# Why Did Lapwings *Vanellus vanellus* in Managed Habitat Advance Egg Laying During a Period without Warming Early Springs?

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# Why did Lapwings *Vanellus vanellus* in managed habitat advance egg laying during a period without warming early springs?

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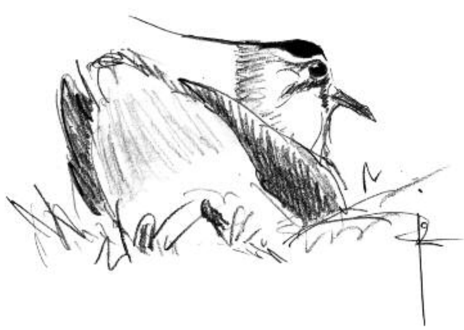
From 1950, spring temperatures in The Netherlands increased. Previous research suggested that advances in first egg dates of Lapwings *Vanellus vanellus* best correlate with climatic factors rather than with changes in farming practices. In an area constantly and uniformly managed especially for breeding meadow birds (the reserve Giethoorn-Wanneperveen), nesting phenology of Lapwings was monitored over almost three decades (1988–2014). During this period local average air temperatures across early spring (1 February – 31 March) showed no change. Although first laying dates of the initial clutches (varying between 7 and 30 March) did not change either, the median laying date of the first egg of all the clutches (varying between 21 March and 8 April) advanced by ten days (from 4 April to 25 March). Interestingly, laying dates were associated with temperatures, in that egg laying usually followed an increase in temperature in the previous weeks. As a consequence, whereas first laying dates of initial clutches correlated with temperatures in the 21 February – 31 March interval, they did not with temperatures in the previous 1–20 February interval. Likewise, median laying dates of the first egg of all the clutches did not correlate with the temperatures in February and early March, but the two variables were strongly correlated in the overlapping 11 March – 10 April interval. We found no associations with precipitation. That median laying dates (but not first laying dates) advanced without changes in the overall average spring temperature nor in habitat management, can only partly be explained by the finding that hatching success steadily increased during the study (note that the more frequent replacement clutches would have delayed the measured median laying date in the earlier years). As hatching success of earlier clutches is higher than that of later clutches, there may now be selection for earlier laying.

Key words: Lapwing, breeding season, spring temperatures, timing, advanced laying date, seasonal reproductive decline, meadow birds



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During the second half of the 20th century, in many parts of Europe spring temperatures increased (Both *et al.* 2005, Charmantier *et al.* 2008). At the same time the grassland habitat of the Northern Lapwing *Vanellus vanellus* has dramatically changed due to agricultural intensification (Schekkerman 2002, Both *et al.* 2005, Schroeder *et al.* 2012). During most of the 20th century, Lapwings in The Netherlands adjusted to agricultural intensification and even increased in numbers, but since 2000, numbers have declined in association with direct habitat loss and increasingly intensive agricultural practices (Schekkerman 2002, Teunissen & Soldaat 2006, Boele *et al.* 2015).

Long-term data on the laying dates of unmarked birds has shown that many species have advanced egg laying during the last decades, which was argued to be a direct consequence of climate change (Crick & Sparks 1999, Walther *et al.* 1997). In the Dutch province of Fryslân there is a long tradition of collecting Lapwing eggs for consumption (Breuker 2015), and the finding of the first egg of the season is still an important social event. A study on the dates when the first Lapwing egg of the season were found in Fryslân showed that from 1897 to 2003 the first egg was found increasingly early (Both *et al.* 2005). This advance was primarily explained by increasing spring temperatures (Both *et al.* 2005). Lapwings also laid earlier after wet winters, with little variance remaining to be explained by habitat change. For a given spring temperature and winter rainfall, the first egg was laid on average three days earlier in 2000 compared with 1900, suggesting that the laying behaviour of Lapwings has changed. However, an analysis of Lapwing breeding on inland meadows in the UK did not find a change in laying date over the period 1962–1999 (Chamberlain & Crick 2003).

In this study on Lapwings breeding in the meadow-breeding bird reserve Giethoorn-Wanneperveen, we provide an analysis of the yearly laying dates of the first egg of all found Lapwing clutches during the period 1988–2014, in relation to temperature and precipitation in the period 1 February – 10 April. This study is interesting for its duration, and for the fact that the Lapwing breeding habitat in the study area has been managed consistently for meadow birds, with changes to landscape (e.g. removal of trees, O. Brandsma in prep.), but without changes to meadow characteristics including ground water level. We examine whether first laying dates and median laying dates advanced over the years, and relate this to changes in the average temperature. Moreover, to interpret the patterns found, we examined whether hatching success differs between years and varies in consistent ways over the course of the spring seasons.

## Study area and methods

The reserve Giethoorn-Wanneperveen is located in the province Overijssel (The Netherlands), bordered by the villages of Steenwijk (52°47.0'N, 06°07.0'E), Giethoorn (52°44.0'N, 06°05.0'E), Wanneperveen (52°42.0'N, 06°07.0'E) and the road Gasthuisdijk, and is a part of wetland De Wieden (Figure 1). De Wieden is a peat-bog area consisting of lakes, pools, swamps, woods and grasslands. The reserve Giethoorn-Wanneperveen consists mostly of grasslands, with some shallow pools

Lapwing breeding habitat in the reserve Giethoorn-Wanneperveen (24 May 2015).

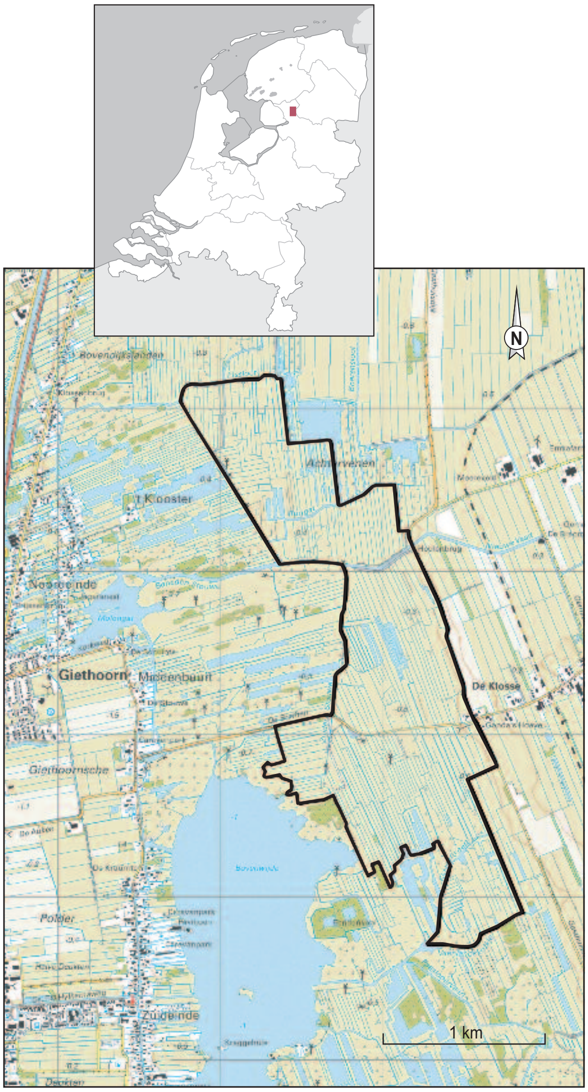


**Figure 1.** Map of the study area Giethoorn-Wanneperveen (De Wieden) in The Netherlands.

and fields with reeds. Most of the grasslands are narrow elongated fields of 1–3 ha, separated from each other by ditches that are 1–3 m wide and about 0.5 m deep. In the study area of 252 ha, the water level in the reserve varied between 5 and 30 cm below field level. In the period 1987–1992, in c. 60% of the study area mowing and grazing were not allowed to occur before 1 June, or mostly later (either 15 June to 1 July). After a re-allotment of land in 1993, the proportion of the study area with late mowing days increased to c. 80%.

Most of the grasslands were supplied yearly with organic dung (maximum 10–20 ton/ha) in early spring (February–March) or in summer (Brandsma 1999, 2012a,b). After the breeding season, grasslands were mowed or grazed with cattle. All grasslands were mowed at least once a year. Narrow canals (<3 m) were cleaned once in about three years, wide canals (3–5 m) once in about five years.

In the period March–June (1988–2014), Lapwing nests were marked with a stick of reed 0.5 m tall, two meters from the nest. Every 7–10 days the nests were checked. Field efforts were deliberately kept constant over the breeding season. A clutch was considered to have hatched if there were little pieces of dry egg shell in the nest. Incomplete nests which were found during laying ($n$ = 328) were used to calculate the first egg laying date. For complete nests found ($n$ = 1079), the hatching date was used to estimate laying date of the first egg by assuming a period of incubation of 28 days to which we added 5 days for the laying of a full clutch (Beintema & Müskens 1981, Beintema *et al.* 1995). For the clutches which were found complete, but were lost before hatching ($n$ = 256), it was not possible to calculate the laying dates. If a clutch is lost, Lapwings may start a new clutch within an average period of 10 days (Beintema *et al.* 1995).

As is usual in these kind of studies (e.g. Crick & Sparks 1999), we could not distinguish between first and second clutches. This means that whilst the first laying date may be little affected by early nest losses leading to replacement clutches, the median laying date in a particular year is. Although in some years many nests were lost due to predation, in the study area the loss of clutches to agricultural activities is negligible due to the high water tables and additional management restrictions.

For an analysis of the effects of air temperatures and precipitation, we used climatic data collected at the Royal Meteorological Institute (KNMI) in Eelde, 80 km north of the reserve Giethoorn-Wanneperveen (www.knmi.nl). Using average daily temperatures, we calculated average temperature (°C) and precipitation (mm) for the periods 1–20 February, 21 February – 10 March, 11–31 March, 1–20 April and 21 April – 10 May. This covers the month before the first laying date and the laying period of all but 19 of the 1407 observations of first eggs in the reserve.

We tested correlations between average temperature and precipitation in different periods in spring on the first and median laying date. To enable a more fine-grained analysis of time effects, rather than exclusive time blocks we additionally used overlapping periods of 20 days between 1 February and 10 April.

As it is likely that not all nests were found before predation occurred, the proportion of successful nests would be an overestimate of nest success (Mayfield

1961, Johnson 1979). To account for this overestimation in the estimation of changing nest success in the period 1988–2014, we calculated daily nest survival rates using the program Mark (White & Burnham 1999) incorporating all Lapwing nests ($n$ = 1663). Daily nest success to the power of the number of nesting days, 33 in Lapwings (Beintema *et al.* 1995), represents the chance that a nest will hatch.

To estimate changes in nest success during the spring, we only used nests where we knew the laying date ($n$ = 328) and tested the relationship between laying date and hatching success. We used a mixed effect generalized linear model with a binomial error structure, with laying date as predictor and year as random effect. We tested whether there was a linear effect and a quadratic effect of laying date. To overcome collinearity of laying date with laying date$^2$ and convergence problems, we scaled laying date around zero with a SD of 1. We used the unscaled parameter for plotting.

To calculate daily nest survival and hatching success, we used R (R Core Team 2016), with the packages RMark (Laake 2013) and LME4 (Bates *et al.* 2015), respectively. The other statistical analyses were carried out in SPSS.

## RESULTS

Although Dutch spring temperatures have increased since 1950 (Both *et al.* 2005), temperatures near the study area in February and March did not change over the study period 1988–2014, except in the first three weeks of April (Figure 2). In the period 1988–2014, 10% of the Lapwing nests were laid before 18 March, 50% before 30 March and 90% before 21 April (Figure 3). With a laying and breeding period of 33 days (Beintema *et al.* 1995), 10% of the nests would have hatched before 20 April, 40% in the period 20 April – 1 May, 40% in the period 2–24 May, with the remaining 10% hatching in late May and June.

The date of the first egg of the initial clutches in a given year varied between 7 and 30 March, with no significant directional change over the study period ($F_{26}$ = 0.91, $r$ = 0.19, $P$ = 0.349). However, median laying date of the first egg of all the clutches, varying between 21 March and 8 April advanced by 10 days from 4 April to 25 March ($F_{26}$ = 10.54, $r$ = 0.5, $P$ = 0.003; Figure 4).

There was a correlation between first laying dates of the initial clutches and the average temperature in the periods preceding laying (21 February – 31 March; Figure 5), but not with temperatures in an earlier 3-week period (1–20 February). The earliest laying date of the initial clutches was after 20 March in only 4 years. The median laying date of the first egg of all clutches was positively correlated with temperature in the period 11 March – 10 April (Figure 5). Precipitation between 1 February and 31 March varied between years, but did not show consistent change over time,

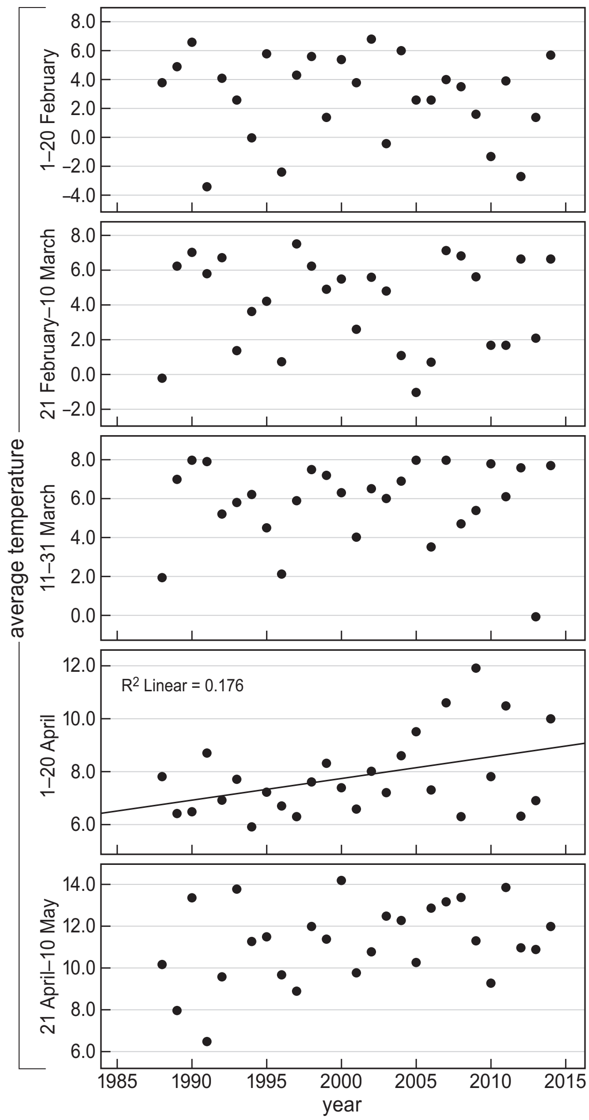


**Figure 2.** Changes in average temperature at Eelde, The Netherlands, from 1988 to 2014 ($n$ = 27) in the periods 1–20 February (no significant change, $F_{26}$ = 0.36, $r$ = 0.12, $P$ = 0.55), 21 February – 10 March (no significant change, $F_{26}$ = 0.06, $r$ = 0.05, $P$ = 0.80), 11–31 March (no significant change, $F_{26}$ = 0.01, $r$ = 0.02, $P$ = 0.91), 1–20 April (significant increase, $F_{26}$ = 5.34, $r$ = 0.42, $P$ = 0.029) and 21 April – 10 May (no significant change, $F_{26}$ = 3.05, $r$ = 0.33, $P$ = 0.093).

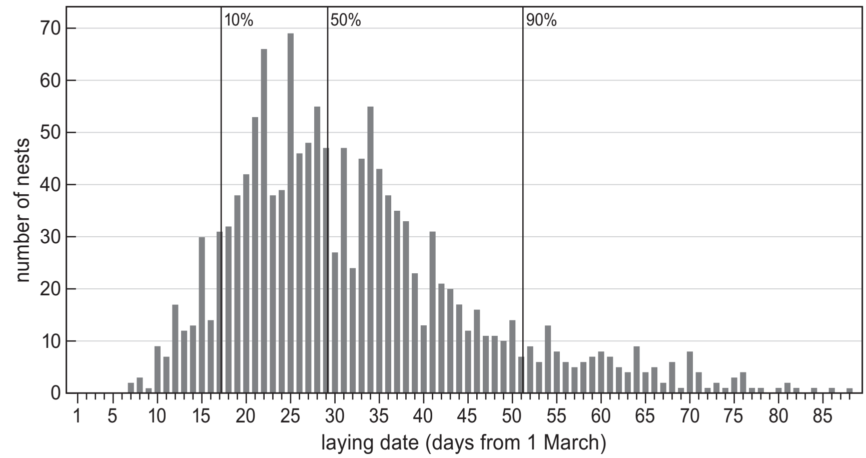


**Figure 3.** Frequency distribution of laying dates of the first Lapwing egg ($n$ = 1407) in the reserve Giethoorn-Wanneperveen 1988–2014 (day number 1 = 1 March). Data include both first and replacement nests.

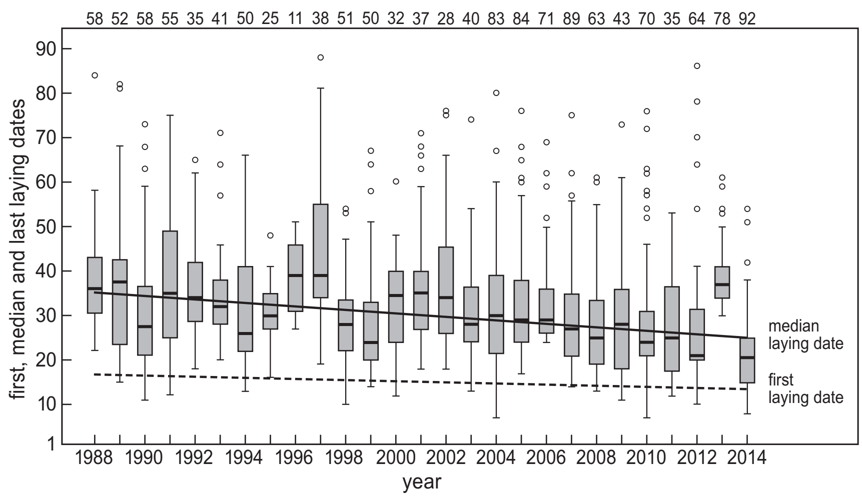


**Figure 4.** First laying dates of the initial clutches and median laying dates of the first egg of all the Lapwing clutches in the reserve Giethoorn-Wanneperveen 1988–2014 ($n$ = 1407; daynumber 1 = 1 March). The lowest points of the boxplot are the yearly first laying date. The dashed line is the regression line of the first laying date. The continuous line is the regression line of the median laying date. The open dots are the outliers.

nor did we detect correlations with either first or median laying dates.

Hatching success increased significantly over the years 1988–2014 from an average of 54% to an average of 73% (Deviance = 22.19, $df$ = 1, $P$ < 0.001; Figure 6). Predation was the major cause of nest failure. As Lapwing pairs losing a clutch early in the season will usually replace it, and as relaying of nests in the sample will take about ten days (Beintema *et al.* 1995), under the assumption of a linearly increasing hatching success over the years 1988–2014, this leads to a three day advance in median laying date (correlation hatching success and median laying date: $F_{26}$ = 3.44, $r$ = 0.35, $P$ = 0.075; Figure 7). This should be beneficial for Lapwings, as averaged over all years, hatching success declined during spring as a consequence of nest predation increasing with time ($\chi_1^2$ = 17.67, $P$ < 0.001, random year effect SD = 0.72). A quadratic relationship of laying date with hatching success was not supported ($\chi_1^2$ = 2.74, $P$ = 0.10). At the start of the breeding season, nests had a probability of 70% to hatch, while at the end of the breeding season, after 1 June, this probability had declined to less than 20% (Figure 8).

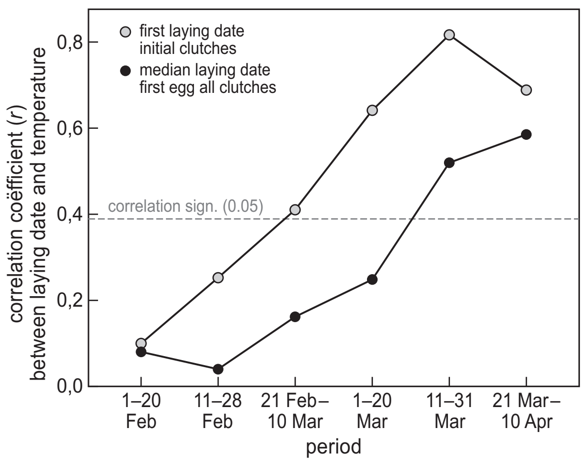


**Figure 5.** Pearson product-moment correlations between yearly first laying dates of the initial clutches and median laying date of the first eggs of all the Lapwing clutches ($n$ = 1407; 1988–2014) in the reserve Giethoorn-Wanneperveen and average temperature across different intervals between 1 February and 10 April. The dotted line indicates the level at which (in the given sample) the correlation coefficient is different from zero at a 5 % significance level.

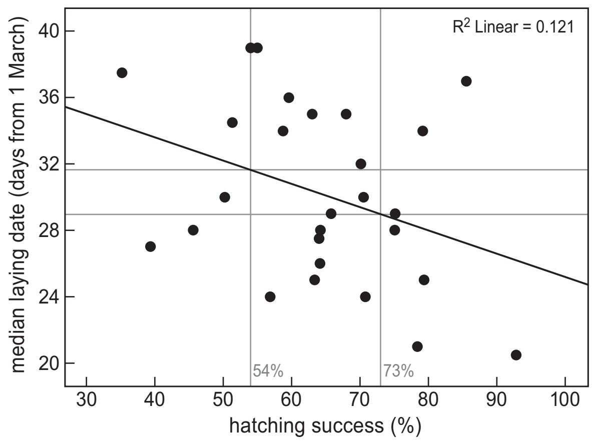


**Figure 7.** The correlation between yearly median laying dates and average hatching success of Lapwings in the reserve Giethoorn-Wanneperveen in 1988–2014.

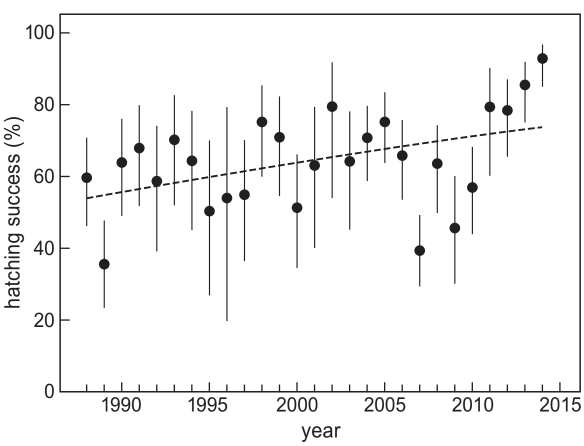


**Figure 6.** Long-term increase in hatching success of Lapwings ($n$ = 1663) in the reserve Giethoorn-Wanneperveen from 1988 to 2014. Vertical lines show the 95% confidence interval.

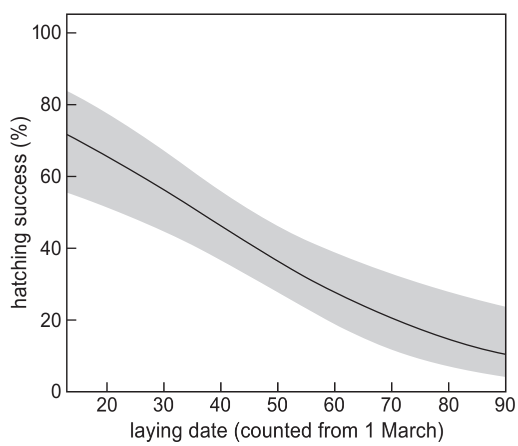


**Figure 8.** Hatching success of Lapwings during spring, between 1988 and 2014 ($n$ = 328), in the reserve Giethoorn-Wanneperveen. Year was modelled as a random effect. Light grey area represents the 95% confidence intervals.

## DISCUSSION

In this study, over 27 years in the meadow bird reserve Giethoorn-Wanneperveen we found a correlation between laying date and average air temperature, but no association with precipitation. Temperature can affect the timing of breeding in Lapwing (Figure 4; Kubelka & Šálek 2013), and first laying date was indeed correlated with the average air temperature in the two weeks just preceding laying. Over the study period 1988–2014, first laying dates of the initial clutches showed no change, but median laying dates of the first egg of all the clutches advanced by 10 days from 4 April to 25 March in the absence of a change in overall average spring temperature. Only in the period 1–20 April was there a significant change in average temperature. This had no effect on the first laying dates of the initial clutches, which all started before 1 April and could only have a small effect on the median laying dates of the first egg of all the clutches, for 55% of the median laying dates occur before 1 April and 78% before 10 April.

The advance of median laying date of the first egg of all the clutches itself is consistent with an earlier study on Lapwing chicks (Beintema *et al.* 1985); between 1910 and 1975, the average date that chicks were ringed advanced by about 20 days. A similar study by Musters *et al.* (2010) showed that laying dates continued to advance in the early 2000s, but that since the 1960s the advances were no longer correlated with increasing spring temperatures. This leaves open the possibility that climate change was a causal agent early on, and changes in agricultural practices influential later. In the reserve Giethoorn-Wanneperveen agricultural practices are kept to a minimum in the breeding season and have been very stable; they cannot, therefore, explain earlier breeding.

For the median laying date of the first egg of all the clutches, varying between 21 March and 8 April, there was no significant correlation with the temperature in February or during the first ten days of March, but there was with the temperature in 11 March – 10 April. Thus, only the temperature in the two weeks before egg laying appears to matter, suggesting that Lapwings start developing their eggs in response to sudden improvements in spring weather.

Now that we know that changes in spring temperature over the years cannot explain the advance of laying, why did the median laying date of the first egg of all the clutches nevertheless advance over time in an area with rather constant management and no agricultural threats? We offer three possible explanations: (1) because of increasing hatching success over years (Figure 6), there would be fewer additional nesting attempts, causing the median laying date to shift forwards, (2) the hatching success of earlier clutches in spring is more successful (Figure 8) and encourages earlier breeding, (3) earlier increases in food availability for chicks results in earlier breeding.

Although Both *et al.* (2005) showed that Lapwing laying date was primarily affected by climatic factors rather than changes in breeding habitat, after controlling for temperature and rainfall in the year 2000 first egg dates, Lapwings were still laying three days earlier than in 1900. In the present study, during spring hatching success declined (Figure 8). Teunissen *et al.* (2005) also found a higher survival of early clutches and increased predation later in the season. This could have resulted in selection for earlier laying. However, although Black-tailed Godwits *Limosa l. limosa* also show seasonal declines in nest survival (Kentie *et al.* 2015, Roodbergen & Klok 2008), they do not show advances in laying date (Schroeder *et al.* 2012).

For birds in general, the timing of breeding seems to be determined by the timing of food availability for chicks and the parental costs of egg laying at a certain time (Drent 2006). Lapwing chicks feed on surface-dwelling organisms, and exploit fauna living inside cow-dung pats. In May, the number of arthropods in grasslands rapidly increases (Beintema *et al.* 1990, Schekkerman & Beintema 2007, T. Piersma, M. Verhoeven, J. Loonstra *et al.* unpubl. data). In June, arthropod abundance may temporarily decrease (Beintema *et al.* 1990). An increase in temperature in the period 1–20 April (Figure 2) could have advanced insect emergence (Högstedt 1974, Kleijn *et al.* 2010), and this may be an important factor now selecting for earlier breeding in Dutch Lapwings.

## ACKNOWLEDGEMENTS

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## SAMENVATTING

Vanaf 1950 nam de temperatuur in het voorjaar toe en veranderde het leefgebied van de Kievit sterk door de intensivering van de landbouw. De verandering in legdatum van het eerste kievitsei stond meer in verband met een veranderd klimaat dan met een verandering van het leefgebied. In het weidevogelreservaat Giethoorn-Wanneperveen zijn bijna drie decennia (1988–2014) lang legsels gemonitord. Gedurende deze periode is de gemiddelde temperatuur in februari en maart niet gestegen. Ook het eerste ei (variërend van 7 tot 30 maart) werd niet eerder gelegd, maar de mediaan van de legdata van de eerste eieren van alle legsels (variërend van 21 maart tot 8 april) is met 10 dagen vervroegd (van 4 april naar 25 maart). De leg van het eerste ei (tussen 7 en 30 maart) wordt beïnvloed door de gemiddelde temperatuur in de periode 21 februari – 20 maart, maar staat los van de temperatuur in de periode 1–20 februari. De mediaan van de legdata van de eerste eieren van alle legsels (tussen 21 maart en 8 april) staat in verband met de temperatuur in de periode 11 maart – 10 april, maar staat los van de temperatuur in de periode hiervoor. Er is geen verband gevonden met de hoeveelheid neerslag in februari en maart. De vervroeging van de mediane legdatum kan voor een klein deel worden verklaard door een toename van het broedsucces in de periode 1988–2014. Een hoger broedsucces leidt tot minder vervolglegsels en een gemiddeld vroegere legdatum. Mogelijk is de Kievit eerder gaan broeden, omdat vroege legsels in het voorjaar succesvoller zijn dan late legsels.

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