



**HAL**  
open science

## Population ecology Earlier colony arrival but no trend in hatching timing in two congeneric seabirds (*Uria* spp.) across the North Atlantic

Benjamin Merkel, Sébastien Descamps, Nigel G Yoccoz, Jóhannis Danielsen, Francis Daunt, Kjell E Erikstad, Aleksey V Ezhov, David Grémillet, Maria Gavriilo, Svein-Håkon Lorentsen, et al.

### ► To cite this version:

Benjamin Merkel, Sébastien Descamps, Nigel G Yoccoz, Jóhannis Danielsen, Francis Daunt, et al.. Population ecology Earlier colony arrival but no trend in hatching timing in two congeneric seabirds (*Uria* spp.) across the North Atlantic. *Biology Letters*, 2019, 10.1098/rsbl.2019.0634 . hal-02328876

**HAL Id: hal-02328876**

**<https://hal.science/hal-02328876v1>**

Submitted on 23 Oct 2019

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

## Research



**Cite this article:** Merkel B *et al.* 2019 Earlier colony arrival but no trend in hatching timing in two congeneric seabirds (*Uria* spp.) across the North Atlantic. *Biol. Lett.* **15**: 20190634. <http://dx.doi.org/10.1098/rsbl.2019.0634>

Received: 27 August 2019

Accepted: 27 September 2019

### Subject Areas:

behaviour, ecology

### Keywords:

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

### Author for correspondence:

Benjamin Merkel

e-mail: [merkel.benjamin@gmail.com](mailto:merkel.benjamin@gmail.com)

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.4690442>.

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

Benjamin Merkel<sup>1,2</sup>, Sébastien Descamps<sup>1</sup>, Nigel G. Yoccoz<sup>2</sup>, Jóhannis Danielsen<sup>3</sup>, Francis Daunt<sup>4</sup>, Kjell E. Erikstad<sup>5,6</sup>, Aleksey V. Ezhov<sup>7,8</sup>, David Grémillet<sup>9,10</sup>, Maria Gavrilov<sup>7,11</sup>, Svein-Håkon Lorentsen<sup>12</sup>, Tone K. Reiertsen<sup>5</sup>, Harald Steen<sup>1</sup>, Geir H. Systad<sup>13</sup>, Pørkell Lindberg Þórarinnsson<sup>14</sup>, Sarah Wanless<sup>4</sup> and Hallvard Strøm<sup>1</sup>

<sup>1</sup>Norwegian Polar Institute, Fram Centre, PO Box 6606 Langnes, 9296 Tromsø, Norway

<sup>2</sup>Department of Arctic and Marine Biology, University of Tromsø-The Arctic University of Norway, 9037 Tromsø, Norway

<sup>3</sup>University of the Faroe Islands, Vestarabryggja 15, 100 Tórshavn, Faroe Islands

<sup>4</sup>Centre for Ecology and Hydrology, Bush Estate, Penicuik, Midlothian EH26 0QB, UK

<sup>5</sup>Norwegian Institute for Nature Research, Fram Centre, PO Box 6606 Langnes, 9296 Tromsø, Norway

<sup>6</sup>Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science and Technology, 7491 Trondheim, Norway

<sup>7</sup>Association Maritime Heritage, Saint Petersburg, Russia

<sup>8</sup>Murmansk Marine Biological Institute, 17 street Vladimirskaia, 183010 Murmansk, Russia

<sup>9</sup>Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175, CNRS-Université de Montpellier-Université Paul-Valéry Montpellier-EPHE, Montpellier, France

<sup>10</sup>FitzPatrick Institute, DST-NRF Centre of Excellence at the University of Cape Town, Rondebosch 7701, South Africa

<sup>11</sup>National Park Russian Arctic, 57 Sovetskikh Kosmonavtovo Avenue, Archangelsk, Russia

<sup>12</sup>Norwegian Institute for Nature Research, PO Box 5685 Sluppen, 7485 Trondheim, Norway

<sup>13</sup>Norwegian Institute for Nature Research, Thormøhlensgate 55, 5006 Bergen, Norway

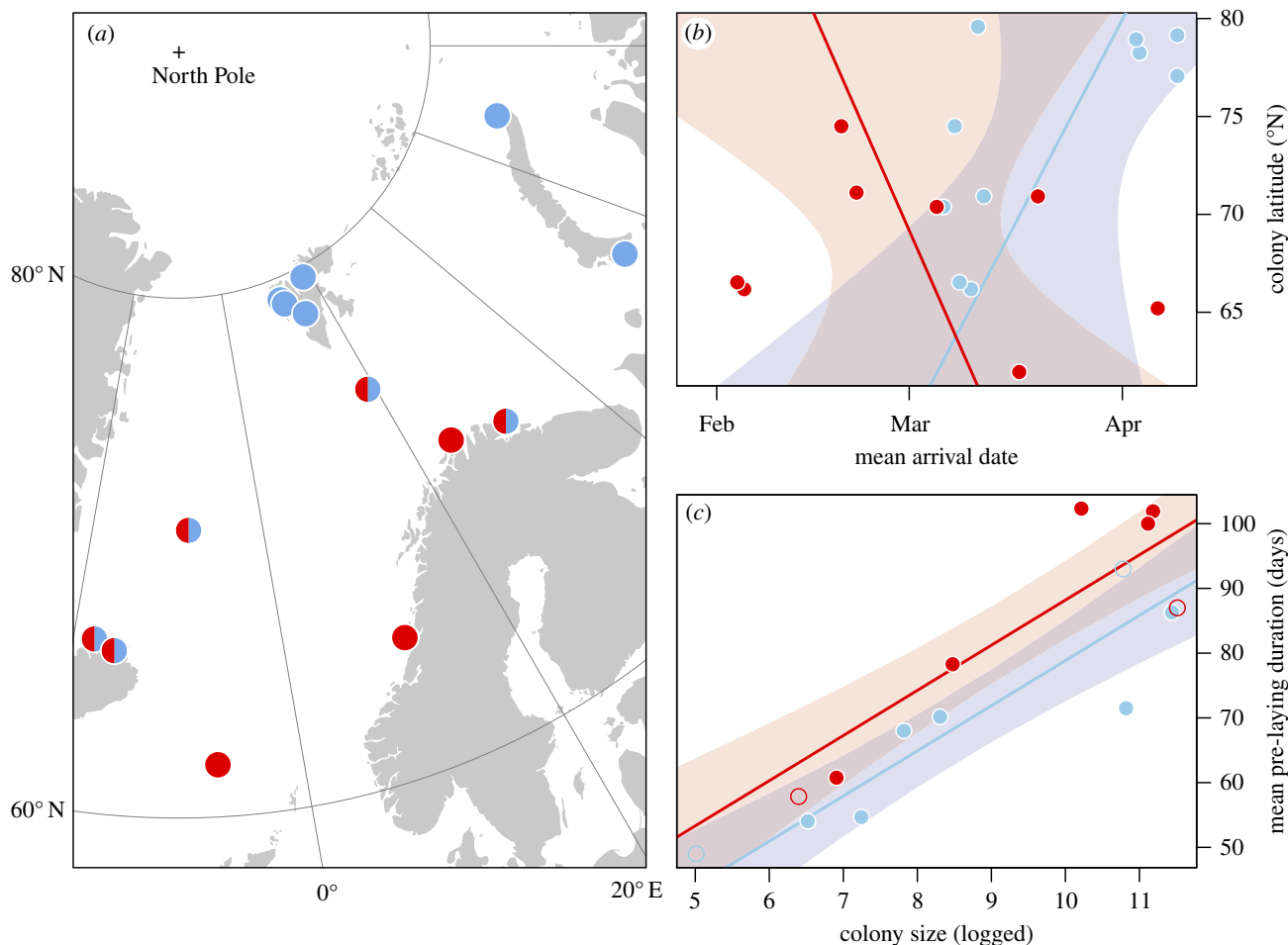
<sup>14</sup>Northeast Iceland Nature Research Centre, Hafnarstétt 3, 640 Húsavík, Iceland

BM, 0000-0002-8637-7655; DG, 0000-0002-7711-9398

A global analysis recently showed that seabird breeding phenology (as the timing of egg-laying and hatching) does not, on average, respond to temperature changes or advance with time (Keogan *et al.* 2018 *Nat. Clim. Change* **8**, 313–318). This group, the most threatened of all birds, is therefore prone to spatio-temporal mismatches with their food resources. Yet, other aspects of the breeding phenology may also have a marked influence on breeding success, such as the arrival date of adults at the breeding site following winter migration. Here, we used a large tracking dataset of two congeneric seabirds breeding in 14 colonies across 18° latitudes, to show that arrival date at the colony was highly variable between colonies and species (ranging 80 days) and advanced 1.4 days/year while timing of egg-laying remained unchanged, resulting in an increasing pre-laying duration between 2009 and 2018. Thus, we demonstrate that potentially not all components of seabird breeding phenology are insensitive to changing environmental conditions.

## 1. Introduction

Timing of life-history events such as reproduction is predicted to have evolved to optimally use temporally favourable conditions in seasonal systems [1]. Breeding phenology is a key adaptation with direct consequences on reproductive success and population dynamics [2,3]. Rapid climate change has led to an



**Figure 1.** (a) The colony locations of COGU (red) and BRGU (blue) included in the study. (b) The relationship between mean arrival date and latitude, while (c) shows the correlation of mean pre-laying duration and colony size. Colonies with less certain pre-laying duration estimates are indicated as open circles. Bands in (b) and (c) indicate 95% CIs for predicted values.

advancement of the annual cycle in many organisms in temperate and polar regions, while species that have not adjusted to climate change seem to be more prone to population declines [4,5]. In seabirds, the timing of egg-laying has been shown to be insensitive to changing climatic conditions globally, highlighting the vulnerability of this group to mismatches with lower-trophic-level resources [6]. Yet, spring arrival at the colony, and the pre-laying period—the time between arrival at the colony and egg-laying—are also important and rarely considered components affecting breeding success. This period allows birds to establish and defend nest sites [7], build up body condition [8,9] and mate [10], which often starts months before egg-laying [11,12].

Here, we took advantage of a large tracking dataset, enabling us to determine arrival dates in two seabird species, across 9 years (2009–2018) and 14 colonies across a large latitudinal gradient (62°N–79°N), to test if arrival date does not exhibit any trend across years, similar to timing of egg-laying [6]. These data were available for two colonial, congeneric species, the common (hereafter COGU, *Uria aalge*) and Brünnich's guillemot (hereafter BRGU, *Uria lomvia*). These species are long-distance migrants [13–15], have similar morphology and life history [16,17], and exhibit no trend in breeding phenology [18], but contrasting population trends [19–21]. Their arrival date is hypothesized to be driven by the timing of food availability in the vicinity of the colony [22,23], which can be roughly approximated by latitude [24], or by colony size through increasing pressure on nest site

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

## 2. Material and methods

### (a) Data acquisition

The date of first arrival at the colony for each colony and species was estimated using salt water immersion data recorded by light-level geolocators deployed on adult breeders. The arrival date was here defined as the date when the pre-laying period commences. It was identified as the date when the majority of tracked individuals attended the colony for the first time after the non-breeding period, using the assumption that first arrival back at the colony is synchronized and independent of sex in guillemots [26–28] (details in the electronic supplementary material). Using a colony-wide first arrival date rather than individual arrival dates resulted in more robust results due to limitations in logger data resolution and accuracy. Tracking data were available from 14 colonies (figure 1a), for 1–8 years (in the period 2009–2018) [29]. BRGU and COGU breed sympatrically at five of these colonies. Three instances of estimated arrival dates could be validated with available time-lapse camera data at two colonies (electronic supplementary material, figure S1). To estimate pre-laying duration as well as temporal changes in phenology, we

gathered annual measures of breeding timing which were available as population-level mean hatching dates at 12 colonies (details in the electronic supplementary material) for 1–7 years (in the period 2009–2018) [24,30–37]. To assess the potential consequences of variable arrival dates on reproductive success, we used annual breeding success for which data were available from five colonies (details in the electronic supplementary material) for 4–6 years (in the period 2010–2017) [30–37].

## (b) Data analysis

### (i) Temporal trends in breeding phenology and their consequences

Colony- and species-specific inter-annual variation in arrival dates was quantified as standard deviation (SD) from mean arrival timing. To test if arrival date changes with year, we applied a linear mixed-effect model (LME, package *lme4*) with relative arrival dates (mean = 0) as response variable ( $n = 79$ ), year and species as fixed effects and id (as combination of colony and species) as random intercept. The same model was applied on a subset of data for which mean hatching date data were available ( $n = 40$ ). Using this subset, we applied the same fixed and random effects to relative pre-laying duration as well as relative mean hatching date as response variables in order to assess if guillemot hatching timing and pre-laying duration have changed over time. Most parsimonious models were selected using the Akaike information criterion [38], resulting in all instances in removal of species and its interaction with year as predictor variables. We calculated the percentage of variance explained by the fixed effects (marginal  $R^2$ ) and fixed and random effects (conditional  $R^2$ ; [39]). In order to assess if a large-scale factor is driving temporal trends in arrival date, we assessed temporal synchrony as mean correlation of relative arrival dates between colonies using the *msynch* function (package *ncf* [40]). To test if potential temporal trends in arrival date had an effect on reproductive output, we applied an LME with standardized breeding success (SD = 1, mean = 0) as response variable, relative arrival date as fixed effect and id as random intercept ( $n = 33$ ).

### (ii) Effect of latitude and colony size on arrival date

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

## 3. Results

### (a) Timing of colony arrival

Annual arrival dates varied between 28 January and 18 April with considerable variation across the Northeast Atlantic (figure 1*b*). Most of this variation is found among colonies

(SD = 21.6 and 16.2 days for COGU and BRGU, respectively, electronic supplementary material, figure S1) and species (SD = 12.8 days across sympatric colonies), while colony- and species-specific inter-annual variation was significantly smaller (mean SD = 7.8 and 4.9 days for COGU and BRGU, respectively).

### (b) Temporal variability in breeding phenology and its consequences

Timing of hatching in guillemots showed no trend over time ( $\beta_{\text{year}} = -0.17$  with SE = 0.23, marg.  $R^2 = 0.01$ , cond.  $R^2 = 0.01$ ; figure 2*c*). By contrast, arrival date at the colony advanced by 1.4 days/year irrespective of 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 mean hatching data:  $\beta_{\text{year}} = -1.7$  with SE = 0.35, marg.  $R^2 = 0.39$ , cond.  $R^2 = 0.39$ ; figure 2*a*). This was also 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 2*b*) as arrival date and pre-laying duration were highly and negatively correlated (−0.86). Colony arrival dates did not display synchrony among each other for either species (COGU: mean correlation = 0.15 with 95% confidence interval (CI) = −0.34–0.55 and BRGU: 0.09 with CI = −0.56–0.71). No consequence of an advancing arrival date was detectable in exhibited breeding success for either species ( $\beta_{\text{std. arrival}} = -0.005$  with SE = 0.02, marg.  $R^2 = <0.01$ , cond.  $R^2 = <0.01$ ; figure 2*d*).

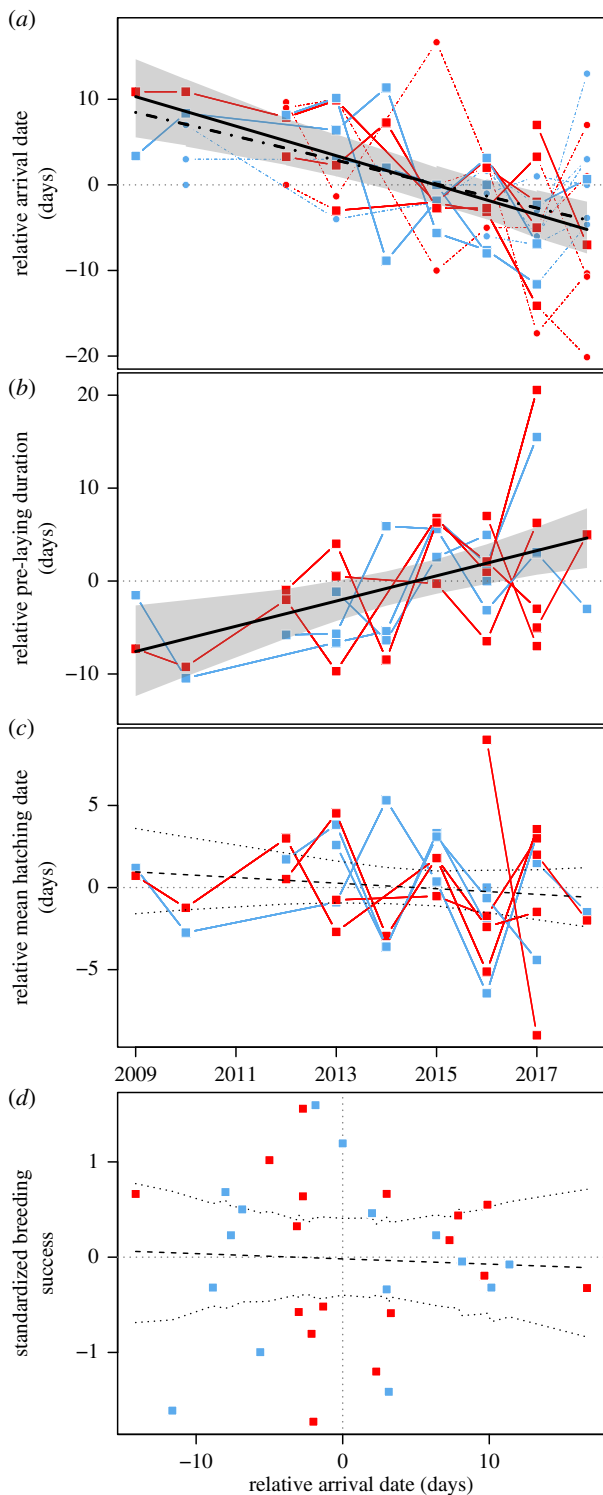
### (c) Does latitude or colony size predict the arrival date?

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

## 4. Discussion

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

Theoretically, the minimum pre-laying duration required in guillemots is 5 days, as females undertake a 4 day long pre-laying exodus away from the colony [42]. Yolk formation (usually 14–15 days [42]) could also occur away from the colony and fertilization occurs very soon after ovulation, which in turn occurs 24 h before the egg is laid [10]. So, copulation right before the pre-laying exodus should be sufficient. Nonetheless, here we identified extensive pre-laying periods of more than one and up to several months with large variability between colonies and species. In an extreme case of a population further south, most breeding birds arrive back



**Figure 2.** Temporal trends in arrival dates at the colony (a), pre-laying duration (b) and mean hatching date (c). The dashed line in (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 (a) illustrates the same model prediction for arrival date using the entire dataset (squares and dots). (d) The relationship between advancing arrival date and breeding success. Bands in all panels indicate bootstrapped 95% CIs for predicted values calculated using the *bootMer* function with 1000 simulations (package *lme4*). Red and blue symbols represent COGU and BRGU, respectively.

at the colony already in the autumn and in at least some years birds attend the breeding sites throughout the winter [11,43]. This variability may have costs and benefits associated with it. During the pre-laying period prospective breeders attend the colonies at regular intervals [26–28] which restricts them

to quasi-central place foraging. This, in turn, limits their available prey options and could even lead to local depletion of food resources before spring bloom at large colonies [44], decreasing their body condition and potentially breeding probability prior to breeding. Alternatively, early return to the breeding sites might help secure nesting sites, mating partners and facilitate courtship [23], or it might be a response to unfavourable conditions experienced by these migrants during the end of their non-breeding period, resulting in an earlier return to the colony.

We showed that colony arrival date advanced in both the Brünnich's and common guillemot across the study area, while their timing of hatching did not display any trend as shown previously in seabirds globally [6] and for alcid in the Atlantic and Pacific [18]. Contrary to these previous studies, concluding that breeding phenology is insensitive to short-term climatic change, we identified a clear trend in arrival dates across both species studied. This advancement resulted in an increasing pre-laying duration as mean hatching date did not advance, suggesting that part of breeding in these seabirds is indeed sensitive to changing conditions, although we cannot derive conclusions regarding the process driving this phenomenon or if it is an adaptation to a changing environment. A potential explanation could be that the cue used to time arrival across the North Atlantic is changing as has been shown in some passerine species [45], but could not be demonstrated in others [46,47].

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

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



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

**Ethics.** All animal research was conducted in accordance with relevant in country protocols and were granted by: the County Governor of Nordland, the County Governor of Finnmark, the Governor of Svalbard, the Norwegian Food Safety Authority (FOTS ID: 6291, 8482, 15603), the National Museum of the Faroe Islands and the Icelandic Institute of Natural History.

**Data accessibility.** Data are available through the Norwegian Polar Data Centre (doi:10.21334/npolar.2019.55169600), SEAPOP reports (www.seapop.no/no/publikasjoner/) and NNA reports (nna.is/wp-content/uploads/2018/12/NNA1804-Bjargfuglavoktun2018\_framvinduskysrsla2.pdf).

## References

- Varpe Ø. 2017 Life history adaptations to seasonality. *Integr. Comp. Biol.* **57**, 943–960. (doi:10.1093/icb/ix123)
- Youngflesh C *et al.* 2017 Circumpolar analysis of the Adélie penguin reveals the importance of environmental variability in phenological mismatch. *Ecology* **98**, 940–951. (doi:10.1002/ecy.1749)
- McLean N, Lawson CR, Leech DI, van de Pol M. 2016 Predicting when climate-driven phenotypic change affects population dynamics. *Ecol. Lett.* **19**, 595–608. (doi:10.1111/ele.12599)
- Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Hoegh-Guldberg O, Bairlein F. 2002 Ecological responses to recent climate change. *Nature* **416**, 389. (doi:10.1038/416389a)
- Møller AP, Rubolini D, Lehikoinen E. 2008 Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proc. Natl Acad. Sci. USA* **105**, 16 195–16 200. (doi:10.1073/pnas.0803825105)
- Keogan K *et al.* 2018 Global phenological insensitivity to shifting ocean temperatures among seabirds. *Nat. Clim. Change* **8**, 313–318. (doi:10.1038/s41558-018-0115-z)
- Kokko H, Harris MP, Wanless S. 2004 Competition for breeding sites and site-dependent population regulation in a highly colonial seabird, the common guillemot *Uria aalge*. *J. Anim. Ecol.* **73**, 367–376. (doi:10.1111/j.0021-8790.2004.00813.x)
- Béty J, Gauthier G, Giroux JF. 2003 Body condition, migration, and timing of reproduction in snow geese: a test of the condition-dependent model of optimal clutch size. *Am. Nat.* **162**, 110–121. (doi:10.1086/375680)
- Sénéchal É, Béty J, Gilchrist HG, Hobson KA, Jamieson SE. 2011 Do purely capital layers exist among flying birds? Evidence of exogenous contribution to arctic-nesting common eider eggs. *Oecologia* **165**, 593–604. (doi:10.1007/s00442-010-1853-4)
- Birkhead TR, Johnson SD, Nettleship DN. 1985 Extra-pair matings and mate guarding in the common murre *Uria aalge*. *Anim. Behav.* **33**, 608–619. (doi:10.1016/S0003-3472(85)80085-3)
- Harris MP, Heubeck M, Shaw DN, Okill JD. 2006 Dramatic changes in the return date of guillemots *Uria aalge* to colonies in Shetland, 1962–2005. *Bird Study* **53**, 247–252. (doi:10.1080/00063650609461439)
- Quillfeldt P, Weimerskirch H, Masello JF, Delord K, McGill RAR, Furness RW, Cherel Y. 2019 Behavioural plasticity in the early breeding season of pelagic seabirds—a case study of thin-billed prions from two oceans. *Mov. Ecol.* **7**, 1. (doi:10.1186/s40462-019-0147-7)
- Frederiksen M *et al.* 2016 Migration and wintering of a declining seabird, the thick-billed murre *Uria lomvia*, on an ocean basin scale: conservation implications. *Biol. Conserv.* **200**, 26–35. (doi:10.1016/j.biocon.2016.05.011)
- Tranquilla LA *et al.* 2013 Multiple-colony winter habitat use by murres *Uria* spp. in the Northwest Atlantic Ocean: implications for marine risk assessment. *Mar. Ecol. Prog. Ser.* **472**, 287–303. (doi:10.3354/meps10053)
- Linnebjerg JF, Frederiksen M, Kolbeinsson Y, Snaethórsson AÖ, Thórisson B, Thórarinnsson TL. 2018 Non-breeding areas of three sympatric auk species breeding in three Icelandic colonies. *Polar Biol.* **41**, 1951–1961. (doi:10.1007/s00300-018-2334-1)
- Benowitz-Fredericks ZM, Kitaysky AS. 2005 Benefits and costs of rapid growth in common murre chicks *Uria aalge*. *J. Avian Biol.* **36**, 287–294. (doi:10.1111/j.0908-8857.2005.03357.x)
- Gaston AJ, Jones IL. 1998 *Bird families of the world. The Auks Alcidae*. Oxford, UK: Oxford University Press.
- Descamps S *et al.* 2019 Diverging phenological responses of Arctic seabirds to an earlier spring. *Glob. Change Biol.* **00**, 1–11. (doi:10.1111/gcb.14780)
- JNCC. 2016 Seabird population trends and causes of change: 1986–2015 report. Peterborough, UK: Joint Nature Conservation Committee.
- Fauchald P *et al.* 2015 The status and trends of seabirds breeding in Norway and Svalbard. In *NINA rapport* (ed. P Fauchald), pp. 1–84. Trondheim, Norway: NINA.
- Garðarsson A, Guðmundsson GA, Lillindahl K. 2019 The numbers of large auks on the cliffs of Iceland in 2006–2008. *Bliki* **33**, 35–46.
- Taylor K, Reid J. 1981 Earlier colony attendance by Guillemots and Razorbills. *Scott. Birds* **11**, 173–180.
- Harris MP, Wanless S. 1989 Fall colony attendance and breeding success in the common murre. *Condor* **91**, 139–146. (doi:10.2307/1368157)
- Burr ZM *et al.* 2016 Later at higher latitudes: large-scale variability in seabird breeding timing and synchronicity. *Ecosphere* **7**, e01283. (doi:10.1002/ecs2.1283)
- Birkhead TR. 1978 Attendance patterns of guillemots *Uria aalge* at breeding colonies on Skomer Island. *Ibis* **120**, 219–229. (doi:10.1111/j.1474-919X.1978.tb06779.x)
- Hatchwell B. 1988 Intraspecific variation in extra-pair copulation and mate defence in common guillemots *Uria aalge*. *Behaviour* **107**, 157–185. (doi:10.1163/156853988X00331)
- Gaston AJ, Nettleship DN. 1981 *The thick-billed murres of Prince Leopold Island*. Ottawa, Canada: Canadian Wildlife Service.
- Wilhelm SI, Storey AE. 2002 Influence of cyclic pre-lay attendance on synchronous breeding in common murres. *Waterbirds: Int. J. Waterbird Biol.* **25**, 156–163. (doi:10.1675/1524-4695(2002)025[0156:IOCPAO]2.0.CO;2)
- Merkel B *et al.* 2019 Data from: Earlier colony arrival but no trend in hatching timing in two congeneric seabirds (*Uria* spp.) across the North Atlantic. *Norwegian Polar Institute* (doi:10.21334/npolar.2019.55169600)

30. Barrett RT, Anker-Nilssen T, Bustnes JO, Christensen-Dalsgaard S, Descamps S, Erikstad K-E, Lorentsen S-H, Strøm H, Systad GH. 2012 Key-site monitoring in Norway 2011. In *SEAPOP Short Report*.
31. Barrett RT *et al.* 2013 Key-site monitoring in Norway 2012, including Svalbard and Jan Mayen. In *SEAPOP Short Report*.
32. Barrett RT *et al.* 2014 Key-site monitoring in Norway 2013, including Svalbard and Jan Mayen. In *SEAPOP Short Report*.
33. Barrett RT *et al.* 2015 Key-site monitoring in Norway 2014, including Svalbard and Jan Mayen. In *SEAPOP Short Report*.
34. Barrett RT *et al.* 2016 Key-site monitoring in Norway 2015, including Svalbard and Jan Mayen. In *SEAPOP Short Report*.
35. Anker-Nilssen T *et al.* 2017 Key-site monitoring in Norway 2016, including Svalbard and Jan Mayen. In *SEAPOP Short Report*.
36. Anker-Nilssen T *et al.* 2018 Key-site monitoring in Norway 2017, including Svalbard and Jan Mayen. In *SEAPOP Short Report*.
37. Kolbeinsson Y, Þórarinnsson PL. 2018 Vöktun bjargfuglastofna 2018 -Framvinduskýrsla. Húsavík, Náttúrustofa Norðausturlands.
38. Pinheiro JC, Bates DM. 2000 *Mixed-effects models in S and S-PLUS*. New York, NY: Springer.
39. Nakagawa S, Schielzeth H. 2013 A general and simple method for obtaining R<sup>2</sup> from generalized linear mixed-effects models. *Methods Ecol. Evol.* **4**, 133–142. (doi:10.1111/j.2041-210x.2012.00261.x)
40. Bjørnstad ON, Ims RA, Lambin X. 1999 Spatial population dynamics: analyzing patterns and processes of population synchrony. *Trends Ecol. Evol.* **14**, 427–432. (doi:10.1016/S0169-5347(99)01677-8)
41. R Development Core Team. 2019 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
42. Birkhead TR, Nevo AJD. 1987 Egg formation and the pre-laying period of the common guillemot *Una aalge*. *J. Zool.* **211**, 83–88. (doi:10.1111/j.1469-7998.1987.tb07454.x)
43. Harris MP, Wanless S. 1990 Breeding status and sex of common murrelets (*Uria aalge*) at a colony in Autumn. *Auk* **107**, 603–605.
44. Ashmole NP. 1963 The regulation of numbers of tropical oceanic birds. *Ibis* **103b**, 458–473. (doi:10.1111/j.1474-919X.1963.tb06766.x)
45. Marra PP, Francis CM, Mulvihill RS, Moore FR. 2005 The influence of climate on the timing and rate of spring bird migration. *Oecologia* **142**, 307–315. (doi:10.1007/s00442-004-1725-x)
46. Both C, Visser ME. 2001 Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* **411**, 296. (doi:10.1038/35077063)
47. Fraser KC, Silverio C, Kramer P, Mickle N, Aepli R, Stutchbury BJM. 2013 A trans-hemispheric migratory songbird does not advance spring schedules or increase migration rate in response to record-setting temperatures at breeding sites. *PLoS ONE* **8**, e64587. (doi:10.1371/journal.pone.0064587)
48. IPCC. 2013 *Climate change 2013: the physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change*. Cambridge, UK and New York, NY: Cambridge University Press.
49. Harris MP, Wanless S. 1995 Survival and non-breeding of adult common guillemots *Una aalge*. *Ibis* **137**, 192–197. (doi:10.1111/j.1474-919X.1995.tb03239.x)
50. Reed TE, Harris MP, Wanless S. 2015 Skipped breeding in common guillemots in a changing climate: restraint or constraint? *Front. Ecol. Evol.* **3**, 1. (doi:10.3389/fevo.2015.00001)
51. Jeschke JM, Harris MP, Wanless S, Kokko H. 2007 How partnerships end in guillemots *Uria aalge*: chance events, adaptive change, or forced divorce? *Behav. Ecol.* **18**, 460–466. (doi:10.1093/beheco/arl109)