E-Article

Nesting Synchrony and Clutch Size in Migratory Birds: Capital versus Income Breeding Determines Responses to Variable Spring Onset

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ABSTRACT: Synchronous reproduction of birds has often been explained by benefits from nesting together, but this concept fails to explain observed intraspecific variation and climate-mediated changes of breeding synchrony. Here, we present a theoretical model of birds that store resources for reproduction (capital breeders) to show how breeding synchrony, clutch size, and offspring recruitment respond to changes in timing of first possible breeding date. Our approach is based on individual fitness maximization when both prebreeding foraging and offspring development are time constrained. The model predicts less synchronous breeding, smaller clutch size, and higher chances for offspring recruitment in capital breeding birds that advance their nesting. For contrast, we also show that birds that need to acquire resources during egg laying (income breeders) do not change nesting synchrony but increase clutch size along with earlier breeding. The prediction of stronger nesting synchronization of capital breeders in years with late nesting onset is confirmed by empirical data on breeding synchrony of a high-latitude capital breeding sea duck, the common eider (*Somateria mollissima*). We predict that in warming high-latitude ecosystems, bird species that depend on stored reserves for reproduction are expected to desynchronize their nesting.

Keywords: clutch size, breeding synchrony, timing of breeding, capital breeding, common eider, dynamic programming.

Introduction

The question of why some birds synchronize their breeding within the annual cycle is a long-debated subject in evolutionary ecology (Darling 1938). One set of explanations is focused on benefits achieved from breeding together, for example, better opportunities for optimal partner choice, more efficient defense, group foraging, and dilution of nest predation risk (Ims 1990a, 1990b; Spottiswoode and Møller 2004). The benefits from breeding at the same time must also outweigh high offspring mortality due to competition for food with peers (Mock and Parker 1997) or predators attracted by an abundant food source (e.g., Mwema et al. 2010). An alternative view is that synchronization emerges from adjustment of individual breeding strategies to seasonal time constraints. Comparative analyses of geographical trends in breeding synchrony, using latitude as a proxy for season length, show that nesting is more synchronized the farther from the equator (Spottiswoode and Møller 2004; Burr et al. 2016). However, the latitudinal trend explains only part of the variability in reproductive synchrony (Stutchbury and Morton 2001; Burr et al. 2016).

On top of seasonality, a life history approach is crucial for understanding the phenology of breeding. Juveniles need sufficient time to reach developmental milestones (e.g., fledging) early enough to successfully migrate and recruit (Verhulst and Nilsson 2008), and advancement of breeding by parents is expected to positively affect their fitness. However, in many bird species, the period before breeding serves as an important determinant of body reserves that

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later contribute to reproduction (Chastel et al. 1995). Advancement of nesting thus increases prospects for offspring development and successful recruitment but will at the same time shorten the time of prebreeding foraging. This evolutionary dilemma, with its potential effect on breeding synchrony, clutch size, and offspring quality, concerns numerous bird species, especially those that rely on stored reserves for breeding. This is referred to as "capital breeding" (cf. Drent and Daan 1980; Jönsson 1997), as opposed to "income breeding," in which reproduction is fueled by concurrent resource acquisition. A capital breeding component has been shown to contribute to reproductive output in a number of species among ducks (eider, diving, and dabbling ducks), geese, swans, waders, gulls, penguins, flamingos, owls, and even some passerine birds (Krapu 1981; Mawhinney et al. 1999; Kullberg et al. 2005; Drent et al. 2006; Langin et al. 2006; Nolet 2006; Hobson and Jehl 2010; Yates et al. 2010; Rendón et al. 2011; Solonen 2014; Poisbleau et al. 2015).

Both capital and income breeding birds are expected to maximize the expected lifetime number of offspring capable of recruiting. While early hatching is ideal from the perspective of each offspring's individual survival (Drent and Daan 1980), it is not necessarily optimal from the perspective of the mother, which can produce an extra chick if she gathers more reserves prior to breeding. This creates a trade-off between quantity of produced eggs and chance of each offspring's recruitment (Ejsmond et al. 2015). This trade-off constitutes a main challenge both for capital breeders, which need to acquire the resources required for reproduction prior to breeding, and for income breeders, which must forage during egg laying in order to produce the full clutch of eggs. Species all along the continuum, from income to capital breeders, thus optimize timing of seasonal activities in order to maximize the expected number of recruits. Current literature focused on climate-driven changes in nesting phenology and clutch size lacks this diversity of strategies and its consequences for breeding and population dynamics.

Here, we follow a life history approach and develop a theoretical model to find the optimal timing of breeding that maximizes the expected number of successful recruits as proxy for fitness (Williams 1966; Jørgensen and Fiksen 2006). A seasonal time constraint is a key element in our model. We model prebreeding behavior and breeding strategies in birds that vary in time of arrival to the breeding grounds. Offspring produced late in the season are assumed to have decreased chances of recruitment, so the timing of hatching affects fitness. This creates a life history trade-off between number of eggs produced and probability of offspring recruitment. Crucially, this trade-off and its consequences depend on whether the bird is a capital or income breeder. Although our model considers pure capital and income breeders, the predictions portray two endpoints of a continuum, and comparing them reveals the pros and cons of the two types of reproductive strategies. In our model, breeding synchrony emerges from optimization of timing and clutch size in a seasonal environment, and the degree of synchrony results from individual breeding strategies that are conditional on the physiological state of females in the modeled population. Predictions of our model are compared with data on breeding synchrony of a high-latitude capital breeding and migratory sea duck, the common eider (*Somateria mollissima*).

Our modeling approach of comparing income and capital breeding birds allowed us to show that spring advancement is expected to trigger contrasting responses in these groups. The novelty of our paper is that we not only focus on optimal timing but also show how breeding synchrony, clutch size, and recruitment success covary systematically, depending on whether the breeders use a capital or income breeding strategy. The emergent breeding dynamics is mediated by the physiological state of individuals, their state-dependent decisions (Houston and McNamara 1999; McNamara and Houston 2008), and whether they can make use of a capital breeding strategy beyond income breeding. Our work elucidates how the breeding strategies adopted by birds are affected by changing spring phenology and have consequences for reproduction at the population level.

Methods

Model Overview

The theoretical model focuses on the response of breeding synchrony and clutch size to shifting spring onset. We first describe the model for capital breeders, then explain how the income breeding model differs. Upon arrival at the breeding grounds, capital breeding females first gather required resources by building reserves, then reproduce. Females foraging for longer during the prebreeding season are able to produce more eggs, but this leaves less time for offspring to develop. In turn, this results in lower per-offspring contribution to fitness. The key decisions are when to start and when to terminate egg laying in order to maximize fitness, where fitness is defined as the number of offspring multiplied with per-offspring recruitment probability (see below). Note that the words "decision" and "strategy" imply no conscious intent or cognitive planning but are used merely to describe physiological and behavioral responses that have evolved through natural selection. The decision of each female depends on the amount of reserves gathered so far and number of eggs already laid. After optimizing the state-dependent timing of nesting, the model simulates a population of females to quantify the distribution

of breeding, clutch size, and probability of offspring recruitment. Whereas our work presents the model parameterized in order to resemble breeding biology of sea ducks, we also performed extensive sensitivity analyses to test the generality of our predictions (appendix, available online).

Optimization of Capital Breeding Strategy

As an inspiration for model design of a capital breeder, we consider the breeding behavior of common eider females nesting in a high-latitude seasonal environment. The model spans the time between spring arrival at the breeding grounds and egg hatching. After migration in spring, the common eider females are in a lean condition and are unable to produce eggs without first foraging to build energy reserves (Waltho and Coulson 2015). Hence, in our model, all females have no energy reserves at the day of their spring arrival—that is, minimal body reserves $S_{min} = 0$—and need to prepare for the upcoming reproduction by foraging prior to egg laying. We refer to this preparation period as the prebreeding season. The total body mass of the modeled bird at day t consists of a lean body mass M_L plus reserves $S(t)$. Foraging and the corresponding daily gain w in energy reserves is given by $S(t + 1) = S(t) + w$, with w parameterized according to Korschgen (1977) and Rigou and Guillemette (2010; see table 1 for the value of this and other parameters). Maximal body mass M_{max}—that is, the sum of lean body mass M_L and maximal reserves S_{max}—was set consistent with observations that mass of reserves in common eider females can reach up to approximately 130% of lean body mass (Milne 1976).

A female in good condition lays up to six eggs (Erikstad et al. 1993) at a rate of one egg per day (Watson et al. 1993), and we assume this to be the maximum clutch size, n_{max} (scenarios with n_{max} other than six are discussed in the appendix). After all eggs are laid, a female starts incubating her clutch (Waltho and Coulson 2015). We further assume that all eggs are the same size (Parker and Holm 1990; Waltho and Coulson 2015) and that egg size does not depend on a female's body size or condition (Swennen and van der Meer 1992). Breeding females need to incubate eggs for 26 days (Parker and Holm 1990). For simplicity, we assume that the reserves used during incubation equal 50% of the energetic costs needed to produce the eggs

Table 1: Model parameters and their baseline values

Parameter	Description	Unit	Value	Comments	References
N	Population size		10,000		
M_L	Lean body mass	Grams	1,100	Mass with no reserves	Milne 1976
M_{max}	Maximal body mass	Grams	2,500	Mass with max reserves $M_{max} = M_L + S_{max}$	Milne 1976; Gabrielsen et al. 1991
S_{max}	Maximal reserves	Grams	1,400	Body reserves	Milne 1976; Gabrielsen et al. 1991
w	Prebreeding weight gain	Gram day^{-1}	15	Estimated linear increase	Korschgen 1977; Rigou and Guillemette 2010
E	Egg mass	Grams	110		Parker and Holm 1990; Waltho and Coulson 2015
L	Egg laying rate		1	Number of eggs laid daily	Watson et al. 1993
c	Coefficient accounting for costs of egg production		1.5	Cost of egg production includes egg laying and incubation	
I	Incubation duration	Days	26	Incubation starts after all eggs are laid	Parker and Holm 1990
D_a	Mean arrival date	Day of year	90	Normal distribution, based on observed arrival dates	Hanssen et al. 2016; A. Ejsmond, personal observation
SD	Standard deviation for D_a	Days	10		
b_s	Earliest possible breeding onset	Day of year	130–170	Observed and reported early and late nesting	A. Ejsmond, personal observation; Waltho and Coulson 2015
D_e	Last possible laying date	Day of year	240	Last day of laying that allows juveniles to develop before autumn migration	Waltho and Coulson 2015

Note: The model was parametrized to resemble the biology of the common eider with supporting references (given in the last column).

(for egg mass and cost of incubation, see table 1). The costs of incubation being independent of clutch size is discussed in the appendix.

Egg laying in birds at high latitudes is constrained by access to nesting sites, for example, due to timing of snow-melt (Chaulk and Mahoney 2012; Waltho and Coulson 2015). The key parameter in our model is the first possible breeding day, b_s (fig. 1A; day of year). Females in our model arrive prior to the breeding season and can start egg laying at any day t on or after b_s (fig. 1B). If females postpone egg laying, offspring have less time to develop before the autumn migration. We assume that the probability of offspring recruitment $f(t)$ is maximal at the first possible breeding day b_s of the earliest breeding season (among all investigated scenarios) and decreases linearly to 0 for those that hatch too late to develop to fledging with a physiological condition that allows autumn migration (fig. 1C). The assumption of decreasing probability of recruitment with the timing of hatching represents the reduced probability of successful offspring development, along with the delayed postbreeding timing (Drent et al. 2003; Dunn 2004; Morrison et al. 2019).

The fitness measure V is a breeding female's expected number of recruits, that is, the number of offspring weighed by their recruitment probability. A capital breeder in our model that decides to stop egg laying and start incubating
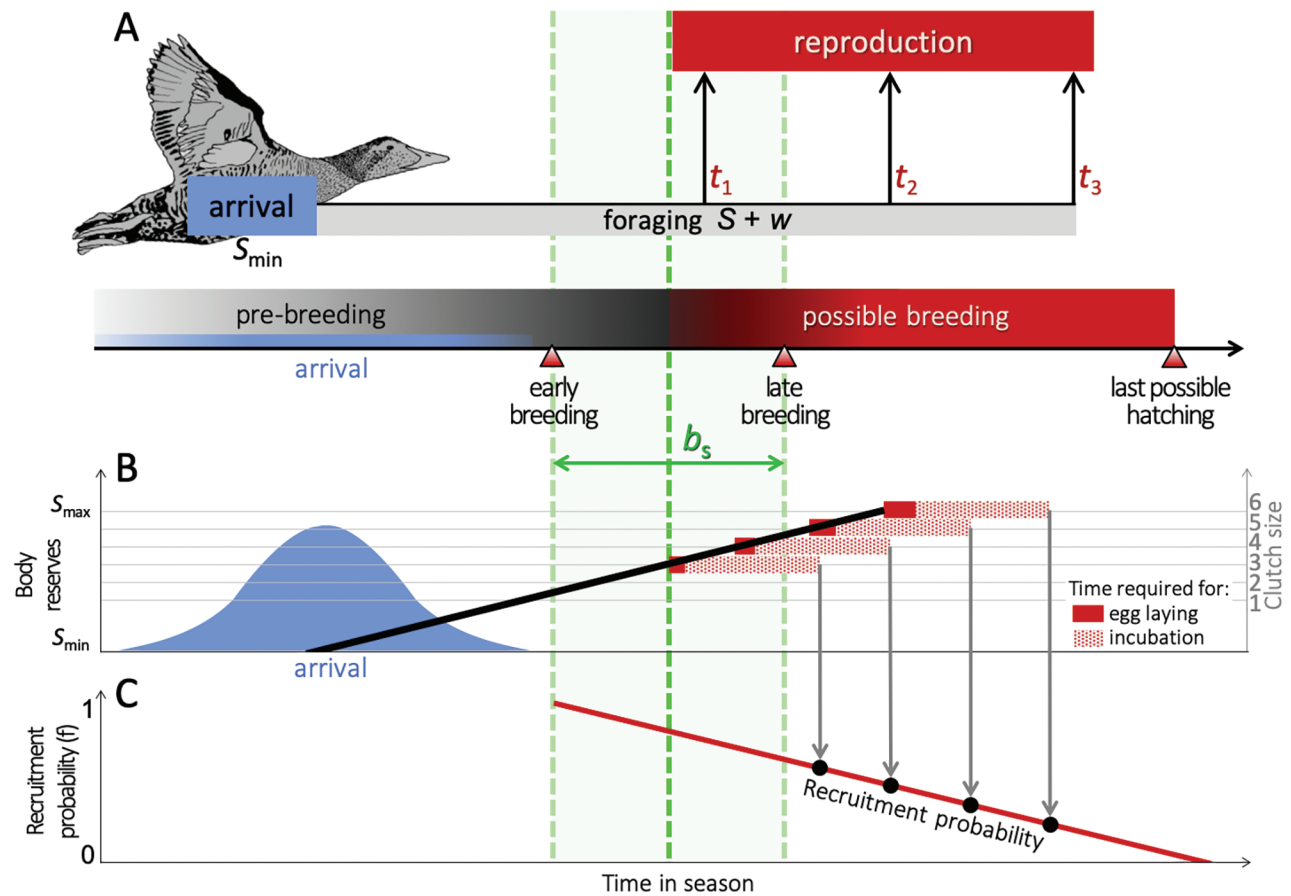

Figure 1: Key components of the model. *A*, The bird arrives at the breeding grounds in spring with minimal body reserves (S_{min}). The arrival is followed by resource acquisition, which increases mass of reserves S as the bird forages $S(t + 1) = S(t) + w$, where w is daily weight gain. The model optimizes timing of reproduction t that may take place from the day of first possible breeding b_s onward (green lines). The model bird decides when to switch from foraging to egg laying and when to start incubation (t_1, t_2, and t_3 represent three hypothetical strategies differing in timing of nesting onset), while gathering more reserves postpones reproduction. *B*, The body reserves increase until maximal body mass S_{max} is reached. Postponed reproduction allows for a larger clutch size due to enlarged reserves, whereas the probability of recruitment f decreases. The distribution of arrival dates is depicted in blue. *C*, The assumed recruitment probability f translates to probability of offspring recruitment that decreases from 1 at time b_s of the earliest scenario to 0. The thick black line in *B* exemplifies a trajectory of condition and clutch sizes mapped onto corresponding probability of recruitment in *C*.

obtains a fitness if breeding V_{incubate} (eq. [1]). After incubation, the offspring hatches, and the chance of recruitment f declines with time:

$$V_{\text{incubate}}(t, n) = nf(t + i), \qquad (1)$$

where n is number of eggs laid and cannot exceed available resources divided by egg production costs, $S(t)/(cE)$. Hatching takes place i days after the last egg was laid and defines the offspring recruitment probability. A female that has not yet produced her maximum clutch size may alternatively decide to continue egg laying, which would lead to fitness if laying V_{lay}:

$$V_{\text{lay}}(S, t, n) = V(S - cE, t + 1, n + 1), \qquad S \geq cE, \quad (2)$$

where E is the mass of one egg and c the multiplicative cost of producing and incubating it in units of energy reserves (see table 1). The female may also continue foraging, which would influence prospects for future fitness due to increasing reserves, according to

$$V_{\text{forage}}(S, t, n = 0) = V(S + w, t + 1, n = 0), \qquad (3)$$

where w is the daily increase in reserves and $S + w$ cannot exceed $S_{\max}$. The third argument $n = 0$ indicates that foraging is only available as long as no eggs have yet been laid; capital breeding females that have already initiated breeding ($n \geq 1$) were not allowed to forage ($V_{\text{forage}} = 0$). Reserves are constrained upward by $S_{\max}$ (see table 1). The model uses dynamic programming (cf. Clark and Mangel 2000) to fill in the matrix of V from the final day of the season and recursively for each day earlier. It does so by comparing V_{forage}, V_{lay}, and V_{incubate} calculated on each day and for each level of energy reserves S and number of eggs laid:

$$V(S, t, n)$$
$$= \max[V_{\text{forage}}(S, t, n = 0), V_{\text{lay}}(S, t, n), V_{\text{incubate}}(t, n)].$$
$$(4)$$

In this way, the model optimizes the day t^* at which a capital breeding female initiates egg laying and day t^{**} at which female starts incubation, by maximizing V (see eq. [3]; fig. 1). At t^*, the female switches from foraging to reproduction, which thus determines the amount of reserves at breeding. At t^{**}, the female terminates egg laying, which sets the clutch size as one egg laid per day. Note that the clutch size is determined not only by condition S because there may not be enough time for females nesting late to utilize all reserves for egg production.

Optimization of Income Breeding Strategy

For income breeders, we used the same parameterization regarding egg size, incubation time, and so on as for the capital breeders. However, income breeding females were allowed to store reserves up to the level equal to production cost of one egg, that is, $S_{\max} = cE$. Thus, while capital breeders can lay one egg per day, income breeding females need to set aside time to forage to produce another egg and thus continue cycles of foraging and egg laying until time t^{**}, when the 26-day period of incubation starts. Hence, the decision about starting incubation at t^{**} determines their clutch size. Income breeding females, in contrast to capital breeders, were allowed to forage and increase their reserves S no matter the number of eggs already laid; compare this with equation (3), which is then $V_{\text{forage}}(S, t, n) = V(S + w, t + 1, n)$. As with capital breeders, the optimal state-dependent strategy for an income breeder was found using dynamic optimization (see eq. [4]).

Simulating Populations of Breeding Females

To obtain distribution of nesting onset and other characteristics of the breeding population, we simulated a population of 10,000 females with normally distributed arrival dates. Behavior of the simulated females followed the state-dependent optimal strategy t^* and t^{**} obtained with backward optimization (eq. [4]). By following individual females arriving at different days, we obtained trajectories of individual reserve levels $S(t)$, day of breeding onset, and clutch size. We ran optimization and simulations for a range of arrival dates and three different scenarios of possible days of breeding onset b_s (fig. 1).

We contrast scenarios for different prebreeding season lengths by varying day of first possible breeding onset b_s from an early ($b_s = 130$) via intermediate ($b_s = 150$) to late ($b_s = 170$) spring and refer to these scenarios as spanning from early to late spring (for other arrival scenarios, see the appendix). The model assumes normally distributed arrival dates (mean arrival day of year $D_a = 90$, SD $= 10$ days) consistent with migration patterns for high-latitude populations of the common eider (Hanssen et al. 2016). The scenarios reflect the high seasonal variation observed in natural systems of diverse migratory bird species.

To test the generality of our predictions, we tested our model for a broad range of assumed maximal clutch size, incubation time, costs of egg production, distribution of arrival dates, and other key parameters to cover the biological variation and to explore whether conclusions are valid for other birds (appendix). All calculations were performed with Matlab R2015b (Matlab 2015).

Empirical Data: Breeding Synchrony of Common Eiders

The theoretical framework allows for predictions regarding changes in the degree of breeding synchrony with shifts in the first possible breeding date. By using gathered data on the degree of breeding synchrony, we confronted our theoretical predictions with empirical patterns of breeding synchrony. We analyzed data from two high-latitude

breeding colonies of common eider: Rif (Iceland, 65°N, 185–620 nests per year) and Longyearbyen (Svalbard, 78°N, 326–445 nests per year). The Iceland colony was monitored in the years 1992–2013; nesting onset was defined as the day when at least one breeding female was observed (with 1–10 nests recorded at day of nesting onset during the long-term monitoring period of 20 breeding seasons; for details, see Jónsson et al. 2017). In Svalbard, a clearly defined nesting area was counted daily in seasons 2016–2019. For both colonies, the degree of breeding synchrony was measured as the time interval between nesting onset and median nest day.

Results

Timing of Nesting

The ability of storing reserves for clutch production allows capital breeding females to benefit from foraging prior to breeding (fig. 1). Among capital breeders, but not income breeders, some individuals therefore postponed breeding beyond the first possible day of nesting (fig. 2). Initially, we focus on the strategy of capital breeding birds exposed to three scenarios differing in the first possible breeding day b_s (fig. 2). When spring was early with rapid snowmelt, even an early-arriving female was unable to gather sufficient reserves by the first possible day of nesting (fig. 2A). Capital breeding females, therefore, postponed reproduction to forage beyond the first possible day of nesting. For intermediate spring onset, females that arrived early have amassed sufficient stores to produce the maximal number of eggs and start nesting as soon as conditions allow (fig. 2B). Those that arrived late needed to postpone reproduction and foraged for longer to maximize the expected number of recruits (fig. 2B). Finally, when spring was late, the time window between arrival and first possible nesting gave enough time for all females, no matter their arrival date, to gather extensive energy reserves. Hence, all females reproduced as soon as conditions allowed and produced maximal clutch size (fig. 2C).

Income breeders differed in that they started nesting earlier than the capital breeding strategy, except when spring was late and both capital and income breeders were forced to nest quickly to allow fledging and development prior to the autumn migration (fig. 2). Although income breeders generally initiated nesting earlier than capital breeders, their chicks hatched later (fig. 2) because income breeders had to forage for each consecutive egg laid.

Clutch Size Variability and Breeding Synchrony

The optimization of individual breeding tactics translates into breeding synchrony, clutch size variation, and num-

ber of recruits per female recorded at the population level. Income breeders synchronized nesting no matter the length of the prebreeding season (fig. 2) because postponement of breeding by an income breeder brings no benefit in terms of clutch size as they cannot store extensive reserves. Additionally, late breeding leaves less time for clutch production, so when first possible breeding onset b_s was late, income breeders had a smaller clutch size, lower probability of recruitment, and, in turn, lower fitness measured by the expected number of recruits per female (figs. 2, 3B).

For capital breeders, reproductive synchrony and variation in clutch size are an outcome of the optimization of the trade-off between time dedicated to gathering reserves and offspring development. To facilitate interpretation of the model outcomes, we divided the gradient of the first possible breeding day b_s into early, intermediate, and late spring onset, respectively (fig. 3). When spring was early, capital breeders were not synchronized as there was significant variability in the condition among individuals at day b_s (fig. 2A). The average clutch size of capital breeders was low, but the probability of recruitment of the produced offspring was relatively high, and both these metrics varied among individuals in the population (fig. 3; early spring onset). Among capital breeders in early springs, production of recruits per female was highest as the production of small clutches was accompanied with a high chance of offspring recruitment (cf. figs. 2, 3). When spring was intermediate, breeding synchrony and average clutch size of capital breeders were higher than when spring was early. Clutch size also showed greatest variability, but recruitment probability was lower compared with the scenarios of early spring onset (fig. 3). When spring was late, the average number of eggs was high and the variation in clutch size very low among capital breeders (fig. 3). Late breeding onset allowed most individuals to gather the reserves for maximum clutch size and breed immediately at day b_s. The average probability of recruitment in the population was uniform but low (fig. 3), as females in good condition had little possibility to advance breeding (fig. 2C). When comparing early versus intermediate spring onset, capital breeders were able to buffer the drop in recruitment probability by increasing the number of produced eggs (fig. 3). Income breeders cannot store reserves during the prebreeding period, and their egg numbers declined in late versus early springs, as opposed to capital breeders, for which clutch size was larger when spring was late (figs. 2, 3).

Climate-Induced Shifts in Breeding Synchrony

Our model predicts trends in breeding synchrony, clutch size, and offspring recruitment that can be interpreted as responses to climate-mediated changes in the date of
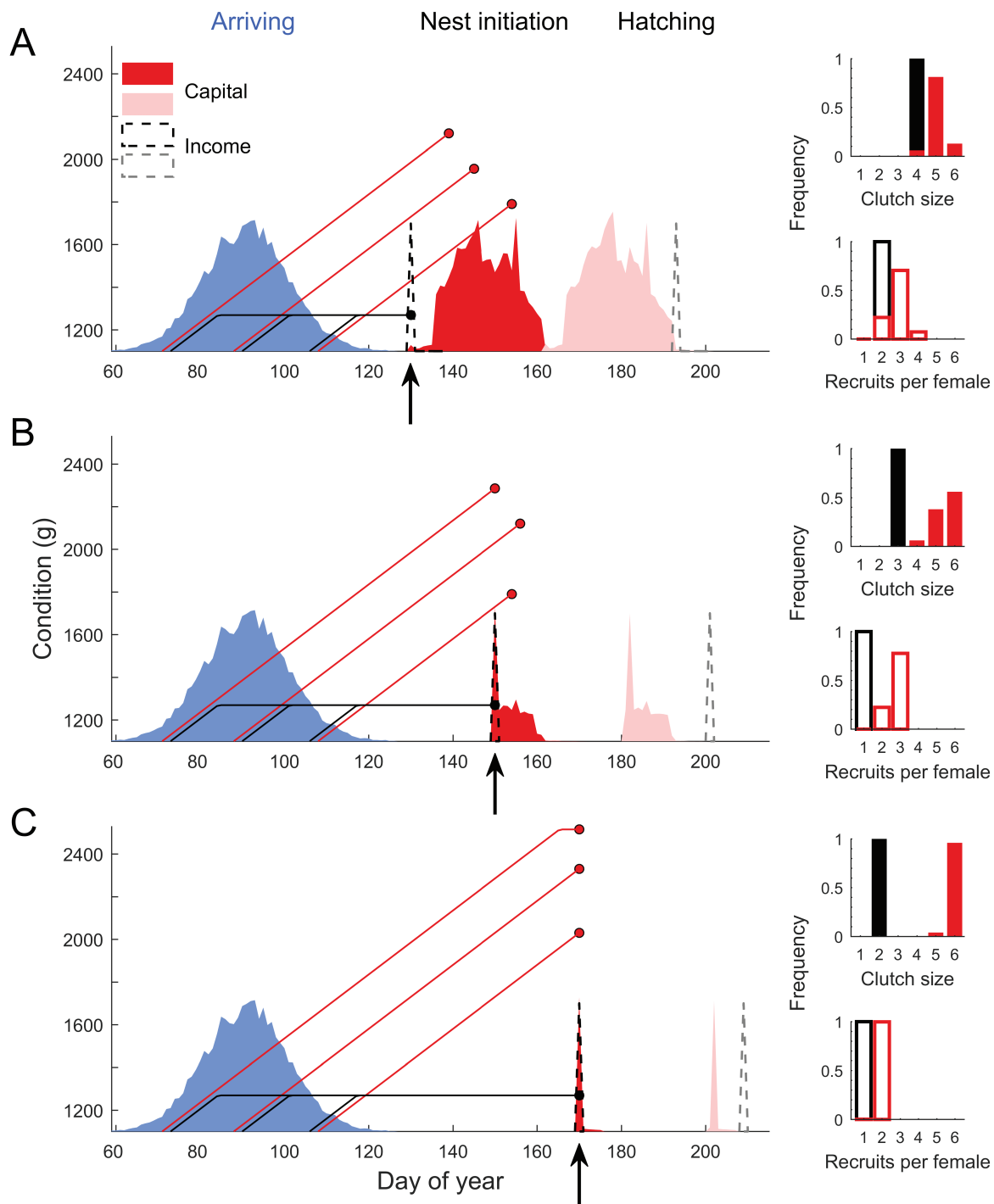
Figure 2: Optimal breeding strategies in three considered scenarios of prebreeding season length. Breeding dates, clutch size, probability of recruitment, and the number of recruits per female are presented for capital breeders (red) and income breeders (green). The main panels illustrate trajectories of body condition (solid red and dashed green lines) of females with given frequency distributions (frequency on Y-axes) of arrival dates (blue), nesting onset of capital breeders (red), and nesting onset of income breeders (dashed). Histograms illustrate the distribution of clutch size, recruitment probability, and recruits' production in the simulated population. Panels represent scenarios with first possible breeding day b_s (black dashed line) set to different prebreeding season lengths: short ($b_s = 130$; A), intermediate ($b_s = 150$; B), and long ($b_s = 170$; C). The timing of arrival for the modeled population of 10,000 females (blue) is sampled from the normal distribution with mean arrival date $D_a = 90$ and SD $= 10$.
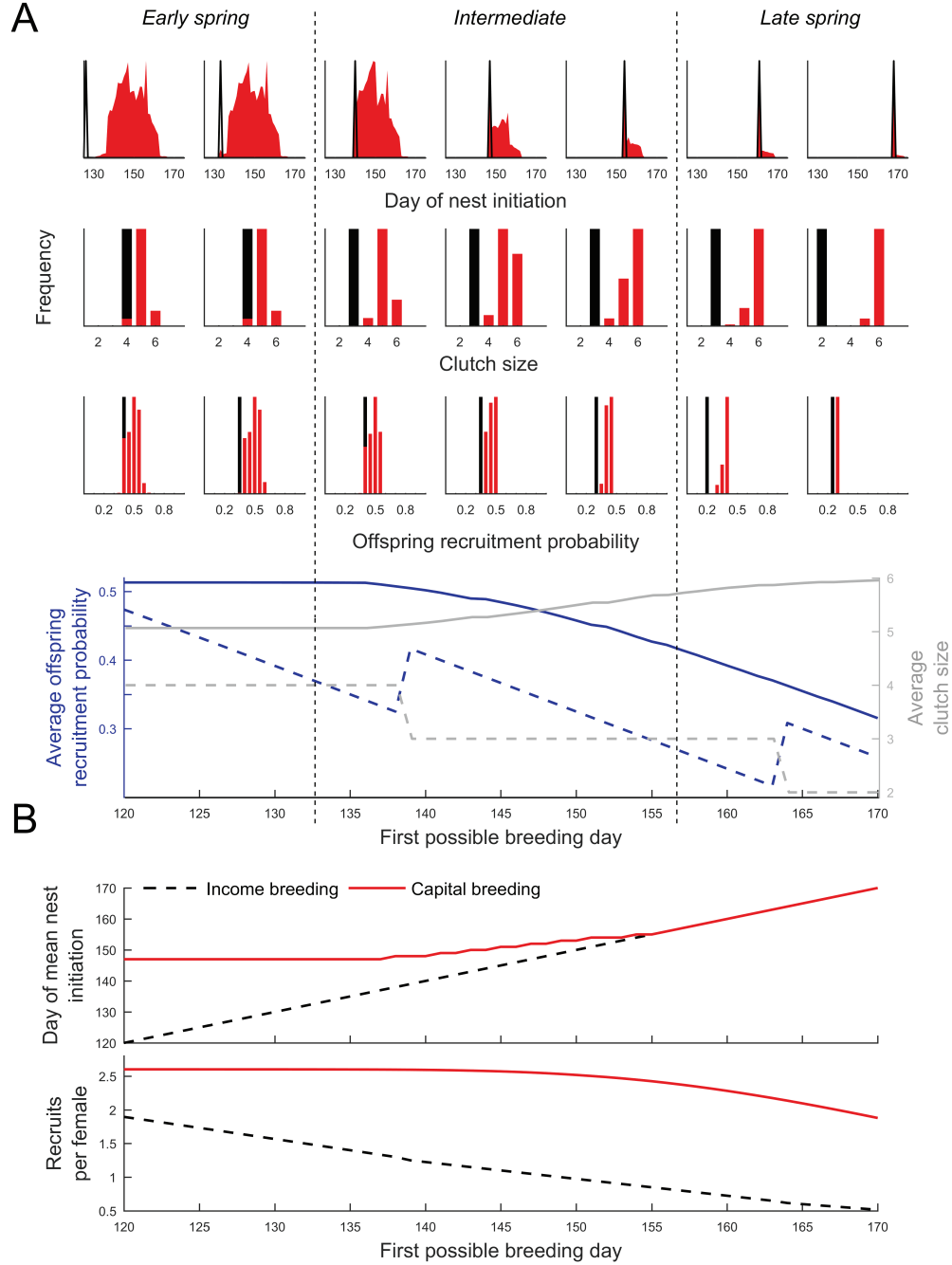
Figure 3: Breeding components and the number of produced recruits for the modeled populations of females. *A*, Breeding dates, clutch size, and probability of recruitment for capital breeders presented on a gradient of first possible breeding day b_s. The figure is divided into values of b_s corresponding to early, intermediate, and late spring onset. The position of normalized frequency distributions representing breeding onset, clutch size, and recruitment probability matches the time points specified by the "First possible breeding day" axis. Average values of the breeding characteristics for modeled populations are represented by solid lines in the bottom panels. *B*, Average breeding onset and recruits production by capital breeders compared with those of income breeders (see legend) presented on a gradient of first possible breeding day b_s.

first possible breeding onset. Specifically, a shift from cold years with late breeding season toward warm years is expected to cause a decreasing degree of synchrony in capital breeders, although income breeders are expected to remain synchronized (figs. 2, 3). Warming is also expected to cause reduction of average clutch size among capital breeders but an increase among income breeders (fig. 2). Importantly, earlier spring onset is expected to increase probability of recruitment and production of recruits for both strategies (fig. 3*B*).

With gradually earlier spring onset, our model suggests that breeding biology will change in phases. For a capital breeding migratory bird with synchronous breeding (i.e., one corresponding with late spring onset in fig. 3), the warming climate allows for earlier breeding and will initially bring no change to breeding synchronization and only little change to average clutch size (fig. 3, right to center). For both capital and income breeders, the breeding onset is expected to shift to earlier dates with an increase in number of produced recruits (fig. 3). An even earlier access to nesting sites (fig. 3, from center to left) would cause nesting by capital breeders to be spread over time, with reduced clutch size, while only modest change is expected to occur for breeding onset. In contrast, income breeders would continue to nest earlier and earlier, and with larger, not smaller, clutch size (fig. 2). The production of recruits by capital breeders is expected to increase only slightly in comparison with the increase in recruitment of income breeders (fig. 3*B*). Under very warm conditions, in which breeding is possible almost right af-

ter arrival, capital breeders are expected to produce small clutches with high probability of recruitment (fig. 3, left part), with variation in breeding dates similar to the variation in arrival dates (cf. fig. 2*A*).

Whereas parametrization of our model was inspired by the biology of common eiders, the sensitivity analysis (see the appendix) showed that the results described above regarding the response of breeding synchrony, timing of nesting, clutch size, and offspring recruitment to shifting spring onset would hold also in case of other capital breeding birds.

Empirical Data

In both monitored colonies of the common eider, the degree of breeding synchrony was higher in years with later nesting onset (fig. 4), as our model predicted for capital breeders. In the Svalbard colony, the first females started nesting as soon as snow melted, but synchrony varied. In years with late snowmelt and, consequently, late breeding onset, the rate of increase in number of breeding females (and thus breeding synchrony) was higher than for early breeding onset (fig. 4*A*). In the Iceland colony, the number of days until median nest decreased with the date of nesting onset across a data set of 20 years (fig. 4*B*).

Discussion

We have modeled capital and income breeding birds to show how their optimal breeding phenology differs in response to climatic variation in the onset of conditions
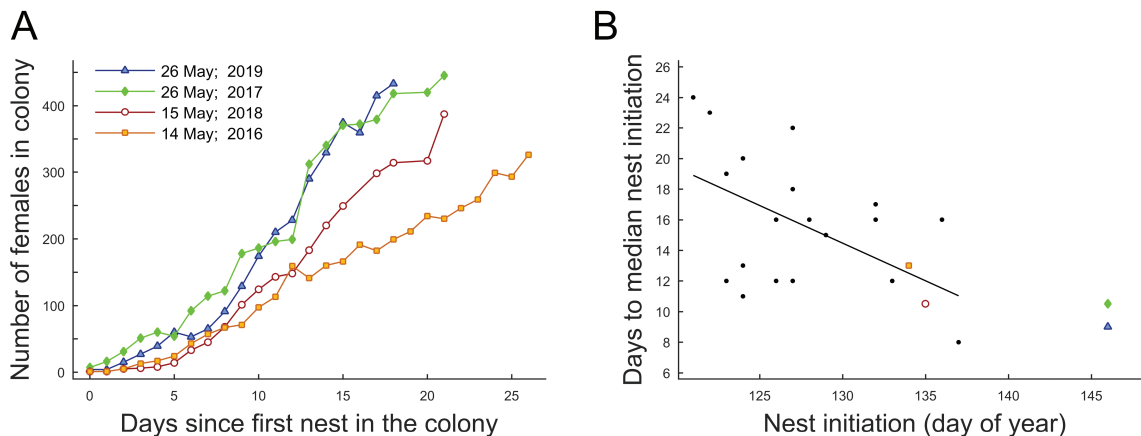

Figure 4: Breeding synchrony in relation to timing of breeding in the monitored common eider populations. *A*, The degree of breeding synchrony in the Svalbard colony presented for 4 years differing in first possible breeding day defined by the timing of snowmelt (first breeders start nesting when snow in the colony melts, based on visual observations). In years with late first-possible breeding onset (2017, 2019), the breeding synchrony was high (steep increase in number of females) in comparison with years (2016, 2018) characterized by early access to nesting sites and early nesting onset. *B*, The relation between the nest initiation date and time to median nest in the Iceland colony for 1992–2013. In years with late nesting onset, there was a higher synchrony of breeding females than in years when nesting started early (slope: −0.49, $P = .015$). For illustrative purposes, colored data points for 2016–2019 from the Svalbard colony were added to the data from the Iceland colony (black circles) but were omitted from the regression analysis.

that allow nesting. Our work predicted that in years when spring is early, both reproductive strategies would breed earlier and with higher success. In contrast, an earlier spring was characterized by diverging predictions for clutch size, which was lower for capital breeders but higher for income breeders, and nesting, which would be less synchronous among capital breeders but remain highly synchronized among income breeders. The reproductive adaptations of storing and preparing for egg production thus have contrasting consequences for these breeding characteristics. We show that the degree to which birds use storage gathered prior to breeding is crucial for predicting and interpreting demographic and ecological consequences. This is particularly relevant in light of the widespread changes in breeding phenology as spring has appeared progressively earlier over the last couple of decades—a trend that is projected to continue with climate change.

While we modeled capital and income breeding as two distinct reproductive strategies, it should be noted that these are endpoints of a continuum where many species represent a strategy in between. There is also an underlying size gradient: small passerines cannot store significant reserves because that would entail high costs in terms of constrained flight ability and increased mortality risk (Kullberg et al. 2005). Birds weighing only a few grams are therefore commonly income breeders, defined as those species unable to produce a full clutch of eggs without feeding. In light of our model predictions, climate-induced changes in breeding ecology reported for small passerines cannot be extrapolated to larger species unless the role of reserves in reproduction is taken into account.

We first discuss optimal timing of nesting, which is the most straightforward prediction from our work. Early access to nesting sites leaves a longer postbreeding period, which is good for offspring survival and recruitment (fig. 3). While income breeding requires little preparation and enables nesting onset soon after arrival, capital breeding necessitates a substantial prebreeding foraging period and, in our model, approaches an asymptote for how early nesting can commence (fig. 3*B*). Although observations from the common eider colony in Svalbard cover only 4 years (fig. 4*A*), it was observed that the first females started laying eggs as soon as the nest site was free of snow. In general, the warming climate has shifted reproduction in many bird species toward earlier nesting dates, which consequently has relaxed the constraints a short postbreeding time may impose on offspring development (Drent et al. 2003; Dunn 2004; Morrison et al. 2019). Such climate-driven changes have caused earlier nesting for many passerines as well as other birds (Halupka and Halupka 2017), including in the High Arctic (Høye et al. 2007). The timing of breeding in some species is suggested to be tightly linked to peak of food availability. For example, offspring recruit-

ment depends on a match with the peak of insect abundance in many passerine birds that have advanced breeding in response to warming (Daan et al. 1989), an effect that is not included in our models. A similar trophic mismatch between offspring production and availability of high-quality food has been observed in capital breeding snow geese (*Chen caerulescens*), where it resulted in reduced recruitment (Dickey et al. 2008; Aubry et al. 2013). However, in other species of capital breeding geese, a match between the availability of high-quality food and timing of nesting was a poor determinant of offspring recruitment, as nesting in some populations took place much earlier than can be expected from timing adjusted to the peak in high-quality food (van der Jeugd et al. 2009). This points to a pivotal role of the mechanisms included in our model: temporal constraints on offspring development and building reserves prior to breeding.

Less straightforward is how earlier arrival of spring conditions desynchronizes nesting among capital breeders but not among income breeders. Income breeders derive few benefits from the prebreeding period, as their stores are quickly maximized, and when spring conditions allow, they can all start breeding. Whereas in our model, income breeders appear highly synchronized, there are numerous mechanisms in real landscapes and populations—for example, stochastic fluctuations of local weather or daily food gain—that introduce variation of nesting onset within the breeding colony or on spatial scales beyond it. Capital breeders require time to maximize their reserves, and only when spring is late will all manage to do so and thus initiate nesting in a highly synchronized manner. If spring starts early, only those that arrived ahead of others in the population or are in good condition for other reasons will be ready to breed. Thus, variation among individuals in their stored capital translates into desynchronized breeding.

Substantial year-to-year variation in breeding synchrony has been reported from seabird monitoring data, and our model helps interpret why synchrony is higher in years when breeding generally is later (Burr et al. 2016), as these species are mostly capital breeders. The empirical observations from the Svalbard and Iceland colonies of capital breeding common eiders fit the predicted change in degree of breeding synchrony: in both colonies, we observed increased synchronization in years of late nesting onset (fig. 4). It should be noted that there is sufficient light for underwater foraging for mussels throughout the winter in Iceland, and eiders can therefore overwinter there without need for an energy-costly migration with a lightweight body. This may explain why the eiders in Iceland breed earlier than predicted by the model with Svalbard parameters, which represent the High Arctic summer much further north. In lapwings (*Vanellus vanellus*), which are migratory birds, a long-term monitoring study spanning

about 50 years of breeding phenology showed that timing of laying initiation moved to earlier dates, but the breeding synchrony, measured as the difference between the first and tenth laid egg, decreased with warmer spring temperatures (Both et al. 2005), which is consistent with our findings for capital breeders. In well-documented experimental studies on the costs and benefits associated with laying date in European kestrel (*Falco tinnunculus*) and European coot (*Fulica atra*), early egg laying was beneficial, but only individuals in good condition could afford to breed early (Daan and Tinbergen 1997; Brinkhof et al. 2002). Differences in condition can be further complicated by carryover effects, as in the capital breeding pink-footed goose (*Anser brachyrhynchus*), for which body condition at a stopover site along the migration route (Norway) determines reproductive success at the nesting site (Svalbard; Drent et al. 2003). Because our model explicitly considers the time needed to gather stores for reproduction, it explains why capital breeding birds in good condition benefit from breeding early but, importantly, also how females in poor condition are forced to breed later since they need to catch up with gathering stores to maximize fitness.

Even more interesting are the counterintuitive predictions about optimal clutch size, where earlier springs are associated with having larger clutches for income breeders but smaller clutches for capital breeders. Key to understanding this result is to focus sharply on the trade-off between foraging prior to breeding and time available for offspring development after hatching. If spring is late, this trade-off is nonexistent for capital breeders, as most have already reached their maximal storage capacity, whereas income breeders experience the same trade-off brutally because each extra egg will require foraging that takes away crucial development time for the whole brood. Conversely, if spring is early, this same trade-off is relaxed for income breeders, whereas capital breeders suddenly experience a drop in postbreeding development time for all offspring if they continue foraging for another egg. This fits with observations among income breeding passerines, which in warmer temperatures reproduce earlier and produce more offspring, in line with our model, or have increased chance for laying replacement or multiple clutches, which our model did not consider (Winkler et al. 2002; Dunn 2004; Morrison et al. 2015, 2019). Contrast this with heavier passerines that may rely more on capital breeding, for example, starlings (*Sturnus vulgaris*), which breed earlier but lay fewer eggs in warm years (Williams et al. 2015). Such a size gradient in capital breeding is also evident among boreal owls, where clutch size depends on food availability prior to breeding for large species but not for the small ones, which presumably respond more to current conditions (Lehikoinen et al. 2011). Unfortunately, we do not have data on clutch size for the eider colonies, a metric that is difficult to obtain for some groups, such as sea ducks including common eider, which have a high degree of conspecific brood parasitism in dense breeding colonies so that the number of eggs in the nest does not necessarily reflect the clutch size of the female (e.g., Waldeck et al. 2004). Thus, these data are not available for the focal eider populations to allow testing the model predictions.

It is further interesting to note how the relationship between clutch size and nesting date is different for capital breeding individuals within one season when compared with population averages across different years. Similar to the model by Rowe and colleagues (1994) for a single population of capital breeders under early spring onset, individual females in sufficient condition to breed early produced larger clutches than females breeding later in the season (see individual condition trajectories in fig. 2A). However, when different spring onsets are considered, capital breeders produced smaller clutches on average in years with early spring onset compared to late breeding onset (cf. fig. 2A–2C, or see fig. 3A). In many bird species that breed earlier in warmer years, changes in reproductive performance—that is, clutch size and offspring recruitment—tend to be more variable in response to increased temperature (reviewed in Dunn 2004). This aligns with the predictions from our model for capital breeders. We thus recommend that the role of reserves prior to reproduction should be considered when clutch size and breeding timing responses to warming are discussed.

Optimal responses in timing of breeding, synchrony, and clutch size translate into overall effects on expected number of recruits (see fig. 3). These can be complex—as potentially many independent factors may interact and cumulatively affect probability of recruitment—and make clear some of the limitations of our models. For example, seasonal trends in food quality are not yet considered but could affect offspring recruitment. The models further assume that conditions for the hatchlings remain unchanged with varying spring phenology, although matching the peak food for offspring needs is a major challenge for some species. Extrapolation beyond birds can be problematic as breeding timing of capital breeders in other taxa is shaped by trade-offs related to physiological features absent in birds, for example, growth continued after maturation (Jørgensen et al. 2006), physiological limits of lactation (Houston et al. 2007), or diapause (Ejsmond et al. 2018). On the other hand, there are important factors that have been omitted in our model but are expected to have little effect on the model predictions. For example, in the model the only origin of variation in body condition is arrival date, although birds may differ in condition already on arrival. However, the conclusions derived from our work hold as long as there is prebreeding variation in body condition, regardless of the mechanisms that introduce this variation.

The theoretical life history approach applied in this study reveals that breeding synchrony and clutch size vary with shifting spring onset in ways that differ between capital and income breeders. Reproductive strategy, effects on individual condition, and a nuanced picture where several traits are interpreted in concert are therefore needed to predict how phenology and breeding strategies of birds have changed and will continue to be affected in warming ecosystems, including the Arctic.

Statement of Authorship

A.E. and C.J. conceived the study, designed the model, and wrote the code. A.E. ran the simulations and performed the analyses with input from Ø.V., C.J., and M.F. Data from Svalbard were collected by A.E. and M.F. J.E.J. provided data from Iceland. A.E. drafted the paper, and all authors contributed to writing.

Data and Code Availability

The computer program used in the work is available on Zenodo (https://doi.org/10.5281/zenodo.4751089; Ejsmond et al. 2021).

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A common eider female on her nest in a high Arctic colony. These capital breeders do not feed during the time of egg incubation; hence, females need to gain extensive body reserves prior to breeding. Photo credit: Anna Ejsmond.