Timing of the Breeding Season of Black-Tailed Godwit Limosa limosa and Northern Lapwing Vanellus vanellus in The Netherlands

Authors: Musters, C.J.M., ter Keurs, W.J., and Snoo, G.R. de

Timing of the breeding season of Black-tailed Godwit *Limosa limosa* and Northern Lapwing *Vanellus vanellus* in The Netherlands

C.J.M. Musters[1,*], W.J. ter Keurs[1] & G.R. de Snoo[1,2]

Long-distance migratory bird species might face larger problems to adapt to local climate change in their breeding area than short-distance migrants. This study investigated the effect of climatic change on the timing of the breeding season of two wader species with contrasting migration strategies, the long-distance migratory Black-tailed Godwit *Limosa limosa* and the short-distance migrant Northern Lapwing *Vanellus vanellus*. We tested the hypothesis that a change in breeding schedule will be stronger in the Lapwing than in the Godwit. Our analyses are based on the ringing dates of around 35,000 Black-tailed Godwit chicks and 112,000 Lapwing chicks from 1960 to 2004 in The Netherlands. The results demonstrate that the Lapwing is breeding earlier than in the 1960s, independent of the species' direct response to warm early springs. In contrast, the Godwit does not exhibit earlier breeding dates other than a direct response to warmer springs. Our observations suggest that the Godwit is not able to advance breeding dates to cope with changes in its breeding habitat. This could mean the species is suffering lower breeding success than would have been the case if it had adapted, and this could be one of the reasons for the stronger decline in The Netherlands of the Godwit population than that of the Lapwing.

Key words: meadow birds, Black-tailed Godwit, Lapwing, timing, breeding season, climate change, agriculture

[1]Institute of Environmental Sciences, Leiden University, P.O. Box 9518, 2300 RA Leiden, The Netherlands; [2]Nature Conservation and Plant Ecology Group, Wageningen University, P.O. Box 47, 6700 AA Wageningen, The Netherlands; *corresponding author (musters@cml.leidenuniv.nl)

All kinds of organisms, including birds, have a tendency to shift their breeding season to earlier in the year because of milder temperatures or changes in precipitation due to climate change (Crick *et al.* 1997, McCleery & Perrins 1998, Bergmann 1999, Parmesan 2006). However, in particular long-distance migratory birds may be unable to fully adapt to local climate change in the breeding area (Both & Visser 2001, Hüppop & Winkel 2006, but Anthes 2004). The need to adapt may depend, among other things, on how the breeding habitat is affected by climate change. For example, if prey abundance does not peak sharply during the breeding season, there may be little need for adaptation (Both *et al.* 2006). Moreover, certain taxonomic groups may be more adaptable than others. The question, then, is whether related bird species, breeding in the same habitat and accustomed to having the same breeding period, differ in their adaptation to climate change according to their migration strategy.

The agricultural grasslands of The Netherlands harbour relatively large populations of wader species. For example, the Dutch population of Black-tailed Godwits *Limosa limosa* is estimated to be 45–50,000 breeding pairs, which is about 45% of the total population within the European Union. The breeding population of the Northern Lapwing *Vanellus vanellus* is estimated at 200–300,000 pairs, some 12% of the EU population (Verhulst 2007). Both species breed relatively early and place their nests on ground of highly productive agricultural grasslands. In the breeding season, Godwits

feed mainly on soil invertebrates like earthworms, and Lapwings on ground-dwelling invertebrates (Beintema *et al.* 1995). Godwit chicks feed on small flying insects, which they pick from blades of grass, while Lapwing chicks pick ground-dwelling insects (Beintema *et al.* 1995). Both species are considered of high conservational value in Europe (Burfield & van Bommel 2004).

In The Netherlands the relationship between agriculture, usually dairy farming, and meadow bird populations has long been the subject of research (Klomp 1954, Verstrael 1987, Beintema 1991, Kruk 1994, Musters *et al.* 2001, Kleijn *et al.* 2001, Verhulst 2007, Kragten & de Snoo 2007, Schekkerman 2008). The shift from extensive to intensive farming that took place in the 20th century is usually regarded as favourable for most of the species concerned, providing them with more food because of the larger amounts of fertilizer used (Beintema *et al.* 1995). Agricultural practices seem to have passed the optimum intensity for most species, however, and the numbers of almost all meadow birds are now declining (Burfield & van Bommel 2004, Teunissen & Soldaat 2006). Between 1990 and 2005 the number of Godwit breeding pairs decreased by about 2–5% annually, while the Lapwing, though seemingly stable between 1990 and 2000, declined by over 3% per year between 2001 and 2005 (Teunissen & Soldaat 2006). High fertilizer inputs combined with lower water tables have resulted in highly productive grassland in early spring, allowing a high density of cattle and early mowing with fast-moving machines covering large areas in a short period of time. This may have shortened the time in which the meadow birds can breed without eggs being trampled or chicks being killed by mowing activities, and is thought to be one of the key reasons for the decline of the two species (Schekkerman 2008).

Based on ringing data, Beintema *et al.* (1985) found a trend toward earlier breeding in meadow birds, including Godwit and Lapwing, between 1911 and 1974. This trend was correlated with mowing date and the actual breeding time would therefore not be shortened (Beintema *et al.* 1985). Both *et al.* (2005) found an ongoing shift in the laying date of Lapwing towards earlier breeding, but contrary to Beintema *et al.* (1985) they explained this change as a result of climate change. The change in laying dates of meadow birds may thus be due to agricultural change, climate change, or both.

The Lapwing is a short-distance migratory species – the Dutch Lapwing stays in Western Europe during winter (Beintema *et al.* 1995) –, while the Godwit is a long-distance migratory species that winters in Africa south of the Sahel (Beintema *et al.* 1995). This raises the question whether the Godwit is able to adapt its breeding season to climate changes or changes in agricultural practice in Western Europe as the Lapwing appears to do. Moreover, earlier analyses suggested that Godwits now start breeding later than they did in the 1960s (unpubl. data). If so, the effective breeding time of Godwits is squeezed in between a later start of the breeding season and an earlier start of ecological processes and agricultural activities. This misfit might contribute to the present decline of the Godwit population in The Netherlands.

The results of our preliminary analyses and Both *et al.* (2005) were based on 'first' observations, i.e. the date of the first ringed chicks and date of the first egg found, respectively. These approaches can be criticized, because phenology assessments based on first observations may be biased and are sensitive to number of observation sites, changes in population abundance and start of the observation period (van Strien *et al.* 2008). Since meadow bird abundance is known to be changing, it is anticipated that changes in population size might be biasing the results of first-date analyses. We therefore chose to analyse ringing data in a way that is more robust and less sensitive to population size. Based on ringing dates we here analyse the influences of climate on the start of the breeding season of the Godwit and Lapwing. We focus on a comparison between the two species and test the hypothesis that if a change in timing of breeding is detected, it will be stronger in the Lapwing than in the Godwit.

METHODS

Ringing dates
The Dutch Bird Ringing Centre in Heteren provided us with the Dutch ringing data compiled between 1911 and 2004 for the Black-tailed Godwit (ca. 40,000) and Lapwing (ca. 130,000). Our analyses are based on the ringing dates of approximately 35,000 Black-tailed Godwit chicks and 112,000 Lapwing chicks from 1960 to 2004. The average number per year was 778.3 ± 432.4 for the Godwit and 2497.6 ± 1025.3 for the Lapwing.

To check whether a change in ringing locations might have affected ringing dates, we calculated the average X- and Y-coordinate of all ringing locations per year for both species. The Dutch Amersfoort X- and Y-coordinates were used, which means that X increases from west to east and Y from south to north. Since the north-east of the Netherland has colder winters (van

Vliet *et al.* 2009), a shift of ringing locations in a northeasterly direction may have resulted in later ringing dates without any actual shift in breeding time. *AverageX* and *AverageY* were included as independent variables in the regression analyses.

Timing of breeding

To measure the timing of breeding we used the day number from 1 January as 'date'. From the ringing data we calculated the dates of the first and last chick ringed in order to explore the data. The date of the 5th percentile was calculated as a measure of the start of the breeding season (cf. Anthes 2004), while the 95th percentile of chicks ringed was used as a measure of the end of the breeding season. The middle of the breeding season was measured by the date of the 50th percentile. In line with van Strien *et al.* (2008), both study species show a different correlation between year and start of the breeding season when taking the date of the first ring as measurement as compared to taking the date of the 5th percentile of all chicks ringed. The difference is especially pronounced in the Lapwing. The 25th percentile, the measure recommended by van Strien *et al.* (2008), was also considered but rejected because of its strong correlation with the date of the 50th percentile. On average, 5% of the chicks ringed per year were 38.9 ± 21.6 for Godwits and 124.9 ± 51.3 for Lapwings. Knowing that Godwits have on average 3.86 eggs per nest and Lapwings 3.85 eggs (Cramp 1983), and assuming that all eggs survive and that ringers ring all chicks of a nest, this means that date of the 5th percentile is based on an average of 10.1 Godwit and 32.4 Lapwing nests per year. Since not all eggs hatch and not all chicks are caught, this is obviously a minimal estimate of the number of broods on which the date of the 5th percentile is based.

Climate change

To include climate change in our regression models, we selected variables characterizing changes in winter, spring, summer and the whole year. Variables for winter and spring climate were chosen because of their possible influence on the start of the breeding season, variables for spring, summer and whole year climate because of their possible influence on the middle and end date of the breeding season.

For changes in winter climate we used the North Atlantic Oscillation (NAO) index (Forchhammer *et al.* 1998, Mysterud *et al.* 2003; http://www.cgd.ucar.edu:80/cas/climind/), which stands for the difference between atmospheric pressure in the winter (December, January, February and March) over Stykkosholmur

(Iceland) and Lisbon (Portugal). When the NAO index is negative it reflects cold, dry winters in The Netherlands; when positive, it leads to warm, wet winters (Opsteegh & Beersema 2000). Additionally we calculated the annual average rainfall in December until March at weather stations in De Bilt, Den Helder and Vlissingen (http://www.knmi.nl/klimatologie/maandgegevens/index.html).

Spring was characterized by the average February and March temperatures of the same three weather stations, summer by averaging June and July temperatures. Year temperatures are available on http://www.milieuennatuurcompendium.nl/, as cited in Both *et al.* (2005).

Data analyses

Multiple regression analyses were performed to analyze effects of climate change on the timing of the breeding season of the Godwit and Lapwing. Climate variables and average coordinates were included in multiple regression models in all the different combinations, with model selection being based on the Akaike Information Criterion (AIC). The model with the lowest AIC, i.e. the model that best explains the data with a minimum of free parameters, was selected as the preferred model and is given in the results, together with the four next best models. Statistical analyses were carried out using the statistical analysis program GenStat 11.0. In all analyses, residuals were checked on deviation from a normal distribution, which was never the case.

RESULTS

Data exploration

When plotting the first and last ringing date per year, it became clear that in the early days of ringing data were too scarce to use for studying phenology (Fig. 1). Up until the 1950s, the first and last dates were so close together that they seemed part of the same cloud of data points. Yet, the progressively earlier start of the breeding season reported by Beintema *et al.* (1985) for both species over the period 1911–1974 can well be recognized. From the 1960s onwards, the difference between first and last ring, i.e. the breeding season, becomes visible.

Climate change was detectable in our data by positive correlations between year and year-round temperature (*TempYear*: $r = 0.63$, $P < 0.001$), NAO-index (NAO: $r = 0.42$, $P = 0.004$), temperature in February and March (*TempFebMarch*: $r = 0.34$, $P = 0.023$) and temperature in June and July (*TempJunJul*: $r = 0.36$,
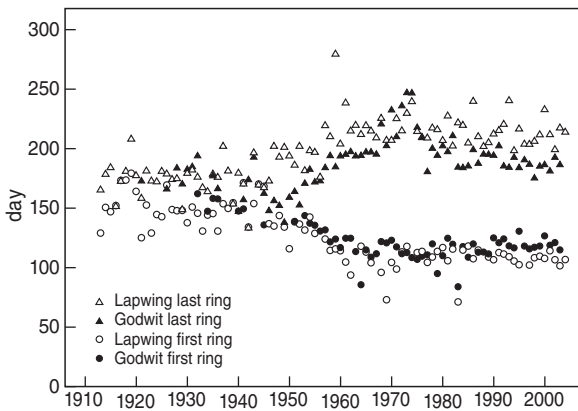
Figure 1. Dates of first and last ringing of Black-tailed Godwit and Northern Lapwing chicks between 1911 and 2004.
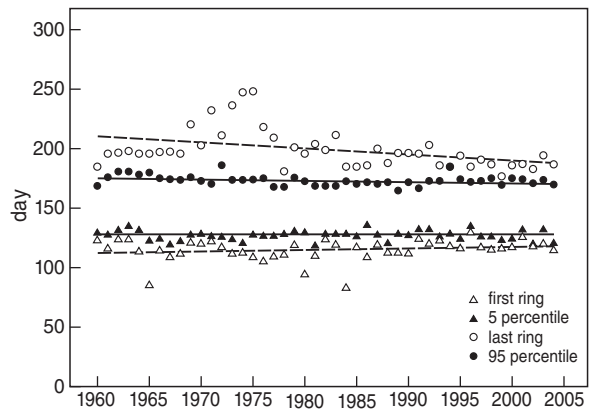

Figure 2. Ringing dates of Black-tailed Godwit chicks between 1960 and 2004.

$P = 0.014$). No correlation was found between year and winter and early spring precipitation (*WinterPrec*: $r = 0.10, P = 0.509$).

Between 1960 and 2004 the date of the 5th percentile of chicks ringed showed no change toward an earlier date for the Godwit (Fig. 2; Table 1), while in Lapwing this date shifted about 8.5 day (Fig. 3; Table 1). The date of the 95th percentile did not change for the Lapwing, while Godwit ringing stopped about five days earlier (Figs 2 and 3; Table 1).

In the Godwit there was neither a west–east shift in ringing locations between 1960 and 2004 (correlation between Year and *AverageX*: $r = -0.04, P = 0.801$), nor a south–north shift (Year and *AverageY*: $r = 0.27, P = 0.073$). In the Lapwing, however, a strong shift towards the north-east could be detected (Year and *AverageX*: $r = 0.68, P < 0.001$; Year and *AverageY*: $r = 0.69, P < 0.001$).

Model selection

In Godwit, the five multiple regression models that best explain the date of the 5th percentile of chicks ringed all included early spring temperature and winter precipitation (Table 2, Appendix 1). None of the other variables tested proved to explain any significant part of the variance. The five best models for the 50th percentile date show no clear pattern in the variables selected and none of the variables explained a significant part of the variance. The same holds for the end of the breeding season: none of the variables tested explained a significant part of the variance. Accounting for effects of climate leads to a marked change in the correlation between year and the 5th and 95th percentile for the Godwit (compare the factor Year in Table 2 with Table 1).
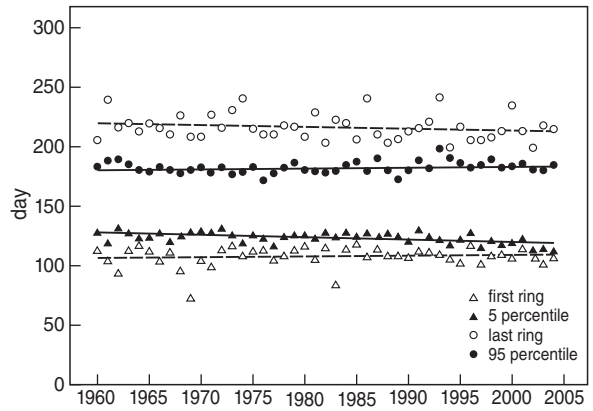
Figure 3. Ringing dates of Northern Lapwing chicks between 1960 and 2004.

Table 1. Correlation between timing of breeding and year for Black-tailed Godwit and Lapwing. Significant r ($P < 0.05$) in bold.

Species	Correlation between year and	Pearson r	P
Black-tailed Godwit	Date first ring	0.180	0.236
	Date 5th percentile	0.009	0.952
	Date 50th percentile	–0.071	0.644
	Date 95th percentile	**–0.320**	0.032
	Date last ring	**–0.417**	0.004
Lapwing	Date first ring	0.097	0.528
	Date 5th percentile	**–0.545**	<0.001
	Date 50th percentile	–0.277	0.065
	Date 95th percentile	0.191	0.208
	Date last ring	–0.173	0.255

For the Lapwing, too, early spring temperature is the most relevant climate variable in the multiple regression models for the date of the 5th percentile of chicks ringed (Table 3, Appendix 2). No other variable contributed significantly to the models. The preferred model of the date of the 50th percentile included early spring temperature and summer temperature. The preferred model of the date of the 95th percentile included summer temperature and the non-significant AverageY. Accounting for climate variables and coordinates leads to a considerable change in the correlation between year and the dates of both the 50th and 95th percentile (compare the factor Year in Table 3 with Table 1). The correlation between year and the 5th percentile remains significant (Table 3).

DISCUSSION

In both the Godwit and the Lapwing the start of the breeding season is negatively correlated with temperature in February and March, i.e. the species start breeding early when spring temperature is relatively high. This was also found by Both *et al.* (2005) for Frisian Lapwings and it makes sense; in this way breeding is synchronized with other relevant time-dependent phenomena such as soil temperature and food availability for chicks. Also, adults may be in a better condition after mild early springs. The temperature in early spring seems to determine the timing of the entire Lapwing breeding population, since in this species we also found a correlation between this variable and the 50th percentile ringing date.

Table 2. Regression models for timing of the Black-tailed Godwit breeding season ($n = 45$).

Date 5th percentile

R^2 adjusted	0.321			
F	7.94			
P	<0.001			
Parameter	Estimate	SE	T	P
Constant	4.0	85.4		
Year	0.067	0.043	1.55	0.130
TempFebMarch	–0.117	0.033	–3.57	<0.001
WinterPrec	–0.007	0.003	–2.19	0.034

Date 50th percentile

R^2 adjusted	0.075			
F	2.19			
P	0.104			
Parameter	Estimate	SE	T	P
Constant	141.6	89.0		
Year	–0.010	0.047	0.22	0.830
TempFebMarch	–0.062	0.033	–1.90	0.064
AverageY	0.058	0.037	1.55	0.128

Date 95th percentile

R^2 adjusted	0.079			
F	2.89			
P	0.067			
Parameter	Estimate	SE	T	P
Constant	330	124		
Year	–0.074	0.066	–1.13	0.265
TempYear	–1.03	1.09	–0.94	0.352

Table 3. Regression models for timing of the Lapwing breeding season ($n = 45$).

Date 5th percentile

R^2 adjusted	0.427			
F	17.43			
P	<0.001			
Parameter	Estimate	SE	T	P
Constant	407.4	83.7		
Year	–0.141	0.043	–3.32	0.002
TempFebMarch	–0.107	0.031	–3.47	0.001

Date 50th percentile

R^2 adjusted	0.268			
F	6.36			
P	0.001			
Parameter	Estimate	SE	T	P
Constant	188.2	82.1		
Year	–0.006	0.043	–0.15	0.885
TempFebMarch	–0.085	0.029	–2.91	0.006
TempJunJul	–0.139	0.058	–2.41	0.020

Date 95th percentile

R^2 adjusted	0.168			
F	3.96			
P	0.014			
Parameter	Estimate	SE	T	P
Constant	96	130		
Year	0.0389	0.074	0.53	0.602
TempJunJul	–0.2276	0.081	–2.82	0.007
AverageY	0.0909	0.050	1.83	0.075

In Godwits we found a negative correlation between the start of the breeding season and winter precipitation: after a rainy winter Godwits start breeding early. This can be explained by the fact that large amounts of winter precipitation result in wet soils which may have a high food abundance and be easy to penetrate by foraging adult Godwits (Beintema *et al.* 1995). The adults can then gain weight quickly and will be ready for breeding early. If this reasoning is correct, it would mean that in Godwits the start of the breeding season is at least partly limited by food availability in the breeding areas. Lapwings, in contrast, may not strongly depend on soil-dwelling food species for getting into condition to breed (Beintema *et al.* 1995, but see also Högstedt 1974 who found a correlation between the abundance of earthworms and laying date in Sweden), so that in this species no correlation with winter precipitation is found.

In contrast to the Godwit, the Lapwing has shifted its breeding season towards an earlier timing since the 1960s, independent of the direct response to warm early springs (Fig. 4). Although this may be a direct reaction to an unknown confounding factor, we think this can be reasonably assumed to be an adaptation to climate change, changes in agricultural practices or a combination of these two factors. We attempted to separate the factors by including a variable for agricultural intensity in the analyses. The only variable available over a large part of our study period (1966–2004) was mowing intensity, expressed as the percentage of land mowed. However, this variable was highly correlated with year ($r = 0.96$) and made it impossible to include both this variable and year in our multiple regression analyses. Hence, the effect of year could well be the effect of agricultural intensity. So, unlike Both *et al.* (2005), we cannot conclude that the timing of the start of the Lapwing breeding season is defined only by climate.

Given that many bird species start their breeding season earlier in response to climate change, combined with the fact that the Lapwing, a species using the same breeding habitat as Godwit, also starts breeding earlier, suggests that the breeding habitat has changed, but that the Godwit did not adapt to these changes. This could mean that the Godwit is suffering lower breeding success than would have been the case if it had adapted and this could be one of the reasons for the relatively strong decline of the Godwit population in The Netherlands compared with that of the Lapwing (Teunissen & Soldaat 2006).

Why is the Godwit unable to start breeding as early as the Lapwing? Is the fact that the Godwit is a long-
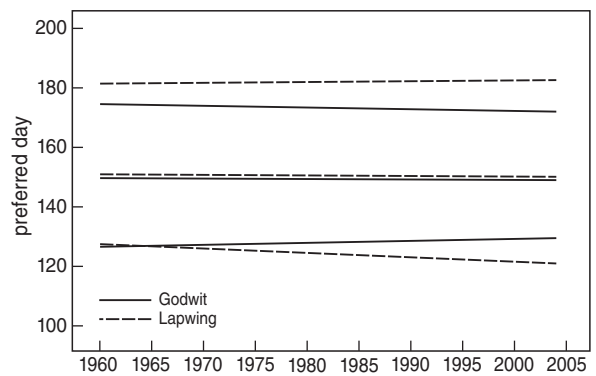

Figure 4. Ringing dates of chicks of Godwit and Lapwing between 1960 and 2004. Given are results of preferred regression models of the dates of the 5th (lower lines), 50th (middle lines) and 95th percentiles (upper lines).

distance migrant, while the Lapwing is not, sufficient reason? This might be the case, although other long-distance migratory waders were able to shift their migration timing, namely *Tringa nebularia, T. erythropus* and *T. glareola* (Anthes 2004). One would therefore expect that under strong selective pressure the timing of migration would shift towards earlier dates. This could mean either that there is no strong selective pressure towards earlier breeding, or that the start of the breeding season is not delimited by the arrival of adults, but by some other factor. The absence of selective pressure towards earlier breeding may be unlikely because it contrasts with our findings for the Lapwing as well as the huge amount of literature showing shifts towards earlier breeding in other birds. However, our results do suggest that in Godwits another delimiting factor may be involved at the start of the breeding season: food availability for adults arriving from their winter grounds. Even if the Godwits were to arrive earlier, there might not be enough food available for the adults to gain weight fast enough to start breeding earlier. That food availability can affect the laying date has been shown for Lapwings in Sweden in the 1970s (Högstedt 1974). As stated before, food availability for Lapwings may not be limited by wet soils in The Netherlands.

Our results suggest that Godwit and Lapwing differ in their change of breeding season. In designing conservation strategies related to the allowance of early agriculture activities on land under agri-environmental schemes, these differences should be taken into consideration. The two species should therefore not be treated as two meadow birds for which one meadow bird policy is applicable, which is now the case in The Netherlands.

ACKNOWLEDGEMENTS

REFERENCES

Anthes N. 2004. Long-distance migration timing of *Tringa* sandpipers adjusted to recent climate change. Bird Study 51: 203–211.

Beintema A.J. 1991. Breeding ecology of meadow birds (Charadriiformes); implications for conservation and management. PhD thesis University of Groningen.

Beintema A.J., Beintema-Hietbrink R.J. & Müskens G.J.D.M. 1985. A shift in the timing of breeding in meadow birds. Ardea 73: 83–89.

Beintema A., Moedt O. & Ellinger D. 1995. Ecologische Atlas van de Nederlandse Weidevogels. Schuyt & Co, Haarlem.

Bergmann F. 1999. Langfristige Zunahme früher Bruten beim Teichrohrsänger (*Acrocephalus scirpaceus*) in einem südwestdeutschen Untersuchungsgebiet. J. Ornithol. 140: 81–86.

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.

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. & Visser M. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature 411: 60–62.

Burfield I. & van Bommel F. (eds) 2004. Birds in Europe. Population estimates, trends and conservation status. BirdLife International, Cambridge.

Cramp S. 1983. Handbook of the birds of Europe, the Middle East and North Africa. Volume III. Waders to Gulls. Oxford University Press, Oxford.

Crick H. Q. P., Dudley C. , Glue D. E. & Thomson D. L. 1997. UK birds are laying eggs earlier. Nature 388: 526.

Forchhammer M.C., Post E. & Stenseth N.C.1998. Breeding phenology and climate. Nature 391: 29–30.

Högstedt. G. 1974. Length of the pre-laying period of the Lapwing *Vanellus vanellus* L. in relation to its food resources. Ornis Scand. 5: 1–4.

Hüppop O. & Winkel W. 2006. Climate change and timing of spring migration in the long-distance migrant *Ficedula hypoleuca* in central Europe: the role of spatially different temperature changes along migrating routes. J. Ornithol. 147: 344–353.

Kleijn D., Berendse F., Smit R. & Gilissen N. 2001. Agri-environment schemes do not effectively protect biodiversity in Dutch agricultural landscape. Nature 413: 723–725.

Klomp H. 1954. De terreinkeus van de Kievit (*Vanellus vanellus*). Ardea 42: 1–139.

Kragten S. & de Snoo G.R. 2007. Nest success of Lapwings *Vanellus vanellus* on organic and conventional arable farms in the Netherlands. Ibis 149: 742–749.

Kruk M. 1994. Meadow bird conservation on modern commercial dairy farms in the western peat district of the Netherlands: possibilities and limitations. PhD thesis Leiden University.

McCleery R.H. & Perrins C.M. 1998. Temperature and egg-laying trends. Nature 391: 30–31.

Musters C.J.M., Kruk M., de Graaf H.J. & ter Keurs W.J. 2001. Breeding birds as a farm product. Conserv. Biol. 15: 363–369.

Mysterud A., Stenseth N.C., Yoccoz N.G., Ottersen G. & Langvatn R. 2003. The response of terrestrial ecosystems to climate variability associated with the North Atlantic Oscillation. Geophys. Monogr. 134: 235–262.

Opsteegh J. D. & Beersma J. J. 2000. De Noord-Atlantische Oscillatie. In: De toestand van het klimaat in Nederland 1999. http://www.knmi.nl/voorl/nader/klim/nao.html.

Parmesan C. 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. Syst. 37: 637–669.

Schekkerman H. 2008. Precocial problems. Shorebird chick performance in relation to weather, farming, and predation. PhD thesis University of Groningen.

van Strien A.J., Plantenga W.F., Soldaat L.L., van Swaay C.A.M. & Wallis de Vries M.F. 2008. Bias in phenology assessment based on first appearance data of butterflies. Oecologia 156: 227–235.

Teunissen W.A. & Soldaat L.L. 2006. Recente aantalsontwikkeling van weidevogels in Nederland. Levende Natuur 107: 70–74.

Verhulst J. 2007. Meadow bird ecology at different spatial scales. Responses to environmental conditions and implications for management. PhD thesis Wageningen University.

Verstrael T.J. 1987. Weidevogelonderzoek in Nederland. Een overzicht van het Nederlandse weidevogelonderzoek 1970–1985. Contactcommissie Weidevogelonderzoek van de Nationale Raad voor Landbouwkundig Onderzoek, Den Haag.

van Vliet J., Musters C.J.M. &. ter Keurs W.J. 2009. Changes in migration behaviour of Blackbirds *Turdus merula* from the Netherlands. Bird Study 56: 276–281.

SAMENVATTING

Hoe groter de afstand tussen het broed- en overwinteringsgebied van vogels is, hoe lastiger het mogelijk voor hen zal zijn om zich aan te passen aan klimaatveranderingen in het broedgebied. Om deze hypothese te toetsen werd onderzocht in hoeverre klimaatverandering doorwerkt op het tijdstip van broeden bij de Grutto *Limosa limosa*, een langeafstandstrekker, en de Kievit *Vanellus vanellus*, een korteafstandstrekker. Onze veronderstelling was dat de Kievit een sterkere verandering van het broedseizoen zou laten zien dan de Grutto. Het tijdstip van broeden werd afgeleid uit de ringgegevens van kuikens van Grutto en Kievit (respectievelijk 35.000 en 112.000 kuikens) die in de jaren 1960–2004 in Nederland zijn geringd. De resultaten laten zien dat de Kievit in de loop van de jaren eerder is gaan broeden, ook als gecorrigeerd wordt voor het warmer worden van het voorjaar. De Grutto reageert wel op hogere temperaturen in het voorjaar, maar laat daarop niet een extra vervroeging zien zoals de Kievit. Dit zou erop kunnen wijzen dat de Grutto niet in staat is te reageren op veranderingen in het broedgebied. Mogelijk draagt dit onvermogen bij aan de achteruitgang van de soort in Nederland. (DH)

Appendix 1. Variables selected in the five best models for timing of the Black-tailed Godwit breeding season. Variables are given in order of P-value. Year was included in all models tested. $n = 45$; (*): $P < 0.1$; *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$, based on F-test for including variable.

	Five best models	ΔAIC
Date 5th percentile	TempFebMarch**, WinterPrec*	0
	TempFebMarch**, WinterPrec*, AverageY	0.951
	TempFebMarch**, WinterPrec*, TempJunJul	1.025
	TempFebMarch**, WinterPrec(*), AverageX	1.126
	TempFebMarch**, WinterPrec*, TempYear	1.723
Date 50th percentile	TempFebMarch(*), AverageY	0
	TempFebMarch(*)	0.204
	AverageY(*), TempYear(*)	0.431
	TempFebMarch(*), AverageX	0.963
	AverageY, TempFebMarch, WinterPrec	1.211
Date 95th percentile	TempYear	0
	TempFebMarch	0.516
	AverageX	0.576
	TempJunJul	0.580
	AverageY	0.749

Appendix 2. Variables selected in the five best models for timing of the Lapwing breeding season. Variables are given in order of P-value. Year was included in all models tested. $n = 45$; (*): $P < 0.1$; *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$, based on F-test for including variable.

	Five best models	ΔAIC
Date 5th percentile	TempFebMarch**	0
	TempFebMarch**, TempJunJul	0.272
	TempFebMarch**, TempJunJul, NAO	0.508
	TempFebMarch**, NAO	1.025
	TempFebMarch(*), TempYear	1.499
Date 50th percentile	TempFebMarch**, TempJunJul*	0
	TempFebMarch**, TempJunJul*, WinterPrec	0.885
	TempFebMarch**, TempJunJul*, NAO	1.507
	TempJunJul(*), TempFebMarch(*), TempYear	1.887
	TempYear**, WinterPrec	1.989
Date 95th percentile	TempJunJul**, AverageY(*)	0
	TempJunJul(*), AverageY(*), TempYear	0.111
	TempJunJul**, AverageY(*), TempFebMarch	0.312
	TempYear**, AverageY(*), WinterPrec(*)	0.362
	AverageY*, TempYear(*), TempJulJun, WinterPrec	0.639