Research article

Nest predation and climate change as drivers of alternative reproductive tactics in a migratory species

Hannu Pöysä [1,2]

[1]Department of Environmental and Biological Sciences, University of Eastern Finland, FI, Joensuu, Finland
[2]Natural Resources Institute Finland, Yliopistokatu, Joensuu, Finland

Correspondence: Hannu Pöysä (hannu.poysa@outlook.com)

Alternative reproductive tactics enable individuals to choose a reproductive tactic relative to their status and prevailing environmental conditions in a way that increases their fitness. For example, females in many avian species show phenotypic plasticity and employ alternative reproductive tactics to cope with changes in predation risk and climate. Conspecific brood parasitism (CBP), in which females lay eggs in nests of conspecifics, is one example of such behaviour. It has been proposed that when prospects for successful nesting are low and/or costs of reproduction are high, females employ tactics of low effort such as non-breeding and parasitic laying. When environmental conditions are ideal and prospects for success high, females can increase their reproductive effort above typical nesting by laying parasitic eggs prior to initiating their own nest. Here, I used this flexible life-history strategy concept and long-term (1994–2022) population level data of the common goldeneye *Bucephala clangula* to study how the rate of parasitic laying varies in relation to variation in nest predation risk and in the timing and length of the breeding season, the latter being measured by the timing of ice breakup. Nest predation rate in the previous year and timing of ice breakup interactively affected parasitic laying, the rate of parasitic laying being particularly high in years with late ice breakup and high nest predation rate in the previous year. Furthermore, the proportion of predated eggs was lower in parasitized nests than in non-parasitized nests, while the opposite was true for the proportion of eggs that failed in other way. As a consequence, the final number of young produced per nest was higher for parasitized nests. The findings of this study show that changes in environmental conditions affect the dynamics of alternative reproductive tactics in goldeneyes, with consequences to population level reproductive output.

Keywords: alternative reproductive tactics, climate warming, conspecific brood parasitism, nest predation risk, reproductive success, timing of breeding

Introduction

Alternative reproductive tactics enable individuals to choose a reproductive tactic relative to their status and prevailing environmental conditions in a way that increases their fitness (Gross 1996). Predation risk is a major environmental factor selecting for plasticity in various behavioural and reproductive traits in birds (Lima 2009, Martin and Briskie 2009). This is not surprising, considering that predation is the major source of nesting mortality in birds (Ricklefs 1969) and an important driver in the evolution of avian breeding biology in general (Lima 2009, Martin and Briskie 2009). More recently, climate change has been recognized as an important force in affecting breeding birds. For example, at northern latitudes climate change-caused shifts in spring temperature and phenology have been found to affect the timing of breeding, the length of the breeding season and the occurrence of second broods in multi-brooded species (Dunn and Winkler 2010, Halupka and Halupka 2017, Marrot et al. 2018, Lv et al. 2020). All in all, a growing body of research indicates that females in many avian species show considerable phenotypic plasticity and employ alternative reproductive tactics (sensu Gross 1996, Taborsky and Brockman 2010) to cope with changes in environmental conditions such as predation risk and climate (Sorenson 1991, McRae 1997, 2011).

Conspecific brood parasitism (CBP), in which females lay eggs in nests of conspecifics, is one example of alternative reproductive tactics (Krüger 2008, Taborsky et al. 2008, Lyon and Eadie 2008). While earlier studies have focused on female traits (e.g. age and body condition), population metrics (e.g. density/availability of hosts) and resource limitation (e.g. nest site availability in hole-nesting species) as possible correlates of CBP, the role of variation in environmental conditions in driving the occurrence of CBP has received little attention (Lyon and Eadie 2017). The few exceptions addressing impacts of environmental conditions on CBP concern effects of drought and flooding on the frequency of CBP in four species of waterfowl (Lyon and Eadie 2017). In one additional study, not mentioned in Lyon and Eadie (2017), it was found for lesser snow geese *Chen caerulescens caerulescens* breeding in Manitoba, Canada, that the rate of parasitism increased in years when nest-site availability was restricted by snow or water (Lank et al. 1989). Other studies have found that the rate of CBP increases under conditions of high nest predation, some females responding to nest loss during the egg laying period by laying their next egg parasitically and some females laying parasitically prior to initiating own clutches (McRae 1997). More generally, it has been suggested that nest predation is an important ecological driver of CBP (McRae 1997, Pöysä 1999, Pöysä and Pesonen 2007) but, again, the idea has not been addressed with long-term data (but see Pöysä and Paasivaara 2016 for a 7 year study in an experimental setting).

Sorenson (1991), being one of the four studies addressing impacts of environmental conditions on CBP (above and Lyon and Eadie 2017), reported that reproductive effort of redhead *Aythya americana* females breeding in the Canadian prairies in Manitoba was reduced in a year when drought conditions reduced the probability of successful nesting: the frequency of normal nesting decreased, as many redhead females switched from typical nesting to parasitic egg laying. Sorenson (1991) presented a conceptual reproductive decision model to explain the varying reproductive tactics of redhead females. He proposed that at the beginning of each breeding season females choose from four reproductive options of increasing reproductive effort: 1) non-breeding, 2) parasitic laying, 3) typical nesting and 4) parasitic laying prior to typical nesting. In general, when prospects for successful nesting are low and/or costs of reproduction are high, females employ tactics of low effort such as non-breeding and parasitic laying. When environmental conditions are ideal and prospects for success high, females can increase their reproductive effort above typical nesting by laying parasitic eggs prior to initiating their own nest. Based on the Sorenson's (1991) model, Lyon and Eadie (2008) proposed that CBP can be considered more generally in the context of a flexible life-history strategy, in which females adjust their reproductive investment and options to prevailing ecological and phenotypic conditions (Eadie and Savard 2015).

Here, I used the flexible life-history strategy concept proposed by Sorenson (1991) and Lyon and Eadie (2008) as a general framework, and long-term (1994–2022) population level data of the common goldeneye (*Bucephala clangula*; hereafter, goldeneye), to study how the rate of parasitic laying varies in relation to variation in nest predation risk and climate change-driven variation in the timing and length of the breeding season. Goldeneye is a cavity-nesting diving duck species, in which the frequency of CBP varies a lot both within and between populations (reviewed by Eadie and Savard 2015). Females typically return to the same nest site if the previous nesting has been successful but not if the previous nesting attempt has been depredated (Dow and Fredga 1983, 1985, Lawson et al. 2017). Parasitically laying goldeneye females prefer safe nest sites: sites that have had a successful nest in year t-1 are parasitized more frequently in year t, information on nest success being gathered through nest site prospecting at the end of the previous nesting season (Pöysä 1999, 2003, 2006, Pöysä et al. 2014a). A field experiment has confirmed that parasitically laying females pursue a flexible safety-seeking tactic in nest selection and that nest predation risk drives spatial and temporal dynamics of CBP in goldeneyes (Pöysä and Paasivaara 2016). However, the experiment addressed only lake-level patterns and used the number of parasitically laying females as a crude proxy for the frequency of CBP. In addition, the role of climatic factors in affecting among-year variation in the frequency of CBP was not considered in that experiment. Furthermore, other studies have found that goldeneye females switch egg laying tactics between years (Eadie 1989, Åhlund and Andersson 2001, Lawson et al. 2017), indicating a flexible life-history strategy.

As to biological traits potentially sensitive to climate change impacts, 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). Considering responses to this shift in spring phenology (earlier ice breakup), breeding of goldeneyes has advanced, settling dynamics and the start of egg laying tracking annual variation in spring temperature and the timing of ice breakup (Clark et al. 2014, Pöysä 2019, 2022, Messmer et al. 2021). Moreover, while individual goldeneye females in general show flexibility in the timing of egg laying in response to between-year variation in spring temperature and ice breakup, not all females do so (Messmer et al. 2021), this difference in response probably reflecting flexible reproductive tactics. In sum, CBP in goldeneyes provides an ideal model system to study the dynamics of alternative reproductive tactics in the face of two fundamental ecological and environmental drivers, viz. predation risk and climate change.

Goldeneye populations include both pure parasites and nesting parasites (Åhlund and Andersson 2001) and parasitic laying via these two tactics probably are driven by different mechanisms (Lyon and Eadie 2008). For example, in the case of pure parasites, laying all eggs in high-quality nest sites of other females enhances breeding success, compared with laying in own low-quality nest. Nesting parasites, in turn, can bypass clutch-size constraint by laying some eggs parasitically, thus increasing total production of young (Lyon and Eadie 2008). Hence, it is reasonable to consider possible impacts of environmental drivers on the rate of parasitism from both tactics' (nesting parasites and pure parasites) point of view. Considering first population level responses to variation in nest predation risk and taking into account the previous findings concerning variation in site-specific risk and females' response to that (above), we may put forward the following hypothesis. When expectations for successful nesting due to high nest predation risk are low (high nest predation rate the previous year), particularly females that have lost their nest to predation the previous year should respond to the high risk either by skipping normal nesting and laying only parasitically or by laying parasitically prior to initiation of their own nest. Either way, the rate of parasitic laying should increase with nest predation rate the previous year.

Considering climate change impacts, it is reasonable to assume that the length of the nesting season can be an important constraint in parasitic laying. As females can lay only one egg per day, each parasitic egg will delay the initiation of the female's own clutch for at least one day, subjecting it to a seasonal decline in clutch size and reproductive success (Perrins 1970, Verhulst and Nilsson 2008, Pärt et al. 2017; see Milonoff et al. 1998, Clark et al. 2014 for goldeneye). So, when it comes to climate change impacts, we may hypothesize two scenarios with opposite predictions, depending on the prevailing tactic of parasitic laying. When expectations for successful breeding due to an early spring are high (i.e. constraint imposed by the length of the nesting season relaxed) especially fecund nesting females may increase their

reproductive success through laying parasitically prior typical nesting (Åhlund and Andersson 2001). Hence, if we assume that most parasitic eggs are laid by nesting parasites, the rate of parasitic laying at the population level should increase with earliness of the breeding season. When expectations for successful breeding due to a late spring are low (constraint imposed by the length of the breeding season strong), some females (e.g. poor-quality or first-time breeders) may skip normal nesting and lay parasitically instead. In this case, if we assume that most parasitic eggs are laid by pure parasites, the rate of parasitic laying at the population level should increase with lateness of the breeding season.

Here, I tested the above population-level predictions, while simultaneously taking into account possible impacts of other potentially important factors on the rate of parasitic laying, including conditions during the previous winter (harsh weather in the wintering area may affect female condition, breeding propensity, and breeding performance; Fredga and Dow 1983, Lehikoinen et al. 2006, Pöysä et al. 2017), population density (population or nest density may affect opportunities for parasitic laying; Rohwer and Freeman 1989, Lyon 2003) and nest predation rate in the same year (parasitic laying may be a response to nest loss in the laying stage in the same season; Yom-Tov 1980, Eadie et al. 1988, Lyon and Eadie 2008). In addition, using annual data of the numbers of nesting attempts and potential nesting females, I assessed the occurrence of non-nesting females and the pure parasite tactic in the population. Finally, I studied population-level consequences of CBP in terms of hatching success and offspring production, i.e. life history parameters potentially important when studying population dynamic implications of CBP (Eadie and Fryxell 1992, Eadie et al. 1998, de Valpine and Eadie 2008). While doing this, I also considered the role of nest predation in affecting variation in these parameters.

Material and methods

Study area and main predator of goldeneye nests

The study area in southeastern Finland (61°35N, 29°40E) is about 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, have a relatively stable water level in summer and are only used by waterbirds for breeding. 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-boxed were made available after an experimental study of CBP (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 nest site limitation per se can be ruled out as a factor affecting the frequency of CBP, because 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 CBP (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 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 common 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. 1997, Sonerud et al. 2023), a long-lived forest-dwelling mustelid species having a fixed home range (Zalewski and Jędrzejewski 2006). Pine martens use natural cavities (e.g. old black woodpecker cavities) for resting and denning sites but have also been observed to use nest boxes provided by man (Brainerd et al. 1995). Clutch predation by pine marten has been found to be spatially clumped for nests of goldeneyes (Dow and Fredga 1983). Pine martens typically take all the eggs (Dow and Fredga 1983, H. Pöysä, unpubl.) and cache some of the eggs in spring for consumption in the following winter (Helldin 1999). Daily movements and use of home ranges of radio-collared pine martens in Poland suggest that the daily hunting range of individuals in spring and summer extends to about 68–118 ha, daily movement distances ranging from 5.5 to 8.6 km (Zalewski et al. 2004).

Winter severity data

I selected three weather stations in western Europe (Berlin–Dahlem, northeast Germany; Groningen, northern Netherlands; Malmö, southernmost Sweden) to represent typical wintering areas of the goldeneyes breeding in Finland as revealed by winter-time ring recoveries of females ringed in Finland (Saurola et al. 2013). For these stations, I downloaded the mean daily temperatures for December, January, and February 1994–2022 from www.ecad.eu (Klein Tank et al. 2002) and calculated the Hellman index (Hellmann 1918) as the sum of mean daily temperatures that were below zero between 1 December and 28 February (winter severity index 'WSI'; note that absolute values were used; see also Pöysä et al. 2019). This index has been found to be useful when studying e.g. effects of harsh wintering conditions on movements of ducks in the European wintering areas (Ridgill and Fox 1990).

Nest data and identification of CBP

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. The first check in a year was typically done well before the breakup of ice cover in the lakes and the start of egg laying in the population (Supporting information), the among-year variation in the timing of the first check tracking the among-year variation in the timing of ice breakup ($r = 0.685$, $p < 0.001$, $df = 27$; year 1994 included, see Supporting information). The frequency of nest box visits varied depending on the annual status of the nest box; nest boxes in which a nesting attempt was recorded were visited more frequently during the egg laying phase to get data on parasitic laying (below) and again near hatching to get reliable data on nest success. Nesting attempts were typically found early in egg laying. New eggs were numbered, and their width and length were measured. 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; that is, 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; see also Pöysä 1999, 2006). All nesting attempts were used to calculate annual nest predation rates. A nest that was deserted during the egg laying was followed for 30 days (i.e. incubation plus 1–2 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).

Parasitized nests were identified using two methods: 1) more than 1 egg laid within 24 h (Eadie 1989, MacWhirter 1989, Eadie et al. 2010) and 2) within-clutch variation of egg width, length, and weight (weights were calculated using the formulae developed by Rohwer 1988 for waterfowl) exceeded a threshold value (maximum Euclidean distance [MED] between any two eggs within a clutch), a method developed by Eadie (1989) for goldeneyes (see Eadie et al. 2010 for verifying the method using DNA fingerprinting) and tested for the current population using protein fingerprinting to determine parentage of individual eggs (Pöysä et al. 2009). In brief, using the three egg measures, Euclidean distance between all pairs of eggs within a clutch was calculated; a nest was considered parasitized if MED > 3.0 (Pöysä 1999, Pöysä et al. 2009). I used the method recommended by Eadie et al. (2010: method A; Lyon and Eadie 2017) to estimate the frequency of the parasitic tactic (nesting parasites and pure parasites) each year in nests that proceeded to incubation (i.e. nests for which the final clutch size was known). First, for each nest identified parasitized, I estimated the number of parasitic eggs as total clutch size minus average clutch size in non-parasitized nests. Average clutch size in non-parasitized nests was 7.6 (SD = 1.8, n = 177); hence, I used an average clutch size of 8 eggs for host clutch size, and all eggs beyond this clutch size were considered parasitic (i.e. same clutch-size threshold as used by Eadie et al. 2010). If the total clutch size in a nest that was identified parasitized was ≤ 8 eggs, I set the number of parasitic eggs 1. In each year, the frequency

of the parasitic tactic was estimated as the proportion of eggs laid parasitically from all the eggs laid in the nests that proceeded to incubation (exclusion of nests that did not proceed to incubation did not cause biases in the data, see Supporting information). This index of the rate of parasitic laying was correlated with the proportion of parasitized nests of the nests that proceeded to incubation ($r = 0.738$, $p < 0.001$, $n = 28$ years; Eadie et al. 2010). Similarly, all comparisons between parasitized and non-parasitized nests were based on nests that proceeded to incubation. These comparisons concerned the annual proportions of eggs that were depredated or failed otherwise (did not hatch), the annual proportions of eggs that hatched and produced at least one young that left the nest (i.e. nest success), and the final number of young produced per nest.

Pair counts and ice-out data

Annual pair count and ice breakup data are from Pöysä (2022, 2023), with two additional years (2021 and 2022), and were derived as follows (additional methodological information in Pöysä 2019, 2022, 2023). A standard waterbird point count (Koskimies and Väisänen 1991) 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). In the point count, a lake is surveyed for waterbirds from one or more fixed vantage points so that all the shoreline and open water areas are visible and carefully observed; detection probability for goldeneye is generally high in point counts (Koskimies and Pöysä 1989). All lakes were monitored within a few days (mean range 2.5 d, SE = 0.1) on each of the four surveys. The first survey in each year coincided with an early stage of ice breakup in the study area (i.e. some lakes had some open water, while other lakes were still fully ice covered), while all the lakes were free of ice during the last (fourth) survey (Supporting information in Pöysä 2019). Goldeneye observations from each survey and lake were interpreted as 'pair numbers' using the species-specific criteria of Koskimies and Väisänen (1991; in the case of goldeneye, an observation of adult male and adult female together on a lake or a lone adult male on a lake indicates a breeding pair). The annual number of breeding pairs for each lake was estimated as the mean of the pair numbers from the survey when the lake was free of ice and the survey before or after the ice-free survey, whichever had a higher pair number; i.e. in each year and for each lake, data from two consecutive surveys were used to estimate the annual number of breeding pairs.

During each of the four waterbird surveys in April–May, the progress of the break-up 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 ice-out date (IOD,

a measure of spring earliness) 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 was calculated as the mean of the lake-specific IOD values.

Statistical analyses

I used general linear models to study the effects of nest predation rate the previous year (predation rate in year t-1; data from 1994–2021) and earliness of the spring (IOD; data from 1995–2022), and their interaction, on the rate of parasitic laying in year t (population-level proportion of parasitic eggs, see above) during 1995–2022. Other potentially influential explanatory variables considered were severity of the previous winter (WSI; data from winters 1994/1995–2021/2022), number of breeding pairs (breeding pairs in year t; data from 1995–2022), number nesting attempts (nesting attempts in year t; data from 1995–2022) and nest predation rate in the same season (predation rate in year t; data from 1995–2022) (see Introduction). Because the total number of explanatory variables was relatively high with respect to the sample size, increasing the risk of overfitting (Peduzzi et al. 1996), I fitted separate models for the explanatory variables in focus ('focal-variable model') and the potential confounding variables ('context-variable model'). If a potential confounding variable was significantly associated with the rate of parasitic laying, I added it into the focal-variable model to examine its effect on the model outcome. I used the most parsimonious focal-variable model for final inference (Johnson and Omland 2004). A full model including all the explanatory variables is presented in Supporting information but not used for inference. All explanatory variables were standardized (mean = 0, SD = 1) to facilitate the comparison of their effects on the response variable and the interpretation of the interaction term in the focal-variable model (Aiken and West 1991, Schielzeth 2010). Interaction plots were graphed following Aiken and West (1991). Mean, maximum and minimum values of the standardized explanatory variables (nest predation rate in the previous year or timing of ice breakup) were used as the fixed values to generate the regression lines of the regression of parasitic laying on the other explanatory variable in the interaction plots. The number of indicated breeding pairs in year t and the number of nesting attempts in year t were not correlated ($r = 0.259$, df = 26, $p = 0.184$), probably because they measure partly different segments of the breeding population, the former including females that skip nesting (Åhlund and Andersson 2001, Milonoff et al. 2004, Lawson et al. 2017); hence, both of these density variables were included in the context-variable model. Model diagnostic was done to assure that the underlying assumptions of the general linear model were met (Zuur et al. 2010). Pair-wise correlations among the explanatory variables were generally low ($|r| < 0.465$ in all cases). Even so, multicollinearity was

checked and appeared not to be a problem as variance inflation factor (VIF) was < 1.8 for the explanatory variables in all models (VIF = 1 / tolerance; tolerance values are given in Table 1). Assumptions of homoscedasticity and normality of model residuals were checked graphically by plotting residuals vs. fitted values and theoretical quantiles, respectively; both assumptions were found to be met. Finally, influential data points (outliers) were screened, and one outlier case was recognized (Cook's distance = 0.643) for the context-variable model. Removing the outlier case did not change the model outcome qualitatively; hence, the context-variable model ran on complete data was retained. Pairwise associations were tested using Pearson parametric correlation. Differences between parasitized and non-parasitized nests in the proportions of depredated eggs, eggs that failed in other way (broken in the nest or did not hatch), and final number of young produced, were tested with Wilcoxon matched-pairs signed-ranks test based on annual values of the proportions or means from 1998–2022 (data from 1995–1997 could not be used for the comparisons between parasitized and non-parasitized nests, because all the nests that proceeded to incubation were parasitized in these years). All statistical analyses were performed in SYSTAT 13.

Results

Parasitic laying in relation to nest predation and spring earliness

During the 1995–2022 study period, the annual rate of parasitic laying varied from 0.075 to 0.404 (mean = 0.228, SD = 0.072), that of nest predation (including 1994) from 13.2% to 83.3% (mean = 52.3%, SD = 17.4), and the timing of ice breakup (IOD) from 21 April to 11 May (Fig. 1). The model including the explanatory variables in focus (predation rate in year t-1, IOD and their interaction) suggested that the rate of parasitic laying increased with nest predation rate the previous year and lateness of the spring, the interaction between these variables being also significant (Table 1, focal-variable model). Probing the interaction term revealed that the rate of parasitic laying increased with nest predation rate the previous year in years with late or average IOD, whereas the opposite was true in years with early IOD (Fig. 2a). Similarly, the rate of parasitic laying increased with IOD if nest predation rate in the previous year was high or average, while the opposite pattern was observed if nest predation rate in the previous year was low (Fig. 2b). Considering the potential confounding variables (WSI, breeding pairs in year t, nesting attempts in year t, predation rate in year t), only nest predation rate in year t was associated with the rate of parasitic laying (Table 1, context-variable model). When nest predation rate in year t was included in the focal-variable model, it was no longer significantly associated with the rate of parasitic laying nor did it influence the association between the explanatory variables in focus and the rate of parasitic laying (Table 1, combined model versus focal-variable model).

Occurrence of putative non-nesting females

In 18 out of the 28 years the number of indicated breeding pairs exceeded that of nesting attempts, the excess of potentially nesting females per year ranging from 3 to 22 females more than recorded nesting attempts (Fig. 3). In other words,

Table 1. General linear models to explain among-year variation in the rate of parasitic laying, ran separately for the explanatory variables in focus (focus-variable model) and potential confounding variables (context-variable model), and by including in the focus-variable model the confounding variables that were significantly associated with the rate of parasitic laying in the context-variable model (combined model). IOD = ice-out date (higher IOD values in the data mean later spring), WSI = winter severity index (higher WSI values in the data mean more severe winter). Tolerance is 1 minus the squared multiple correlation between the explanatory variable and the other explanatory variables in the model.

|	β	SE	Tolerance	t	p-value
Focus-variable model					
Intercept	0.222	0.009		23.452	0.000
Nest predation rate in year t-1	0.035	0.010	0.964	3.693	0.001
IOD	0.021	0.010	0.967	2.171	0.040
Nest predation rate in year t-1*IOD	0.037	0.011	0.992	3.205	0.004
Overall model: $r^2 = 0.593$, $F_{3,24} = 11.669$, $p = 0.000$					
Context-variable model					
Intercept	0.228	0.012		19.910	0.000
Nest predation rate in year t	0.038	0.013	0.835	2.900	0.008
Number of nesting attempts	−0.011	0.013	0.913	−0.833	0.413
Number of breeding pairs	0.006	0.014	0.760	0.437	0.666
WSI	0.012	0.013	0.884	0.910	0.373
Overall model: $r^2 = 0.358$, $F_{4,23} = 3.205$, $p = 0.031$					
Combined model					
Intercept	0.223	0.009		24.022	0.000
Nest predation rate in year t-1	0.030	0.010	0.815	2.901	0.008
IOD	0.021	0.009	0.967	2.212	0.037
Nest predation rate in year t-1*IOD	0.029	0.012	0.816	2.362	0.027
Nest predation rate in year t	0.016	0.011	0.694	1.455	0.159
Overall model: $r^2 = 0.628$, $F_{4,23} = 9.688$, $p = 0.000$					
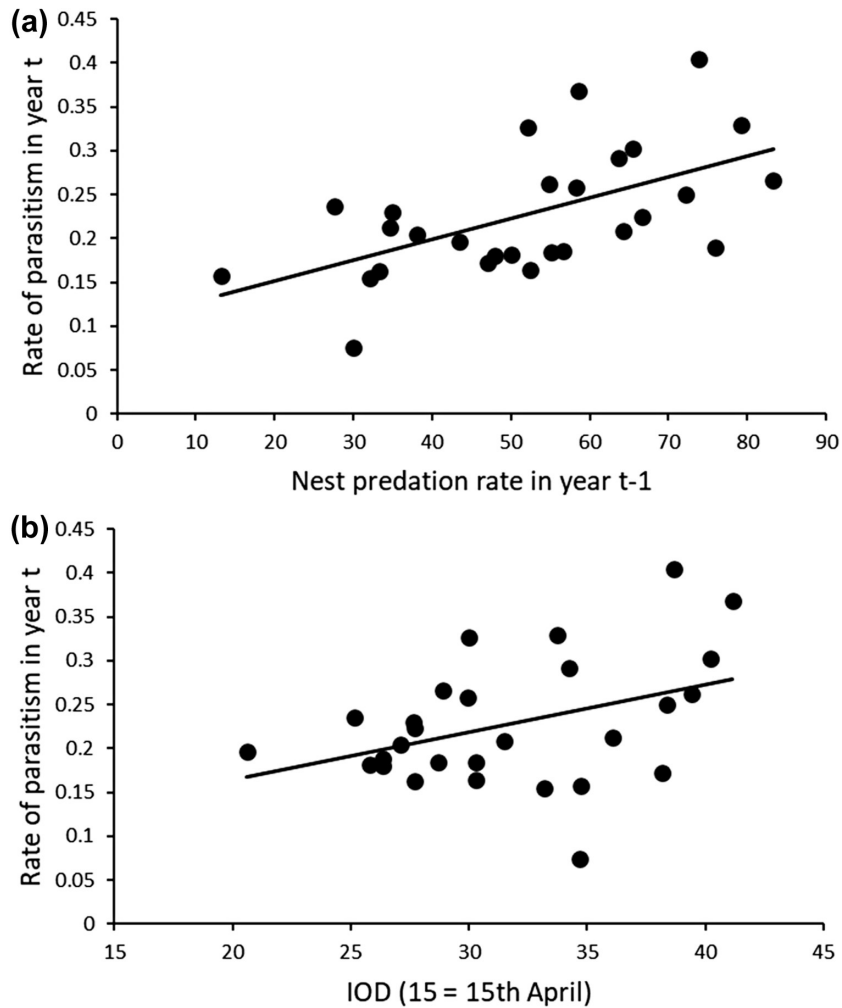
Figure 1. Rate of parasitic egg laying in relation to nest predation rate the previous year (a) and the timing of ice breakup (IOD) (b). Trend lines, showing a regression through the raw data points, are given only for illustrative purposes. See Fig. 2 for plots of the interactive effect of nest predation risk the previous year and the timing of ice breakup on the rate of parasitic laying.

in those years, 7–56% (mean 29%) of females probably did not have a nest of their own.

Parasitic laying, nest predation and nest success

The proportion of predated eggs was lower in parasitized nests than in non-parasitized nests (Wilcoxon's matched-pairs signed-ranks test, $Z=3.135$, $p=0.002$, $n=25$; Fig 4a), while the opposite was true for the proportion of eggs that failed in other way (Wilcoxon's matched-pairs signed-ranks test, $Z=2.166$, $p=0.030$, $n=25$; Fig. 4b). All in all, the proportion of failed eggs (Fig. 4c; depredated, broken or failed to hatch) was lower (Wilcoxon's matched-pairs signed-ranks test, $Z=2.597$, $p=0.009$, $n=25$) and the final number of young produced per nest (Fig. 4d) higher (Wilcoxon's matched-pairs signed-ranks test, $Z=4.200$, $p < 0.001$, $n=25$) in parasitized nests. Annual nest success (the proportion eggs that produced an offspring that left the nest) was not related to the rate of parasitic laying ($r=-0.057$, df$=26$,

$p=0.773$), but it decreased with increasing nest predation rate ($r=-0.497$, df$=26$, $p=0.007$).

Discussion

The findings of this study show that changes in environmental conditions affect the dynamics of alternative reproductive tactics in goldeneyes. As predicted, the rate of parasitic laying increased with increasing nest predation rate the previous year. However, this association appeared to depend on the timing of ice breakup, a phenological feature affected by climate change. Similarly, the rate of parasitic laying was associated with the timing of ice breakup, this effect in turn depending on nest predation rate in the previous year. Because of this joint effect, parasitic laying was particularly frequent in years with late ice breakup and high nest predation rate in the previous year. Of the two predictions concerning possible climate change impacts on the rate of parasitic laying, the one predicting increasing rate of parasitic laying with lateness of
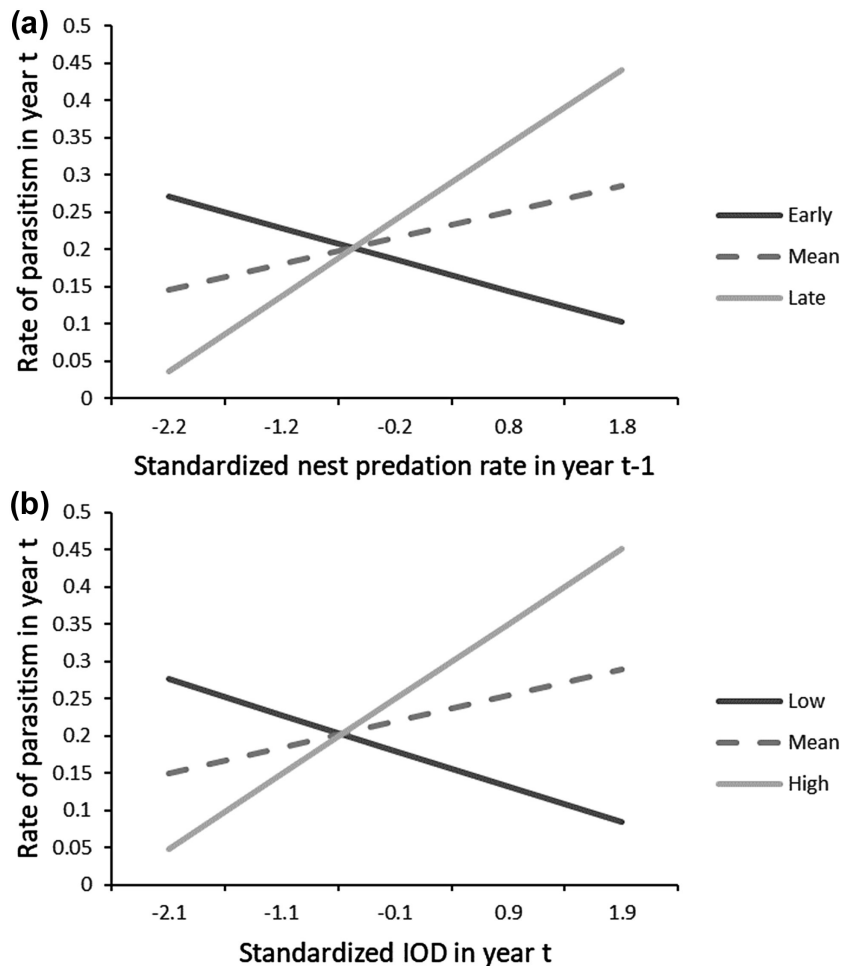
Figure 2. Plots of the interaction between predation risk the previous year and the timing of ice breakup in explaining variation in the rate of parasitic laying, as revealed by the focus-variable model in Table 1. The relationship between the rate of parasitic laying and nest predation rate the previous year is depicted for years with early (black line), mean (dashed line) and late (grey line) ice breakup (a), while that between the rate of parasitic laying and the timing of ice breakup is depicted for years with low (black line), mean (dashed line) and high (grey line) nest predation rate in the previous year (b). Mean, maximum and minimum values were used as the three fixed values for the timing of ice breakup (panel a) and nest predation rate in the previous year (panel b) to generate the regression lines of the regression of parasitic laying on the other explanatory variable.

the spring was generally supported, while the opposite prediction was not. However, answers to these predictions were modulated by nest predation rate in the previous year. All in all, climate change seems not to be promoting CBP in goldeneyes through warming-induced lengthening of the breeding season, because the rate of parasitic laying did not generally increase with earlier ice breakup. This study also found that the proportion of predated eggs was lower in parasitized nests than in non-parasitized nests, while the opposite was true for the proportion of eggs that failed in other way than due to predation. All in all, the final number of young produced per nest was higher in parasitized nests. Annual nest success (the proportion eggs that produced an offspring that left the nest) was driven by nest predation.

Considering the impact of nest predation risk, it seems unlikely that nesting females that return to the same successful nest site would engage in extensive parasitic laying.

First, because their own nest site is safe, as evidenced by the experience from the previous season (Pöysä 1999, 2003), there is no need for them to engage in parasitic laying to safeguard reproduction. They should derive limited benefits from spreading the eggs and reducing the time of their own nests at risk, a hypothesized advantage of parasitic laying (Andersson and Åhlund 2012) that may work for females facing higher nest predation risk. Second, because they typically start egg laying earliest within a season (Dow and Fredga 1984), low availability of potential nests obviously limits possibilities for parasitic laying. The overall seasonal decline of reproductive success, as documented for goldeneyes (Dow and Fredga 1984, Milonoff et al. 1998, Clark et al. 2014), would make engaging in parasitic laying unprofitable for early nesting females as success of their own nests would be reduced (Sorenson 1991). By contrast, females that have lost their nest to predation the previous
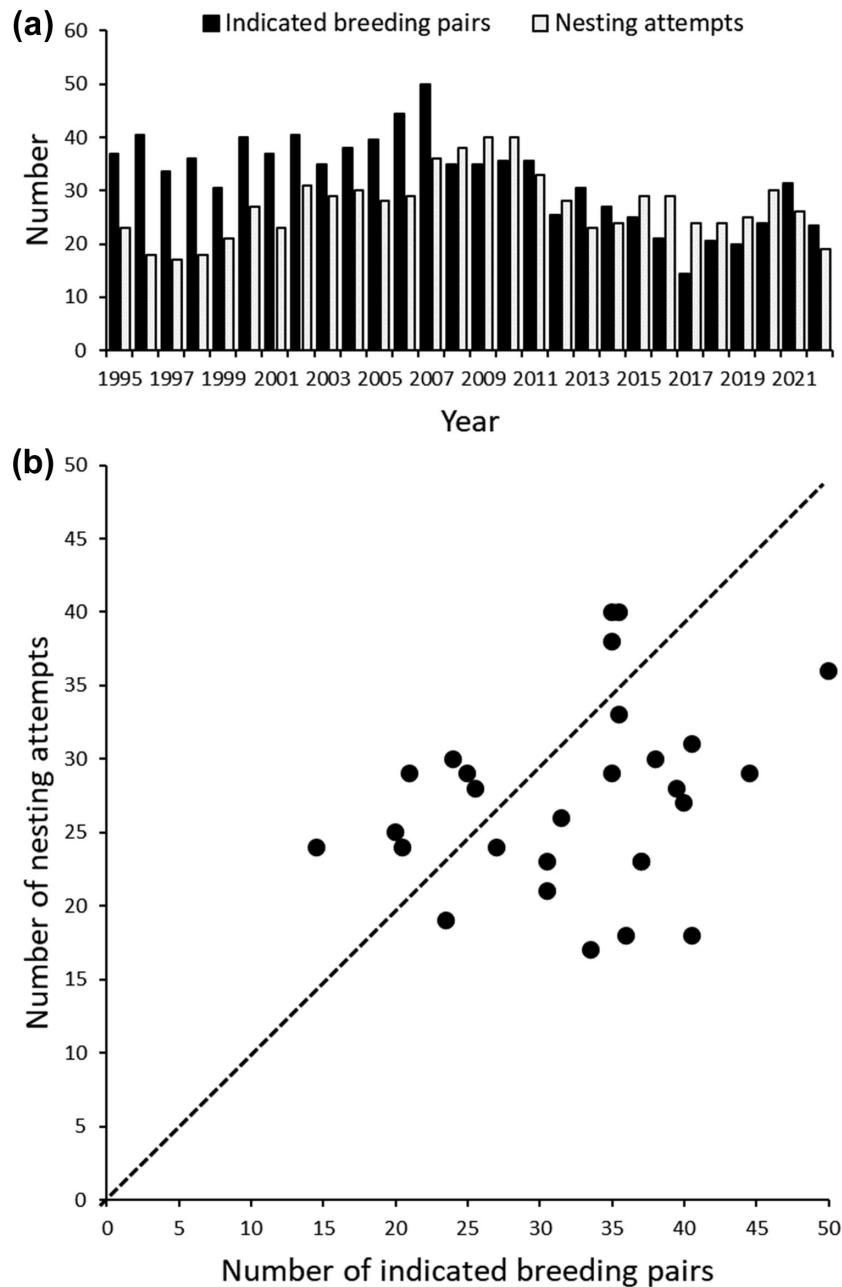
Figure 3. Numbers of indicated breeding pairs and recorded nesting attempts in each year during 1995–2022 (a) and plotted against each other (b). The dashed 1:1 line in panel (b) indicates equal numbers for the two variables.

year face fundamentally different conditions (Pöysä and Paasivaara 2016). Earlier studies have shown that goldeneye females that fail to breed successfully move to a new nest site the next season (Dow and Fredga 1983). Changing nest site between years will result in later egg laying, smaller clutch size and less young (Dow and Fredga 1983, 1984). The safest nest sites are occupied by early nesting, previously successful females. Therefore, if females that failed the previous year due to nest predation intend to have their own nest, they are forced to select from less safe nest sites, facing an additional cost due to later nesting. Under such circumstances,

it is profitable to lay parasitically in nests of hosts occupying safer sites, prior to initiating own nest or skipping nesting entirely. That the rate of parasitic laying was associated with nest predation rate in the same season in a model that did not include nest predation rate in the previous year may reflect this constraint, rather than response to nest loss within the same season (Pöysä 1999). This is because a year with high nest predation rate often is followed by another year with high nest predation rate (nest predation rate in year t versus nest predation rate in year t-1, $r = 0.395$, $df = 26$, $p = 0.037$; data from 1994–2022).
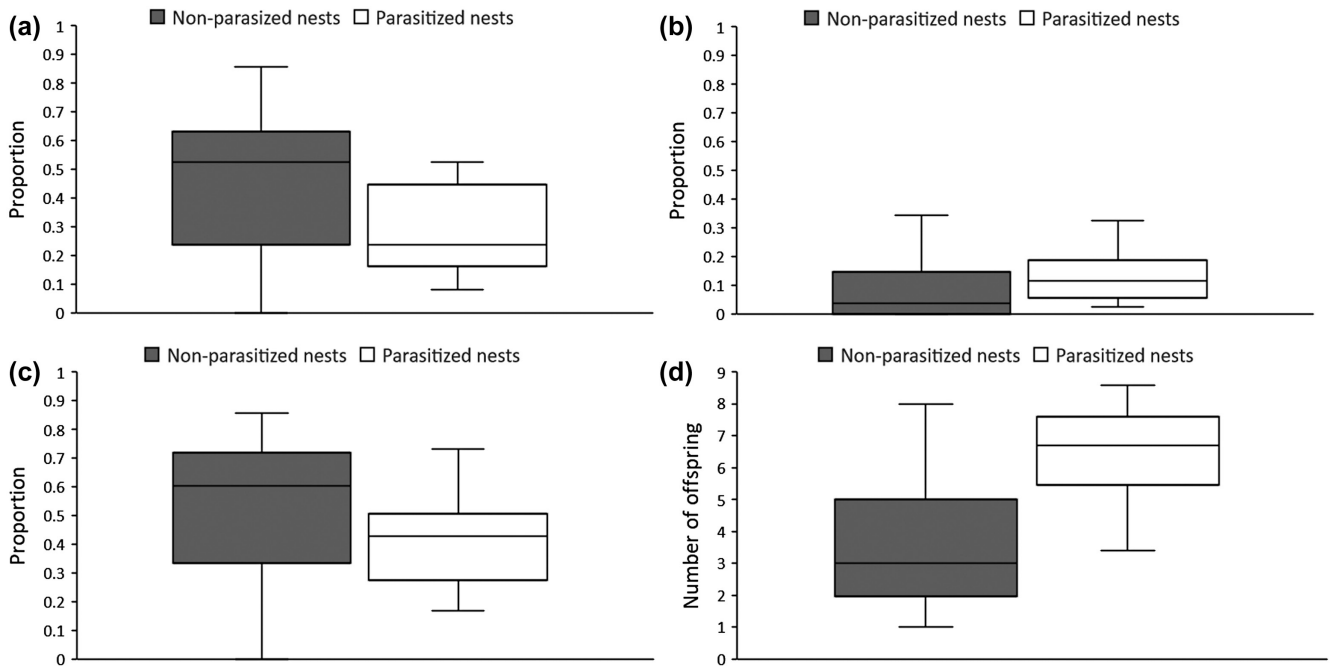
Figure 4. Box plots showing the proportion of predated eggs (a), the proportion of eggs that failed otherwise than due to predation (b), the overall proportion of failed eggs (panels (a) and (b) together) (c), and the number of offspring produced per nest (d) for non-parasitized and parasitized nests. Boxes show upper and lower quartiles (horizontal line within boxes gives the mean) of the data and whiskers indicate variability outside the quartiles. Each box is based on annual values (n = 25) of proportions (a)–(c) or means (d) from 1998–2022.

In this study, nesting tactics of individual females was not known. However, the finding that in most of the study years the number of indicated breeding females (pairs) exceeded that of recorded nesting attempts suggests that many females either laid only parasitically (pure parasites) or skipped egg laying entirely (non-nesting). It is unlikely that females nesting in natural cavities in the study area could explain the relatively high number of excess females (Material and methods). On the other hand, in some years the number of recorded nesting attempts was higher than the number of indicated breeding pairs, probably due to renesting attempts by females that failed early in egg laying. Besides being an indirect and crude method to assess the occurrence of non-breeding females each year, comparing numbers between indicated breeding females and recorded nesting attempts probably underestimates the proportion of such females. This is because the annual numbers of nesting attempts also included renesting attempts of females that lost the eggs early in laying. Laying tactics of individual goldeneye females have been reported in other studies. Eadie (1989) found for intensively followed goldeneye females in British Columbia, Canada, that most (23 out of 33 females) of the parasitically laying females acted as pure parasites in a given year, the rest (10) of the putative parasites laying both parasitically and in their own nests. Based on protein fingerprinting data from all the eggs laid by individually known goldeneye females (i.e. maternity of eggs was known) in one breeding season at Lake Mjörn, southwest Sweden, Åhlund and Andersson (2001) reported that approximately one third of egg laying females were pure parasites, i.e. laid only in the nests of other females.

Lawson et al. (2017) in turn used multistate capture–mark–recapture models to estimate breeding probability of goldeneye females in their study population in Interior Alaska, USA. Most females (83%) in the Alaska population attempted to breed every year (Lawson et al. 2017). These authors reported on a smaller segment of non-breeders (17%), of which some were laying parasitic eggs, i.e. were pure parasites. Although it has not been possible to separate non-breeding and parasitically laying females in all these studies, the findings of this study and those of the other studies together suggest that pure parasitic laying is a frequent although variable alternative reproductive tactic in goldeneye populations. It would be interesting to study how much of this variation is attributable to heterogeneity in individual quality as has been found in some demographic traits in goldeneyes (Lawson et al. 2017).

It has been found that the relative timing of first reproduction is affected by winter severity, recruits (first-time breeders) breeding later relative to the population mean after cold winters (Pöysä et al. 2017). One possible explanation for this is that their weaker physiological condition prevented earlier nest initiation after harsh winters. It is not known if the first-time breeders in such circumstances lay parasitic eggs before initiating their own clutch. Eadie (1989) found that parasitic laying was slightly more common among first-time breeders but was frequently employed also by older females. Lawson et al. (2017) in turn reported that seven of the eight putative pure parasite females they encountered were first-time breeders. Lateness of the spring (later ice breakup) will affect forage conditions negatively during the energetically demanding egg production period, extending to incubation

(Mallory and Weatherhead 1993, Alisauskas and Devink 2015). Limited forage conditions probably are more critical in years with a late spring and late ice breakup, because in such years, typically all the lakes in the study area are covered by ice for a prolonged period (Pöysä 2022, H. Pöysä unpubl.). This may affect the nesting and egg laying decisions of especially inexperienced and poor-quality females, resulting in increased rate of parasitic laying, as found here at the population level in years with late springs. Because the effect of late spring on parasitic laying was conditional to nest predation rate in the previous year, it seems likely that this effect concerned poor-quality females that had experienced nest loss in the previous year, rather than inexperienced first-time breeders of poor quality. Another mechanism that could affect variation in the frequency of parasitic laying along the early vs. late spring continuum is renesting. In years with an early spring, females that have lost the first clutch early in egg laying may be more prone to attempt renesting, instead of switching to parasitic laying, because they have more time to accomplish successful nesting. On the other hand, if the spring is very early, those females could, after losing the first clutch, lay some parasitic eggs before renesting. This could at least partially explain the finding that the rate of parasitic laying decreased with IOD (hence, was somewhat higher in years with an early ice breakup) if nest predation rate was low in the previous year. This finding is also in line with the idea that especially fecund nesting females may increase their reproductive success through laying parasitically prior typical nesting, as found in goldeneyes (Åhlund and Andersson 2001).

Given that parasitically laying goldeneye females prefer safe nest sites in egg laying (Pöysä 1999, 2003, Pöysä et al. 2014b, Pöysä and Paasivaara 2016), it was not surprising that the proportion of predated eggs in parasitized nests was lower than that in non-parasitized nests. On the other hand, the risk that eggs failed in other way than due to predation was higher in parasitized nests, probably because of inaccurate timing of parasitic laying (parasitic eggs were laid after the incubation had started and did not have time to hatch) and higher nest desertion rate due to disturbance caused by parasitism. However, at the population level, the net outcome of parasitic laying was positive, as indicated by the higher overall hatching success and production of young per nest in parasitized nests compared to non-parasitized nests. Providing that success of host eggs and offspring are not affected by parasitic eggs and offspring, as typically is the case in goldeneyes (Pöysä 2004; see Clawson et al. 1979, Eadie et al. 1998, Dugger and Blums 2001, Jaatinen et al. 2009a, b, Craik et al. 2018 for mixed findings in other precocial species), CBP could act as a buffering mechanism against high nest predation, as more females are able to produce offspring, resulting in higher population-level reproductive output. This is an important finding, given that the existing theoretical models of the effects of CBP on population dynamics (reviewed by de Valpine and Eadie 2008) have not considered the role of nest predation and the interplay between nest predation and parasitic laying. Interestingly, by considering different types of parasitism and including multiple biological aspects (but

not nest predation) in their models, de Valpine and Eadie (2008) demonstrated that CBP may have drastically different impacts on population size and stability, depending on whether parasitism increases or decreases average fitness in the population. Results of this study show that, indeed, informed non-random parasitic laying may result in increased population-level offspring production (Pöysä and Pesonen 2007). However, there obviously is a threshold level of parasitism above which the impact will turn into negative (Semel et al. 1988, Semel and Sherman 2001; see also Eadie et al. 1998). Further empirical research and modelling work is needed to identify such thresholds and to explore the influence of the whole range of fitness consequences of parasitic laying on population dynamics.

Considering that avian breeding seasons at northern latitudes are coming earlier and longer due to warming springs, results of this study imply that such changes can relax the pressure on females (probably inexperienced or poor-quality) to engage in parasitic laying. Whether this will translate into changes in average fitness and, consequently, impacts on population dynamics depends on how nest predation rate will change with warming springs, as the latter appeared to be a more important driver of nest success, at least in this population. Some works suggest that nest predation rate in shore birds has been increasing at northern latitudes due to climate-induced shifts in predator-prey interactions (Kubelka et al. 2018). In principle, such climate-driven changes in predator-prey interactions and consequent changes in nest predation rates could occur also in systems of cavity-nesting species like the one studied here. Predation of goldeneye eggs (alternative prey for the pine marten) has been found to respond to changes in the abundance of small rodents (typical prey for the pine marten) (Pöysä et al. 2016). Climate warming, in turn, potentially affects small rodent abundances and dynamics (Andreassen et al. 2021). However, current data do not indicate such climate-related changes in predator-prey interactions in this system, as nest predation rate was not correlated with climate warming-caused advancement of ice breakup (nest predation rate versus IOD, $r = 0.090$, $df = 26$, $p = 0.648$; data from 1995–2022). Even so, the interaction between the timing of ice breakup and nest predation risk in affecting the rate of parasitic laying, as found in this study, highlights that impacts of climate change are complex and should be studied in concert with other drivers of reproductive decisions. All in all, possible impacts of climate change on the dynamics of CBP should be studied in other populations and species, as evidence of the ability of females to respond via parasitic laying to climate-related changes in environmental conditions has now been found for several species (Lank et al. 1989, Sorenson 1991, McRae 2011, this study, Lyon and Eadie 2017). Interestingly, it has been found in rails that parasitism rates are higher in populations with shorter nesting seasons (McRae 1997, 2011, Jamieson et al. 2000). Given that climate change may affect avian reproduction via multiple mechanisms and have unexpected impacts (Husby et al. 2009, Chamberlein and Pearce-Higgins 2013, this study), with effect on offspring

production varying according to ecological and life history traits of species (Halupka et al. 2023), more research of impacts of climate change on alternative reproductive tactics in general is needed.

In conclusion, based on long-term data, this study showed that the dynamics of alternative reproductive tactics, here parasitic egg laying in conspecifics' nests, are affected interactively by nest predation risk and climate warming. Interestingly, climate warming can have a positive effect at the individual level, in that earlier springs seem to alleviate the pressure on females to engage in parasitic laying, although this effect depends on the level of nest predation risk. This may have consequences to population dynamics, again, depending on whether nest predation rate will also change. The findings of this study further suggest that nest predation, and the ability of females to adjust their reproductive tactic in response to changes in it, are important ecological and behavioural aspects that need more attention when modelling population dynamic consequences of CBP. More research on the role of environmental drivers, such as predation risk and climate change, in affecting the dynamics of alternative reproductive tactics is warranted.

Transparent peer review

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.wwpzgmss6 (Pöysä et al. 2024).

Supporting information

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

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