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Research article

Climate change and nest predation affect shifts in timing and duration of breeding as well as reproductive success in a migratory species

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While it is well known that the overall timing of avian breeding in northern latitudes has generally advanced due to climate change, it is still unclear how climate warming has affected the beginning, end, and duration of the breeding period and reproductive success of birds. This is because changes in the phenological breeding metrics have often been studied using ringing data that are based on successful nests only and impacts of local factors such as nest predation have not been analysed simultaneously. This study used both successful and failed nesting attempts to estimate the annual timing and duration of breeding in common goldeneyes *Bucephala clangula*. There was strong evidence that the beginning of breeding has advanced during 1995–2022 but only weak evidence that the end of breeding has advanced. Consequently, the duration of the breeding period lengthened, although statistical evidence for the trend was only weak. The relative importance of climate change and nest predation in affecting the timing and duration of breeding as well as breeding success was also studied. Among-year variation in the beginning of breeding was mainly governed by the timing of ice breakup, an indicator of climate change, whereas nest predation rate in the previous year was the main driver of the end of breeding, the duration of breeding being affected by both the timing of ice breakup and nest predation rate. Annual nest-stage success was best explained by nest predation rate. However, final reproductive success (proportion of nest-left ducklings that survived until independence) decreased with advancing timing of ice breakup, suggesting that climate change has negatively affected the production of independent offspring in the study population. The findings of this study underline the importance of also considering local ecological factors when analysing climate change impacts on phenological breeding metrics and breeding success of birds.

Keywords: Breeding phenology, breeding season length, breeding success, egg laying, precocial species



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Introduction

Climate change has affected breeding of birds in several ways. One widely documented impact is the advancement of the timing of egg laying due to warming springs across the Northern Hemisphere (Crick et al. 1997, Dunn and Winkler 2010, Kluen et al. 2017). It is less clear, however, whether the duration of the breeding period has also changed. For example, a meta-analysis of 65 long-term studies of 54 species found that single-brooded species have generally shortened the season, whereas multi-brooded species have lengthened it (Halupka and Halupka 2017). Moreover, while shifts in the overall timing of avian breeding have now been widely documented (Romano et al. 2023), we still have limited understanding of how climate change affects reproductive output of bird populations (Halupka et al. 2021, 2023), this being a critical gap in the information needed to understand recent and predict future population changes. It has been found for some multi-brooded species that the frequency of second broods may increase due to lengthening of the breeding season, resulting in increased reproductive output, but impacts of climate change on breeding success of single-brooded species is less clear (Halupka et al. 2021, 2023). One reason for this uncertainty is that climate change may influence avian offspring production through complex interactions with other processes that affect reproductive success, such as nest predation, but these processes typically have not been studied simultaneously with climate change impacts (Halupka et al. 2023).

Nest predation has long been recognized as a major source of nest failure and nestling mortality in birds (Ricklefs 1969). For example, a global comparison of studies from five continents showed that the proportion of failed nesting attempts in birds ranged from approximately 50% to 75%, most (approximately 65% to 95%) of the nest failures being due to predators (Remeš et al. 2012). In addition, nest predation rates have been found to vary seasonally, with both decreasing and increasing nest predation rates from the start of the breeding season towards the end (Klett and Johnson 1982, Roos 2002, Roy Nielsen et al. 2006, Decker et al. 2012). Ignoring possible effects of nest predation and its seasonal variation on avian breeding may not only complicate interpretations of climate change impacts on breeding success, but also confound analyses focusing on finding changes in the timing and duration of the breeding period. For example, a recent analysis based on extensive ringing data of birds from Finland showed that, on average, bird species have contracted their breeding period over the last few decades (Hällfors et al. 2020). The observed contraction was mainly due to a faster advance of the end compared with the beginning of the breeding period. The analysis by Hällfors et al. (2020) used the timing of ringing of nestlings in a nest of a species as an indicator for breeding time, i.e. only successful nests were included. However, omitting failed nesting attempts may bias measures of breeding time and confound patterns interpreted to be caused by climate change.

The multi-species analysis by Hällfors et al. (2020) on the timing and duration of breeding in birds included common goldeneye *Bucephala clangula* (hereafter goldeneye), a hole-nesting single-brooded migratory species. The authors found for goldeneyes that both the beginning and end of breeding has advanced, and the duration of the breeding period contracted during about three decades (data for goldeneye covered the period of 1985–2017 in Hällfors et al. 2020). The contraction in goldeneyes was because the end of the breeding had advanced more (approximately 0.7 days/year) than the beginning (approximately 0.3 days/year) (Fig. 4 in Hällfors et al. 2020). However, as pointed out above, the analysis was based on data from successful nests only, being thus open for biases. In general, nest predation may affect differently the beginning and end of the breeding period in birds. Considering its within-season effects, high nest predation rate early in egg laying or incubation increases the number of re-nesting attempts, affecting both the timing and duration of breeding in a population. Re-nesting after a failed attempt is frequent in many bird species (Arnold et al. 2010, Becker and Zhang 2010, Gates et al. 2013). If only successful nesting attempts are analysed (i.e. early failed nests not included), we may find that, at the population level, the beginning of breeding is later and the duration of breeding shorter than they actually are. In addition, nest predation rate may both increase (Nielsen et al. 2006, Öberg et al. 2014) and decrease (Roos 2002, Decker et al. 2012) with the progress of breeding, causing noise and unpredictable biases in the analyses of the timing and duration of breeding if only data from successful nests are used.

Impacts of climate change on breeding success of goldeneyes have also been studied earlier, specifically in terms of duckling production (number of ducklings that leave the nest) as well as production of broods and female recruits, and no effects of climate change on these measures have been detected (Clark et al. 2014, Pöysä 2019, Halupka et al. 2023). However, a critical gap in our understanding of climate change impacts is how they may realize during the relatively long brood rearing period of goldeneyes and other precocial species, probably affecting production of independent offspring. Goldeneye ducklings leave the nest within 24–36 hours of hatching, and the female attends the brood for several weeks but deserts it before fledging (Pöysä 1992, Eadie et al. 1995, Pöysä et al. 1997a). Newly hatched nidifugous young are vulnerable to unfavourable weather conditions and other mortality factors, mortality of young being highest during the first week of life after the young have left the nest (Savard et al. 1991, Paasivaara and Pöysä 2007).

Here, I used data of both successful and failed nesting attempts and studied shifts in the timing and duration of breeding, and associated changes in breeding success, in goldeneyes in relation to climate change-induced shifts in spring phenology and among-year variation in nest predation rate. Goldeneye is an early migrating and early nesting species in the European boreal areas, being fully dependent on open water for feeding and other activities including breeding.

Therefore, the timing of ice breakup in breeding lakes is fundamentally important for the timing of the breeding season. Ice breakup has become earlier in lakes across the Northern Hemisphere due to climate warming (Sharma et al. 2016, Hewitt et al. 2018, Lopez et al. 2019), the timing of ice breakup being strongly governed by spring air temperature (Korhonen 1996, Jylhä et al. 2014, Lopez et al. 2019, Pöysä 2022). Therefore, the timing of ice breakup provides a useful natural integrator of spring phenology and an effective indicator of climate change (Bradley et al. 1999, Adrian et al. 2009). Settling dynamics and start of egg laying of goldeneyes track among-year variation in spring temperature and timing of ice breakup, and breeding of goldeneyes has generally advanced as a response to the shift in spring phenology (earlier ice breakup) (Clark et al. 2014, Pöysä 2019, 2022, Messmer et al. 2021). Hence, goldeneyes breeding in boreal lakes provide an excellent model system to tackle climate change impacts on avian breeding performance.

In goldeneyes, and probably other species with similar nesting tactics, nest predation may also have impacts on the timing of breeding between consecutive seasons, the effect arising through the processes of nest site selection. Females that have bred successfully in a given nest site typically return to the same site the next year and are the first to start egg laying (Dow and Fredga 1983, 1984). Hence, there will be a segment of early breeding females (and nests) in the population every year, and therefore the beginning of the breeding period may more easily track changes in spring phenology rather than be affected by variation in nest predation rate. Unsuccessful females, on the other hand, change nest site and start egg laying later in the year after an unsuccessful nesting attempt (Dow and Fredga 1983, 1984). Hence, because nest predation in the previous year affects nest site use and selection differently in successful and unsuccessful females, we can make the following prediction: at the population level, high nest predation rate in year $t-1$ may not affect the beginning of the breeding period (successful females use the same site and start egg laying early anyway) but can delay the end of breeding (unsuccessful females select a new site and start egg laying later) and, consequently, lengthen the duration of the breeding period in year t . As a corollary prediction, the beginning of breeding should be more strongly governed by spring phenology than by measures of nest predation.

This study had three main aims. First, I studied if results and conclusions concerning long-term changes in the three phenological metrics (i.e. beginning, end, and duration of the breeding period) in goldeneyes differ from those of Hällfors et al. (2020) when both successful and failed nesting attempts are included in the analysis. Second, I studied the relative importance of climate change and nest predation in affecting the timing (beginning and end) and duration of the breeding period in goldeneyes. Specifically, I tested the prediction that the beginning of breeding is more strongly governed by variation in spring phenology, whereas the end of breeding is more strongly affected by nest predation rate, especially in the previous year. Finally, I studied the roles of climate change and nest predation in affecting nest-stage

success and final reproductive success (production of independent offspring) of goldeneyes.

Material and methods

Study area

The study area in southeastern Finland (61°35N, 29°40E) is approximately 59 km² and dominated by pine *Pinus sylvestris* or mixed (pine, birch *Betula* spp. and spruce *Picea abies*) forests interspersed with lakes of varying size and luxuriant, emergent vegetation. The 37 study lakes (mean size 3.5 ha, range 0.05–24.0 ha) are covered by ice during winter and have a relatively stable water level in summer. There has been a varying number of nest boxes available for goldeneyes in the study area, and nesting attempts and success in the boxes have been recorded annually since 1992. There were 14 old nest boxes available before 1992. In 1992–1994, new nest boxes were erected in three phases, making together 64 nest boxes on 30 lakes from 1994 onwards (Pöysä 1999, Pöysä and Pöysä 2002). In 2008, 30 additional nest boxes were made available after an experimental study of conspecific brood parasitism (Pöysä and Paasivaara 2016), resulting in a total of 94 nest boxes on the 30 lakes from 2008 onwards. The extent of the study area has remained unchanged since 1994. Some nest boxes were lost due to forestry activities during the study period, but since the nest box addition in 1992–1994, there has been no nest site limitation that could have affected breeding parameters; the proportion of unoccupied nest boxes has been high (range from 48% to 78% per year) throughout the 1995–2022 study period used here for recording the timing of breeding and breeding success (Pöysä 2024: Supporting information). There are some natural cavities in the study area, such as cavities excavated by black woodpeckers *Dryocopus martius*. However, the number of females currently nesting in those cavities is probably small, because an earlier nest box addition experiment in the study area suggested that females may switch from nesting in natural cavities to using nest boxes (Pöysä and Pöysä 2002).

The main predator of goldeneye clutches in the present study area and in European boreal areas in general is the pine marten *Martes martes* (Dow and Fredga 1983, Pöysä et al. 1997b, Sonerud et al. 2023), a long-lived forest-dwelling mustelid species having a fixed home range (Zalewski and Jędrzejewski 2006; see also Pöysä and Paasivaara 2016, Pöysä 2024). Pine martens may occasionally also kill the incubating female (Sonerud et al. 2023, H. Pöysä unpubl.).

Ice-out data

As the timing of ice breakup (hereafter, IOD = ice-out date) has been found to be a sensitive and useful phenological indicator of climate change impacts in northern lake ecosystems and to affect breeding performance of goldeneyes (Introduction), it was used as a general measure of climate change in the analyses. Annual IOD data are from Pöysä (2024), in which

all the methodological details concerning field work and data processing are explained (Pöysä 2019, 2022). In brief, a waterbird survey was made on each lake four times in April–May at an interval of approximately seven days (mean survey interval = 7.0 d, SE = 0.1) each year from 1991 to 2022 (data from 1995–2022 used here). During each of the four waterbird surveys, the progress of the breakup of ice cover on each lake was marked on a field map and later scored as follows (open water score): 0 = lake fully ice-covered, 1 = small openings along shoreline, central parts fully ice-covered, 2 = half of the shoreline open, central parts fully ice-covered, 3 = more than half of the shoreline open, central parts partially (< 50%) open, 4 = shoreline fully open, small ice rafts or buildups here and there, 5 = lake fully open. An annual IOD for each lake was estimated as the mean of the dates of two consecutive surveys when the open water scores were 4 and 5; if the lake was already free of ice (score 5) during the first visit, the IOD was estimated as the date of the first survey minus 3.5 days (i.e. the mean difference in days between two consecutive surveys divided by 2). The annual mean IOD (used in the analyses) was calculated as the mean of the lake-specific IOD values. The annual mean IOD in the study area is strongly correlated with mean April temperature (Pöysä 2022).

Breeding and nest predation data

All nest boxes were checked frequently from about mid-April through early June in each year for nesting attempts (at least one egg laid) and to determine the fate of the nesting attempts (annual timing of the first five nest checks and annual numbers of nesting attempts are given in Supporting information). The first check in a year was usually done well before the breakup of ice cover in the lakes and the start of egg laying in the population (Supporting information). Nesting attempts were typically found early in egg laying. The date on which the first egg was laid in a nest (start of egg laying) was determined by back-dating, using the criterion that it takes 1.32 days for a female to lay one egg (Fredga and Dow 1983). Goldeneye females typically lay one egg every other day (Eadie et al. 1995), meaning that it typically takes 1.5 days for a female to lay one egg. However, even though the difference is negligible, the use of 1.32 days (instead of 1.5 days) as a criterion in back dating is probably more appropriate as it better adjusts the estimate of the start of egg laying for possible parasitic eggs. A nesting attempt was deemed successful (at least one duckling departed the nest box), deserted (clutch deserted during egg laying or incubation), or depredated (clutch depredated during egg laying or incubation). In the case of depredated nests, either all eggs were taken (this usually was the case) or at least one egg disappeared, and the nest was deserted, i.e. if a clutch was deserted due to partial clutch predation, all the eggs were deemed failed due to predation (Pöysä 1999, 2006, 2024). A nest that was deserted during the egg laying was followed for 30 days (i.e. incubation plus 1–1.5 days that it takes before the ducklings leave the nest) or until it was depredated, starting from the day after which no new eggs were found in the nest, to determine the final fate

(depredated or not). All nesting attempts were used to calculate annual timing of breeding and nest predation rate (nest predation rates are same as used in Pöysä 2024).

To make the comparisons between the results of this study and those of Hällfors et al. (2020) easier, I used the same three phenological metrics as used by Hällfors et al. (2020) to measure the timing and duration of the breeding period in a given year: the 5th (beginning of breeding) and 95th (end of breeding) percentiles of the annual start-of-laying distribution, as well as the difference between the upper and lower quantiles (duration of the breeding period).

Data for nest-stage success and final reproductive success

The total number of eggs laid in the nests (eggs from all nesting attempts included) and the total number of ducklings that left the nests were used to calculate annual nest-stage success (nest-stage success = the proportion of eggs that produced an offspring that left the nest). The annual numbers of independent offspring were estimated using data from brood surveys made on each of the study lakes each year three times between mid-June and late July/early August (Pöysä 2019, Pöysä and Paasivaara 2021 for details) and additional visits to the lakes where goldeneye broods were observed during the three regular brood surveys (Pöysä and Pöysä 2002). All the brood surveys and additional visits to brood-rearing lakes were done in each year by the same person (HP). A principally similar approach (brood surveys) has been used in several earlier studies for estimating reproductive output and success of ducks for study areas encompassing several small lakes and ponds (Nudds and Cole 1991, Fournier and Hines 1998, Elmberg et al. 2003, Arzel et al. 2014). While females often move broods from a nesting lake to a rearing lake and may change the rearing lake several times during the first 1–2 weeks after leaving the nest (Wayland and McNicol 1994, Paasivaara and Pöysä 2008), older young typically stay at the rearing lake until fledging. Rearing lakes were visited frequently to keep track of the age, growth and development of goldeneye young and to identify possible fledged juveniles that arrived at the rearing lakes from outside the study area (these were not included when estimating local production of independent offspring). The age class of goldeneye young is easy to define in the field according to the development stage of the plumage; seven age classes, each approximately 7.5 d (i.e. age classes Ia–c, IIa–c, III in Pirkola and Högmander 1974). Juvenile plumage is complete by approximately 50–55 d, and juveniles typically can fly at the age of 60–65 d (Eadie et al. 1995, H. Pöysä unpubl.). Goldeneye females always abandon the young before they can fly (Pöysä 1992, Pöysä et al. 1997a, H. Pöysä unpubl.). Mortality of goldeneye ducklings is highest during the first week of life and starts to level off at the age of two to three weeks (Savard et al. 1991, Eadie et al. 1995, Paasivaara and Pöysä 2007). For example, using data from radio-marked females and their broods, Paasivaara and Pöysä (2007) calculated, on a per-brood basis, the daily survival rate of ducklings for every seven-day period

from nest exodus until the ducklings were all dead or had fledged. The authors found that the daily survival rate of ducklings was only 0.80 during the first week after hatching, increased to approximately 0.97 at the age of 15–22 days and was approximately 1.0 at the age of 42–49 days and older. Hence, the total number of young that reached the age class IIc/III (approximately 45 days old) was used to estimate the production of independent offspring in the study area each year during 1995–2020 (Pöysä and Pöysä 2002). Final population level reproductive success was calculated as the proportion of nest-left ducklings that survived until independence. Because ducklings were not marked, it was not possible to recognize ducklings that possibly had arrived at the study ponds from outside the study area. However, I consider such movements negligible, except in one case. In one year (1996), the estimated number of independent offspring was higher than the number of nest-left young, probably because a beaver-flooded lake at the northeastern edge (close to the border between Finland and Russia) of the study area attracted broods from lakes outside the study area (Pöysä and Pöysä 2002). To ensure that the beaver-flooded lake did not confound the results and conclusions concerning final reproductive success, I conducted a separate analysis using data from which the observations (annual numbers of nest-left ducklings and independent offspring) of the beaver-flooded lake were excluded, changing the final reproductive success values as follows: beaver-flooded lake included: mean = 0.285, SD = 0.273, range 0–1.269; beaver-flooded lake excluded: mean = 0.245, SD = 0.209, range 0–0.808. The results did not differ qualitatively between models including data versus those excluding data from the beaver-flooded lake (results based on the data from which the observations from the beaver-flooded lake are excluded are given in Supporting information); hence, results from the analysis in which all data are included are reported in the results. Other cases in which the study lakes attracted broods from outside the study area were not observed and, in general, possible movements of broods into or out of the study area were assumed to be compensatory. All in all, considering the trends and patterns found in final reproductive success (Results), it is unlikely that such movements, while possibly adding noise into the data, could have caused influential biases in the data. The data for the two breeding success measures (nest-stage success and final reproductive success) are from 1995–2020 only, because complete brood surveys were not done on all lakes in 2021 and 2022.

Statistical analyses

All statistical analyses were done at the population level using annual values (annual averages or proportions during 1994–2022 as specified below) as sample units in the analyses. I used Sen's (1968) estimate of regression coefficient based on Kendall's rank correlation (i.e. Sen slope) to calculate trends (days/28 years) in the three phenological metrics (beginning, end, and duration of the breeding period) during 1995–2022 and Mann–Kendall test to assess statistical significance of the trends (two-tailed trend test). Sen slope

is a robust and frequently used non-parametric alternative to estimate and study trends in various environmental time series data (Libiseller and Grimvall 2002, Benson et al. 2012, Gocic and Trajkovic 2013). I used general linear models to study effects of IOD, nest predation rate in the previous year (predation rate in year $t-1$; data from 1994 to 2021) and nest predation rate in the current year (predation rate in year t ; data from 1995 to 2022) on among-year variation in the three phenological metrics during 1995–2022 and to study effects of IOD and nest predation rate (year t) on annual nest-stage success and final annual reproductive success in 1995–2020. The explanatory variables were standardized (mean = 0, SD = 1) to facilitate the comparison of their effects on the response variables for models with multiple predictors (Schielzeth 2010). A model diagnostic was done to ensure that the underlying assumptions of the general linear model were met (Zuur et al. 2010). Multicollinearity was checked and found not to be a problem as variance inflation factor (VIF) was < 1.215 for the explanatory variables in all models (VIF = $1/\text{tolerance}$; tolerance values are given in the connection of each model). Even though the VIFs indicated absence of multicollinearity among the explanatory variables and the number of explanatory variables in the models was small, I used an all-possible-models approach to make sure that spurious effects or masking effect of potential suppressor variables did not confound interpretations based on the full models including all explanatory variables (Mac Nally 2000). Specifically, I fitted in each case all possible models (combinations of explanatory variables) to the data and used the regression coefficients of the models and hierarchical partitioning to assess the independent effect of each explanatory variable (Mac Nally 2000, Murray and Conner 2009; see the latter reference for the technique and equation to calculate independent effects). Assumptions of homoscedasticity and normality of model residuals were checked graphically by plotting residuals versus fitted values and theoretical quantiles, respectively; both assumptions were found to be met. Influential data points (outliers) were screened, and one suspect case was found for the nest-stage success model (Cook's distance = 0.521) and the final reproductive success model (Cook's distance = 0.769). Removing the outlier cases did not change the model outcomes qualitatively; hence, the nest-stage success and final reproductive success models ran on complete data were retained. Concerning all models, if both the response and explanatory variables showed a temporal trend (correlation with year), alternative models were run by including year as an additional explanatory variable to ensure that the common trend in the time series did not confound the effect of the explanatory variables in focus (Freckleton 2002, Lindström and Forchhammer 2010, Iler et al. 2017). All other response variables, except nest-stage success, showed some correlation with year (beginning of breeding: $r = -0.584$, $p = 0.001$, $n = 28$; end of breeding: $r = -0.328$, $p = 0.089$, $n = 28$; duration of breeding: $r = 0.390$, $p = 0.043$, $n = 28$; nest-stage success: $r = -0.060$, $p = 0.772$, $n = 26$; final reproductive success, including beaver-flooded lake: $r = -0.703$, $p < 0.001$, $n = 26$; final reproductive

success, excluding beaver-flooded lake: $r = -0.675$, $p < 0.001$, $n = 26$). However, inclusion of year in the models as an additional explanatory variable did not change the results qualitatively (models including year as an additional explanatory variable are presented in Supporting information), indicating that possible associations between a response variable and the explanatory variables in focus are not confounded with common trends. Hence, results from models that did not include year are reported in the results. Pairwise associations were tested using Pearson parametric correlation. When reporting p -values, I used the evidence-based language and terminology recommended by Muff et al. (2022) as an alternative to the traditional null-hypothesis significance testing with a fixed cutoff value of p (Wasserstein et al. 2019). All statistical analyses were performed in SYSTAT 13.

Results

Long-term trends in breeding phenology

There was strong evidence for the advancement of the beginning of the breeding period during 1995–2022 (13.1 days; Sen's slope = -0.467 , 95% CL, lower -0.744 , upper -0.185 ; $Z = -2.847$, $p = 0.004$), but only weak evidence for the advancement of the end of the breeding period (5.2 days; Sen's slope = -0.185 , 95% CL, lower -0.457 , upper 0.060 , $Z = -1.699$, $p = 0.089$) (Fig. 1a, b). Consequently, duration of the breeding period showed an increasing trend during 1995–2022, although evidence for the trend was only weak (Sen's slope = 0.301 , 95% CL, lower -0.014 , upper 0.654 ; $Z = 1.877$, $p = 0.061$) (Fig. 1c).

Explaining among-year variation in breeding phenology

The three phenological breeding metrics varied considerably between years (Fig. 1). Among-year variation in the beginning of breeding was explained by IOD and nest predation rate in year t , IOD having the strongest evidence and highest explanatory power; the beginning of breeding advanced with advancing IOD (Table 1). Among-year variation in the end of breeding, in turn, was best explained by nest predation rate in year $t-1$, IOD and nest predation rate in year t having only negligible explanatory power (Table 1); the higher the nest predation rate in the previous year, the later the end of breeding. While IOD, nest predation rate in year t and nest predation rate in year $t-1$ all seemed to affect the duration of breeding, the first mentioned variable had the highest explanatory power (Table 1). In general, the earlier the IOD and the higher the nest predation rate, the longer the duration of breeding.

Effects of climate change and nest predation on nest-stage success and final reproductive success

The total number of eggs laid annually varied from 100 to 347 (mean = 227.4, SD = 64.6), that of nest-left ducklings from 26 to 216 (mean = 91.8, SD = 44.7), and that of independent offspring from 0 to 56 (mean = 21.1, SD = 14.4). Nest-stage success (the proportion of eggs that produced an offspring that left the nest) decreased with increasing nest predation rate but there was little evidence for it being affected by IOD (Table 2, Fig. 2a). There was strong evidence that final reproductive success (the proportion of nest-left

Table 1. Models to explain among-year variation in the start, end, and duration of breeding. IOD = ice-out date (higher IOD values in the data mean later spring). Tolerance is 1 minus the squared multiple correlation between the explanatory variable and the other explanatory variables in the model. Independent effect of each explanatory variable represents the average contribution of the variable to the variance in the response variable over all possible models (see statistical analyses for further details).

Explanatory variable	β	SD	Tolerance	t	P	Independent effect	
						Value	Weight
Start of breeding							
Intercept	-11.386	1.006		-11.321	0.000		
IOD	4.668	1.041	0.969	4.486	0.000	0.409	0.799
Nest predation rate in year t	-2.574	1.115	0.843	-2.308	0.030	0.094	0.184
Nest predation rate in year $t-1$	0.607	1.128	0.824	0.538	0.595	0.009	0.017
Overall model: $r^2 = 0.512$, $F_{3,24} = 8.382$, $p = 0.001$							
End of breeding							
Intercept	18.416	0.948		19.428	0.000		
IOD	0.805	0.981	0.969	0.821	0.420	0.035	0.137
Nest predation rate in year t	-0.252	1.051	0.843	-0.240	0.812	0.012	0.047
Nest predation rate in year $t-1$	2.609	1.063	0.824	2.453	0.022	0.209	0.816
Overall model: $r^2 = 0.256$, $F_{3,24} = 2.754$, $p = 0.065$							
Duration of breeding							
Intercept	29.802	0.756		39.413	0.000		
IOD	-3.863	0.782	0.969	-4.937	0.000	0.262	0.504
Nest predation rate in year t	2.322	0.838	0.843	2.769	0.011	0.108	0.208
Nest predation rate in year $t-1$	2.002	0.848	0.824	2.360	0.027	0.150	0.288
Overall model: $r^2 = 0.624$, $F_{3,24} = 13.298$, $p < 0.001$							

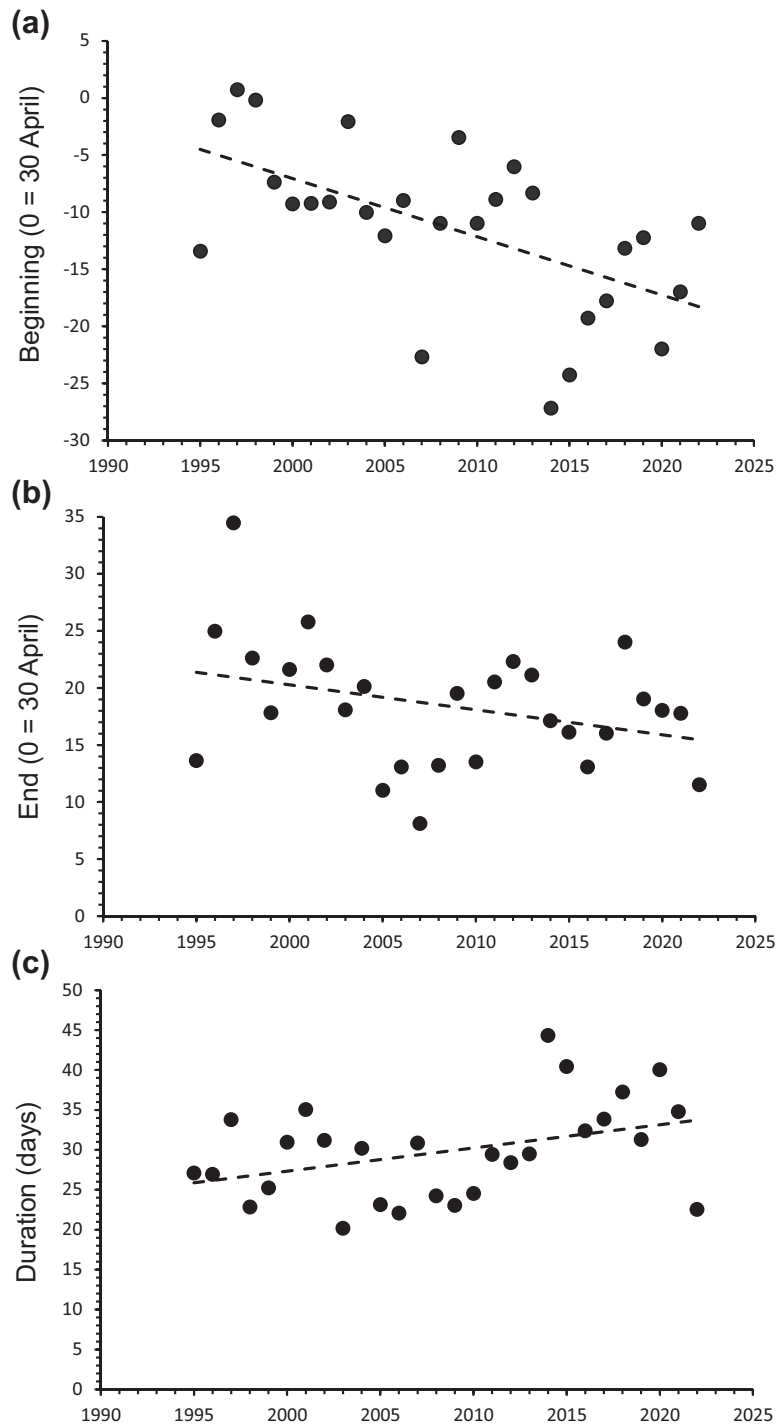


Figure 1. Trends in the beginning (a), end (b), and duration (c) of the breeding period in goldeneyes. Trend lines, showing a regression through raw data points, are given only for illustrative purposes (see the main text for tests of statistical evidence for the trends based on Sen's slope).

ducklings that survived until independence) decreased with earlier IOD (Table 2, Fig. 2b). It is also worth noting that final reproductive success decreased during the study period of 1995–2020 independently of variation in IOD (Supplementary information).

Discussion

This study found that, while there was strong evidence that the beginning of the breeding period advanced in goldeneyes during 1995–2022, evidence for the advancement of end of

Table 2. Models to explain among-year variation in nest-stage success (the proportion of eggs that produced an offspring that left the nest) and final reproductive success (the proportion of nest-left ducklings that survived until independence). IOD = ice-out date (higher IOD values in the data mean later spring). Tolerance is 1 minus the squared multiple correlation between the explanatory variable and the other explanatory variables in the model. Independent effect of each explanatory variable represents the average contribution of the variable to the variance in the response variable over all possible models (see statistical analyses for further details).

Explanatory variable	β	SD	Tolerance	t	p	Independent effect	
						Value	Weight
Nest-stage success							
Intercept	0.303	0.018		22.985	0.000		
IOD	0.006	0.018	0.992	0.320	0.752	0.001	0.002
Nest predation rate in year t	-0.107	0.018	0.992	-6.047	0.000	0.613	0.998
Overall model: $r^2=0.614$, $F_{2,23}=18.310$, $p=0.000$							
Final reproductive success							
Intercept	0.287	0.045		6.343	0.000		
IOD	0.151	0.045		3.334	0.003		
Overall model: $r^2=0.317$, $F_{1,24}=11.117$, $p=0.003$							

the breeding period was only weak. These shifts resulted in lengthening of the breeding period, although evidence for this change was only weak. Furthermore, among-year variation in the beginning of breeding was best explained by the timing of ice breakup (IOD, an indicator of climate change), whereas among-year variation in the end of breeding was best explained by nest predation rate in the previous year, these findings being in line with the predictions. This study revealed further that annual nest-stage success (proportion of eggs that produced an offspring that left the nest) decreased with increasing annual nest predation rate but was not associated with IOD, whereas final reproductive success (proportion of nest-left ducklings that survived until independence) decreased with advanced IOD.

Nest predation should also be considered when analysing changes in avian breeding phenology

Even though evidence for the shifts in the end and duration of the breeding period was only weak in this study, the patterns in the shifts were opposite to the findings of Hällfors et al. (2020) who reported that the end of breeding has advanced more than the beginning and, consequently, the duration of breeding has contracted. The differences between the findings of this study and those of Hällfors et al. (2020) could be due to the difference in the nature of the data. While both successful and failed nesting attempts were included in this study to estimate the timing and duration of breeding, the analysis by Hällfors et al. (2020) was based only on data from successful nests, the phenological metrics of breeding being measured by the day when nestlings were ringed. While Hällfors et al. (2020) did not explicitly consider the bias towards successful nests, they referred to another study that addressed the issue and concluded that ringing data provide a reliable source of information on breeding time (Eeva et al. 2012). However, the study by Eeva et al. (2012) considered the overall timing of breeding (first egg laying day estimated on the basis of ringing day of nestlings; Eeva et al. 2012) in one species, the crested tit *Lophophanes cristatus*, but did not assess the suitability of ringing data to analyse separately the beginning, end, and duration of breeding. Analyses based only on

successful nests may produce distorted results if all the three phenological breeding metrics are in focus. In goldeneyes, females that have lost the eggs to predators early in the egg laying phase may lay a replacement clutch or, alternatively,

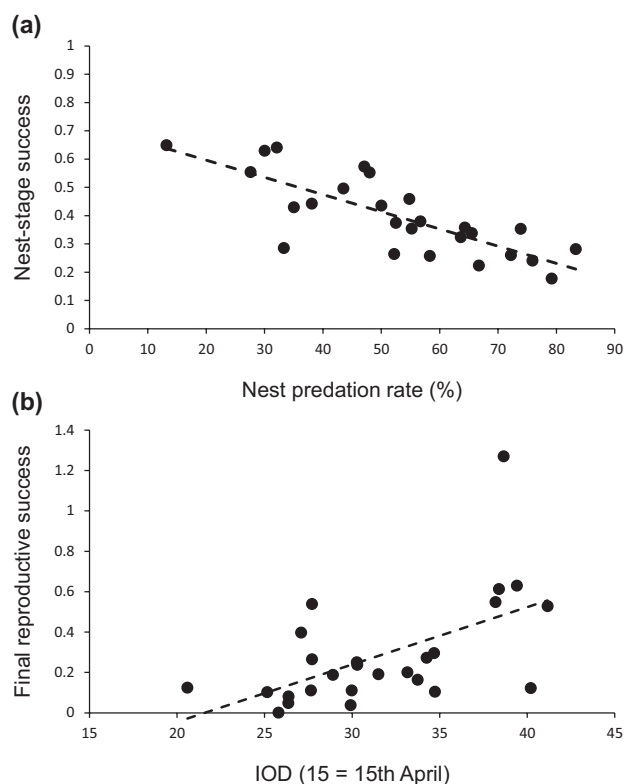


Figure 2. Nest-stage success (proportion of eggs that produced an offspring that left the nest) in relation to nest predation rate (a) and final reproductive success (proportion of nest-left ducklings that survived until independence) in relation to the timing of ice breakup (ice-out date, IOD; higher IOD values in the data mean later spring) (b) in goldeneyes. Trend lines, showing a regression through raw data points, are given only for illustrative purposes (see Table 2 for test statistics). Note that exclusion of data from a beaver-flooded lake that resulted in an unrealistically high reproductive success value at the population level (1.269) in panel (b) did not change the result qualitatively (see material and methods for further information).

lay the rest of the eggs parasitically in nests of other females, the option of parasitic laying being often adopted also by females of other species with conspecific brood parasitism (Stouffer and Power 1991, McRae 1997, 2024). Hence, lack of information on the first, unsuccessful nesting attempt, and the delayed start of egg laying of the replacement clutch (included in the data of successful nests), will shift both the beginning and the end of breeding later. Whether the duration of the breeding period will be affected depends on which one, beginning or end, shifts more. Contraction of the breeding period could also be caused by increased failure of late nesting attempts that have been found to have higher predation rates in some species (Nielsen et al. 2006, Öberg et al. 2014). Similarly, Clark et al. (2014) found for goldeneyes that egg laying had started earlier in successful nests than in nests deserted during incubation. In general, if nest predation rate, or nest failures due to other reasons than predation, change directionally across years, findings of trends in the timing and duration of breeding based on ringing data may not demonstrate response of birds to climate change but response to changes in nest failure.

It is unclear if the potential biases specified above have affected the goldeneye and other species-specific results reported by Hällfors et al. (2020). While climate change-related increasing nest predation rates have been reported for some species (Kubelka et al. 2018; see also Bulla et al. 2019, Kubelka et al. 2019), no such changes have been found for goldeneyes in this study area (Pöysä 2024). Moreover, neither the beginning nor the end of breeding was associated with nest predation rate in the same season in this study, suggesting that the absence of depredated nests from the analysis of Hällfors et al. (2020) may not explain the differences in the results between this study and Hällfors et al. (2020). Explanations for the finding that nest depredation did not affect the end of the breeding season within the same year include: 1) nest depredation may have occurred mainly during the incubation stage, after which renesting is not feasible, and 2) females that faced nest depredation during the egg-laying stage shifted to parasitic laying instead of renesting (see also above). However, as found in this study, impacts of nest predation on the timing and duration of breeding may also realize with a time lag, i.e. between successive seasons. As predicted, high nest predation rate in the previous year delayed the end of breeding. Two nest predation-associated and probably interrelated processes can explain this effect. First, while females that have bred successfully in a given nest site typically return to the same site the next year and are the first to start egg laying, unsuccessful females change nest site between years and start egg laying later in the new nest site (Dow and Fredga 1983, 1984). This difference in nest site selection will especially affect the end of breeding, hence also the duration of breeding (see Introduction). Second, high nest predation rate in year $t-1$ increases the rate of parasitic laying (i.e. conspecific brood parasitism, Eadie et al. 1988, Lyon and Eadie 2008) in year t in goldeneyes (Pöysä 2024). In particular, females that have lost their nest to predation in the previous year may engage in parasitic laying in the

current year (discussion in Pöysä 2024). Parasitically laying females that also have their own nest typically first lay some parasitic eggs before initiating their own clutch (Åhlund and Andersson 2001, Andersson and Åhlund 2012), delaying the beginning of their own breeding, hence affecting the end of breeding at the population level.

The ringing data used by Hällfors et al. (2020) were gathered by ringers anywhere in southern and central Finland, meaning that the effect of potentially influential local factors, such as nest predation addressed in this study, were mingled in the data. Indeed, Milonoff et al. (1998) found significant differences in basic breeding parameters among seven goldeneye study populations in southern and central Finland. More than 50% of the goldeneye ringing data analysed by Hällfors et al. (2020) are from one intensively studied goldeneye population, Maaninka, in central Finland (Milonoff et al. 1998, Saurola et al. 2013). In the Maaninka study area, nest predation is exceptionally low; for example, the overall nest predation rate in 1999–2005 was estimated at 6% in Paasivaara et al. (2010). On the other hand, the proportion of deserted nests (similarly not included in the data analysed by Hällfors et al. 2020) was relatively high, and the total proportion of unsuccessful nests (depredated or deserted) was considerable, ranging from 17% to 35% (mean 25%) in 1999–2005 (Paasivaara et al. 2010).

Whatever are the reasons for the differences between the findings of this study and Hällfors et al. (2020), the contradicting results for goldeneyes underline the importance of assessing possible biases in the data if changes in phenological breeding metrics of birds are analysed using successful nests only. Particularly, impacts of nest predation on those metrics should be considered simultaneously. One could argue that the relatively high nest predation rate in the current study area has influenced the breeding phenology and reproductive tactics of goldeneyes in an atypical way, causing the trend patterns of the phenological breeding metrics to differ from those reported by Hällfors et al. (2020). This is unlikely, however, since the annual nest predation rates in the study population compare well with those found in two other goldeneye populations in Finland (Pöysä et al. 2016: Figure 2) and globally in other species (Remeš et al. 2012), and conspecific brood parasitism has also been found to be frequent in other goldeneye populations (Eadie and Savard 2015). Hence, the findings of this study concerning the impacts of nest predation are based on representative data and provide novel insights on the dynamics of avian breeding phenology under changing environmental conditions.

Impacts of climate change and nest predation on breeding success

The result that nest-stage success was not associated with IOD is in line with an earlier finding for goldeneyes that temperature during the period from pre-laying (March) until incubation (May–June) does not affect the number of young (hatched ducklings) per nesting attempt (Halupka et al. 2023; goldeneye-specific results not shown in the original

article). Similarly, that nest-stage success was governed by nest predation is an expected result and in line with earlier findings for the species (Pöysä 2024). By contrast, that the final reproductive success was associated with IOD is a novel finding and suggests that climate change has affected negatively the production of independent offspring in this goldeneye population. Asynchronous warming of spring weather could be one explanation for the observed association, i.e. temperature in early spring may have increased more than in late spring or early summer, as has been found in a study of climate change impacts on population demography and dynamics of precocial black grouse *Tetrao tetrix* in Finland (Ludwig et al. 2006). If March–April temperatures have increased, resulting in earlier start of breeding by goldeneyes, but May–June temperatures have not, the start of breeding may have been too early in relation to the weather conditions prevailing when young hatch and leave the nest. Cold hardness of newly hatched goldeneye young is relatively high (Koskimies and Lahti 1964), and typical variation in temperature has not been found to affect duckling mortality (Paasivaara and Pöysä 2007). Nevertheless, atypical cold weather faced by newly hatched ducklings in years of exceptionally early breeding seasons could increase mortality, especially if coupled with rainy and windy weather (Schmidt et al. 2006). It is also possible that warming of spring temperatures has made the maintenance of optimal incubation temperature challenging, which may have affected the quality of hatchlings (Hepp and Kennamer 2012, Durant et al. 2013a, Andreasson et al. 2020). It has been found in another precocial hole-nesting duck, the wood duck *Aix sponsa*, that variation in incubation temperature affects variation in body size and growth of newly hatched young (Hepp and Kennamer 2012, Durant et al. 2013b, Hope et al. 2020), these being traits associated with survival probability of wood duck young (Hepp and Kennamer 2012). All in all, while our understanding of impacts of climate warming on parental behaviour and nestling growth and success of altricial bird species has increased in recent years (Andreasson et al. 2020), we know little of climate change impacts on breeding performance and reproductive success of precocial species. Results of this study emphasize the need to study such impacts in precocial species, especially possible differences between nest and brood stage in vulnerability to impacts of extreme and asynchronously changing spring and early summer temperatures.

Final reproductive success declined over the study period independently of changes in IOD, suggesting that other long-term environmental changes than climate change may also have affected reproductive success. As discussed in the context of another study (Pöysä and Paasivaara 2021; see also Pöysä 2022), eutrophication and brownification (increase in water colour due to increasing dissolved organic carbon and iron concentrations), both being processes that affect water quality and aquatic food webs (Creed et al. 2018, Kritzberg et al. 2020, Shuvo et al. 2021), probably have occurred in at least some of the lakes in the study area. While impacts of eutrophication on goldeneye populations are unclear (Pöysä et al. 2023, Holopainen et al. 2024), brownification probably affects

goldeneye young negatively. Browning of freshwaters across the Northern Hemisphere is a process that has negatively affected aquatic invertebrates (Arzel et al. 2020, Turunen and Aroviita 2024), an important food resource of waterbirds including goldeneye young. Moreover, negative impacts of brownification on goldeneye food abundance are probably accelerated by the recovery of lakes from acid deposition, a process that has been recognized as one of the drivers of brownification (Kritzberg et al. 2020). As water quality in previously acid boreal lakes has improved due to this recovery process, populations of the perch *Perca fluviatilis* have increased, causing a decline in aquatic invertebrates that are important food of both perch and goldeneye young (Rask et al. 2001). Hence, in addition to the overall brownification-caused decrease in aquatic invertebrates, increased food competition between perch and goldeneye probably has decreased further the quality of boreal lakes as brood habitats for goldeneyes (Pöysä et al. 1994, Nummi et al. 2012). All in all, the effects of both eutrophication and brownification on aquatic ecosystems may have been accelerated by climate change via increased temperature and precipitation and shorter ice duration (Moss et al. 2011, Williamson et al. 2017, Woolway et al. 2020).

The observed long-term decline of goldeneye reproductive success is alarming, and its connections with climate change and other anthropogenic stressors deserve further research, as clarifying the relative importance of different explanatory factors would greatly improve our understanding of the overall decline of waterbirds in the boreal breeding areas (Lehikoinen et al. 2016, Elmberg et al. 2020, Pöysä et al. 2023, Holopainen et al. 2024). In line with the finding of this study, the Finnish national waterbird monitoring data suggest that the production of ducklings (measured as number of ducklings per number of pairs) has decreased during 1989–2024 in goldeneye and some other duck species (Piha et al. 2024). However, because the Finnish monitoring scheme provides information only on numbers of indicated pairs, broods, and ducklings, it does not allow us to identify whether the decline is due to decreased survival of nests, eggs, or ducklings. While additional research is needed, this study adds critical new information to this undertaking as it identified the importance of the brood stage (separated from the nest stage) in the decline of reproductive success of a waterbird species in boreal lakes.

Conclusions

Changes in the timing (beginning and end) and duration of the breeding period have often been analysed using ringing data that are based only on successful nests, potentially introducing biases in the data. This study used both successful and failed nesting attempts to estimate the timing and duration of breeding in goldeneyes and found that the beginning of breeding has advanced, whereas evidence for the advancement of the end of breeding was only weak. Consequently, and contrary to the findings of an earlier study, the duration of the breeding period lengthened, although evidence for the

trend was only weak. Because the beginning of breeding was mainly governed by IOD (an indicator of climate change), it was not a surprise to find an advancing trend in the beginning of breeding. However, high nest predation rate in the previous year was the main driver of the end of breeding, potentially confounding effects of climate change on this phenological breeding metric. Because climate change-related processes are governing the beginning of breeding and nest predation-related processes the end of breeding, the duration of breeding is affected by both global climate change and local nest predation rate in the studied goldeneye population. These findings emphasize that local ecological factors should also be considered, and both successful and failed nesting attempts should be included, when analysing climate change impacts on phenological breeding metrics of birds. Nest-stage success appeared not to be associated with climate change, whereas final reproductive success was, suggesting that climate change has negatively affected the production of independent offspring in this goldeneye population. This finding calls for more research on climate change impacts at the brood stage in precocial species, including possible impacts deriving from sub-optimal incubation conditions.

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.2bvq83c1k> (Pöysä 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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