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Contact CEH NORA team at
noracch@ceh.ac.uk

1 Title: Earlier colony arrival but no trend in hatching timing in two congeneric seabirds (*Uria* spp.)
2 across the North Atlantic

3 Authors: Benjamin Merkel^{1,2,*}, Sébastien Descamps¹, Nigel G Yoccoz², Jóhannis Danielsen³, Francis
4 Daunt⁴, Kjell E Erikstad^{5,6}, Aleksey V Ezhov^{7,8}, David Grémillet⁹, Maria Gavrilov^{7,10}, Svein-Håkon
5 Lorentsen¹¹, Tone K Reiertsen⁵, Harald Steen¹, Geir H Systad¹², Porkell Lindberg Þórarinnsson¹³, Sarah
6 Wanless⁴, Hallvard Strøm¹

7 Affiliations:

8 ¹ Norwegian Polar Institute, Fram Centre, P.O. Box 6606 Langnes, 9296 Tromsø, Norway

9 ² Department of Arctic and Marine Biology, University of Tromsø - The Arctic University of Norway, 9037 Tromsø,
10 Norway

11 ³ University of the Faroe Islands, Vestarabryggja 15, FO-100 Tórshavn, Faroe Islands

12 ⁴ Centre for Ecology & Hydrology, Bush Estate, Penicuik, Midlothian EH26 0QB, UK

13 ⁵ Norwegian Institute for Nature Research, Fram Centre, P.O. Box 6606 Langnes, 9296 Tromsø, Norway

14 ⁶ Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science and Technology, 7491
15 Trondheim, Norway

16 ⁷ Association Maritime Heritage, Saint Petersburg, Russia

17 ⁸ Murmansk Marine Biological Institute, 17 str. Vladimirskaia, 183010 Murmansk, Russia

18 ⁹ Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175, CNRS - Université de Montpellier - Université Paul-Valéry
19 Montpellier - EPHE, Montpellier, France. & FitzPatrick Institute, DST-NRF Centre of Excellence at the University of
20 Cape Town, Rondebosch 7701, South Africa.

21 ¹⁰ National Park Russian Arctic, 57 Sovetskikh Kosmonavtovo ave., Archangelsk, Russia

22 ¹¹ Norwegian Institute for Nature Research, P.O. Box 5685 Sluppen, 7485 Trondheim, Norway

23 ¹² Norwegian Institute for Nature Research, Thormøhlensgate 55, 5006 Bergen, Norway

24 ¹³ Northeast Iceland Nature Research Centre, Hafnarstétt 3, 640 Húsavík, Iceland

25 *Corresponding author, email: merkel.benjamin@gmail.com

26
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28 supervised the study; all authors provided data, contributed to article drafts, approved the final version of this
29 manuscript and agree to be held accountable for the content.

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47 Abstract

48 A global analysis recently showed that seabird breeding phenology (as timing of egg-laying and hatching)
49 does not, on average, respond to temperature changes or advance with time [1]. This group, the most
50 threatened of all birds, is therefore prone to spatio-temporal mismatches with their food resources. Yet,
51 other aspects of the breeding phenology may also have a marked influence on breeding success, such as
52 the arrival date of adults at the breeding site following winter migration. Here, we used a large tracking
53 dataset of two congeneric seabirds breeding in 14 colonies across 18° latitudes, to show that arrival date
54 at the colony was highly variable between colonies and species (ranging 80 days) and advanced 1.4
55 days/year while timing of egg-laying remained unchanged, resulting in an increasing pre-laying duration
56 between 2009 and 2018. Thus, we demonstrate that potentially not all components of seabird breeding
57 phenology are insensitive to changing environmental conditions.

58 Introduction

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

70 Here, we took advantage of a large tracking dataset, enabling us to determine arrival dates in two
71 seabird species, across nine years (2009 - 2018) and 14 colonies across a large latitudinal gradient (62°N -
72 79°N), to test if arrival date also does not exhibit any trend across years, similar to timing of egg-laying
73 [1]. This data was available for two colonial, congeneric species, the common (hereafter COGU, *Uria*
74 *aalge*) and Brünnich's guillemot (hereafter BRGU, *Uria lomvia*). These species are long-distance migrants
75 [13-15], have similar morphology and life history [16, 17], and exhibit no trend in breeding phenology
76 [18], but contrasting population trends [19-21]. Their arrival date is hypothesized to be driven by timing
77 of food availability in the vicinity of the colony [22, 23], which can be roughly approximated by latitude

78 [24], or by colony size through increasing pressure on nest site defence displayed as longer pre-laying
79 periods in larger colonies [11, 25, 26]. We tested the hypothesis that arrival date is without trend across
80 years, same as egg-laying date. Further, we examined if arrival date is delayed with latitude, similar to
81 timing of egg-laying [24], or determined by colony size due to pressure on nest site defence.

82

83 Material and Methods

84 *Data acquisition*

85 The date of first arrival at the colony for each colony and species was estimated using salt water
86 immersion data recorded by light-level geolocators deployed on adult breeders. Arrival date was here
87 defined as the date when the pre-laying period commences. It was identified as the date when the
88 majority of tracked individuals attended the colony for the first time after the non-breeding period, using
89 the assumption that first arrival back at the colony is synchronized and independent of sex in guillemots
90 [26-28] (details in SI). Using a colony-wide first arrival date rather than individual arrival dates resulted in
91 more robust results due to limitations in logger data resolution and accuracy. Tracking data were
92 available from 14 colonies (figure 1A), for one to eight years (in the period 2009 - 2018) [29]. BRGU and
93 COGU breed sympatrically at five of these colonies. Three instances of estimated arrival dates could be
94 validated with available time-lapse camera data at two colonies (figure S1). To estimate pre-laying
95 duration as well as temporal changes in phenology, we gathered annual measures of breeding timing
96 which were available as population-level mean hatching dates at twelve colonies (details in SI) for one to
97 seven years (in the period 2009 - 2018) [24, 30-37]. To assess the potential consequences of variable
98 arrival dates on reproductive success, we used annual breeding success for which data was available
99 from five colonies (details in SI) for four to six years (in the period 2010 - 2017) [30-37].

100 *Data analysis*

101 *Temporal trends in breeding phenology and their consequences* - Colony- and species-specific inter-
102 annual variation in arrival dates was quantified as standard deviation (SD) from mean arrival timing. To
103 test if arrival date changes with year we applied a linear mixed effect model (LME, package `lme4`) with
104 relative arrival dates (mean = 0) as response variable (n = 79), year and species as fixed effects and id (as
105 combination of colony and species) as random intercept. The same model was applied on a subset of
106 data for which mean hatching date data were available (n = 40). Using this subset, we applied the same
107 fixed and random effects to relative pre-laying duration as well as relative mean hatching date as

108 response variables in order to assess if guillemot hatching timing and pre-laying duration have changed
109 over time. Most parsimonious models were selected using Akaike information criterion [38], resulting in
110 all instances in a removal of species and its interaction with year as predictor variables. We calculated
111 the percentage of variance explained by the fixed effects (marginal R^2) and fixed and random effects
112 (conditional R^2 ; [39]). In order to assess if a large-scale factor is driving temporal trends in arrival date,
113 we assessed temporal synchrony as mean correlation of relative arrival dates between colonies using the
114 `msynch` function (package `ncf` [40]). To test if potential temporal trends in arrival date had an effect on
115 reproductive output, we applied a LME with standardized breeding success ($SD = 1$, $mean = 0$) as
116 response variable, relative arrival date as fixed effect and `id` as random intercept ($n = 33$).

117 *Effect of latitude and colony size on arrival date* - To test for the effect of latitude on arrival date at the
118 colony, we applied a linear model with mean species- and colony-specific arrival date as the response
119 variable ($n = 19$) and latitude and species and their interaction as predictors. Further, if latitude drives
120 arrival date, we would expect that colonies close to each other would exhibit similar arrival timing.
121 Hence, we used a Mantel-correlation test with 1000 permutations (package `ade4`) to test if spatial
122 proximity can explain mean arrival date in either species. Alternatively, to test if arrival date and
123 consequently pre-laying duration can be instead linked to colony size, we applied a linear model with
124 mean species- and colony-specific pre-laying duration as the response variable ($n = 15$) and colony size
125 on the log-scale and species as predictors. Population counts are taken from a similar time period to
126 account for the contrasting population trends (table S1). To account for collinearity, we also tested
127 latitude against colony size, but found no overall latitudinal trend (linear model, $\beta_{\text{latitude}} = -0.10$ with
128 standard error (SE) = 0.10, $adj. R^2 = <-0.01$). R (version 3.5.1, [41]) was used for all statistical analyses.

129

130 Results

131 *Timing of colony arrival*

132 Annual arrival dates varied between January 28 and April 18 with considerable variation across the
133 Northeast Atlantic (figure 1B). Most of this variation is found among colonies ($SD = 21.6$ and 16.2 days
134 for COGU and BRGU, respectively, figure S1) and species ($SD = 12.8$ days across sympatric colonies),
135 while colony- and species-specific inter-annual variation was significantly smaller (mean $SD = 7.8$ and 4.9
136 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 ($\beta_{\text{year}} = -0.17$ with SE = 0.23, marg. $R^2 = 0.01$,
139 cond. $R^2 = 0.01$; figure 2C). In contrast, arrival date at colony advanced by 1.4 days/year irrespective of
140 species (full dataset: $\beta_{\text{year}} = -1.4$ with SE = 0.28, marg. $R^2 = 0.24$, cond. $R^2 = 0.24$; subset with available
141 mean hatching data: $\beta_{\text{year}} = -1.7$ with SE = 0.35, marg. $R^2 = 0.39$, cond. $R^2 = 0.39$; figure 2A). This was also
142 visible as prolonged pre-laying duration ($\beta_{\text{year}} = 1.4$ with SE = 0.40, marg. $R^2 = 0.23$, cond. $R^2 = 0.23$; figure
143 2B) as arrival date and pre-laying duration were highly and negatively correlated (-0.86). Colony arrival
144 dates did not display synchrony among each other for either species (COGU: mean correlation = 0.15
145 with 95% confidence interval (CI) = -0.34 - 0.55 and BRGU: 0.09 with CI = -0.56 - 0.71). And, no
146 consequence of an advancing arrival date was detectable in exhibited breeding success for either species
147 ($\beta_{\text{std. arrival}} = -0.005$ with SE = 0.02, marg. $R^2 = <0.01$, cond. $R^2 = <0.01$; figure 2D).

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

149 Mean arrival date at the colony could not be explained by latitude and the two species exhibited
150 opposite trends ($\beta_{\text{latitude BRGU}} = 1.63$ with SE = 1.24 and $\beta_{\text{latitude * COGU}} = -2.73$ with SE = 2.19, adj. $R^2 = 0.23$;
151 figure 1B). Similarly, there was weak evidence for an effect of proximity on arrival dates for COGUs
152 (Mantel correlation = 0.19, $p = 0.14$), but somewhat stronger evidence in BRGUs (Mantel correlation =
153 0.29, $p = 0.034$). Contrastingly, pre-laying duration showed substantial variability among colonies (mean
154 = 75 days, SD = 19, range = 49 - 102) and was highly correlated with colony size ($\beta_{\log(\text{size})} = 6.96$ with SE =
155 0.97, adj. $R^2 = 0.82$; figure 1C).

156 Discussion

157 The main findings of our study are that timing of first arrival at the colony of both guillemot species and
158 all colonies was highly variable and advanced through time despite no visible trend in mean hatching
159 date. This advancement had apparently no effect on guillemot average breeding success. Further, the
160 duration of the pre-laying period and hence timing of arrival is not determined by latitude, but is better
161 explained by the size of the colony, being longer in large colonies.

162 Theoretically, the minimum pre-laying duration required in guillemots is five days, as females undertake
163 a four day long pre-laying exodus away from the colony [42]. Yolk formation (usually 14-15 days [42])
164 could also occur away from the colony and fertilization occurs very soon after ovulation, which in turn
165 occurs 24 hours before the egg is laid [10]. So, copulation right before the pre-laying exodus should be
166 sufficient. Nonetheless, here we identified extensive pre-laying periods of more than one and up to
167 several months with large variability between colonies and species. In an extreme case of a population
168 further south, most breeding birds arrive back at the colony already in the autumn and in at least some
169 years birds attend the breeding sites throughout the winter [11, 43]. This variability may have costs and
170 benefits associated with it. During the pre-laying period prospective breeders attend the colonies at
171 regular intervals [26-28] which restricts them to quasi central place foraging. This in turn limits their
172 available prey options and could even lead to local depletion of food resources before spring bloom at
173 large colonies [44], decreasing their body condition and potentially breeding probability prior to
174 breeding. Alternatively, early return to the breeding sites might help secure nesting sites, mating
175 partners and facilitate courtship [23], or it might be a response to unfavourable conditions experienced
176 by these migrants during the end of their non-breeding period, resulting in an earlier return to the
177 colony.

178 We showed that colony arrival date advanced in both the Brünnich's and common guillemot across the
179 study area, while their timing of hatching did not display any trend as shown previously in seabirds
180 globally [1] and for alcids in the Atlantic and Pacific [18]. Contrary to these previous studies, concluding
181 that breeding phenology is insensitive to short-term climatic change, we identified a clear trend in arrival
182 dates across both species studied. This advancement resulted in an increasing pre-laying duration as
183 mean hatching date did not advance, suggesting that part of breeding in these seabirds is indeed
184 sensitive to changing conditions, although we cannot derive conclusions regarding the process driving
185 this phenomenon or if it is an adaption to a changing environment. A potential explanation could be that

186 the cue used to time arrival across the North Atlantic is changing as has been shown in some passerine
187 species [45], but could not be demonstrated in others [46, 47].

188 Although overall timing in both species exhibits the same trend, arrival time series were not
189 synchronized between species and colonies. This indicates that short-term fluctuations in arrival date
190 were not parallel through time among species and/or colonies, which suggests the interaction between
191 large-scale environmental trends acting on the entire species combined with more local features.
192 However, environmental conditions, although exhibiting the same trend, do not change homogenously
193 across the genus' range [48], which encompasses most of the North Atlantic for these species breeding
194 within the study area [13-15]. Hence, synchrony is not necessarily expected. As of now we could not
195 detect any immediate consequences of advancing arrival dates on population-wide reproductive success.
196 As we used adult breeders to estimate arrival times, we cannot make any inference of the potential
197 effect of advancing arrival dates on breeding propensity. Not all birds breed every year [49, 50] and the
198 egg laying and hatching dates as well as the recorded breeding success may reflect only individuals with
199 sufficient body condition, i.e. the ones that managed to get enough energy during the pre-laying period
200 in order to breed [8].

201 Pre-laying duration and hence arrival timing at the colony could be linked with colony size [11, 25, 26]
202 rather than latitude. This could explain the displayed large-scale variability in arrival timings between
203 colonies as well as the lack of synchronicity between time series. Although guillemots typically show high
204 nest site fidelity, site changes are documented which usually increase nest site quality for the usurper
205 and decrease it for the usurped [51] underlining the importance of nest site defence as potential driver
206 of arrival date resulting in the pressure to arrive earlier in larger colonies [11, 25, 26]. But, the influence
207 of environmental conditions on arrival timing cannot be ruled out, as unfavourable weather has already
208 been shown to affect pre-laying colony attendance in BRGU [27] although the same could not yet be
209 shown for arrival timing.

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

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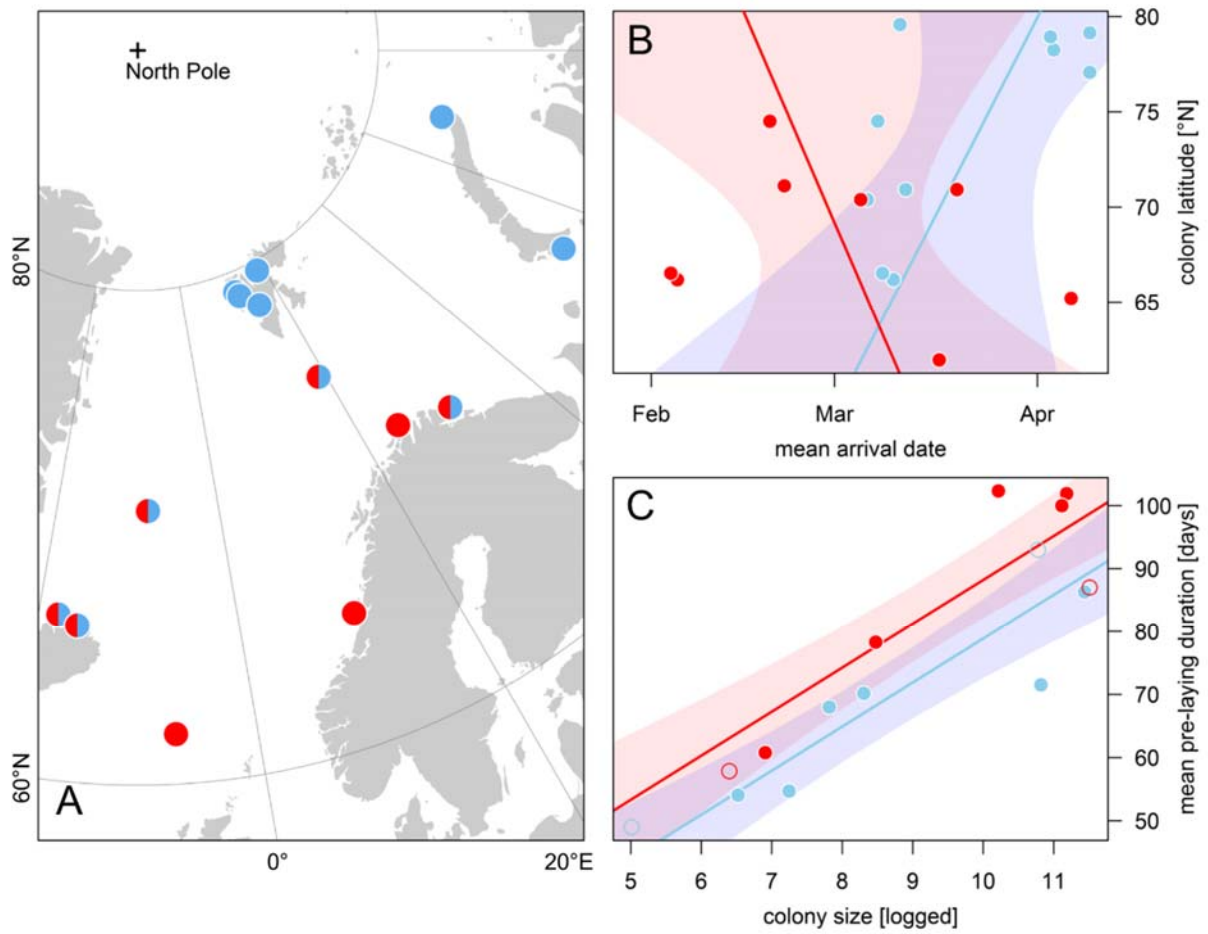
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349

350 Figures



351

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

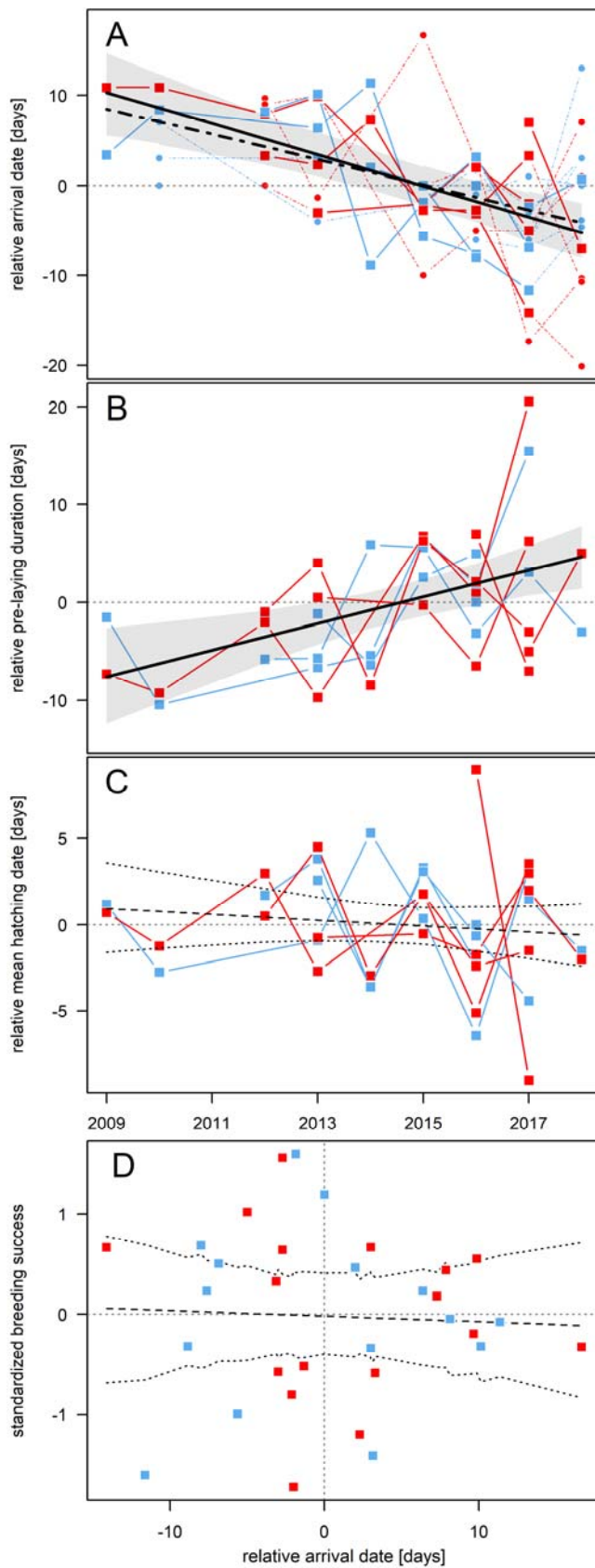


Figure 2. Temporal trends in arrival dates at the colony (Panel A), pre-laying duration (Panel B) and mean hatching date (Panel C). Dashed line in panel A represents linear mixed effect model predictions for the subset of data for which hatching timing information was available (squares), while the solid 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.