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Warming springs and habitat alteration interact to impact timing of breeding and population dynamics in a migratory bird

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Abstract

In seasonal environments, increasing spring temperatures lead many taxa to advance the timing of reproduction. Species that do not may suffer lower fitness. We investigated why black-tailed godwits (*Limosa limosa limosa*), a ground-breeding agricultural grassland shorebird, have not advanced timing of reproduction during the last three decades in the face of climate change and human-induced habitat degradation. We used data from an 11-year field study to parameterize an Integral Projection Model to predict how spring temperature and habitat quality simultaneously influence the timing of reproduction and population dynamics. We found apparent selection for earlier laying, but not a correlation between the laying dates of parents and their offspring. Nevertheless, in warmer springs, laying dates of adults show a stronger positive correlation with laying date in previous springs than in cooler ones, and this leads us to predict a slight advance in the timing of reproduction if spring temperatures continue to increase. We also show that only in landscapes with low agricultural activity, the population can continue to act as a source. This study shows how climate change and declining habitat quality may enhance extinction risk.

KEYWORDS
agricultural intensification, climate change, Integral Projection Model, phenology, shorebirds, source and sink

1 | INTRODUCTION

We live in an era during which environments are changing rapidly due to large-scale human-induced habitat alterations, which range from complete destruction of habitats to effects induced by global climate change (Sala et al., 2000). Numerous studies have revealed that timing of reproduction has advanced in many species breeding in seasonal environments in response to increasing spring temperatures (Parmesan, 2007). Yet, the phenology of some species has not

altered sufficiently to maintain a match between local peaks in resource availability and the time of highest energy demands for offspring in the growing phase (Both, Bouwhuis, Lessells, & Visser, 2006; Plard et al., 2014; Reneerkens et al., 2016; Visser, Noordwijk, Tinbergen, & Lessells, 1998). Likewise, individuals also need to optimize their phenology to, for instance, breeding site availability or predator occurrence which may vary within the season. As shown for mammals (e.g., Plard et al., 2014), birds (e.g., Both et al., 2006;

Saino et al., 2011), plankton and fish (e.g., Edwards & Richardson, 2004), any phenological mismatch may reduce fitness and population size. This reduction in fitness has been shown to be greater in habitats which have been significantly altered by humans in recent decades (Forister et al., 2010).

Modification of habitats often impacts survival and reproductive rates (e.g., Allen et al., 2017; Piersma et al., 2016), for example, by altering food availability, introducing predators or making the habitat more suitable for predators. If reproduction becomes sufficiently suppressed that it cannot counter losses due to mortality, populations become "sinks" (Pulliam, 1988). Without a contribution from source areas, where more recruits are produced than adults die, such sink populations will decline in size and eventually go extinct. In addition, rapidly deteriorating habitats may impact environmental cues associated with optimally timed reproduction (Bourgault, Thomas, Perret, & Blondel, 2010; Winkler et al., 2014), making the combination of climate change and altered habitats especially difficult for populations to adapt to. Several integrative studies have disentangled climate or habitat effects on population dynamics (e.g., Gamelon et al., 2017; van der Meer, Jacquemyn, Carey, & Jongejans, 2016; Simmonds & Coulson, 2015) or have studied correlations between timing of reproduction and population growth (e.g., Both et al., 2006; Dunn & Møller, 2014). To our knowledge, the interactive mechanistic effects of habitat quality, climate change and timing of reproduction on population growth have not been examined before.

Agricultural landscapes have seen a higher rate of change in the past decades than any other type of landscape, and this change may well continue given projected human population growth (Foley et al., 2005; Tilman et al., 2001). On temperate agricultural grasslands, landscape-scale changes in agriculture, including increased fertilizer use and drainage of excess rain- and groundwater, combined with increasing spring temperatures have triggered earlier grass growth, insect emergence dates and advanced agricultural schedules (Kleijn et al., 2010). Bird communities breeding here have been affected by advancing agricultural practices such as mowing. Mowing alters reproductive outputs (Grüebler, Schuler, Horch, & Spaar, 2012; Kragten & De Snoo, 2007; Schekkerman, Teunissen, & Oosterveld, 2008) by placing nests at risk of physical destruction as well as reducing available cover of remaining nests (Kentie, Both, Hooijmeijer, & Piersma, 2015), and cover and food availability for the precocial chicks (Kentie, Hooijmeijer, Trimbos, Groen, & Piersma, 2013; Schekkerman & Beintema, 2007). These climatic and land use changes are associated with advanced arrival dates and timing of reproduction in species that reproduce on agricultural landscapes (Brandsma, Kentie, & Piersma, 2017; Gill et al., 2014; Smith, Steenhof, Mcclure, & Heath, 2017).

Arrival and laying dates of migratory black-tailed godwits (*Limosa limosa limosa*) breeding on agricultural grasslands in Western Europe have not advanced since 1975 (Kleijn et al., 2010; Meltofte, Amstrup, Petersen, Rigét, & Tøttrup, 2018; Schroeder et al., 2012). Over a similar period, their population has declined by 75% (Kentie, Hooijmeijer, Verhoeven, Senner, & Piersma, 2016), primarily due to reproductive failure on intensified agricultural grasslands (Roodbergen, van der Werf, & Hötker, 2012; Schekkerman et al., 2008). In such habitats,

mowing advanced by 0.7 day/year (Kleijn et al., 2010). One hypothesis to explain the failure of some migratory species to advance laying dates is that at the wintering grounds, they are unable to predict climatic conditions on the breeding grounds (Both & Visser, 2001; Lok, Veldhoen, Overdijk, Tinbergen, & Piersma, 2017). However, black-tailed godwits arrive on average 6 weeks before the onset of laying (Lourenço et al., 2011), which seem to allow them sufficient time to adjust laying dates to local spring conditions, as other shorebirds needed between 1 and 3 weeks (Gill et al., 2014).

In this study, we modelled the effects of spring temperature and agricultural land use intensity on laying dates while simultaneously examining how laying date affected fitness, and consequently population growth rates. We parameterised our structured model (Ellner & Rees, 2006; Smallegange & Coulson, 2013) using data from a long-term demographic study (2007–2017). We then used the model to (a) predict laying dates at different spring temperatures at different agricultural land use intensities, (b) explain why black-tailed godwits laying dates have not advanced in recent decades, (c) investigate the effects of spring temperature and agricultural land use intensity on population growth, and (d) predict population persistence and laying date in each of the different agricultural land use intensities if spring temperatures would continue to increase.

2 | MATERIALS AND METHODS

### 2.1 | Model framework: Integral Projection Model

We constructed an Integral Projection Model (IPM) to investigate how spring temperature and agricultural land use intensity influenced timing of reproduction and population dynamics of black-tailed godwits. An IPM is a discrete-time population projection model structured by a continuous trait (Coulson, 2012). Instead of body size, which is primarily used as continuous trait, we used laying date. We built the IPM from functions describing how laying date (z) in year t influenced: (a) adult survival to $t + 1$, $S(z, t)$; (b) laying date in year $t + 1$, $G(z'|z, t)$; (c) recruitment of offspring to the population at year $t + 1$, $R(z, t)$; and (d) offspring laying date at $t + 1$, $D(z'|z, t)$, where z' denotes the laying date at time $t + 1$. These functions were parameterized for three different habitat types and three spring temperature scenarios using predictions from field data. The IPM can be written as:

$$n(z', t + 1) = \int [G(z'|z, t)S(z, t) + D(z'|z, t)R(z, t)]n(z, t)\,\mathrm{d}z,$$

where $n(z, t)$ is the distribution of character traits z at time t, and $n(z', t + 1)$ is the distribution of character traits z' at time $t + 1$. From the IPM, we calculated the long run population growth rate and mean laying date, and assessed the relative contribution of each parameter to laying date and growth rate with a sensitivity analysis.

2.2 | Parameterisation of IPMs

Separate stochastic IPMs were constructed for habitats with low, intermediate and high agricultural land use intensity, and for three
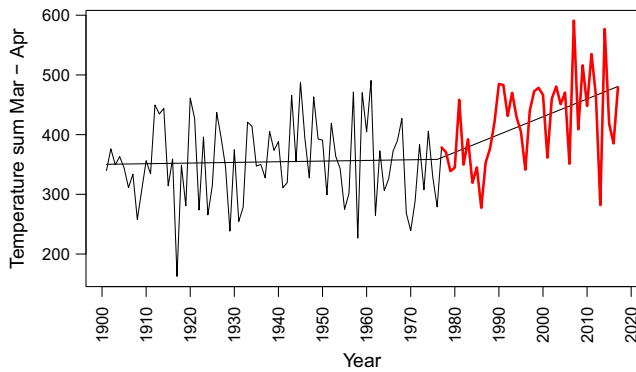
FIGURE 1 Sum of daily average temperatures of March and April (Tsum), extrapolated from weather station De Bilt to fit the weather in our study area from 1900 until 2017. The thick (red) line represents the period when temperatures started to rise [Colour figure can be viewed at wileyonlinelibrary.com]

stochastic spring temperature scenarios reflecting springs before spring temperatures rose (~1900–1975), the present (2007–2017) (Figure 1) and an assumed warmer future spring (~2040 if temperature increases linearly). Although only one-third of godwits return to breed in their second year of life (Kentie, 2015), we opted to keep the model simple; we assumed that each individual attempted to breed each year, and we did not construct an age-structured model, nor took repeat breeding attempts after failure and dispersal between habitat types into account. We used field data of uniquely marked female godwits (unless stated otherwise) of a demographic study spanning 2007–2017 to parameterize the functions defining the IPMs. We included effects of spring temperature and land use intensity if they sufficiently explained observed variation in the demographic data (see below for details of the statistical analyses). As laying date is a labile trait (Childs, Sheldon, & Rees, 2016), we also tested effects of spring temperature in $t + 1$ for functions $G(z'|z, t)$ and $D(z'|z, t)$.

2.3 | Study area

Field data were collected between 2007 and 2017 in a region of dairy farming in southwest Friesland, the Netherlands (52°55′N, 5°25′E; Kentie et al., 2015). In 2007, we monitored godwits on 8,970 ha of agricultural land, but expanded the study area in 2012 to include an adjacent area of 2,445 ha (see for a description Groen et al., 2012; Howison, Piersma, Kentie, Hooijmeijer, & Olff, 2018). We categorized agricultural fields into low, intermediate and high land use intensity using change in vegetation structure measurements of the Sentinel-1 C-SAR (active radar) satellite and verified with detailed ground surveys (see Howison et al., 2018 for a detailed description). In general, grasslands of low land use intensity show little seasonal change in vegetation height; they are characterized by high water tables, herb-rich vegetation, and mowing is delayed until after 15 June as they are often part of an agri-environmental conservation scheme. In contrast, grasslands with high land use intensity are intensely managed for dairy farming, with mowing occurring as

early as mid-April and frequently (every 3–4 weeks) throughout the summer, where early mowing coincides with the incubation stage of the godwits (Kentie et al., 2015). To enable early mowing, water tables are kept low, and the vegetation consists of a monoculture of fast-growing rye grasses *Lolium* sp., onto which fertilizers are applied (Groen et al., 2012; Howison et al., 2018). Intermediate land use intensity consists of fields grazed by livestock or mown less frequently than intensively managed fields. The categorization of land use is based on the situation in 2016, and some fields might have changed during the study period. Our field crews, however, observed that ~80% of fields have stable management schemes throughout the study period. In 2016, the sizes of the study area for low, intermediate and high land use intensity were respectively, 3,935, 2,669 and 4,814 ha (Howison et al., 2018).

2.4 | Spring temperatures

To define spring temperatures during field work years, we used data from Stavoren weather station within our study area (Royal Netherlands Meteorological Institute [KNMI]; www.knmi.nl). For each year, we calculated spring temperature sum (Tsum) by adding up daily average temperatures in March and April. In these months, godwits arrive and start to incubate. This measure of spring temperature showed a strong negative correlation with median first mowing dates, which we estimated in 2008–2016 from randomly chosen fields in our study area of which we annually recorded first mowing dates and which did not have mowing restrictions or grazing cattle (N between 34 and 41, $F_{1,6} = 15.45$, $p = 0.008$, $R^2 = 0.72$). Between 2007 and 2017, Tsum varied between 229 and 589°C with a mean of 450°C (Figure 1).

To investigate past spring temperatures in our study area, we extrapolated spring temperatures for the period from 1900 to 2017 from the weather station De Bilt, because Stavoren weather station started measuring weather data from 1990 onwards (90 km from Stavoren; Tsum Stavoren = −28 + 0.97 × Tsum De Bilt, $R^2 = 0.94$; www.knmi.nl). We used R package "segmented" (Muggeo, 2008) to analyse the start of spring temperature rise in our study area (Figure 1).

2.5 | Timing and demographic field data of godwits

Godwits breed on the ground; their nests were located and positions stored in a GPS. Because nests were almost always found during the incubation stage, we estimated laying date by floating the eggs in water and measured the float angle (Liebezeit et al., 2007). A nest was considered successful if at least one chick was found in the nest, or if we found an indication of successful hatching (Kentie et al., 2015). From 2008 onwards, 1-day-old chicks were marked with a flag-ring with a unique code. Adults were caught on the nest and uniquely marked with a flag and four plastic colour rings and a numbered metal ring. Chicks older than 10 days, including recaptured chicks wearing a flag-ring with a code, were also marked with a flag and four plastic colour rings and a numbered metal ring. Every year we scanned birds for colour rings on a daily basis throughout the

breeding period. Colour marked black-tailed godwits were linked to the nest by observing returning parents from a distance, or by placing camera traps at the nest site. We collected a blood sample to genetically determine sex (see Trimbos et al., 2013 for details), but if a blood sample was lacking, we used morphological measurements to sex adults (Schroeder et al., 2008; 8% of 649 individuals).

2.6 | Statistical demographic analyses for S(z,t)

We used Cormack–Jolly–Seber mark–recapture models (White & Burnham, 1999) to test whether apparent adult survival probability was constant or was associated with laying date, Tsum and land use intensity of their breeding location in the year it was captured (N = 649). We only included sightings of females if they were seen at least twice within a breeding season in our research area. Resighting rate was modelled to be constant, to vary between years, and to vary between land use intensities. Because godwits are site faithful (Kentie, Both, Hooijmeijer, & Piersma, 2014), we assumed that apparent survival is close to true survival. Not all nests were found, and not all found nests could be linked to an individually marked godwit. Therefore, we do not have each individual's laying date for each year, and we used laying date of the year a bird was first captured. In a preliminary test, where laying date only affected survival in the year of which we used laying date—the first year after marking—we found similar results.

2.7 | Statistical demographic analyses for G(z′|z, t)

Within-individual development of laying dates accounts for the flexibility of laying from 1 year to the next. Godwits can lay repeat clutches if the first failed (Senner, Verhoeven, Hooijmeijer, & Piersma, 2015). Including these repeat attempts would lead to a bias in the relationship between laying date at time t and at time $t + 1$. However, usually we were unaware whether we found the first or a repeat nest. From laying dates of confirmed repeat nests (N = 67), we estimated that 95% of the repeat nests occurred after 27 April. To establish the relationship between laying date at time $t + 1$ and at time t within individuals, we used a linear model with a Gaussian error structure with laying dates until 27 April (N = 174, 37, 41 for low, intermediate and high land use intensity). Because laying date can be a labile trait and is more likely defined by spring temperature in the year of breeding, we included Tsum at $t + 1$ as direct laying date cue instead of Tsum at t. We tested for effects of laying date at t, and Tsum at $t + 1$ and its interaction on laying date at $t + 1$, and included land use intensity as factor. We estimated the variance around the intercept to include in the IPM model.

2.8 | Statistical demographic analyses for R(z, t)

To estimate reproductive success, we separately estimated nest survival and first-year survival probability. We assumed 3.7 hatched eggs per successful nest (Kentie, 2015) and equal sex ratios at hatch (R. Kentie, A. H. J. Loonstra, T. Piersma, unpublished data).

We used binomial generalized linear models to test models for nest survival using all nests of which we knew when it was laid (N = 4,018, 951 and 966 nests for low, intermediate and high land use intensity, respectively). To account for nests, we have not found before they were lost, nest age when found was included as a covariate. A nest which is found shortly after it was initiated has a higher chance to get predated while being under observation than a nest which is due to hatch soon. We assumed a linear relationship between the covariate nest age when found and nest success, and kept it zero when extracting parameter estimates, so that nest survival was estimated from the moment of laying. We analysed nest survival with covariates laying date, quadratic laying date, land use intensity, Tsum and all two-way interactions.

We used Cormack–Jolly–Seber mark–recapture models with an age structure to estimate survival from hatch day until the following year. We always included land use intensity as predictor based on previous results (Kentie et al., 2013, 2014), and we tested models with laying date of their birth nest, Tsum, and each interaction between laying date, land use intensity and Tsum as predictors for survival rate of the first age class (N = 2239 hatchlings). Survival probability after the first year was kept constant. Based on earlier results (Kentie et al., 2014), resighting probability always contained age class (first year and adult), whether a bird was ringed with a flag-ring or a more visible colour ring combination (3.6% of chicks) and was either constant or could vary between years. A preliminary test showed no evidence of a quadratic effect of laying date (dAIC > 44 than in the best model without quadratic effects), which we therefore not included in the models.

2.9 | Statistical demographic analyses for D(z′|z, t)

We tested for a parent–offspring association in laying dates with a linear model using a Gaussian error structure and estimated the variance around the intercept. Because most young godwits start breeding in their second year after hatching, we excluded earlier breeding attempts (N = 8) to exclude potential age effects. We included all chicks to increase the sample size (N females 19, N males 9, N unknown sex 8). A preliminary test did not find a difference in laying dates between males and females ($F_{1,26} = 0.05$, $p = 0.8$). Too few godwits recruited successfully from fields of intermediate and high land use intensity (4 and 3, respectively, of N = 36) to account for effects of land use intensity. We therefore tested only for an effect of parents laying date, Tsum when hatched, and Tsum at $t + 2$.

2.10 | Statistical demographic analyses: model selection and inferences

Statistical analyses were carried out in R 3.4.3 (R Core Team, 2017). We used RMark (Laake, 2013) for mark–recapture models. Goodness-of-fit was checked with program release from within R (release.gof). We used a variance inflation factor, or ĉ, of 1.5 for the data set with birds ringed as adults as the data were overdispersed (Test 2: $\chi^2 = 81.38$, $df = 22$, $p < 0.001$, Test 3: $\chi^2 = 27.11$, $df = 50$,

p > 0.5). Goodness-of-fit test showed no signs of overdispersion for the data set of birds marked as chicks (Test 2: χ^2 = 23.0, *df* = 3, *p* = 0.9). Model selection was based on Akaike's information criterion adjusted for small sample sizes (AICc; Burnham & Anderson, 2002). Model selection procedures are described in the Supporting Information. We used Tsum/100 to reach model convergence.
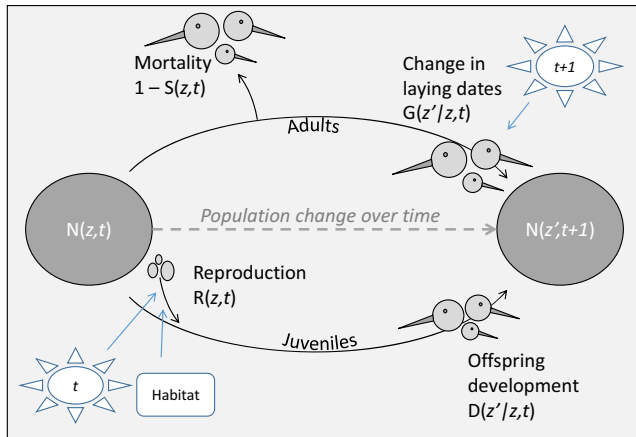
FIGURE 2 Life-cycle diagram of our model system, showing the processes influencing population size *N* with trait distribution *z* (laying date) between time *t* and time *t* + *1*. The dark grey circles represent the population size and the distribution of trait *z*. The upper curved arrow is the trajectory for individuals who were adults at time *t*, while the lower curved arrow is the trajectory for new recruits. As external factors, habitat (land use intensity) and spring temperature at time *t* (shown as the sun) influenced reproductive output, while spring temperature at time *t* + *1* influenced laying dates of adults [Colour figure can be viewed at wileyonlinelibrary.com]

2.11 | IPM modelling

As demographic relationships both depend on Tsum at time *t* and at time *t* + *1*, we built stochastic IPMs with simulated yearly fluctuating Tsums (see Figure 2 for a life-cycle diagram). The IPM contained matrices of 250 discrete bins of laying dates, which ranged between −10 and 80. We built separate IPMs for fields with low, intermediate and high land use intensity, with past, present and future spring temperature scenarios. The three spring temperature scenarios had a mean Tsum of 350, 450 and 550°C, for "past," "present" and "future" respectively, and a standard deviation of 70, which corresponds to the standard deviation of the temperatures between 1900 and 1975 (see Supporting Information Figure S1 for simulated Tsums). Future spring scenario represents 2040 if Tsum will continue to increase at the same rate. The temperature scenarios were generated randomly for a 5,000-year time span. We then started with 100 individuals laying at 24 April, and followed the population trajectories for each. We inspected the results, then discarded the first 100 time steps and stored laying date, population structure and growth rate (natural log lambda) of the remaining 4,900 time steps. Sensitivities of the vital rates were tested for the models with a current temperature scenario, by subsequently changing each parameter by 0.1%.

3 | RESULTS

3.1 | Are there population level changes in laying dates?

The annual mode of laying date, which corresponds to peak laying dates (and thus independent of repeat clutches), did not advance between 2007 and 2017 (Figure 3a). The yearly mode was
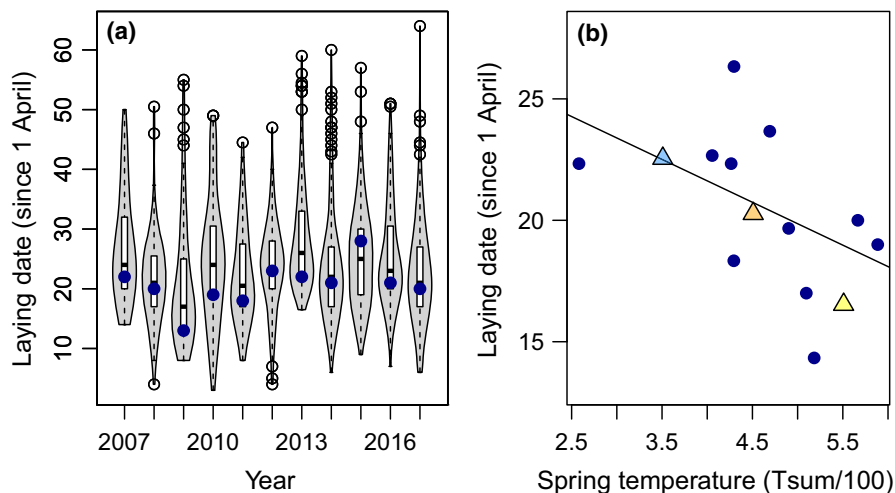
FIGURE 3 (a) Laying dates of black-tailed godwits in our study area. Boxplots (white) showing the interquartile range, with the median (black line) and outliers (open points), and mode (closed dark blue points). The violin plot shows the distribution of the laying date per year. (b) Relationship between the annual mode of observed laying date in black-tailed godwits and spring temperature sum (March to April) during 2007–2017 (closed dark blue points) and model predictions from the IPMs (triangles, colours match Figure 6) for godwits breeding on fields of low land use intensity (past, present and future spring temperatures corresponded to Tsums of 350, 450 and 550, respectively) [Colour figure can be viewed at wileyonlinelibrary.com]

negatively correlated with spring temperature (R^2 = 0.12, p = 0.03), but not with land use intensity (Tsum: 186.6 AICc, df = 3; null-model: 189.3 AICc, df = 2; Tsum + land use: 190.8 AICc, df = 5; land use: 193.3 AICc, df = 4; Figure 3b). Between 2007 and 2017, the mode of laying date was on average 21 April.

3.2 | Demographic and laying date functions

Adult females survived with a probability of 0.86 (0.84–0.87 95% CI) to the next year (Table 1a). The best-supported model had a constant survival and resighting probability. See Supporting Information for all model comparisons. Resighting rate was 0.88 (0.87–0.90 95% CI; see Supporting Information). Survival of newly hatched chicks until the following year declined with laying date in interaction with

TABLE 1 Model parameter estimates used for the functions in the IPMs. Model selection procedures are described in the Supporting Information

| Parameters	Estimate	SE
(a) Adult survival (logit)		
Intercept	1.790	0.061
(b) Juvenile survival (logit)		
Intercept–adult	1.482	0.190
Young	−1.272	0.644
Young × Laying date	−0.063	0.012
Young × Tsum	−0.005	0.096
Young × Intermediate land use	0.239	1.104
Young × High land use	2.191	1.211
Young × Tsum × Intermediate land use	−0.167	0.263
Young × Tsum × High land use	−0.583	0.287
(c) Nest survival (logit)		
Intercept	−0.177	0.282
Laying date	0.073	0.013
Laying date^2	−0.002	0.000
Tsum	−0.135	0.039
Intermediate land use	0.173	0.393
High land use	−1.423	0.418
Age of nest when found	0.111	0.006
Tsum × Intermediate land use	−0.132	0.086
Tsum × High land use	0.158	0.091
(d) Laying date at t + 1		
Intercept	36.256	7.735
Laying date	−0.359	0.354
Tsum t + 1	−6.079	1.672
Laying date × Tsum t + 1	0.193	0.076
Variance (intercept)	18.184	1.547
(e) Parent–offspring relationship		
Intercept	24.264	1.318
Variance (intercept)	60.84	11.7

Note. Tsum is divided by 100.

land use intensity and spring temperature (Table 1b). First-year survival was highest for chicks hatched on fields of low land use intensity in cold springs, and lowest when hatched on fields of high land use intensity in warm springs. The effect of spring temperature was largest for chicks hatched on high land use intensity fields. Nest survival showed a quadratic relationship with highest survival for a laying date of 21 April. Additionally, survival was highest for nests on low land use fields in cold springs and lowest for nests on high land use fields. We also found support for an interaction between spring temperature and land use intensity: The effect of spring temperature, with warmer springs leading to lower nest survival, was highest on intermediate land use fields and absent on high land use fields (Table 1c). The combined effects of reproduction show that later laying and higher land use intensity correlate with lower numbers of recruits, and that higher spring temperatures correlate with lower numbers of recruits most notably on the intermediate and high land use fields (Figure 4).

Laying dates of individual females were more repeatable between consecutive years in warm springs at t + 1 (i.e., had a slope closer to x = y) and were not correlated with land use intensity (Table 1d, Figure 5a). Laying date of young godwits 2 years after hatching did not correlate with Tsum when hatched, Tsum 2 years after hatching, nor laying dates of their parents (Table 1e; Figure 5b). We found this lack of relationship after removing a suspicious outlier, which was a nest with a laying date of 25 May. This appeared to be a second breeding attempt, as this individual was seen nest building on 11 April.

3.3 | IPM: effect of habitat, spring temperature and laying date on population growth rate and laying date

The results of the IPMs predict that mean laying dates did not differ much between different land use intensities and showed a wide standard deviation of the mean (Figure 6a). The predicted laying dates for past and present spring temperature scenarios are close to the observed peak laying date; a difference of 1–2 days (see also Figure 3b). The wide standard deviation shows that mean laying dates are predicted to vary substantially per year. On fields with low land use intensity, mean laying date advanced from past to present spring scenarios by 2 days and is predicted to advance to future spring scenarios by 4 days. On fields with intermediate and high land use intensity, mean laying date is predicted to advance by 6 days.

Mean predicted annual population growth rates differed between land use intensities and spring temperature scenarios (Figure 6b). On fields with low land use intensity, growth rates were positive in the past, present and future scenarios. On fields with intermediate and high land use intensity, predicted growth rates approached zero in past temperature scenarios and are predicted to be negative for present and future scenarios. Note that in the past, fields with a comparably high land use intensity did not exist.
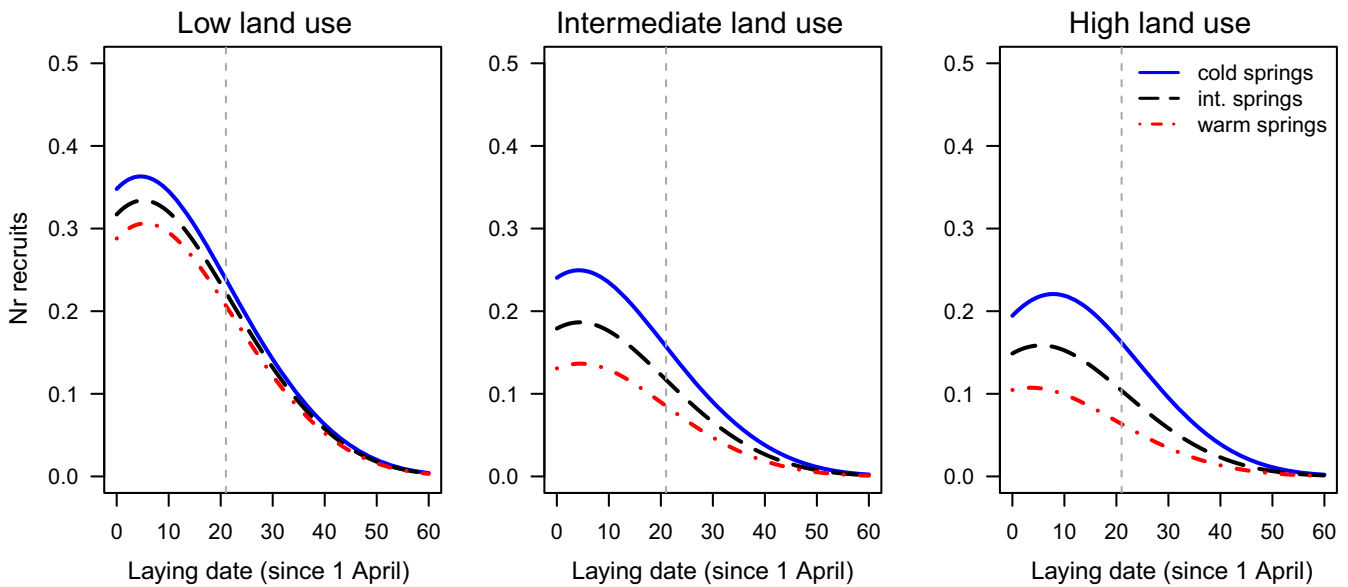
FIGURE 4 Number of recruits of black-tailed godwits related to laying date on low, intermediate and high land use fields for three spring temperature scenarios. We combined model predictions from nest survival and first-year survival models, and assumed 3.7 eggs hatched per successful nests, and equal sex ratio of chicks. Cold is Tsum of 350, intermediate is Tsum of 450, and warm is Tsum of 550. The dotted line is observed peak laying date [Colour figure can be viewed at wileyonlinelibrary.com]
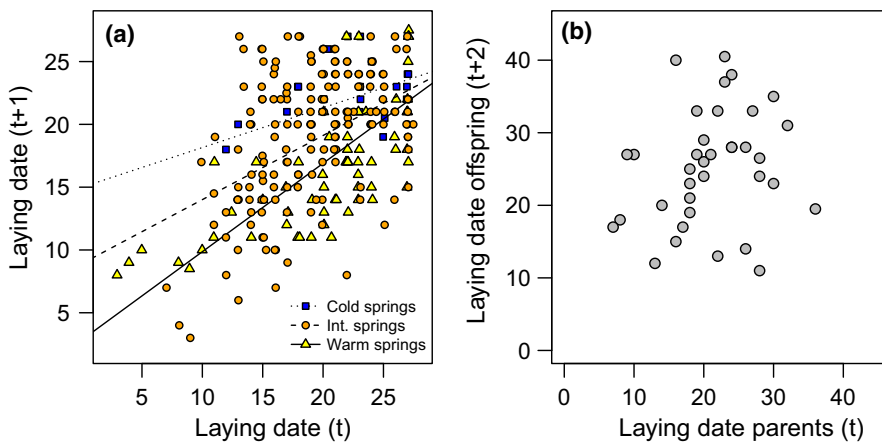
FIGURE 5 (a) The relationship between laying date at year *t* and laying date in the following year, year *t+1*, of adult godwits for cold (Tsum of 350), intermediate ('int.') (Tsum of 450), and warm springs (Tsum of 550) in year *t+1*. (b) Laying date of parents at year *t* and laying date of their offspring when they started to reproduce at *t+2*. We could not find a relationship [Colour figure can be viewed at wileyonlinelibrary.com]

3.4 | Sensitivity analysis

The sensitivity analysis showed that population growth rates were mostly affected by a change in laying dates and reproductive parameters (Figure 7). The strongest effect would be caused by a change in the intercept of the function $G(z'|z, t)$ that describes the within-individual development of laying dates; a positive change would lead to later laying dates which will have a negative effect on population growth rate. The magnitude of the effects on population growth rates differed between land use intensities; for instance, on fields with high land use intensity a positive change in the intercept of first-year survival and its relationship with spring temperature would lead to a larger positive change in population growth rates than on low land use intensity. Laying dates were most affected by the

function $G(z'|z, t)$ and were hardly affected by changes in demographic rates.

4 | DISCUSSION

4.1 | Timing of reproduction; are godwits able to respond to a warming world?

Previous studies have shown that black-tailed godwits have not advanced their laying dates since the early 1980s (Kleijn et al., 2010; Schroeder et al., 2012) or possibly even the 1930s (Meltofte et al., 2018), which contrasts most temperate species that advanced their reproductive timing in response to increasing spring temperatures (Crick & Sparks, 1999; Parmesan, 2007). This is surprising as we
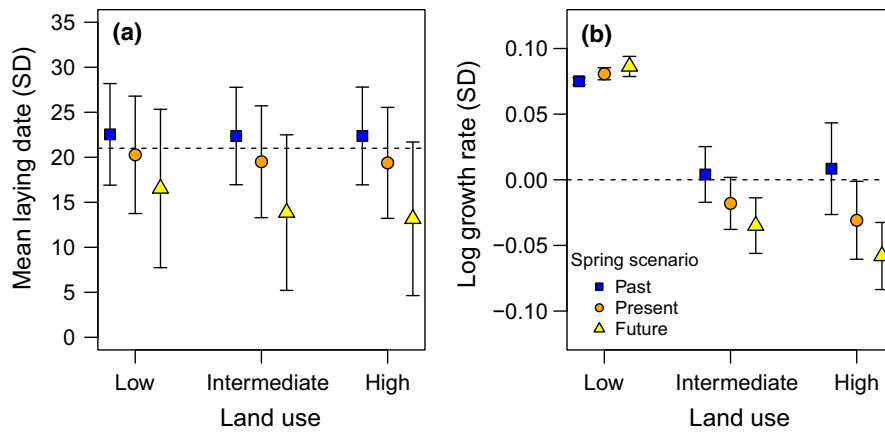
FIGURE 6 Projected annual mean laying dates (a) and mean log population growth rates (b) from IPMs of godwits breeding on fields with low, intermediate or high land use intensity and under a spring temperature scenario reflecting the past, present and future. The error bars are standard deviations of the means. Note that in the period reflecting the past spring temperature scenario, fields were all managed in what we now call low land use intensity. Dashed line in (a) represents observed peak laying date. Dashed line in (b) represents stable population size: below the population declines, above the population grows [Colour figure can be viewed at wileyonlinelibrary.com]
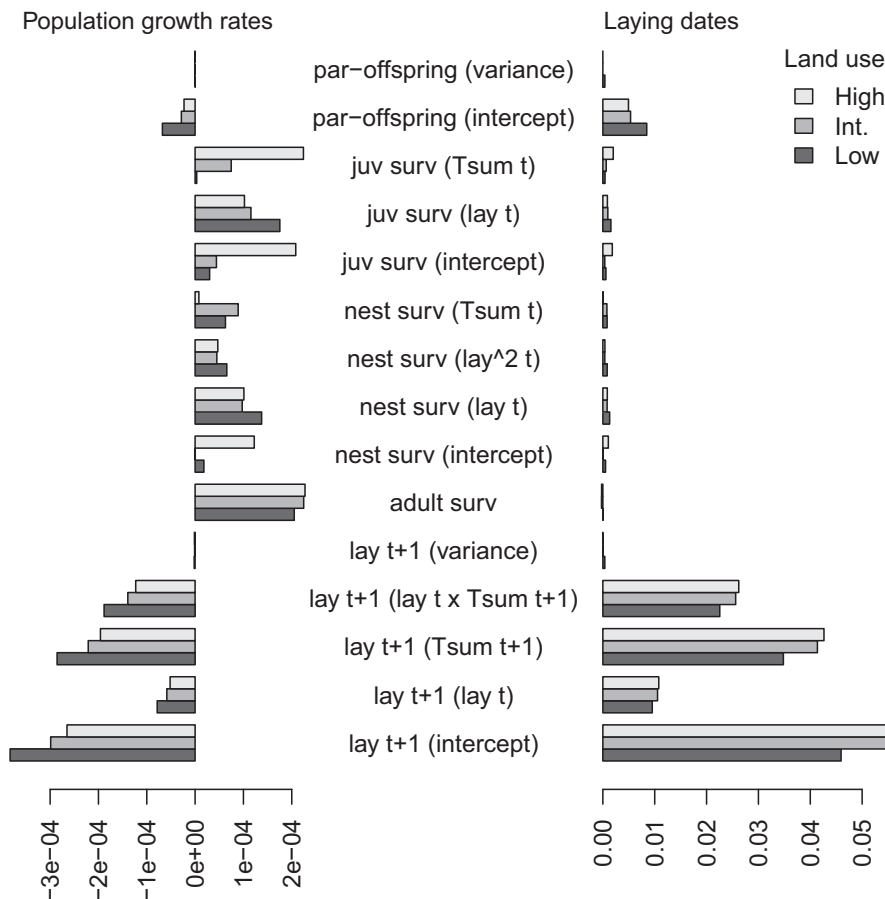
FIGURE 7 Results of sensitivity analysis for the models with present temperature scenario; relative effects on population growth rates (log lambda) and laying dates by subsequently changing each parameter 0.1%

showed that godwits would have higher fitness if they bred earlier. Are they unable to respond to a warming world? Over the past decade, we did not observe advancement of laying dates. However, we did find that the yearly mode of laying dates (the mean or median could be biased by repeated nesting attempts in years with low nest survival) negatively correlated with spring temperatures, although

the slope of the correlation was shallow. Large variation in spring temperatures in the last 11 years may have masked any increasing trend of spring temperatures, and possibly an advancement of laying date over time.

Our models predicted only a slight advance in laying dates if spring temperature was to increase from temperatures before 1976 to the average temperatures experienced during the study period: 2 days on fields with low agricultural land use intensity and 3 days on fields with intermediate and high land use intensity. This change may be too modest to be empirically detected in previous studies, particularly as variation in laying dates between years can be large. We predict that, if springs become warmer, mean laying dates will advance by 4–6 days—not enough to match the optimal timing of offspring production. As we did not find a correlation between laying dates of the parents and laying dates of their offspring, the predicted shift in laying dates was entirely caused by phenotypic flexibility of the adults. The low number of recruits prevented us from carrying out more formal tests for heritability of laying dates (Charmantier & Gienapp, 2014).

The subspecies of black-tailed godwits breeding on Iceland (*Limosa l. islandica*) also faces warming springs and agricultural intensification (Gill et al., 2007; Jóhannesdóttir, Alves, Gill, & Gunnarsson, in press), but spring warming at this more northern latitude and the relative low level of agricultural intensification so far seems to have benefitted the birds. The Icelandic black-tailed godwits seem to be more flexible in general; laying dates within pairs were not repeatable and advanced by 2.5 days per year (and 4 day/°C June temperature) during the last 11-year period, but little is known about how individual arrival affects laying date in this population. Furthermore, Icelandic godwits were able to advance arrival date by 2 weeks over the last 20 years (Gill et al., 2014), whilst the continental West-European godwit population did not advance arrival dates since at least 1970 (Kleijn et al., 2010).

To explain these timing phenomena, Gill et al. (2014) suggested a mechanism that does not require phenotypic plasticity or evolution of phenology: Early hatched offspring would winter at higher quality wintering grounds, which would allow for earlier migration to the breeding grounds. Although wintering location also affects arrival and laying date in Dutch godwits—those who winter at the most southern location arrive and lay earlier than those wintering at northern sites (Kentie et al., 2017)—it is currently not known what influences winter site choice. Nevertheless, we did not find a relationship between laying dates of parents (i.e., hatching date of their offspring) and that of their recruits in subsequent years, so indirect evidence is lacking. Spring temperature during the year that recruits hatched or in the year that they started to breed did not affect their laying date either. So, to unravel what makes a bird an early breeder, and thus how and where individual life histories develop, we need to get more insight into the ontogenetic pathways shaping adult timing behaviour (Senner, Conklin, & Piersma, 2015).

Mechanisms that influence phenology and habitat choice could thus differ in closely related subspecies. It is also possible that over time, mechanisms influencing timing of reproduction will change,

such as shown with an increase in heritability of laying dates in great tits (*Parus major*; Husby, Visser, & Kruuk, 2011). Our sensitivity analysis showed that changes in the flexibility of adult laying dates have the relative strongest effect on population laying dates and growth rates, which makes this a potential mechanism to select upon. Showing their potential to react to temperature, we observed that during a cold spell in the Netherlands in early spring 2013, black-tailed godwits returning from West-African wintering sites were able to respond by delaying their arrival and laying dates (Senner, Verhoeven, Abad-Gómez, et al., 2015). Yet, perhaps a cold spring causes a direct behavioural response due to an immediate lack of food, while they are less sensitive to slower ecological processes such as a mismatch between reproduction and food peaks of which the outcomes —lower reproductive success—are less directly experienced.

4.2 | Population consequences: sources and sinks

The Dutch godwit population started to decline in the same period when spring temperatures started to increase and agricultural intensification accelerated (Harms, Stortelder, & Vos, 1987; Kentie et al., 2016). Our estimated growth rates of past and current spring temperature scenarios and habitats of different land use intensity match this long-term observed population trajectory. Mean population growth rate was only positive on fields of low land use intensity, and close to zero in past spring scenarios on fields with intermediate and high agricultural land use intensity. Note that we simplified the models, for instance, we did not include an age structure or second nesting attempts in the models, which likely produced a bias in opposite directions, nor did we include parameter estimate uncertainty, which would increase the standard deviations around the mean. On fields with intermediate and high land use intensity, we predicted a negative mean growth rate for present and future temperature scenario. Nevertheless, godwits continue to breed here (Howison et al., 2018), albeit in lower densities. Young godwits disperse larger distances than adults and seem to be less discerning about habitat quality (Kentie et al., 2014), suggesting that intermediate and intensive agricultural areas are sinks, which are maintained by godwits breeding on fields with low land use intensities which act as sources (Pulliam, 1988).

The effects of spring temperature and land use intensity on reproductive output is a combination of mowing dates and food availability for the chicks. On intensive agricultural fields, warmer springs enhance grass growth and mowing starts earlier in the season than in cold springs. Mowing destroys the nests, or, if marked by local volunteers so that farmers can spare them, removes cover and increases depredation probability (Kentie et al., 2015). Mowing also poses a threat for prefledged chicks, which may partly explain the decrease in first-year survival during the season, as most mortality happens in the first week after hatching (Schekkerman, Teunissen, & Oosterveld, 2009). Additionally, late hatched chicks have a lower body condition (Loonstra, Verhoeven, & Piersma, 2018), possibly caused by a mismatch relative to the insect food peak, or due to a decline in insect biomass caused by mowing (Schekkerman & Beintema, 2007). Godwit families with prefledged chicks are mobile and,

if in the vicinity, families from mown fields can move to grassland with delayed mowing regimes. Most grassland with low land use intensity is especially managed to protect breeding birds; here agricultural activity is delayed until at least 15 June regardless of spring temperature, that is, after the nesting phase (Kentie et al., 2015). Yet, on fields where mowing is postponed, chicks hatched from nests laid after 26 April (assuming 25 incubation days and 25 prefledging days) also have a high mortality risk due to agricultural activities.

There are only few studies that identify the possible mechanisms that underlie (the lack of) phenological change and integrate this with population dynamics (but see Vedder, Bouwhuis, & Sheldon, 2013; Weegman, Arnold, Dawson, Winkler, & Clark, 2017). Our model suggests that for black-tailed godwits, climate change has considerably stronger negative effects in areas with most human-induced habitat alterations, compared to habitats which are less affected by humans. This stronger effect is caused by demographic differences between these habitats rather than phenological differences. Habitat degradation is a much greater risk, and for black-tailed godwits, as dependent as they are on agricultural landscapes not only during reproduction but also in the rest of the year, a serious threat. Many other species also live in habitats both affected by habitat and climate change, while when modelling extinction risks often only climate change are taken into account (Urban, 2015). Although species may adapt to climate change, either through phenotypic plasticity or evolution, large-scale human-induced habitat change may accelerate species extinctions even more. It is therefore important to preserve landscapes in which species are able to keep up with global climate change.

CONFLICT OF INTEREST

We have no competing interests.

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