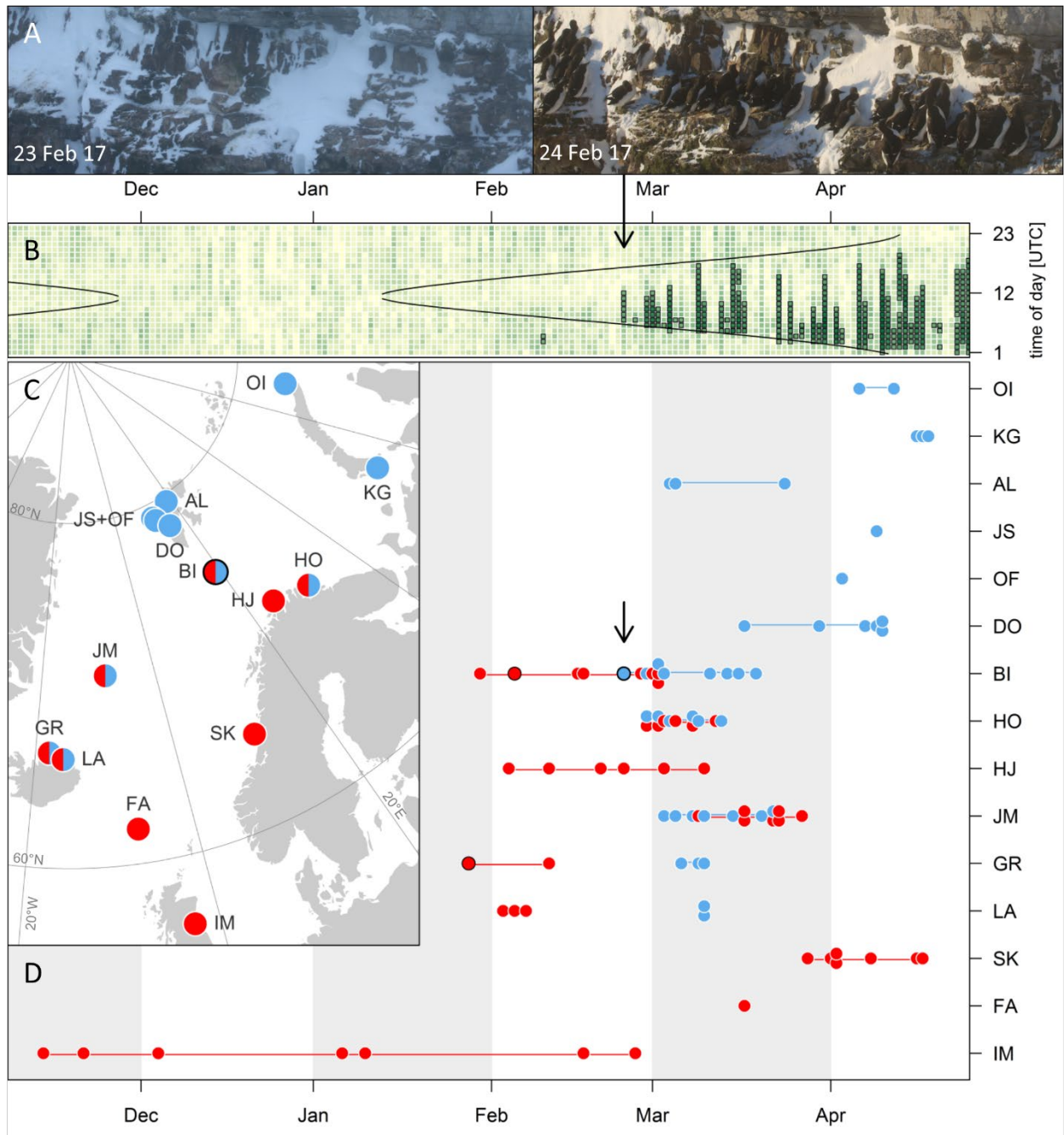
32 *Estimation of breeding success*

33 To estimate breeding success, individual nests have been inspected at variable time intervals with on  
34 average 52 monitored nests (SD = 39, range = 5 – 157, table S1). Depending on colony, individual  
35 breeding success was defined differently (e.g. chick age of 20 days or medium-sized chick present)  
36 and hence all estimates have been standardized (SD = 1, mean = 0) for each colony and species to  
37 make them comparable.

38 **Table S1.** Available data for each colony and species including colony size and number of years with available data for arrival timing at the colony, mean hatching date and  
 39 breeding success.

colony	acronym	colony location	colony size (pairs* 1000)	Year of count/estimate	Common guillemot (COGU)							Brünnich's guillemot (BRGU)										
					colony trend	trend over x years	years with colony arrival date	mean # individuals tracked each year (min-max)	years with mean hatching date	mean # of nests monitored each year (min-max)	years with breeding success data	colony trend	trend over x years	years with colony arrival date	mean # individuals tracked each year (min-max)	years with mean hatching date	mean # of nests monitored each year (min-max)	years with breeding success data				
Isle of May	IM	56.18°N 2.58°W	16 [4]	2007	↗ [5]	15	7	17 (10-21)	4	716 (644-760)	-	-	0	-	-	-	-	-	-	-		
Faroe Islands (Lonin)	FA	61.95°N 6.80°W	100 [6]	2005/06	↘ [6]	15	1	6	1 <sup>b</sup>	-	-	0	-	-	-	-	-	-	-	-		
Sklinna	SK	65.22°N 10.97°E	0.6 [7]	2006	↗ [8]	10	7	17 (7-26)	1 <sup>b</sup>	-	-	0	-	-	-	-	-	-	-	-		
Langanes	LA	66.18°N 15.99°W	27.3 [9]	2007	↘ [10]	20	3	12 (9-18)	2 <sup>d</sup>	87 (82-91)	-	-	2.5 [9]	2007	↗ [10]	20	2	10 (5-15)	1 <sup>d</sup>	57	-	-
Grimsey	GR	66.53°N 17.99°W	67.3 [9]	2007	↘ [10]	20	2	11 (5-16)	2 <sup>d</sup>	15 (14-15)	-	-	4 [9]	2007	↘ [10]	20	3	11 (9-15)	2 <sup>d</sup>	54 (53-54)	-	-
Jan Mayen	JM	71.02°N 8.52°W	1 [11]	2010	↘ [8]	7	7	13 (8-20)	6	14 (10-18)	6	17 (14-21)	50 [11]	2010	↘ [8]	7	7	19 (8-31)	6	50 (25-63)	6	73 (58-102)
Hjelmsøya	HJ	71.07°N 24.72°E	3.1 [12]	2004	↗ [8]	10	6	9 (5-14)	-	-	5	38 (5-141)	?	-	↘ [8]	-	-	-	-	-	-	-
Hornøya	HO	70.38°N 31.15°E	4.8 [13]	2006	↗ [8]	10	6	26 (21-38)	4	31 (23-41)	4	32 (29-39)	0.4 [14]	2006	↘ [8]	10	-	-	-	-	-	-
Bjørnøya	BI	74.50°N 18.96°E	72 [15]	2006	↗ [8]	10	8	22 (7-28)	7	47 (37-61)	6	102 (53-137)	93 [15]	2006	↘ [8]	10	8	17 (7-29)	7	25 (20-31)	6	52 (39-60)
Diabasodden	DO	78.25°N 15.51°E	0	-	-	-	-	-	-	-	-	-	1.4 <sup>a</sup>	2007	↘ [8]	10	6	11 (5-16)	4	60 (10-131)	4	86 (26-157)
Ossian Sarsfjellet	OF	78.94°N 12.49°E	0	-	-	-	-	-	-	-	-	-	0.8 <sup>a</sup>	2011	↘ [8]	10	1	7	1	41	-	-
John Scottfjellet	JS	79.15°N 11.96°E	0	-	-	-	-	-	-	-	-	-	0.1 <sup>a</sup>	2011	?	-	1	3 <sup>e</sup>	1 <sup>c</sup>	-	-	-
Alkefjellet	AL	79.59°N 18.46°E	0	-	-	-	-	-	-	-	-	-	48 <sup>a</sup>	2009	(↗) <sup>a</sup>	4	3	15 (12-18)	1 <sup>b</sup>	-	-	-
Kara Gate	KG	70.59°N 55.02°E	0	-	-	-	-	-	-	-	-	-	?	-	?	-	3	20 (9-26)	-	-	-	-
Oranskie islands	OI	77.07°N 67.64°E	0	-	-	-	-	-	-	-	-	-	?	-	?	-	2	12 (7-16)	-	-	-	-

40 <sup>a</sup> S. Descamps unpublished data; <sup>b</sup> rough estimate based on chick sightings while visiting the colony; <sup>c</sup> assumed to be the same as OF as they are in close proximity to each other; <sup>d</sup> based on  
 41 mean egg laying date; <sup>e</sup> only used for approximate pre-laying duration due to low sample size



42

43 **Figure S1.** First annual arrival dates at the colony (panel D) for common (COGU, red) and Brünnich's guillemots  
 44 (BRGUs, blue) breeding across the Northeast Atlantic (panel C). In panel D, each point represents arrival timings  
 45 in a given year. Colonies in panel D are sorted from southwest to northeast similar to their depiction in panel C.  
 46 Panel B illustrates an example average salt water immersion dataset in hourly bins for BRGU from Bjørnøya (BI,  
 47 outlined in black in panel C) in 2016/17 (n=15) with day of the year on the x-axis and time of day (in UTC) on  
 48 the y-axis. Light green indicates that all individuals were submerged in salt water. Conversely, dark green  
 49 indicates all individuals being dry, while black framed bins specify the majority of tracked individuals being dry.  
 50 Black lines display timings of sunrise and sunset at the colony across the year. The arrow indicates the  
 51 estimated arrival timing for this example which is also indicated in panel D. Black framed points in panel D are  
 52 validated with camera trap data, of which one is illustrated in panel A and corresponds to the example in panel  
 53 B.



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