Climatic change explains much of the 20th century advance in laying date of Northern Lapwing Vanellus vanellus in The Netherlands

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Published in:
Ardea

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Both C., Piersma T. & Roodbergen S.P. 2005. Climate change explains much of the 20th century advance in laying date of Northern Lapwing *Vanellus vanellus* in The Netherlands. Ardea 93(1): 79–88.

Long time series allow us to look back in time and examine how birds responded to changes in their environment. During the second half of the 20th century, not only did Northern Lapwing *Vanellus vanellus* experience an increase in spring temperatures, their meadow habitat also changed dramatically due to agricultural intensification. In The Netherlands, eggs of Lapwing have been collected for consumption for ages, especially in the province of Fryslân, and as the finding of the first egg of the season has been an important social event till today, first egg dates are archived. Here we present data on the dates at which the first egg of the season was found in Fryslân, in 1897–2003. Somewhat to our surprise we found that the advance in the first egg date was primarily explained by increasing spring temperatures. Lapwings also laid earlier after wet winters, with little variance remaining to be explained by habitat changes. Still, at the same spring temperatures and winter rainfall, the first egg was laid on average three days earlier in 2000 compared with 1900. A complementary dataset on the date that the first egg was found in the 10th successive Friesian municipality, confirmed the strong effect of temperature and the additional effect of winter rainfall. The number of days between the first egg date for the province and the 10th municipality yielded a measure of breeding synchrony. The start of egg laying was more synchronous during cold springs. Our analysis thus shows that Lapwing laying date was primarily affected by climatic factors rather than by the considerable changes in breeding habitat.

Key words: breeding – climate change – meadowbirds – phenology – temperature effects – timing – waders

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INTRODUCTION

The time scales that we experience depend largely on our age. As a child, one of the most striking features of nature is the change of seasons. When one grows older, nature appears to change more than just seasonally: the trees in the garden grow, and where once all the trees were cut, new saplings sprout and a forest grows. When one comes of age, the landscape appears no longer as it was in one's youth. Some changes, such as the rapid transition from a rural to an urban landscape, are obvious. Others are more subtle. During a hot summer month most of us 'believe' in global warming, but when the next summer is miserable, it is difficult to judge from mere experience whether we witness a directional change or not. And of course, there are phenomena with time scales that we cannot directly observe during a lifetime.

The longer the time scale, the more difficult it is to detect how changes affect the life of birds. The fossil record is usually unhelpful, the genetic record hard to access, and on the ground we are often too late to observe how birds have responded. The moment we realise that the world is changing, many birds have already anticipated or disappeared from the scene. Glimpses from the past can be gleaned from comparisons between published data and current observations, and the best observations come from determined people that have collected the same data year after year in a consistent way. With respect to the arrival and breeding dates of birds, we are fortunate that amateur and professional biologists have collected data for decades. These data enable us to see whether and how birds are affected by climate and other environmental changes.

Decade-long time series of laying date show that many bird species have advanced their egg laying date during the last decades, most likely as a direct consequence of climate change (Crick *et al.* 1997, Crick & Sparks 1999, Walther *et al.* 2002). Not all species have done so, and even within species some populations have, and others have not advanced laying date (Dunn & Winkler 1999, Both *et al.* 2004). Such populations sometimes live close to one another, experiencing similar climatic conditions (Visser *et al.* 2003). So far we do not understand why one species or population adjusts laying date in response to climate change, while others do not, and there is no insight in the effects of habitat type and habitat change on the relationships between climate and breeding phenology. Analyses for possible climate change effects on laying date have been notably lacking for the waders that breed in open habitats (Piersma & Lindström 2004). An analysis for Northern Lapwing *Vanellus vanellus* (henceforth called Lapwing) breeding on inland meadows in the UK did not find a change in laying date (Chamberlain & Crick 2003), despite the fact that climatic changes affected the breeding phenology of many bird species in the region (Crick *et al.* 1997, Crick & Sparks 1999).

The recent advance in laying date reported for so many passerines has statistically been attributed to local climate warming, but this does not exclude that other changes in the environment could contribute to phenological changes too. For waders breeding in the Dutch meadows, it was observed that between 1910 and 1975 the average date that chicks of Black-tailed Godwits *Limosa limosa* and Lapwings were ringed had advanced by about 20 days (Beintema *et al.* 1985). Although two studies suggest that in warmer years Lapwings and Black-tailed Godwits lay earlier (Kooiker 1993, Kruk *et al.* 1996), this advance nevertheless tended to be explained by changes in agricultural practice. Increased use of fertilisers and better drainage led to earlier grass growth, advancing mowing and grazing. Simultaneously, the earlier growing season may have advanced the insect and earthworm availability enabling the birds to lay earlier (Högstedt 1974). However, because late nests had increasing chances to be destroyed by mowing and grazing (Beintema *et al.* 1995), we need to be certain that the reported advance is more than an artefact of an increasing lack of late-ringed chicks. Although the loss of late nests would select against late laying, we require *direct* data on laying dates to establish whether the birds indeed have changed their behaviour over time. If climate change would be responsible for an earlier laying in meadow breeding waders, we expect that laying date correlates better with temperature (or other climatic variables) than with time.

The subject of this study, Lapwings, are the most common breeding wader species of Dutch meadows (Beintema *et al.* 1995, Bijlsma *et al.* 2001, SOVON Vogelonderzoek Nederland 2002). Dutch breeders mostly winter in the UK, France and Spain, and return to their territories from late

February onwards (Imboden 1974, Kooiker 1993). During most of the 20th century, Lapwings appeared to be able to adjust to agricultural intensification, and even increased in numbers, but since 1980 numbers have declined in The Netherlands due to direct habitat loss and agricultural practices that became too intensive to cope with (Bijlsma *et al.* 2001). In the province of Fryslân, The Netherlands, eggs of Lapwing have been collected for consumption, an old tradition that continues to this day (Roodbergen *et al.* 1991, Roodbergen 1999). Because of financial and ceremonial rewards (e.g. presentation to the Queen or her provincial representative), there has always been a high incentive to find the very first egg in the season. Therefore, the search intensity in the early season is extremely high and has probably been so since the beginning of the time series presented here. Reports on the award ceremonies usually are published in local newspapers and these reports enable us to look back far beyond the start of our own lives. The dates at which the first Lapwing egg was found in Fryslân are now available since 1897. Additionally, for the years since 1955 we have data on the dates that the first egg was found in the 10th successive Friesian municipality. In combination with the first egg date, a measure of seasonal synchrony is obtained. To the best of our knowledge this dataset is one of the longest available for an examination of changes in the timing of avian reproduction.

METHODS

Collection of egg laying data

To establish a rationale for a variable yearly closure date of the Lapwing egg-collecting season, SPR assembled first egg dates for the province of Fryslân in the period to 2003, mainly on the basis of reports in local newspapers. Parts of this data set have been published (van Dijk 1967, Roodbergen 1999, Roodbergen 2003), but several small corrections were incorporated in the data set that can be found in Appendix 1. In a few cases, two eggs were found in the first nest, and in this case we took the day before the nest was found as the first egg date. No date is available for 2001, when access to the land and searches for Lapwing eggs were forbidden due to foot and mouth disease epidemic. In addition, SPR assembled the dates that the first egg was found in the 10th successive Friesian municipality from newspaper sources for years since 1955 (also found in Appendix 1). The number of days between the first egg date for the province and the 10th municipality yielded a measure of breeding synchrony.

Weather data

We used climatic data collected at the Royal Meteorological Institute (KNMI) in De Bilt in the centre of The Netherlands, about 100 km south of the province of Fryslân. Data for the years since 1901 were available on the web site (WWW.KNMI.NL/PRODUCT/). We calculated the average temperature for the pre-laying period (16 February – 15 March) using average daily temperatures. This period is rather arbitrary, but covers the 30-day period before the median first egg over the whole period of years was recorded (18 March); the period begins well before the first egg (4 March). It means that during early years birds had already started their laying about halfway the period over which the temperature was averaged, while in late years the first egg was laid two weeks after the end of this period (latest first egg: 31 March).

Partly as a control, we calculated the average temperature during the preceding winter (1 November – 15 February), a time when the Dutch Lapwings would have been found further south, and we calculated the total precipitation in the months November until February (data available since 1907). Winter temperatures may nevertheless be important for Lapwings, because during large-scale spells of cold weather they would migrate further south. Winter rainfall may have an effect on laying date because soil moisture may affect food availability and the warming capacity of the soil. The different weather variables were correlated: in order of decreasing fit these were winter and spring temperatures ($r = 0.43$, $n = 99$, $P < 0.001$), winter temperatures and rainfall

(r = 0.36, n = 95, P < 0.001), spring temperature and winter rainfall (r = 0.29, n = 95, P < 0.001).

Analyses

We tested for the effects of climatic variables and year in general linear models. To account for possible non-linear effects quadratic terms for each independent variable were included if simultaneous exclusion of the linear and quadratic term yielded a significant increase in deviance compared to the inclusion of the linear term only. Interactions between year and climatic variables were considered, but none of the interactions were significant. Non-significant interactions and quadratic terms are not mentioned in the text.

RESULTS

Over the 20th century the date that the first Lapwing egg was found in Fryslân varied between March 4 (in 1989) and March 31 (in 1969) (Fig. 1A). Since the early 1950s the first egg date advanced by about ten days (Fig. 1A). The date that the first egg was found in the 10th successive Friesian municipality was highly correlated with first egg date (r = 0.96, n = 48, P < 0.001). On average, the difference between the first and the tenth municipality egg was 2.94 days, and from 1955 to 2003 the 10th municipality egg date also advanced, with about 8 days (Fig. 1B). During the 20th century the spring temperature first slightly decreased and since the early 1950s it increased (Fig. 1C). This yielded an inverse of the trend in

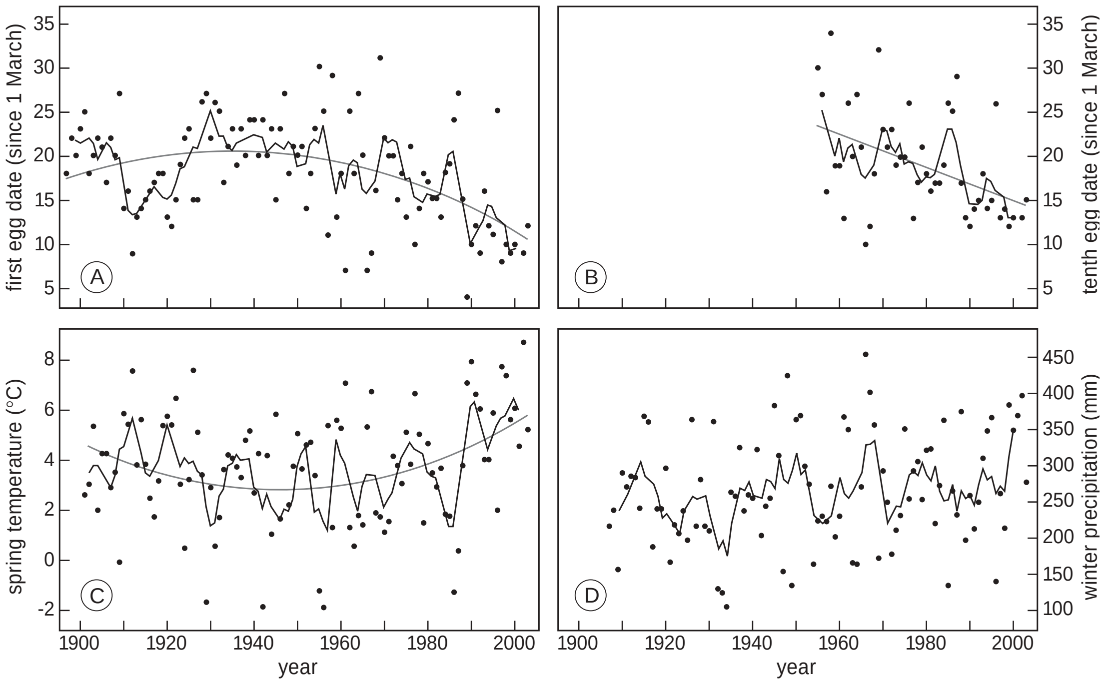

Figure 1. Laying dates of Lapwings in Fryslân over the years. (A) The annual first egg; (B) The date the first egg in the tenth municipality was found; (C) Average temperature in the period 16 Feb – 15 Mar; (D) Average winter precipitation in the period Nov–Feb. In all figures the moving average per five years is given by the solid line, and the curve of the linear regression including year and its square are depicted by the grey curves: (A) $F_{2,102}$ = 13.20, P < 0.001, (B) $F_{1,46}$ = 11.58, P = 0.001, (C) $F_{2,100}$ = 6.14, P = 0.003.

Table 1. Results of GLM analyses of climatic variables and year on laying dates of Lapwings in the province of Fryslân (The Netherlands). In case the quadratic term was significant, we present the significance of simultaneous deletion of the linear and quadratic term. Analyses are given for the first egg in the period 1901–2003, and for the tenth municipality egg from 1955–2003.

	First egg				Tenth egg			
	F	*df*	*P*	*Beta*	*F*	*df*	*P*	*Beta*
Year				5.32	2.31	1,43	0.14	
Year^2	7.98	2, 91	0.006	–0.001				
Winter temperature	0.06	1,90	0.81		2.94	1,44	0.09	
Spring temperature	105.5	1,91	<0.001	–1.64	72.08	1,45	<0.001	–1.64
Winter rainfall	5.24	1,91	0.024	–0.011	10.78	1,45	0.002	–0.021

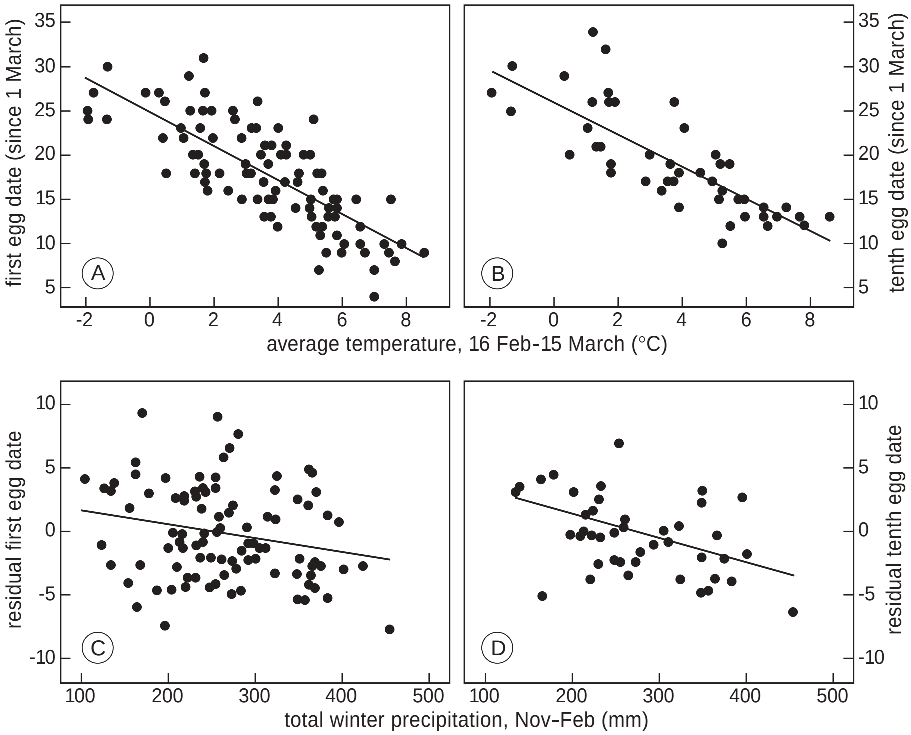

Figure 2. The effects of spring temperature (A-B) and winter precipitation (C-D) on laying dates of Lapwings in Fryslân. In (A) and (C) the date of the first annual eggs is given, in (B) and (D) the date of the tenth municipality egg. For statistics see Table 1.

laying date (Fig. 1A). The increase in winter rainfall (Fig. 1D) was close to significance ($F_{1,95}$ = 3.86, P = 0.052).

Both the first and the 10th municipality egg were found earlier during warm springs and after wet winters (Table 1, Fig. 2). Nevertheless, additional to these effects (explaining 63% of the variance), the first egg was found earlier over the years: with the same temperature and rainfall the first egg is on average three days earlier in 2000 compared with 1900 (and this additional effect of year explained 5% additional of the variance in the model). In contrast, the advancement of the date of the eggs found in the 10th municipality was only explained by the climatic variables (explaining together 70% of the variance).

The difference in days between the date of finding of the10th municipality egg and the first egg was smaller in cold than in warmer years (Fig. 3). Winter rainfall, winter temperature or year did not have additional explanatory power. Lapwings thus lay earlier but less synchronously in warm years.

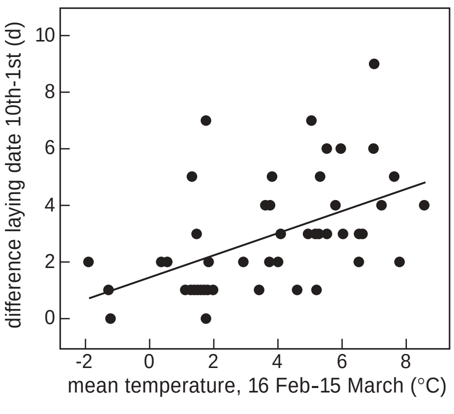

Figure 3. Synchrony of the start of laying in Lapwings in relation to spring temperature. As measure of synchrony we take the difference in days between the first egg date and the tenth municipality egg date for Fryslân. A synchrony of 0 means that lay dates in both data sets started on the same day. GLM results: spring temperature: $F_{1,46}$ = 15.42, P < 0.001.

DISCUSSION

The unique dataset of more than a century presented here enabled us to look back on how Lapwings responded to enormous environmental changes in terms of the date of laying and the synchrony of their laying effort. Over this time period, the Dutch meadows transformed from colourful flower-rich, low intensity grazing pastures and hayfields, into monoculture pastures with the highest fertilisation load in Europe which are mowed and grazed as frequently as possible (Beintema *et al.* 1995, Potter 1997, Bijlsma *et al.* 2001). Perhaps it is surprising that during these immense changes of their habitat, Lapwings and other meadowbirds were able to maintain populations at all; it hardly comes as a surprise that Lapwings in The Netherlands now lay earlier than a hundred years ago. This was in contrast to Lapwings in the UK, which did not show an advance in laying date, but these data are probably more heterogeneously in how they were collected (Chamberlain & Crick 2003). However, our data show that most of the advance in laying date was explained by increases in spring temperatures and winter rainfall. Only a few days of the 8–10 day advance were statistically explained by other than climatic causes.

Indeed, the effect of climate change on laying date is strong in Lapwings. Since the 1950s laying date of both the first egg of the province and in the 10th successive municipality advanced by about 10 days. During cold years eggs were laid later but the start of laying was more synchronous than in warmer springs. These findings are consistent with results on other birds showing that earlier laying can statistically be accounted for by changes in climatic characteristics (Crick *et al.* 1997, Visser *et al.* 1998, Crick & Sparks 1999, Both & Visser 2001, Walther *et al.* 2002, Visser *et al.* 2003, Dunn 2004). The best evidence that climate change indeed causes phenological advancements comes from a Europe-wide comparison of trends in laying date in Pied Flycatchers *Ficedula hypoleuca*, in which the strength of the advancement could be related to the local change in temperature (Both *et al.* 2004).

One may object that the strong correlation between laying date and spring temperature could be caused by observer bias. However, if observers would be more active in warmer years, we expect that in warm years the synchrony of laying would be higher, yet we found that it was lower (Fig. 3). If over time the searching intensity for Lapwing eggs had increased and thus explained the long-term change in lay date, we would have expected year to be a stronger explanatory variable than temperature. This was not the case (Table 1).

That climate had a greater effect on lay date of Lapwings than changes in agricultural practise contrasts with the conclusions of earlier studies (Beintema *et al.* 1985) based on an advancement of the average ringing date of chicks between 1910 and 1975 (Beintema *et al.* 1995). In contrast to the 20-day advancement of ringing date found by Beintema *et al.*, the first egg laying date did not advance if we select the data on first egg-dates for the 1910–1975 period (Appendix 1). Not only was the additional statistical effect of year small in the whole dataset, it was not found in the date of the 10th municipality egg since 1955, the period during which farming increasingly turned into agri-industry (Mak 1996, Potter 1997, Bijlsma *et al.* 2001, Jukema *et al.* 2001). In fact, the year effect found for the entire dataset since 1897 may be an artefact of using a fixed temperature window while laying dates shifted, with increasing likelihood in recent years that Lapwings laid their first egg before the end of the time window over which the temperatures were calculated.

Why would Lapwings lay earlier during warm springs and after wet winters? There are two, not mutually exclusive, classes of explanation: (1) proximate explanations try to understand the internal and external cues organisms use to start laying (e.g. temperature in this case), (2) ultimate explanations seek the fitness consequences of a certain laying date. Under the proximate hypothesis birds may react to temperature as a cue, and lay earlier because it is warmer; in a more indirect way they may also react to the amount of food they need to produce and incubate eggs, with food being correlated with temperature. The ultimate hypothesis considers the fitness consequences of laying at a certain temperature, taking into account that laying at low temperatures may be detrimental to female survival, or that late hatching chicks have low survival because of low food availability. We have no knowledge on proximate cues that Lapwings use to lay their eggs, but food availability may play a role, since in Sweden variation in laying date among individual territories was explained well by earthworm availability (Högstedt 1974). That in our dataset higher winter rainfall leads to earlier laying dates may thus reflect the suggestion that earthworm availability is a function of soil humidity (Grant 1955, Buckerfield 1992). Note that, especially for females, food availability can also be an ultimate explanation, because an abundance of earthworms may lower the energetic and/or survival costs for females to lay early in the year.

The ultimate consequences of laying date are better known, albeit only from descriptive work. Early Lapwing nests survive less well than later nests due to predation (Beintema & Müskens 1987), while late nests, partly as a consequence of cattle trampling and mowing, have low hatching success (Beintema & Müskens 1987) and probably low chick survival as well (Bil & Schuurs 2001). These opposing selection pressures may lead to an optimal laying date that is not too early and not too late, which gives maximal fitness (Fig. 4). This optimal date depends on the prevailing selection pressures. Most likely selection for laying date has shifted for Lapwings breeding in The Netherlands. One change is the increase in temperature, probably leading to an advance of the different components of the grassland foodweb, shifting the fitness curve to earlier dates without affecting its shape (Fig. 4A). The other is due to anthropogenic influences such as advanced mowing date, affecting only one component of the fitness curves and thereby both advancing the optimal laying date and compressing the fitness peak more in time (Fig. 4B). Adapting to the temperature change requires that Lapwings lay earlier if it is warmer and thus using temperature or a related cue as a proximate mechanism: our correlations support

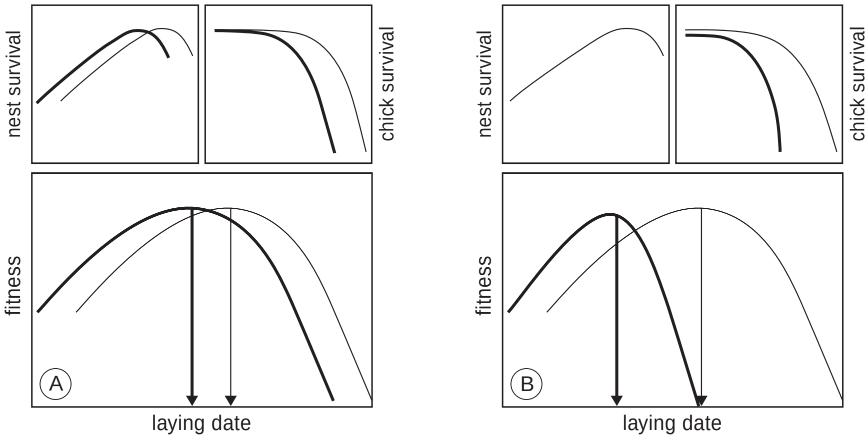

Figure 4. Hypothetical impact of changes in (A) climate and (B) mowing date on fitness components of Lapwings, with the thin curves showing an early, and the bold curves a late situation. Nest survival increases but chick survival decreases over time, yielding an optimal laying date at intermediate dates. Climate change pushes curves to earlier dates, but advanced mowing also affects the shape of the curve, making it more important to lay at the right time of year.

this idea. In contrast, adaptation to changed agricultural practises is more difficult, because at the time of egg-laying Lapwings have no idea when mowing will start and therefore they lack proximate cues or have not evolved the cues yet that have predictive power of when to expect mowing. The slight advance in laying date on top of climate-related variables may thus represent the minor response to this part of the environmental change encountered in the course of the last century, or alternatively may have been a response on selection on genetic variation in laying date (van Noordwijk *et al.* 1981). We do not know whether the observed advance of laying date has been sufficient to cope with the changing climate, but given the declines in breeding population size most likely caused by low reproduction in the current agricultural landscape, we hypothesise that the advance in laying date is not enough to cope with stronger selection for early breeding imposed by current agricultural practises.

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SAMENVATTING

Ons vermogen om terug te kijken in de tijd wordt bepaald door onze leeftijd. Dit maakt het moeilijk om langetermijneffecten van omgevingsveranderingen op vogels te onderzoeken. Gelukkig bestaan er lange tijdseries van waarnemingen gedaan door verschillende generaties onderzoekers, die het mogelijk maken om terug te kijken in de tijd. Wij maken hier gebruik van een van de langste biologische tijdseries: de vondst van het eerste kievitsei sinds 1897 in Fryslân. Sinds die tijd heeft het Nederlandse weidelandschap enorme veranderingen ondergaan en is ook het klimaat geleidelijk veranderd. In de meer dan 100 jaar lange reeks gegevens vonden we een duidelijk effect van temperatuur in de late winter op de eerste eivondst: hoe warmer hoe eerder het eerste ei, maar ook na natte winters werd het eerste ei eerder gevonden. Als het warm is, leggen de vogels niet alleen eerder, maar ook minder synchroon. Deze effecten van klimaatsvariabelen verklaren het grootste deel van de variatie in eileg, maar boven op deze effecten is er nog een kleine vervroeging in de loop der jaren. Deze zou veroorzaakt kunnen worden doordat Kieviten *Vanellus vanellus* ook hebben gereageerd op veranderingen in de landbouw, zoals betere ontwatering en vroeger maaien. In een eerdere studie lieten Beintema et al. (1985) al zien dat de gemiddelde datum waarop jonge Kieviten die in de periode 1910–1975 waren geringd, 20 dagen naar voren was verschoven. Deze verschuiving is gelijk aan de vervroeging van de maaidatum. Beintema et al. suggereerden dat de vogels hier hun legdatum op hebben aan-

gepast. In onze visie is de vervroeging van de gemiddelde ringdatum echter het directe gevolg van maaien, doordat late broedsels nauwelijks nog jongen opleveren. Kieviten lijken hun legdatum niet direct aan te passen aan deze veranderingen in de landbouw, maar lijken wel sterk op klimaatsfactoren te reageren. We denken dat kieviten zich zowel aan klimaatsfactoren als aan veranderende landbouwmethoden zouden moeten aanpassen, omdat beide een effect hebben op de fitness van de vogels. Aanpassing aan veranderende landbouwmethoden is echter moeilijk, omdat Kieviten de maaidata niet kunnen voorspellen wanneer zij hun eieren leggen. Gezien de afnemende grootte van de Nederlandse broedpopulatie is de vervroeging van legdatum kennelijk niet genoeg om de veranderingen in de leefomstandigheden het hoofd te bieden.

Corresponding editor: Rob G. Bijlsma
Received 28 September 2004; accepted 25 February 2005

Appendix 1: Laying dates of Lapwings in Fryslân since 1897. Dates are days in March. For each year we give the annual mean temperature (0°C) for the period 15 Febr – 15 Mar in De Bilt (temp), the first egg date (first), and the date the first egg in the tenth municipality was found (tenth). The latter was only available since 1955. Data for 2001 are lacking.

Year	Temp	First	10th	Year	Temp	First	10th	Year	Temp	First	10th	Year	Temp	First	10th
1897		18		1924	0.44	22		1951	3.59	21		1978	4.96	14	17
1898		22		1925	3.17	23		1952	4.53	14		1979	1.44	18	21
1899		20		1926	7.49	15		1953	4.65	18		1980	4.60	17	18
1900		23		1927	5.02	15		1954	3.33	23		1981	3.41	15	16
1901	2.57	25		1928	3.38	26		1955	–1.25	30	30	1982	2.87	15	17
1902	3.03	18		1929	–1.69	27		1956	–1.90	25	27	1983	3.61	13	17
1903	5.33	20		1930	2.86	22		1957	5.30	11	16	1984	1.80	18	19
1904	1.97	22		1931	0.50	26		1958	1.26	29	34	1985	1.72	19	26
1905	4.24	21		1932	1.67	25		1959	5.50	13	19	1986	–1.30	24	25
1906	4.24	17		1933	3.57	17		1960	5.20	18	19	1987	0.33	27	29
1907	2.90	22		1934	4.15	21		1961	6.97	7	13	1988	3.72	15	17
1908	3.47	20		1935	3.99	23		1962	1.27	25	26	1989	6.97	4	13
1909	–0.10	27		1936	3.69	19		1963	0.51	18	20	1990	7.81	10	12
1910	5.79	14		1937	3.22	23		1964	1.74	27	27	1991	6.53	12	14
1911	5.39	16		1938	4.75	20		1965	1.40	20	21	1992	5.95	9	15
1912	7.43	9		1939	5.11	24		1966	5.26	7	10	1993	3.94	16	18
1913	3.74	13		1940	2.66	24		1967	6.66	9	12	1994	3.95	12	14
1914	5.56	14		1941	4.22	20		1968	1.82	16	18	1995	5.80	11	15
1915	3.80	15		1942	–1.88	24		1969	1.67	31	32	1996	1.93	25	26
1916	2.44	16		1943	4.11	20		1970	1.07	22	23	1997	7.64	8	13
1917	1.72	17		1944	1.01	23		1971	1.48	20	21	1998	7.24	10	14
1918	3.16	18		1945	5.75	15		1972	4.08	20	23	1999	5.50	9	12
1919	5.33	18		1946	1.59	23		1973	3.67	15	19	2000	5.98	10	13
1920	5.68	13		1947	–3.13	27		1974	3.01	18	20	2001	4.46		
1921	5.34	12		1948	2.18	18		1975	5.04	13	20	2002	8.58	9	13
1922	6.40	15		1949	3.70	21		1976	3.79	21	26	2003	5.14	12	15
1923	3.00	19		1950	5.00	20		1977	6.54	10	13				