



Trends in breeding phenology across ten decades show varying adjustments to environmental changes in four wader species

Hans Meltofte, Ole Amstrup, Troels Leuenhagen Petersen, Frank Rigét & Anders P. Tøttrup

To cite this article: Hans Meltofte, Ole Amstrup, Troels Leuenhagen Petersen, Frank Rigét & Anders P. Tøttrup (2018) Trends in breeding phenology across ten decades show varying adjustments to environmental changes in four wader species, Bird Study, 65:1, 44-51, DOI: [10.1080/00063657.2018.1444014](https://doi.org/10.1080/00063657.2018.1444014)

To link to this article: <https://doi.org/10.1080/00063657.2018.1444014>



Published online: 20 Mar 2018.



Submit your article to this journal [↗](#)



Article views: 49



View related articles [↗](#)



View Crossmark data [↗](#)

Trends in breeding phenology across ten decades show varying adjustments to environmental changes in four wader species

Hans Meltofte^a, Ole Amstrup^b, Troels Leuenhagen Petersen^c, Frank Rigét^a and Anders P. Tøttrup^c

^aDepartment of Bioscience, Aarhus University, Roskilde, Denmark; ^bAmphi Consult, Aalborg, Denmark; ^cCenter for Macroecology, Evolution and Climate, University of Copenhagen, Copenhagen, Denmark

ABSTRACT

Capsule: During 1928–2016, initiation of egg-laying advanced in two wader species, remained unchanged in one, and was delayed in one species. The changes across years and variation among species can be explained by climatic variables and differences in migratory strategies.

Aims: To document possible changes in initiation of egg-laying in common Danish wader species since the early part of the 20th century and seek possible correlations between egg-laying, timing of arrival and environmental factors.

Methods: Annual records of the first eggs and chicks found on the scientific reserve of Tipperne in western Denmark 1928–2016 were analysed using linear regression to determine patterns in timing of egg-laying, pre-breeding length and influence of climate factors.

Results: Two short/medium-distance migrant wader species, Northern Lapwing *Vanellus vanellus* and Common Redshank *Tringa totanus* advanced breeding initiation by about one week, with winter North Atlantic oscillation Index and spring temperature as important predictors. By contrast, two long-distance migrants, Black-tailed Godwit *Limosa limosa* and Ruff *Calidris pugnax*, did not advance egg-laying, and Ruff actually delaying it. As a result, the pre-laying period was significantly prolonged in both Black-tailed Godwit (21 days) and Ruff (52 days), while there was no significant change for Common Redshank.

Conclusion: Long-distance migrants are able to adjust spring arrival but unlike short/medium-distance migrants, do not necessarily adjust breeding initiation.

ARTICLE HISTORY





Received 8 May 2017

Accepted 19 February 2018

Much research is aimed at gaining a more thorough understanding of responses to global change at all trophic levels of ecosystems (Parmesan 2007, Jørgensen *et al.* 2016, de Keyser *et al.* 2017). This includes adjustments in reproductive phenology, and whether change is related to the climatic variations and other factors likely to affect the reproductive cycle (Parmesan 2007). Birds need to time breeding in order for the chicks to optimally exploit peak food abundance (Kam *et al.* 2004, Both *et al.* 2006, but also see Jonzén *et al.* 2007), which in turn is affected by soil productivity and climate. Phenotypic plasticity in birds allows, to some extent, quick adjustments of phenology (Berthold 2001, Fiedler 2009, Tøttrup *et al.* 2010) and a growing number of studies find evidence for micro-evolutionary adaptations to current climatic changes (Brandsma *et al.* 2017, Källander *et al.* 2017).

Spatial and temporal responses to climate change differ between species and across trophic levels, because some organisms rely on endogenous factors that are more or less independent of the environment

(Berthold 2001, Both & Visser 2001, Walther *et al.* 2002, Both *et al.* 2006, Jørgensen *et al.* 2016). Changes in breeding phenology of sedentary organisms (e.g. some birds, most invertebrates and plants) are presumably affected differently from those of migratory animals, because the resident species will experience the entire annual cycle in the ecosystem and hence have the opportunity to adjust their physiology throughout the year (Berthold 2001, Fiedler 2009). To avoid disadvantages in interspecific competition, for example for best breeding sites, migrants need to adequately adjust timing of arrival and breeding to the conditions at the breeding grounds; conditions that they are not able to predict during the winter. Both & Visser (2001) showed that inadequate changes in breeding phenology in the Pied Flycatcher *Ficedula hypoleuca*, a long-distance migrant, caused local population declines of up to 90% due to mistiming and competition with Great Tits *Parus major*. Such maladaptation might cause a micro-evolutionary bottleneck by strong selection for early egg-laying

CONTACT Hans Meltofte  mel@bios.au.dk  Department of Bioscience, Aarhus University, Frederiksborgvej 399, DK-4000 Roskilde, Denmark; Anders P. Tøttrup  aptottrup@snm.ku.dk  Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, Universitetsparken 15, DK-2100 Copenhagen, Denmark

(Both & Visser 2001, Both *et al.* 2006, but also see Jonzén *et al.* 2007). However, studies on a nearby population also showed that advances in egg-laying actually benefitted recruitment of offspring into the population (Tomotani *et al.* 2017).

In a previous study, we demonstrated advanced arrival time at the breeding area for three of the wader species analysed in this study – Black-tailed Godwit *Limosa limosa* (13 days earlier), Common Redshank *Tringa totanus* (14 days earlier) and Ruff *Calidris pugnax* (42 days earlier) – over an 80-year period (1929–2008; Petersen *et al.* 2012), whereas arrival of Northern Lapwing *Vanellus vanellus* could not be established because the species was also frequently present during winter.

In this study we present an analysis of breeding initiation observations based on an even longer time period (1928–2016) for the same four wader species in the same area. We include analyses of changes in length of the pre-breeding period and assess how climate impacts the timing of breeding. Our data represent the longest available time series on egg-laying phenology of birds in Denmark and, except for the Northern Lapwing (Both *et al.* 2005), possibly in waders worldwide.

Methods

The study was carried out at the scientific reserve of Tipperne located in the brackish lagoon of Ringkøbing Fjord in western Denmark (55°53' N 8°13' E). The reserve includes 700 ha meadows and reed beds largely without changes in habitat management during the study period. For details of the environment and the birds of Tipperne, see Møtøfte (1987), Thorup (1998) and Møtøfte & Clausen (2011, 2016).

During most of the study years, the Northern Lapwing population numbered around 100–275 pairs, the Black-tailed Godwit population 40–200 pairs, the Ruff population 25–300 breeding females and the Common Redshank population 50–800 pairs (Thorup 1998 and in litt.). For all four species the breeding populations varied around relatively moderate levels up to the late 1970s, after which they increased significantly to a peak in around 1990, followed by a return to more or less previous levels from around 2000.

Egg-laying data (*date of first egg laid*) for the four species were compiled from observers' diaries and breeding phenology forms kept at the reserve during the entire study period. We have solely used dates of first completed clutch and explicit observations of *the first nest this year* to calculate first egg dates (laying intervals: Northern Lapwing: 42 hours, Ruff: 24 hours, Black-

tailed Godwit: 24 hours, Common Redshank: 38 hours (Cramp *et al.* 1983)). Similarly, we have extracted all available data on the first hatched young from the same sources and converted these to first egg dates using 33 days for laying and incubation in Northern Lapwing, 27 days in Black-tailed Godwit and Ruff, and 29 days in Common Redshank (Thorup 1998 and in litt.).

Data on first egg dates are potentially affected by a relatively high predation pressure early in the season compared to just a few weeks later (Thorup 1998) and to the fact that it is more difficult to find the first nest than to find 15 nests one week later. However, the constant effort exerted in locating nests mitigates the potential bias in changes over time in our data.

Individual phenological repeatability in birds remains poorly understood (but see Lourenço *et al.* 2011, Thorup *et al.* 2013). As a proxy measure for the pre-laying period at the population level, we used the difference in number of days between the first arrival and first egg date (see Høgestedt 1974, who used female arrival). Date of arrival and hence length of the pre-laying period could not be determined in Northern Lapwing because, as mentioned, this species occurred irregularly throughout the winter on Tipperne (Møtøfte & Clausen 2016).

Climate data for the entire period were available at national level only and were obtained from the online archives of the Danish Meteorological Institute (Cappelen 2016). As an attempt to integrate spring conditions both covering the general characteristics of western Europe and the local phenology for invertebrate food and vegetation growth, we correlated first egg dates with three-month averaged mean monthly temperature and precipitation for January–February–March (*JFM*) for the early breeding Northern Lapwing and Black-tailed Godwit and for February–March–April (*FMA*) for later breeding Ruff and Common Redshank. Furthermore, we tested for a correlation with the North Atlantic Oscillation (NAO) Index for the winter period of December through to March (*DJFM*) (Hüppop & Hüppop 2003, Hurrell 2016), which is the dominant mode of climate variability in the North Atlantic region (IPCC 2010).

Determination of the wintering area of the populations occurring in Denmark was based on Bønløkke *et al.* (2007) using estimates of spring migration distances to Tipperne from Google Earth (2010, ver. 4.3) and classifying <4000 km as short/medium-distance and >4000 km as long-distance. This classified Northern Lapwing and Common Redshank as short/medium-distance migrants and Black-tailed Godwit and Ruff as long-distance migrants (Petersen *et al.* 2012), that are wintering in western Europe/Mediterranean and tropical Africa, respectively.

For the statistical analyses all data were converted to Julian days (where 1 = 1 January). Ordinary linear regression was then used to determine species-specific temporal patterns in timing of egg-laying and pre-breeding length. Prior to the regression analyses, possible outliers were identified and removed, if they had influence values higher than Cooks Distance (Weisberg 1985). In order to assess possible year-to-year correlations between first egg dates and date of observation of the first individuals, the potentially confounding temporal effect on both variables was removed. This was done by regression analyses of both variables on year and then extracting the residuals from these two regressions. A Spearman correlation analysis of these two sets of residuals was then used to test the relationship between year-detrended first egg dates and observation of first individuals.

Results

We found significant advances in first egg dates for Northern Lapwing (-0.0858 days/year) and Common Redshank (-0.0683 days/year) while a significant delay was noted for Ruff (0.0908 days/year) (Table 1 and Figure 1). In total, the mean initiation of the earliest clutches advanced by 7.6 and 6.1 days, respectively, over the study period 1928–2016 for the two short/medium-distance migrants, Northern Lapwing (from approximately 10 April to 3 April) and Common Redshank (from approximately 2 May to 26 April) during the 89-year study period. Initiation of egg-laying was delayed by 8.1 days in the long-distance migrant, the Ruff (from approximately 2 May to 9 May), and remained largely unchanged in the similarly long-distance migrant, the Black-tailed Godwit (mean 21 April; Figure 1).

Over the study period, the pre-laying period became significantly longer in the long-distance migrants Ruff (0.596 days/year, $P < 0.0001$) and Black-tailed Godwit (0.214 days/year, $P = 0.001$) (Table 1 and Figure 2). In Ruff, we found a longer pre-laying period in years with higher spring temperatures (3.225 days/ $^{\circ}\text{C}$, $P = 0.048$) and more precipitation (0.448 days/mm, $P = 0.039$), but no effect of winter conditions (Table 1). We found no significant correlation between year-detrended first egg dates and first observation date of arrival for Black-tailed Godwit ($P = 0.59$) and Common Redshank ($P = 0.49$), whereas such a correlation was found for Ruff ($P = 0.001$).

When changes in timing to the start of breeding were compared with advances in arrival, the pre-laying period was prolonged by 21.1 days (from 22.3 to 43.4 days) in Black-tailed Godwit and 52.4 days (from 9.5 to 61.9

days) in Ruff. The apparent prolonged pre-laying period of 7.7 days in Common Redshank was not statistically significant (Table 1).

For all four species, timing of first egg was earlier in springs following mild winters (positive NAO values). Furthermore, breeding initiation was also earlier in years with higher temperatures for Northern Lapwing, Black-tailed Godwit and Common Redshank. In Black-tailed Godwit and Common Redshank, we also found that breeding was earlier in years with more precipitation (Table 1).

Discussion

We demonstrate earlier initiation of egg-laying by one week for the two short/medium-distance migratory waders, Northern Lapwing and Common Redshank, and unchanged or delayed initiation of egg-laying for two long-distance migrants, Black-tailed Godwit and Ruff. The pre-laying period was consequently prolonged in the long-distance species while a small expansion in the short/medium-distance Common Redshank was not statistically significant (we do not have arrival data for Northern Lapwing). Overall, winter NAO and spring temperature were found to be the most important predictors. This is in accordance with our previous findings on spring arrival (Petersen *et al.* 2012); i.e. timing of arrival in waders can be explained by local temperature and precipitation as well as winter conditions (NAO, winter index) and species-specific migration distances.

Thorup (1998) found no change in Northern Lapwing and Common Redshank breeding phenology during 1928–92 on Tipperne, but this is not necessarily contradictory to our results because Thorup used population-wide breeding phenology, which may show a slower trend than analyses of first egg dates, where a single nest counts. On the other hand, the data we present here are based on a time series that is 25 years longer than that of Thorup, and we consider first egg/chick dates to have been more consistently recorded on the reserve than the population-wide laying phenology. Yet, as in our study, the long-distance migrant, Black-tailed Godwit, showed no change in breeding phenology in Thorup's study (see also Kentie *et al.* 2017), whereas breeding in Ruff was delayed according to a more recent analysis (Thorup 2016).

Given the marked advancement in its arrival, the unchanged breeding phenology in Black-tailed Godwit was surprising (see below). Even more surprising was delayed egg-laying in Ruff, which Thorup (2016) ascribed to the likely effects of greatly increased grazing by Barnacle Geese *Branta leucopsis* since the

Table 1. Trends in egg-laying initiation dates and length of pre-laying period in four wader species on Tipperne 1928–2016 estimated by linear regression analyses. The pre-laying period of Northern Lapwing could not be established due to irregular occurrence of the species in mild winters. Significant effects are shown in bold.

Species				Year			Temperature (JFM/FMA)			Precipitation (JFM/FMA)			NAO (DJFM)		
	<i>N</i>	mean	se	days/year	<i>P</i>	<i>R</i> ²	days/°C	<i>P</i>	<i>R</i> ²	days/mm	<i>P</i>	<i>R</i> ²	days/NAO	<i>P</i>	<i>R</i> ²
First egg dates															
Northern Lapwing	78	97	0.79	−0.086	0.004	0.10	−1.201	0.001	0.14	−0.041	−0.410	0.01	−1.212	0.002	0.12
Black-tailed Godwit	70	111	0.67	0.012	0.642	<0.01	−0.668	0.029	0.07	−0.105	0.010	0.09	−0.725	0.022	0.08
Ruff	67	126	0.81	0.091	0.003	0.13	−0.303	0.481	0.01	−0.027	0.665	<0.01	−0.957	0.013	0.09
Common Redshank	68	119	0.70	−0.068	0.006	0.11	−1.619	<0.001	0.28	−0.148	0.005	0.11	−1.333	<0.001	0.24
Pre-laying period															
Black-tailed Godwit	34	34	1.99	0.214	0.001	0.28	1.091	0.217	0.05	−0.013	0.908	<0.01	0.943	0.314	0.03
Ruff	45	40	2.84	0.596	<0.001	0.78	3.225	0.048	0.09	0.448	0.039	0.07	1.220	0.380	0.02
Common Redshank	32	38	1.57	0.087	0.168	0.06	−0.226	0.790	<0.01	0.090	0.453	0.02	−0.667	0.316	0.03

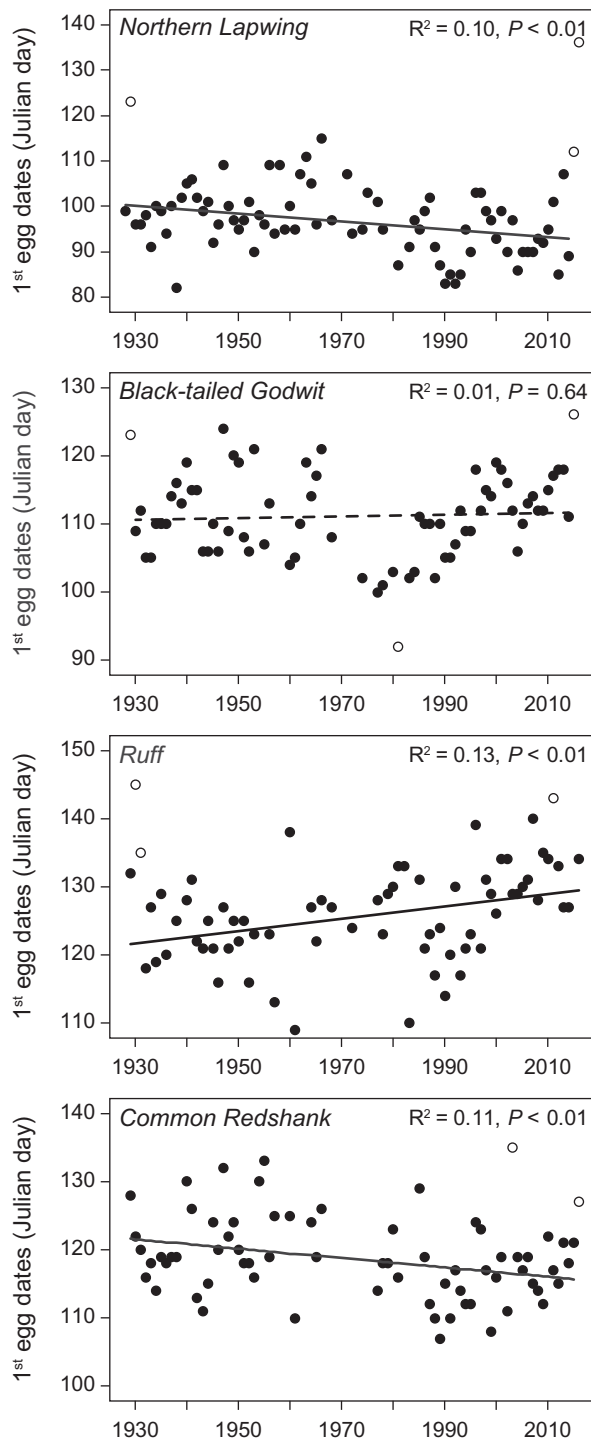


Figure 1. Temporal trends in first egg dates in four wader species on Tipperne 1928–2016. Lines represent the results from linear regressions, where significant regression lines are solid and one non-significant is dashed. Open circles are outliers as defined by Cooks Distance (Weisberg 1985).

late 1990s. Increased grazing would delay the appearance of sufficiently tall nest cover and could potentially be another factor influencing changes in egg-laying timing.

Breeding initiation appears to be highly influenced by food supply prior to and during egg-laying, which in turn

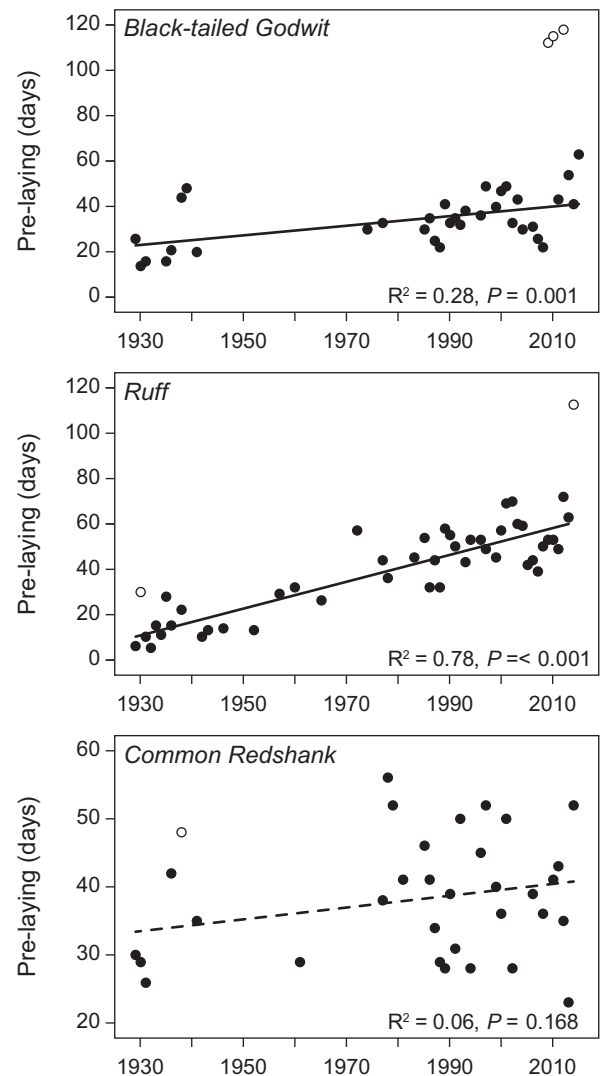


Figure 2. Temporal trends in the length of the pre-laying period in three wader species on Tipperne 1928–2016. Lines represent the results from linear regressions. Open circles are outliers as defined by Cooks Distance (Weisberg 1985).

is affected by temperature and precipitation together with timing of snow melt in northern areas (Kam *et al.* 2004, Meltofte *et al.* 2007, Fiedler 2009; see also Ettrup & Bak 1985 for temperature dependent egg-laying in Danish Northern Lapwings). Explanations for lack of response to global warming, e.g. in Black-tailed Godwit, could be lack of adaptation, unchanged prey phenology or bias in our first egg dates (see discussion in Musters *et al.* 2010). No data on prey phenology was available from Tipperne, but we have information on prey abundance. For example, Thorup (1998) found largely unchanged invertebrate abundance on the meadows between studies conducted in 1938–43 and 1987–89. However, Common Redshank, in particular, just prior to and during egg-laying obtain a large part of their food on the shallow mudflats surrounding the Tipperne meadows (O. Thorup in litt.), and here prey

densities have increased considerably during the study period (Møltøfte & Clausen 2016). Predation pressure might counteract earlier egg-laying because predation is most intense early in the breeding season (Thorup 1998). On the other hand, advanced breeding initiation increases the opportunity for more replacement clutches due to the longer breeding season.

In a Dutch study on meadow birds, Beintema *et al.* (1985) found that in the 1980s breeding phenology had already advanced by 2–3 weeks in all six wader species studied, including the four species from this study. Spring temperature was discarded as the cause, and the phenological changes were attributed to intensified agricultural management, especially fertilizer application leading to soil fauna phenology advancement. Since then egg-laying phenology in meadowbirds has been studied extensively in the Netherlands with the aim to unravel the impact of climate versus changes in habitat management, e.g. in form of fertilizers, soil humidity, timing of mowing, etc. (Both *et al.* 2005, Kleijn *et al.* 2010, Musters *et al.* 2010, Schroeder *et al.* 2012, Senner *et al.* 2015, Brandsma *et al.* 2017). The results show a mixed picture with varying influence of both agricultural practices and climate variables in the individual species and periods of time. On Tipperne, effects of habitat management can largely be excluded because management of the meadows has been restricted to grazing (from May at the earliest) and late summer mowing (from July at the earliest), while fertilizers have not been used (Thorup 1998). However, in the Netherlands a similar difference was found between egg-laying advancement during the last half century in the short-distance migrant, Northern Lapwing, and no change in the long-distance migrant, Black-tailed Godwit (Musters *et al.* 2010). Also in accordance with our results, Both *et al.* (2005) found that advancement of egg-laying in Northern Lapwing apparently began before the middle of the 20th century and has accelerated since then.

Gill *et al.* (2014) suggest that earlier breeding could be the mechanism leading to earlier arrival in a population of short-distance migrant Icelandic Black-tailed Godwits *Limosa l. islandica*. This is driven by earlier born young being able to select better wintering habitats and thereby arrive earlier in Iceland at the time they start breeding. Our data do not include individual data to further study this mechanism. Still, for our short/medium-distance species, this could potentially be an explanation to study further.

Unlike the long-distance migratory waders covered in this study, the long-distance migrant, Pied Flycatcher, has shortened the pre-laying period on their Dutch breeding grounds (Both & Visser 2001). The Pied Flycatcher breeds earlier now, but not early enough

compared to prey phenology. As shown by Both & Visser (2001), a pre-laying period which was at the minimum required, plus insufficient advancement of arrival, hampered adequate advancement of egg-laying which subsequently led to severe population declines in this species. The two short/medium-distance migrants, Northern Lapwing and Common Redshank, do lay their eggs earlier and thus have an advantage in interspecific competition. They gain more time for replacement clutches and possibly are better able to synchronize hatching with an advanced peak in invertebrate abundance on the meadows, assuming that prey phenology on Tipperne has also advanced.

Högestedt (1974) showed a strong negative correlation between the length of the pre-laying period and prey abundance in a Swedish Northern Lapwing population in a study based on female arrivals and first egg dates. Högestedt suggested a minimum pre-laying period of about 13 days. However, given the increasingly sedentary behaviour of Northern Lapwing on Tipperne, a minimum pre-laying period could hardly have been a limiting factor for Lapwing breeding phenology in the reserve in recent decades. We do not know to which degree our breeders are sedentary, so the year-round presence of the species makes further exploration impossible within this current data.

Thorup (2004) addressed different possible causes of declining Ruff and Black-tailed Godwit populations in Denmark, and stressed that climate change is unlikely to be the cause because Danish temperatures have not risen above that of the former French, Hungarian and Ukrainian breeding sites of these species. Rising temperatures should nevertheless not be neglected as a future cause of population decline as a result of a slower adaptation to the changed breeding ground phenology (e.g. prolonged pre-laying periods) compared to that of sedentary and short-distance migratory waders (this study).

Invertebrate biomass varies between years at Tipperne (Thorup 1998) and abundance is especially low after a severe winter followed by a dry spring (Larsen 1949). Hence, less frequent winter frosts and increased precipitation (IPCC 2010) predict good conditions for invertebrates. Warmer winters might be especially advantageous for meadow breeders, because Black-tailed Godwit chick survival was higher with moderate temperatures and precipitation (Groen & Hemerik 2002). Higher temperatures are believed to be especially favourable for Northern Lapwing because the chicks are much less dependent on brooding in periods with higher temperatures (Beintema & Visser 1989). However, a potentially negative effect of warmer springs is that grass may be higher and denser at an

earlier time, which could make it difficult for the birds to capture their invertebrate prey.

Our results show that long-distance migrants may adjust timing of spring arrival, but breeding initiation is not necessarily adjusted, as it is in short/medium-distance migrants. This indicates that records of spring arrival alone may not be sufficient to assess climate change impacts on timing of breeding. Understanding the link between timing of spring arrival and breeding initiation time is essential if conservation or management actions are to be implemented.

Acknowledgements

We thank Preben Clausen, Aarhus University, and Ole Thorup, Amphi Consult, for providing help and supplementary data and other information on Tipperne. Nick Quist Nathaniels kindly checked our English, and two anonymous referees provided highly valued suggestions for improvement of the manuscript.

Funding

APT thanks the Aage V Jensen Foundation for support and the Danish National Research Foundation for supporting the Center for Macroecology, Evolution and Climate [grant number DNRF96].

References

- Beintema, A.J. & Visser, G.H. 1989.** The effects of weather on time budgets and development of chicks of meadow birds. *Ardea* 77: 181–192.
- Beintema, A.J., Beintema-Hietbrink, R.J. & Müskens, G.D.J.M. 1985.** A shift in the timing of breeding in meadow birds. *Ardea* 73: 83–89.
- Berthold, P. 2001.** *Bird Migration. A General Survey*, 2nd ed. Oxford University Press, Oxford.
- Bønløkke, J., Madsen, J.J., Thorup, K., Pedersen, K.T., Bjerrum, M. & Rahbek, C. 2007.** *The Danish Bird Migration Atlas*. Rhodos A/S (in Danish, with English summary).
- Both, C. & Visser, M.E. 2001.** Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* 411: 296–298.
- Both, C., Piersma, T. & Roodbergen, S.P. 2005.** Climatic change explains much of the 20th century advance in laying date of Northern Lapwing *Vanellus vanellus* in The Netherlands. *Ardea* 93: 79–88.
- Both, C., Bouwhuis, S., Lessells, C.M. & Visser, M.E. 2006.** Climate change and population declines in a long-distance migratory bird. *Nature* 441: 81–83.
- Brandsma, O.H., Kentie, R. & Piersma, T. 2017.** Why did Lapwings *Vanellus vanellus* in managed habitat advance egg laying during a period without warming early springs? *Ardea* 105: 19–26.
- Cappelen, J. (ed.) 2016.** *Denmark – DMI Historical Climate Data Collection 1768–2015*. DMI Report No. 16-02.
- Cramp, S., Simmons, K.E. & Ferguson-Lees, J. 1983.** *Handbook of the Birds of the Europe, the Middle East and North Africa. The Birds of the Western Palearctic*. Vol. 3. Oxford University Press, Oxford.
- de Keyser, C.W., Rafferty, N.E., Inouye, D.W. & Thomson, J.D. 2017.** Confounding effects of spatial variation on shifts in phenology. *Glob. Change Biol.* 23: 1783–1791.
- Ettrup, H. & Bak, B. 1985.** Breeding season, clutch size and young production of Danish Lapwings *Vanellus vanellus*. *Dansk Orn. Foren. Tidsskr.* 79: 43–55 (in Danish, with English summary).
- Fiedler, W. 2009.** *Bird ecology as an indicator of climate and global change*. In Letcher, T.M. (ed) *Climate Change: observed impacts on planet earth*, Ch. 9: 181–195. Elsevier B.V., Amsterdam.
- Gill, J.A., Alves, J.A., Sutherland, W.J., Appleton, G.F., Potts, P.M. & Gunnarsson, T.G. 2014.** Why is timing of bird migration advancing when individuals are not? *P. Roy. Soc. B* 281: 20132161.
- Google Earth 2010.** 4.3.7284.3916 (beta), online: kh.google.com (02-03-2010).
- Groen, N.M. & Hemerik, L. 2002.** Reproductive success and survival of Black-tailed Godwits *Limosa limosa* in a declining local population in the Netherlands. *Ardea* 90: 239–248.
- Högestedt, G. 1974.** Length of the pre-laying period in the Lapwing *Vanellus vanellus* L. in relation to its food resources. *Ornis Scand* 5: 1–4.
- Hüppop, O. & Hüppop, K. 2003.** North Atlantic Oscillation and timing of the spring migration in birds. *Proc. R. Soc. Lond. B* 279: 233–240.
- Hurrell, J. 2016.** North Atlantic Oscillation (NAO) Index (station-based). <https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based> (13 May 2016).
- IPCC 2010.** Intergovernmental Panel on Climate Change. <http://www.ipcc.ch/pdf/technical-papers/climate-changes-biodiversity-en.pdf> (23-03-2010).
- Jonzén, N., Hedenström, A. & Lundberg, P. 2007.** Climate change and the optimal arrival of migratory birds. *Proc. R. Soc. Lond. B* 274: 269–274.
- Jørgensen, P.S., Bohning-Gaese, K., Thorup, K., Tøttrup, A.P., Chylarecki, P., Jiguet, F., Lehtikainen, A., Noble, D.G., Reif, J., Schmid, H., van Turnhout, C., Burfield, I.J., Foppen, R., Voříšek, P., van Strien, A., Gregory, R.D. & Rahbek, R. 2016.** Continental-scale global change attribution in European birds – combining annual and decadal time scales. *Glob. Change Biol.* 22: 530–543.
- Källander, H., Hasselquist, D., Hedenström, A., Nord, A., Smith, H.G. & Nilsson, J.-Å. 2017.** Variation in laying date in relation to spring temperature in three species of tits (Paridae) and pied flycatchers *Ficedula hypoleuca* in southernmost Sweden. *J. Avian Biol* 48: 83–90.
- Kam, J. van de, Ens, B., Piersma, T. & Zwarts, L. 2004.** *Shorebirds. An Illustrated Behavioural Ecology*. KNNV Publishers, Zeist.
- Kentie, R., Marquez-Ferrando, R., Figuerola, J., Gangoso, L., Hooijmeijer, J.C.E.W., Loonstra, A.H.J., Robin, F., Sarasa, M., Senner, N., Valkema, H., Verhoeven, M.A. & Piersma, T. 2017.** Does wintering north or south of the Sahara correlate with timing and breeding performance in black-tailed godwits? *Ecol. Evol.* 7: 2812–2820.

- Kleijn, D., Schekkerman, H., Dimmers, W.J., van Kats, R.J.M., Melman, D. & Teunissen, W.A. 2010. Adverse effects of agricultural intensification and climate change on breeding habitat quality of Black-tailed Godwits *Limosa l. limosa* in the Netherlands. *Ibis* **152**: 475–486.
- Larsen, E.B. 1949. The influence of the severe winters of 1939–1942 on the soil fauna of Tipperne. *Oikos* **1**: 184–207.
- Lourenço, P.M., Kentie, R., Schroeder, J., Groen, N.M., Hooijmeijer, J.C.E.W. & Piersma, T. 2011. Repeatable timing of northward departure, arrival and breeding in Black-tailed Godwits *Limosa l. limosa*, but no domino effects. *J. Ornithol.* **152**: 1023–1032.
- Meltofte, H. 1987. The occurrence of staging waders Charadrii at the Tipperne reserve, western Denmark, 1928–1982. *Dansk Orn. Foren. Tidsskr* **81**: 1–108 (in Danish, with English summary).
- Meltofte, H. & Clausen, P. 2011. The occurrence of swans, ducks, Coot and Great Crested Grebe in the Tipperne Reserve 1929–2007 in relation to environmental conditions in the brackish lagoon, Ringkøbing Fjord, Denmark. *Dansk Orn. Foren. Tidsskr.* **105**: 1–120 (In Danish, with extensive English summary).
- Meltofte, H. & Clausen, P. 2016. Trends in staging waders on the Tipperne Reserve, western Denmark, 1929–2014 with a critical review of trends in flyway populations. *Dansk Orn. Foren. Tidsskr.* **110**: 1–72.
- Meltofte, H., Høye, T.T., Schmidt, N.M. & Forchhammer, M.C. 2007. Differences in food abundance cause inter-annual variation in the breeding phenology of High Arctic waders. *Polar Biol.* **30**: 601–606.
- Musters, C.J.M., ter Keurs, W.J. & de Snoo, G.R. 2010. Timing of the breeding season of Black-tailed Godwit *Limosa limosa* and Northern Lapwing *Vanellus vanellus* in The Netherlands. *Ardea* **98**: 195–202.
- Parmesan, C. 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Glob. Change Biol.* **13**: 1860–1872.
- Petersen, T.L., Meltofte, H. & Tøttrup, A.P. 2012. Advanced spring arrival of avian migrants on Tipperne, western Denmark, during 1929–2008. *Dansk Orn. Foren. Tidsskr.* **106**: 65–72.
- Schroeder, J., Piersma, T., Groen, N.M., Hooijmeijer, J.C.E.W., Kentie, R., Lourenco, P.M., Schekkerman, H. & Both, C. 2012. Reproductive timing and investment in relation to spring warming and advancing agricultural schedules. *J. Ornithol.* **153**: 327–336.
- Senner, N.R., Verhoeven, M.A., Hooijmeijer, J.C.E.W. & Piersma, T. 2015. Just when you thought you knew it all: New evidence for flexible breeding patterns in Continental Black-tailed Godwits. *Wader Study* **122**: 18–24.
- Thorup, O. 1998. The breeding birds on Tipperne 1928–1992. *Dansk Orn. Foren. Tidsskr* **92**: 1–192 (in Danish, with extensive English summary).
- Thorup, O. 2004. Status of populations and management of Dunlin *Calidris alpina*, Ruff *Philomachus pugnax* and Black-tailed Godwit *Limosa limosa* in Denmark. *Dansk Orn. Foren. Tidsskr.* **98**: 7–20.
- Thorup, O. 2016. Timing of breeding in Ruff *Philomachus pugnax*: a crucial parameter for management and use of wet grassland in Western Europe. *Wader Study* **123**: 49–58.
- Thorup, K., Vardanis, Y., Tøttrup, A.P., Kristensen, M.W. & Alerstam, T. 2013. Timing of songbird migration: individual consistency within and between seasons. *J. Avian Biol.* **44**: 486–494.
- Tomotani, B.M., van der Jeugd, H., Gienapp, P., De La Hera, I., Pilzecker, J., Teichmann, C. & Visser, M.E. 2017. Climate change leads to differential shifts in the timing of annual cycle stages in a migratory bird. *Glob. Change Biol.* DOI:10.1111/gcb.14006.
- Tøttrup, A.P., Rainio, K., Coppack, T., Lehikoinen, E., Rahbek, C. & Thorup, K. 2010. Local temperature fine-tunes the timing of spring migration in birds. *Integr. Comp. Biol.* **50**: 293–304.
- Walther, G., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J., Hoegh-Guldberg, O. & Bairlein, F. 2002. Ecological responses to recent climate change. *Nature* **416**: 389–395.
- Weisberg, S. 1985. *Applied Linear Regression*. 4th ed. Wiley, New York, NY.