

The early birds and the rest: do first nesters represent the entire colony?

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Abstract Climate change studies have detected earlier spring arrival of breeding birds. However, first nest dates (date first nests were found), which commonly provide the metric for earlier arrival, can be biased by population size or sampling effort. Our aims were to determine if: 1) first nest dates and median nest date (date when at least 50 % of all females have nested) were equivalent predictors for the spring arrival and 2) first nest date or median nest date were related to nest numbers. We recorded first and median nest dates and nest numbers at the common eider (*Somateria mollissima*) colony at Rif, Iceland, during 1992–2013. First nest date was advanced by 11 days during the study, but median nest date was advanced by only 4 days. First nest date and median nest date were correlated, but this relationship was only a small improvement over the null model (Nagelkerke $R^2 = 30\%$). We found a relationship with nest count for both first and median nest dates once the analysis had accounted for inter-annual variability. First nest date may not represent the colony as a whole but rather the physically fittest or the most determined individuals,

which may be more prone to nest early than the general population. Nesting birds must decide how much to advance breeding based on nest numbers and other non-temporal cues which necessitate earlier breeding. We argue that nest numbers affect the birds in a biological sense and that the advancement was not explained solely by increased nest numbers.

Keywords First nest date · Arrival date · Nest numbers · Eider · Climate change

Introduction

Individual birds make different adjustments to environmental changes that facilitate earlier nest initiation (Ahola et al. 2012; Arzel et al. 2014). Early nesting individuals generally are in optimal physical condition, often lay large clutches or attain a high nesting success (Erikstad et al. 1993; Arnold et al. 2004; Bêty et al. 2004). Clutch size commonly is inversely related to nest date and survival of subsequent young can be negatively related to hatch date (Traylor and Alisauskas 2006; Öst and Steele 2010; Clark et al. 2014; Westneat et al. 2014). A potential drawback of very early nesting and subsequent early hatch is a temporary high exposure to predators, which can incur costs on the earliest individuals (Lepage et al. 2000; Bêty et al. 2004; Pálsdóttir 2016).

Climate change has affected spring arrival dates of migratory birds in recent decades (Jonzen et al. 2006; Miller-Rushing et al. 2008; Moe et al. 2009; Dolenc et al. 2011; Schroeder et al. 2012). Although such changes can cause mis-timings with availability of prey for some species (Both et al. 2006; Saino et al. 2009; Watanuki et al. 2009), some species or populations seem to benefit from

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climate change or have altered their behavior or otherwise adapted to environmental changes (Mace et al. 2010; Jonker et al. 2011; 2012). However, spring arrival dates can depend on factors besides climate, most notably cohort sizes and annual changes in the sizes of migratory populations (Miller-Rushing et al. 2008; Ahola et al. 2012). Findings on spring arrival date also depend on the exact indices used; in a study of 32 migratory species, Miller-Rushing et al. (2008) found that earliest arrivals 1970–2002 were delayed 0.20 days each decade whereas conversely, mean arrival dates for each species were advanced 0.78 days each decade.

Common eider (*Somateria mollissima*) breeds in the Arctic and sub-Arctic regions, Western Europe and the Baltic Sea and is considered an indicator species for climate change in the Arctic and sub-Arctic regions (Merkel and Gilchrist 2010). Common eider responds to climate change because females that attain the best body condition in late winter generally become the first nesters in a given year (Bolduc et al. 2005; Öst et al. 2008) and earlier nesting generally is positively related to hatching success (Öst et al. 2011), more exogenous protein use for egg formation relative to later nesters (Sénéchal et al. 2011), and increased clutch sizes (Lehikoinen et al. 2006; Jónsson et al. 2009; Mehlum 2012). Unfavorable winter weather can interfere with accumulation of endogenous reserves for breeding, cause nest desertion and affect levels of yolk hormone, nest site selection or immune function (Robertson 1995; Descamps et al. 2010; Love et al. 2010; Sénéchal et al. 2010; Jónsson and Lúðvíksson 2013).

Like other seabirds (Mergini), common eider spring arrival responded to local weather parameters, ice cover, the North Atlantic Oscillation (NAO) index and fertilizer release (Lehikoinen et al. 2006; Jónsson et al. 2009; Love et al. 2010; Zipkin et al. 2010; Laursen and Møller 2014). In northwest Iceland, spring icecover generally is absent but females arrived later following warm winters with strong westerly winds (positive NAO values; Jónsson et al. 2009), whereas females in southwest Iceland nested earlier following milder winters (D’Alba et al. 2010). Furthermore, clutch sizes increased following warm and wet spring seasons in northwest Iceland (Jónsson et al. 2009).

For common eider, different variables have been used to index spring arrival date but these are not always available simultaneously. For example, D’Alba et al. (2010) presented first nest date (the dates in May first nests were observed) for Nordurkot, southwest Iceland, and so did Jónsson et al. (2009) for Laekur, Northwest Iceland. Both studies reported a relationship between first nest date and winter weather. For the third colony, Bíldsey in West Iceland, first nest date was not recorded but multiple nest surveys during nest initiation, along with final nest counts,

were used to estimate the date in May where 50 % of all nests for the colony have been found (median nest date; Jónsson et al. 2009).

Population trends potentially can bias recorded first nest dates toward a seemingly earlier spring arrival, i.e., for a growing population the chance of observing an early nest increases with higher number of nesters (Miller-Rushing et al. 2008; Waltho and Coulson 2015). Such variation is well possible for common eider in Iceland where trends in nest numbers differ between the 40 colonies studied to date (Jónsson et al. 2009; Jónsson and Lúðvíksson 2013; Jónsson et al. 2013). D’Alba et al. (2010) reported an advanced first nest date and a positive trend for nest numbers at Nordurkot, southwest Iceland 1977–2006 but did not show a correlation between first nest date and nest numbers, despite an increase in nest numbers during the study period. Waltho and Coulson (2015) criticized this finding, claiming that first nest dates were always inversely related to population sizes. For first nest date of common eider at our study site at Rif, West Iceland (and probably for many other eider colonies in Iceland), such sampling effect is unlikely because the eider farmer (S JL) prepares the colony in advance for nest initiation of females (see Jónsson 2001; Kristjánsson and Jónsson 2011), i.e., visits the 2.34 ha colony regularly daily from late April and thus accurately documents the first nesters independently of nest numbers. At Rif, the colony is visible from an adjacent hill-top (see photograph in Jónsson and Lúðvíksson 2013) and the presence of males until the first weeks of June makes the eider pairs highly visible to observers (Kristjánsson and Jónsson 2015).

At Rif, first nest date and median nest date were recorded at this colony 1992–2013. There should be a strong biological selection for earlier laying dates because the nesting density has increased since 1992 (Jónsson and Lúðvíksson 2013). Thus, early breeding may not be advantageous on its own but a necessity under increased population density which increases competition for preferred nest sites (Ahola et al. 2012). The main goal of this study was to identify and compare potential sources of variation in first nest date with that of the median nest date. The comparison between nest numbers, first nest date, and median nest date can serve as a model for these questions: (1) Are first nest dates and median nest date equivalent predictors for the spring arrival of the study population, as would be indicated by a linear relationship of first nest dates with median nest date? (2) Do advances in first nest date or median nest date have a biological meaning or are they simply a function of changes in nest numbers? We predicted that increased nest numbers would advance first nest dates or median nest dates in this study, after accounting for annual variation in the data.

Methods

Study area

We studied the common eider colony at Rif, Snaefellsnes peninsula in West Iceland (Fig. 1; GPS: 64°55′14″N; 23°49′23″W). Number of nests has been counted annually since colony establishment in 1972, and females have been leg-banded since 1993. The studied breeding population is wild and free-ranging, although the colony was originally established by humans.

The colony is comprised of two islands, which are 40 m apart and surrounded by a 2.34 ha pond (Jónsson and Lúðvíksson 2013). Both islands were originally man-made, one comprised of rocks in 1972 and the other a grass island separated from the coast in 1990 by a ditch. When the study began in 1992, the rock island had been a nest site for 20 years, which almost equals the highest life spans of common eiders that have been banded at Rif (Smári J. Lúðvíksson, unpublished data). Conversely, the grass island was first nested in 1990 and probably received most of the new recruits as the colony increased in nest numbers

1992–2008. The overall area for nests has remained the same since 1990 (the rock island is approx. 120 m² and the grass island is approx. 600 m²). Both islands have driftwood logs and car tires as nesting shelters, but larger vegetation is absent. During 1993–2008, the colony (both islands combined) increased from 248 nests to 606 nests. The rock island increased from 150 nests to 200 nests (average 186 nests). The first nests were found in the grass island in 1990, and nest numbers there increased from 35 nests in 1992 to 306 nests in 2013 (average 221 nests).

Generally, eider nests can be initiated any time between 1 May and 16 June within a year (last recorded brood exodus was July 24, 1994, Smári J. Lúðvíksson unpublished data), making the individual variation in nest initiation date 47 days within a season or even greater. The Rif colony has a very high nest density (1.7 nests/m²) where most nest bowls are used every year, and some bowls are used in succession by two females (where the later-nesting female nests where the first female has successfully led out her brood; Kristjánsson et al. 2016). In other colonies in Iceland, each bowl usually is used by only one female each season and up to one-third of nest sites may be new every

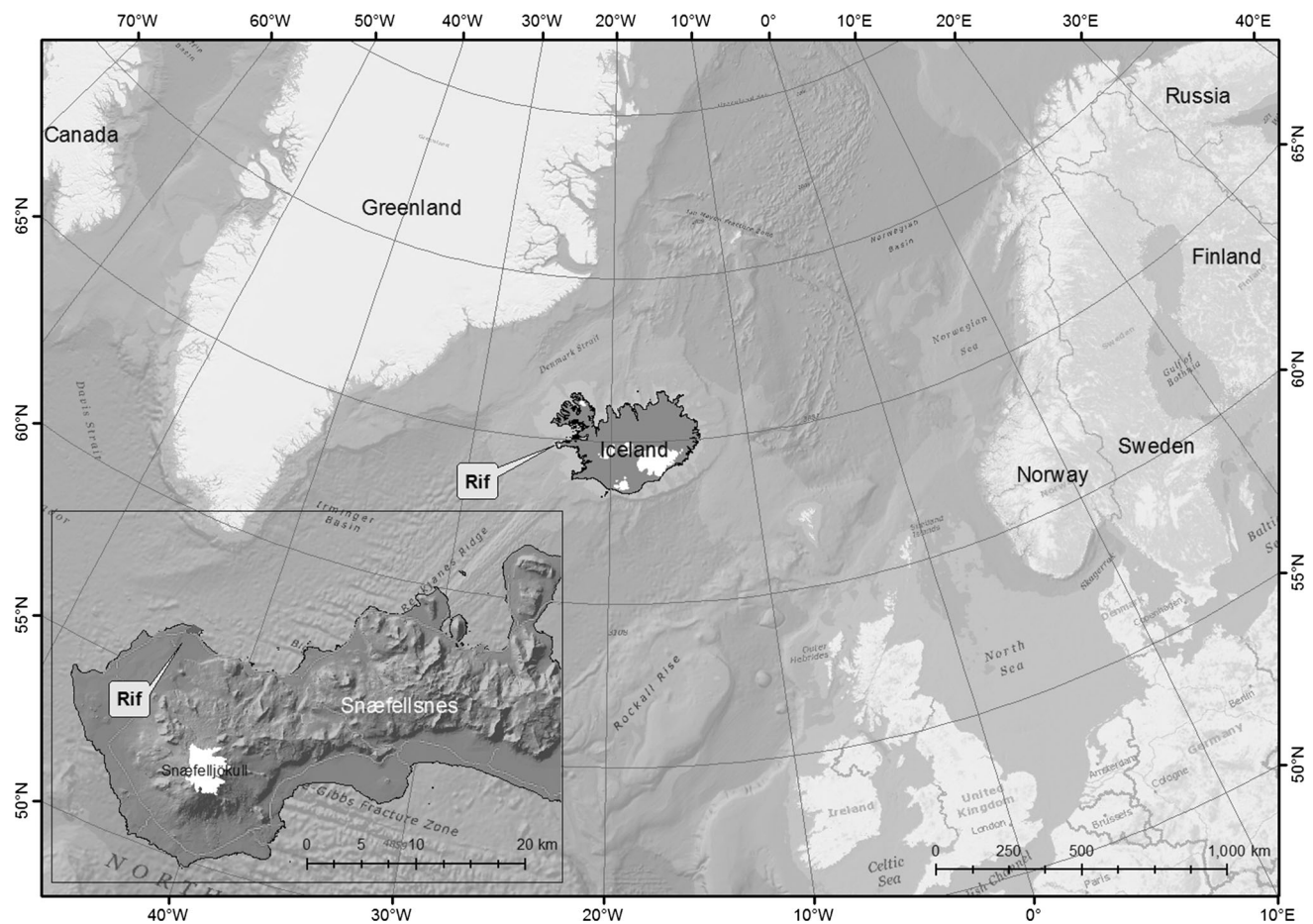


Fig. 1 Map of the North Atlantic, showing Iceland and the location of Rif eider colony within the Snaefellsnes peninsula, west Iceland

year. Furthermore, the Rif colony has some females that partially share nest attendance and over 20 % of the nests have parasitic egg laying (Kristjánsson and Jónsson 2015), i.e. individuals that lay their eggs in other females nests (Waldeck et al. 2011).

Data

We collected data on three variables 1992–2014, specific to each island, i.e., the rock island and grass island: (1) total number of nests, obtained from the final nest count every year; (2) first nest date, the date where the first 1–10 nests were found (Jónsson et al. 2009; D’Alba et al. 2010); and (3) median nest date, the date where 50 % of nests had been initiated, estimated by interpolating between 3 and 5 nest counts within the month of May (Lehikoinen et al. 2006; see also Jónsson et al. 2009). There were no data on first nest date and median nest date in 2003 and 2004 although a final nest count was obtained; these years are missing from our analysis ($n = 20$ years).

Statistical analyses

Our methodology for analysis followed the recommendations/approach of Zuur et al. (2009). The main issues addressed were to determine the models that best fit data for inference regarding the influence of total nest number on first nest date and median nest date. We investigated whether: (1) general linear models, with fixed effects of year and total nest numbers, predicted first nest date and median nest date; (2) these models appropriately fit the data by examining variance inflation factors (VIF); and (3) generalized linear mixed models with total nest number as the sole fixed effect and year as a nuisance random variable with a temporal covariance structure appropriately fit the data.

To evaluate the first set of general linear models, we used VIF to evaluate possible interrelationships between the candidate explanatory variables with year for evidence of multicollinearity (PROC REG, SAS Institute, Inc., Cary, NC). An interrelationship between nest numbers with year would be consistent with our predictions, specifically that nest initiation would be earlier when nest numbers increased from the previous year and delayed when nest numbers decreased from the previous year. We assessed VIF between nest numbers with year and between nest numbers, differenced between years, as annual change in nest numbers.

To evaluate the generalized linear models, we followed the general procedure for constructing and selecting

generalized linear models (PROC GLIMMIX, SAS Institute, Inc., Cary, NC; Faraway 2006; Gbur et al. 2012) selecting link function and probability distributions outlined by Bolker et al. (2008) and selecting temporal covariance structures following Zuur et al. (2009). Based on these procedures, we first constructed fully parameterized models, including nest number and year, that differed in link function (model-level transformation) and probability distribution, selected a fit statistic (AICc) to identify the most appropriate model structure (i.e., link and probability distribution combination), evaluated multiple temporal covariance structures (by \hat{c} e.g., first- and second-order autoregressive, Toeplitz, variance components, and unstructured), and, lastly, determined statistical significance of the explanatory variables based on the best fitting model (no link transformation and normal probability distribution).

We combined the two islands for analysis but point out that in a preliminary analysis with the islands segregated, first nest date and median nest date were on average 4–5 days earlier in the rock island throughout the study period. During model fitting, there were year trends in all variables, i.e., nest numbers were positively related to year whereas first nest date was positively related to year and median nest date was weakly positively related to year. Thus, our analysis treated year as a covariate but moderated the influence of inter-annual variability by using the R-side covariance matrix (Gbur et al. 2012), because sampling was repeated annually. It should be noted that the subject of the sampling was the uniquely assignable breeding season each year, which does influence the dependent variables, however, does not need to be assigned a unique random intercept (e.g., a random G-side covariance approach) because inference in this model was across the length of the study; therefore, this analysis acknowledges that year was a source of variability, but once accounted, year was not part of the inference. An unstructured covariance matrix fit our data best, presumably because the influence of year is proximally independent (i.e., the year effect is not strengthening or weakening in a discernable pattern, like an autoregressive structure). For interpretation, variation explained by the final model was estimated by improvement over the null model by Nagelkerke (1991) R^2 (i.e., the sample size adjusted ratio of the full model to null model likelihoods represented increased variance explained by the full model over the null model; Hair et al. 2010). Finally, we estimated, by z test, the probabilities of observed first nest dates, given nest numbers to illustrate the relationship between first nest date with number of nests.

Results

Descriptive statistics

Final nest count increased from 185 nests to 506 nests during 1992–2013 (Fig. 2). The rock island reached a plateau of 200–230 nests during 2005–2013, whereas the more recently established grass island reached a plateau of 300–316 nests during 2010–2013. First nest date was advanced on average 11 days during the study, i.e., from 17 May to 6 May whereas median nest date was advanced on average 4 days, i.e., from 29 May to 25 May (Fig. 3).

Analysis of trends

Analyses of VIF between nest numbers with year resulted in an unacceptably high VIF of 5.4, strongly indicating multicollinearity. Conversely, the annual change in nest numbers did not exhibit multicollinearity with year (VIF = 1.4). Overall, increased nest numbers appeared to explain advancing first nest date and median nest date, despite a weak relationship between first nest date and median nest date. The relationship between first nest date with median nest date was weak ($F_{1,18} = 7.93$, $p = 0.01$, Nagelkerke $R^2 = 0.30$; Fig. 4), suggesting that the advancing first nest date was not simply a function of an advancing median nest date (i.e., the first nest date became earlier because the whole nesting period became earlier). Increased total numbers of nests did well explain the advance in first nest date ($F_{1,18} = 18.9$, $p < 0.01$, Nagelkerke $R^2 = 0.49$, Fig. 5) and, to a lesser degree, median nest date ($F_{1,18} = 18.9$, $p < 0.01$, Nagelkerke $R^2 = 0.24$, Fig. 5). Importantly, in each model, the unstructured covariance matrix best fit the data, indicating that the influence of among-year variation was simply the magnitude in the increase in the number of nests during the

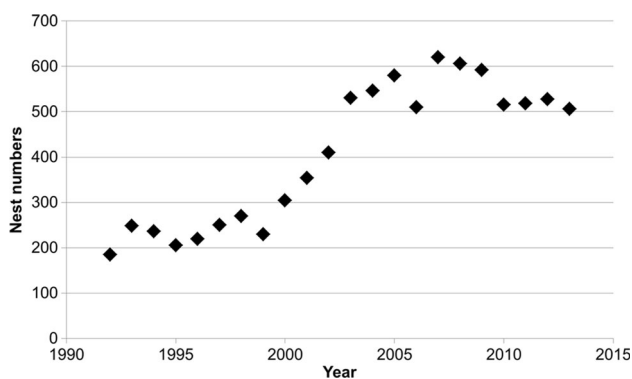


Fig. 2 Relationships between year (1992–2013) and final nest numbers, for common eider nesting at Rif, West Iceland. A second-order polynomial model gave a better fit here than either linear or power model

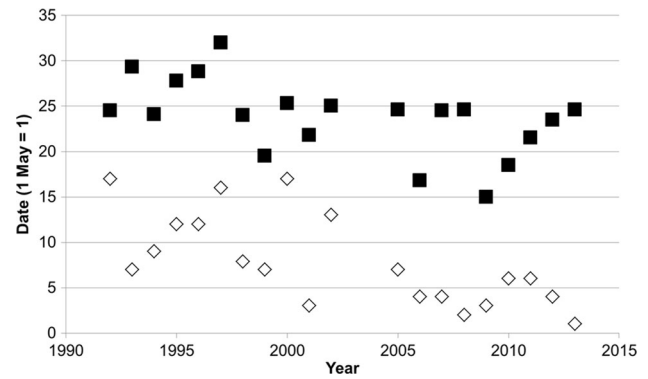


Fig. 3 Year trends in first nest date (open symbols) and median nest date (close symbols), for common eider nesting at Rif, West Iceland 1992–2013. A second-order polynomial model gave a better fit for median nest date than either linear or power model. A power model gave a better fit for first nest date than either linear or polynomial model

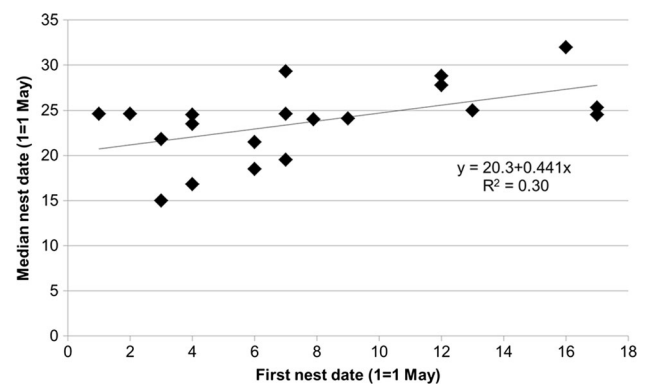


Fig. 4 Relationships between first nest date and median nest date, for common eider nesting at Rif, West Iceland 1992–2013. The model shown here is the general linear mixed model between first and median nest data with nest number with year as a random effect

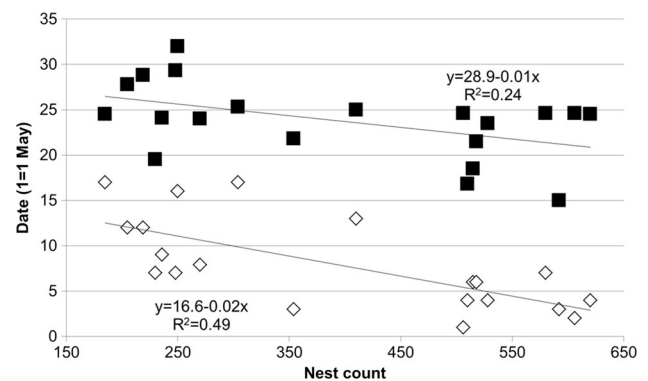


Fig. 5 Relationship between first nest date (open symbols) and median nest date (close symbols), for common eider nesting at Rif, West Iceland 1992–2013. The model shown here is the general linear mixed model between first and median nest data with nest number with, year as a random effect

previous year(s) (i.e., variance components) or a trend based primarily on the passage of time (i.e., autoregressive structure). The high among-year variation unexplained by similarity in serial measurements indicated that another, possibly stochastic, process may be occurring.

To further illustrate the relationship between nest number and first nest date, we used a z test to estimate probabilities of the observed first nest dates (or an earlier date), given the number of nests for the years 2005–2013. If drawn from a simulated random sample of first nest dates, with the same mean and variance as the observed data, the mean first nest date would be 16 May (± 1.25 days standard deviation) for numbers of nests between 505 and 620, which corresponded to the number of nests between 2005 and 2013. However, the observed first nest dates were between 6 May (2013; 506 nests) and 13 May (2005; 580 nests). These dates were significantly earlier (13 May 2005 z -score -100.8 , $p < 0.01$; 10 May 2006 z -score -111.4 , $p < 0.01$; 10 May 2007 z -score -100.8 , $p < 0.01$; 8 May 2008 z -score -133.7 , $p < 0.01$; 9 May 2009 z -score -126.1 , $p < 0.01$; 12 May 2010 z -score -100.8 , $p < 0.01$; 12 May 2011 z -score -100.9 , $p < 0.01$; 10 May 2012 z -score -113.3 , $p < 0.01$; 6 May 2013 z -score -127.8 , $p < 0.01$) than would have been expected from a random sample of first nest dates.

Discussion

First nest date was advanced 11 days during 1992–2013, but the median nest date only by 4 days. First nest date and median nest date were weakly correlated and probably represent different parts of the study population. First nesters probably are the physically fittest or the most determined individuals, which may be more prone to nest early than the general population. Conversely, females nesting near the median nest date probably represent the average individuals and perhaps better index all individuals within the study colony.

Furthermore, both first nest date and median nest date were affected by nest numbers, after accounting for annual variation in the data. This finding indicates that eiders respond to the crowding (increased nest density) in the colony. Common eider's decisions to initiate nesting will partially depend on density and the choices of other females in the colony, either as a result of observing the actions or nest success of others ("public information") or that females are attracted to the high nest densities, perhaps seeing the crowding as a sign of safety (Danchin et al. 1998; Valone 2007; Öst et al. 2011). Such individuals could be reluctant to nest early and wait to initiate their own nests until they see sufficient conspecifics on their nests. The z tests confirmed that observed nest dates for the

period 2005–2013 were much earlier (6 May through 13 May) than would be predicted in random sample (15–17 May). Therefore, the trend in the data is larger than would occur simply by increasing number of nests, suggesting that a behavior or other biological process may have occurred.

Effects of density dependence on nest numbers are rarely observed for common eiders (Coulson 2010; Jónsson et al. 2013) but are undoubtedly present at Rif, which has one of the highest nest densities reported for common eiders (see Kristjánsson and Jónsson 2015). Competition for preferred nest sites between females may cause differing nest initiation agendas between individuals. For example, increased nest numbers may represent more pressure for birds that prefer to arrive early, whereas other individuals are reluctant to nest until the bulk of their fellow colonials have arrived.

During model fitting, the inclusion of year was very important in obtaining the best fitting model, strongly suggesting that some inter-annual differences occurred, in either environmental conditions or the decision-making process of birds. Of the findings, the most important was that the variability appeared to be independent of patterns from the previous year or the magnitude of the increase in nest number during the previous year. The strong but essentially trendless, inter-annual variation suggests either an environmental cue or behavioral response is the underlying factor behind the pattern. Environmental patterns generally exhibit temporal trends (e.g., warmer waters tend to stay warmer); therefore, because temporal trends were rejected by these models, the better explanation is behavioral, at least among possible explanations.

Which individuals are the first nesters?

A relevant question here is whether the same individuals are likely to be among the first nesters every year or whether individual nest dates are direct functions of body condition within a given year. In black-tailed godwits (*Limosa limosa*), spring arrival dates are highly consistent between years for individuals but advances in spring arrival dates are driven by earlier arrivals of the younger birds (Gill et al. 2014). However, for common eiders, body condition could alter nest initiation schedules of individuals, and body condition in the common eider can vary within individuals among years (Öst et al. 2007).

Higher clutch sizes in common eiders are associated with higher nest densities and the most densely nested islands are the ones least likely to suffer egg predation (Mehlum 2012; Pratte et al. 2016). Thus, dense nest sites, such as Rif, can be advantageous for common eiders. At least three individual traits can drive individual females to arrive early and try to obtain a favored nest site. One

obvious candidate is body condition and its relationship with stress or nest initiation date (Öst and Steele 2010; Seltmann et al. 2012) especially because body condition of individual eiders can vary from year to year (Öst et al. 2007). The choice or ability to compete for best nest sites each year could thus be positively related to body condition.

Secondly, age probably affects the earliness of nesting but also the nest choice as experienced females select the more concealed or centrally located nest sites and often lay the largest clutches (Öst and Steele 2010). We know from banding data in our study colony (Jónsson and Lúðvíksson 2013) that early nesters at Rif often are recaptures, i.e., at least somewhat experienced females. The variety of nest shelter types at Rif probably promotes active preference of nest sites by the females. However, the islands probably are too small to observe an edge effect, i.e., older and calmer individuals may not be able to nest noticeably farther from the shoreline, like observed for eiders in Finland (Seltmann et al. 2014). The absence of trees or other large vegetation also somewhat limits effects of topography as a driver of nest selection at Rif.

A third possible factor is the personality of common eider (Seltmann et al. 2014) which could possibly explain which individuals strive to arrive early (i.e., “bold” personality types, possibly more independent in character than later nesters). Other individuals are more likely to rely on public information or find safety among mid- to late arrivals (i.e., “shy” personality types). A future research question is whether first nesters are individuals that respond to environmental conditions within a given year, or whether they are phenotypically (or personality-wise) fixed as competitive nesters, with determined preferences for certain types of nest bowls or nest sites. Interestingly, individual females do not seem influenced by the nest sites but rather the females show consistent, individual patterns in nest site selections (D’Alba et al. 2011; Seltmann et al. 2014).

Females that strive to nest early may be those which wish to avoid parasitic egg laying (Waldeck and Andersson 2006) which is common at Rif, particularly in the rock island (Kristjánsson and Jónsson 2015). Interestingly, the rock island generally initiated nesting 4–11 days earlier but also had a higher occurrence of clutches with 7 eggs or higher (32.4–17.3 % in 2012, the authors, unpublished data). Thus, late nesters may have increased their chances of avoiding parasitic nesters by choosing the grass island as a nest site. Banding data from Rif show that many females will switch between the islands during their lifetime (Jónsson and Lúðvíksson 2013). The choice between the two islands each spring may be affected by affinities for parasitic egg laying, their own or that of other individuals. Eiders may switch between islands at Rif after

unsuccessful early nest initiation attempts in the previous years. We suspect that at Rif, parasitic egg laying (Waldeck et al. 2011) can occur if the first eggs are predated (see Hanssen and Erikstad 2013), employed as a salvage strategy favored over a second nesting attempt.

Conclusion

There is general agreement that spring arrival of common eider is influenced by climate variation, both in higher-Arctic conditions where ice covers the nest sites until spring and in sub-Arctic or temperate locations where spring ice cover is absent and low-pressure winters delay first nest dates (Lehikoinen et al. 2006; Jónsson et al. 2009; D’Alba et al. 2010; Love et al. 2010; Chaulk and Mahoney 2012; Mehlum 2012). Thus, the importance of such parameters cannot be understated for study of this species, which is often too numerous and/or dispersed to count annually. Our results illustrate that different parameters used to estimate “arrival” in common eider can agree poorly with one another. A metric that somehow takes into account most of the individuals, such as median nest date, or average laying date of first egg for females (Love et al. 2010), may be the preferred choice but often unavailable for practical reasons. We hypothesize that first nest date represents only a handful of the fittest or most determined individuals, whereas the 50 % threshold at least awaits the arrival of half the population and may better represent the general public. An alternative hypothesis is to view common eiders as pioneers and followers, where such grouping of each individual could be determined by personality (Seltmann et al. 2014), body condition (Parker and Holm 1990; Öst and Steele 2010), affinity for public information (Valone 2007) or an interaction of these factors (Seltmann et al. 2012). Our study colony of common eiders is somewhat unique in being densely occupied by nesters and also having high incidence of nest parasitism but probably is representative for other such colonies and also valuable in providing insights into a population that is healthy and stable, with high adult survival (Jónsson and Lúðvíksson 2013).

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References

- Ahola MP, Laaksonen T, Eeva T, Lehtikainen E (2012) Selection on laying date is connected to breeding density in the pied flycatcher. *Oecologia* 168:703–710. doi:[10.1007/s00442-011-2135-5](https://doi.org/10.1007/s00442-011-2135-5)
- Arnold J, Hatch J, Nisbet I (2004) Seasonal declines in reproductive success of the common tern *Sterna hirundo*: timing or parental quality? *J Avian Biol* 35:33–45. doi:[10.1111/j.0908-8857.2004.03059.x](https://doi.org/10.1111/j.0908-8857.2004.03059.x)
- Arzel C, Dessborn L, Poysa H, Elmberg J, Nummi P, Sjöberg K (2014) Early springs and breeding performance in two sympatric duck species with different migration strategies. *Ibis* 156:288–298. doi:[10.1111/ibi.12134](https://doi.org/10.1111/ibi.12134)
- Bêty J, Giroux JF, Gauthier G (2004) Individual variation in timing of migration: causes and reproductive consequences in greater snow geese (*Anser caerulescens caerulescens*). *Behav Ecol Sociobiol* 57:1–8. doi:[10.1007/s00265-004-0840-3](https://doi.org/10.1007/s00265-004-0840-3)
- Bolduc F, Guillemette M, Titman RD (2005) Nesting success of common eiders *Somateria mollissima* as influenced by nest site and female characteristics in the Gulf of the St. Lawrence. *Wildl Biol* 11:273–279. doi:[10.2981/0909-6396\(2005\)11\[273:NSOCES\]2.0.CO;2](https://doi.org/10.2981/0909-6396(2005)11[273:NSOCES]2.0.CO;2)
- Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2008) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol Evol* 24:127–135. doi:[10.1016/j.tree.2008.10.008](https://doi.org/10.1016/j.tree.2008.10.008)
- Both C, Bouwhuis S, Lessells CM, Visser ME (2006) Climate change and population declines in a long-distance migratory bird. *Nature* 441:81–83. doi:[10.1038/nature04539](https://doi.org/10.1038/nature04539)
- Chaulk KG, Mahoney ML (2012) Does spring ice cover influence nest initiation date and clutch size in common eiders? *Polar Biol* 35:645–653. doi:[10.1007/s00300-011-1110-2](https://doi.org/10.1007/s00300-011-1110-2)
- Clark RG, Poysa H, Runko P, Paasivaara A (2014) Spring phenology and timing of breeding in short-distance migrant birds: phenotypic responses and offspring recruitment patterns in common goldeneyes. *J Avian Biol* 45:457–465. doi:[10.1111/jav.00290](https://doi.org/10.1111/jav.00290)
- Coulson JC (2010) A long-term study of the population dynamics of common eiders *Somateria mollissima*: why do several parameters fluctuate markedly? *Bird Study* 57:1–18. doi:[10.1080/00063650903295729](https://doi.org/10.1080/00063650903295729)
- D’Alba L, Monaghan P, Nager RG (2010) Advances in laying date and increasing population size in relation to climate change in an Icelandic eider colony. *Ibis* 152:19–28. doi:[10.1111/j.1474-919X.2009.00978.x](https://doi.org/10.1111/j.1474-919X.2009.00978.x)
- D’Alba L, Spencer KA, Nager RG, Monaghan P (2011) State dependent effects of elevated hormones: nest site quality, corticosterone levels and reproductive performance in the common eider. *Gen Comp Endocrinol* 172:218–224. doi:[10.1016/j.ygcen.2011.03.006](https://doi.org/10.1016/j.ygcen.2011.03.006)
- Danchin E, Boulinier T, Massot M (1998) Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. *Ecology* 79:2415–2428. doi:[10.1890/0012-9658\(1998\)079\[2415:CRSABH\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[2415:CRSABH]2.0.CO;2)
- Descamps S, Yoccoz NG, Gaillard J-M, Gilchrist HG, Erikstad KE, Hanssen SA, Cazelles B, Forbes MR, Bêty J (2010) Detecting population heterogeneity in effects of North Atlantic oscillations on seabird body condition: get into the rhythm. *Oikos* 119:1526–1536. doi:[10.1111/j.1600-0706.2010.18508.x](https://doi.org/10.1111/j.1600-0706.2010.18508.x)
- Dolenec Z, Dolenc P, Møller AP (2011) Warmer springs, laying date and clutch size of tree sparrows *Passer montanus* in Croatia. *Curr Zool* 57:414–418
- Erikstad KE, Bustnes JO, Moum T (1993) Clutch-size determination in precocial birds: a study of the common eider. *Auk* 110:623–628. doi:[10.2307/4088426](https://doi.org/10.2307/4088426)
- Faraway JJ (2006) Extending the linear model with R: generalized linear, mixed effects and nonparametric regression models. Chapman and Hall, Boca Raton
- Gbur EE, Stroup WW, McCarter KS, Durham S, Young LJ, Christman J, West M, Kramer M (2012) Analysis of generalized linear mixed models in the agricultural and natural resource sciences. American Society of Agronomy, Madison, Wisconsin
- Gill JA, Alves JA, Sutherland WJ, Appleton GF, Potts PM, Gunnarsson TG (2014) Why is timing of bird migration advancing when individuals are not? *Proc R Soc B* 281:20132161. doi:[10.1098/rspb.2013.2161](https://doi.org/10.1098/rspb.2013.2161)
- Hair JF, Black WC, Babin BJ, Anderson RE (2010) Multivariate data analysis, 7th edn. Prentice Hall, Upper Saddle River
- Hanssen SA, Erikstad KE (2013) The long term consequences of egg predation. *Behav Ecol* 24:564–569. doi:[10.1093/beheco/ars198](https://doi.org/10.1093/beheco/ars198)
- Jonker RM, Kuiper MW, Snijders L, Van Wieren SE, Ydenberg RC, Prins HHT (2011) Divergence in timing of parental care and migration in barnacle geese. *Behav Ecol* 22:326–331. doi:[10.1093/beheco/arq208](https://doi.org/10.1093/beheco/arq208)
- Jonker RM, Kurvers RHJM, van de Bilt A, Faber M, Van Wieren SE, Prins HHT, Ydenberg RC (2012) Rapid adaptive adjustment of parental care coincident with altered migratory behaviour. *Evol Ecol* 26:657–667. doi:[10.1007/s10682-011-9514-6](https://doi.org/10.1007/s10682-011-9514-6)
- Jónsson J (2001) Æðarfugl og æðarrætt á Íslandi. Mál og Menning, Reykjavík (In Icelandic)
- Jónsson JE, Lúðvíksson SE (2013) A choice between two adjacent islands: is switching nest sites related to weather or nest density in the common eider (*Somateria mollissima*)? *Ornis Fennica* 90:73–85
- Jónsson JE, Gardarsson A, Gill JA, Petersen Æ, Gunnarsson TG (2009) Seasonal weather effects on a subarctic capital breeder: common eiders in Iceland over 55 years. *Clim Res* 38:237–248. doi:[10.3354/cr00790](https://doi.org/10.3354/cr00790)
- Jónsson JE, Gardarsson A, Gill JA, Pétursdóttir UK, Petersen Æ, Gunnarsson TG (2013) Relationships between long-term demography and weather in a sub-Arctic population of common eider. *PLoS One* 8:e67093. doi:[10.1371/journal.pone.0067093](https://doi.org/10.1371/journal.pone.0067093)
- Jonzen N, Linden A, Ergon T, Knudsen E, Vik JO, Rubolini D, Piacentini D, Brinch C, Spina F, Karlsson L, Stervander M, Andersson A, Waldenström J, Lehtikainen A, Edvardsen E, Solvang R, Stenseth NC (2006) Rapid advance of spring arrival dates in long-distance migratory birds. *Science* 312:1959–1961. doi:[10.1126/science.1126119](https://doi.org/10.1126/science.1126119)
- Kristjánsson TO, Jónsson JE (2011) Effects of down collection on incubation temperature, nesting behaviour and hatching success of common eiders (*Somateria mollissima*) in west Iceland. *Polar Biol* 34:985–994. doi:[10.1007/s00300-010-0956-z](https://doi.org/10.1007/s00300-010-0956-z)
- Kristjánsson TO, Jónsson JE (2015) Cooperative incubation behaviour in a super dense common eider colony. *B Study* 62:146–149. doi:[10.1080/00063657.2014.993591](https://doi.org/10.1080/00063657.2014.993591)
- Kristjánsson TO, Jónsson JE, Svavarsson J (2016) Variation in nest composition and abundances of ectoparasites between nests in colonially breeding common eiders *Somateria mollissima*. *B study* (in press). doi:[10.1080/00063657.2016.1182965](https://doi.org/10.1080/00063657.2016.1182965)
- Lehtikainen A, Kilpi M, Öst M (2006) Winter climate affects subsequent breeding success of common eiders. *Glob Change Biol* 12:1355–1365. doi:[10.1111/j.1365-2486.2006.01162.x](https://doi.org/10.1111/j.1365-2486.2006.01162.x)

- Laursen K, Møller AP (2014) Long-term changes in nutrients and mussel stocks are related to numbers of breeding eiders *Somateria mollissima* at a large Baltic colony. *PLoS One* 9:e95851. doi:10.1371/journal.pone.0095851
- Lepage D, Gauthier G, Menu S (2000) Reproductive consequences of egg-laying decisions in snow geese. *J Anim Ecol* 69:414–427. doi:10.1046/j.1365-2656.2000.00404.x
- Love OP, Gilchrist HG, Descamps S, Semeniuk CAD, Bêty J (2010) Pre-laying climatic cues can time reproduction to optimally match offspring hatching and ice conditions in an Arctic marine bird. *Oecologia* 164:277–286. doi:10.1007/s00442-010-1678-1
- Mace GM, Collen B, Fuller RA, Boakes EH (2010) Population and geographic range dynamics: implications for conservation planning. *Philos Trans R Soc B* 365:3743–3751. doi:10.1098/rstb.2010.0264
- Mehlum F (2012) Effects of sea ice on breeding numbers and clutch size of a high Arctic population of the common eider *Somateria mollissima*. *Polar Sci* 6:143–153. doi:10.1016/j.polar.2012.03.004
- Merkel F, Gilchrist HG (2010) Indicator # 05. Seabirds—common eider. In: Arctic Biodiversity Trends—Selected Indicators of Change. CAFF International Secretariat, Akureyri, Iceland, May 2010, pp 38–40
- Miller-Rushing AJ, LLOYD-EVANS TL, PRIMACK RB, SATZINGER P (2008) Bird migration times, climate change, and changing population sizes. *Glob Change Biol* 14:1959–1972. doi:10.1111/j.1365-2486.2008.01619.x
- Moe B, Stempniewicz L, Jakubas D, Angelier F, Chastel O, Dinessen F, Gabrielsen GW, Hanssen F, Karnovsky NJ, Rønning B, Welcker J, Wojczulanis-Jakubas K, Bech C (2009) Climate change and phenological responses of two seabird species breeding in the high-Arctic. *Mar Ecol-Prog Ser* 393:235–246. doi:10.3354/meps08222
- Nagelkerke NJD (1991) A note of a general definition of the coefficient of determination. *Biometrika* 78:691–692. doi:10.1093/biomet/78.3.691
- Öst M, Clark CW, Kilpi M, Ydenberg R (2007) Parental effort and reproductive skew in coalitions of brood rearing female common eiders. *Am Nat* 169:73–86. doi:10.1086/510213
- Öst M, Wickman M, Matulionis E, Steele B (2008) Habitat-specific clutch size and cost of incubation in eiders reconsidered. *Oecologia* 158:205–216. doi:10.1007/s00442-008-1139-2
- Öst M, Steele B (2010) Age-specific nest site preference and success in eiders. *Oecologia* 162:59–69. doi:10.1007/s00442-009-1444-4
- Öst M, Lehikoinen A, Jaatinen K, Kilpi M (2011) Causes and consequences of fine-scale breeding dispersal in a female-philopatric species. *Oecologia* 166:327–336. doi:10.1007/s00442-010-1855-2
- Parker H, Holm H (1990) Patterns of nutrient and energy expenditure in female common eider nesting in the high Arctic. *Auk* 107:660–668. doi:10.2307/4087996
- Pálsdóttir AE (2016) Breeding habits of common eider (*Somateria mollissima*) and nest predation in Breiðafjörður, West Iceland. MS thesis, Faculty of Life and Environmental sciences, University of Iceland (In Icelandic with an English abstract)
- Pratte I, Davis SE, Maffei M, Mallory ML (2016) Aggressive neighbors and dense nesting: nest site choice and success in high-Arctic common eiders. *Polar Biol* (in press). doi:10.1007/s00300-015-1884-8
- Robertson GJ (1995) Factors affecting nest site selection and nesting success in the common eider *Somateria mollissima*. *Ibis* 137:109–115. doi:10.1111/j.1474-919X.1995.tb03226.x
- Saino N, Rubolini D, Lehikoinen E, Sokolov LV, Bonisoli-Alquati A, Ambrosini R, Boncoraglio G, Møller AP (2009) Climate change effects on migration phenology may mismatch brood parasitic cuckoos and their hosts. *Biol Lett* 5:539–541. doi:10.1098/rsbl.2009.0312
- Schroeder J, Piersma T, Groen NM, Hooijmeijer JCEW, Kentie R, Lourenc PM, Schekkerman H, Both C (2012) Reproductive timing and investment in relation to spring warming and advancing agricultural schedules. *J Ornithol* 153:327–336. doi:10.1007/s10336-011-0747-5
- Seltnmann M, Öst M, Jaatinen K, Atkinson S, Mashburn K (2012) Stress responsiveness, age and body condition interactively affect flight initiation distance in breeding female eiders. *Anim Behav* 84:889–896. doi:10.1016/j.anbehav.2012.07.012
- Seltnmann M, Jaatinen K, Steele B, Öst M (2014) Boldness and stress responsiveness as drivers of nest-site selection in a ground-nesting bird. *Ethology* 120:77–89. doi:10.1111/eth.12181
- Sénéchal É, Bêty J, Gilchrist HG (2010) Interactions between lay date, clutch size, and postlaying energetic needs in a capital breeder. *Behav Ecol* 22:162–168. doi:10.1093/beheco/arq189
- Sénéchal É, Bêty 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
- Traylor JJ, Alisauskas RT (2006) Effects of intrinsic and extrinsic factors on survival of white-winged scoter (*Melanitta fusca deglandi*) ducklings. *Auk* 123:67–81. doi:10.1642/0004-8038(2006)123[0067:EOIAEF]2.0.CO;2
- Valone TJ (2007) From eavesdropping on performance to copying the behavior of theirs: a review of public information use. *Behav Ecol Sociobiol* 62:1–14. doi:10.1007/s00265-007-0439-6
- Waldeck P, Andersson M (2006) Brood parasitism and nest takeover in common eiders. *Ethology* 112:616–624. doi:10.1111/j.1439-0310.2005.01187.x
- Waldeck P, Hanssen SA, Andersson M (2011) Indeterminate laying and flexible clutch size in a capital breeder, the common eider. *Oecologia* 165:707–712. doi:10.1007/s00442-010-1762-6
- Waltho C, Coulson J (2015) The common eider. T & AD Poyser, London
- Watanuki Y, Ito M, Deguchi T, Minobe S (2009) Climate-forced seasonal mismatch between the hatching of rhinoceros auklets and the availability of anchovy. *Mar Ecol-Prog Ser* 393:259–271. doi:10.3354/meps08264
- Westneat DF, Bókony V, Burke T, Chastel O, Jensen H, Kvalnes T, Lendvai AZ, Liker A, Mock D, Schroeder J, Schwagmeyer PL, Sorci G, Stewart IR (2014) Multiple aspects of plasticity in clutch size vary among populations of a globally distributed songbird. *J Anim Ecol* 83:876–878. doi:10.1111/1365-2656.12191
- Zipkin EF, Gardner B, Gilbert AT, O'Connell AF Jr, Royle JA, Silverman ED (2010) Distribution patterns of wintering sea ducks in relation to the North Atlantic Oscillation and local environmental characteristics. *Oecologia* 163:893–902. doi:10.1007/s00442-010-1622-4
- Zuur AF, Barbraud C, Ieno EN, Weimerskirch H, Smith GM, Walker NJ (2009) Estimating trends for Antarctic birds in relation to climate change. In: Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (eds) Mixed effects models and extensions in ecology with R. Springer-Verlag, New York. doi:10.1007/978-0-387-87458-6