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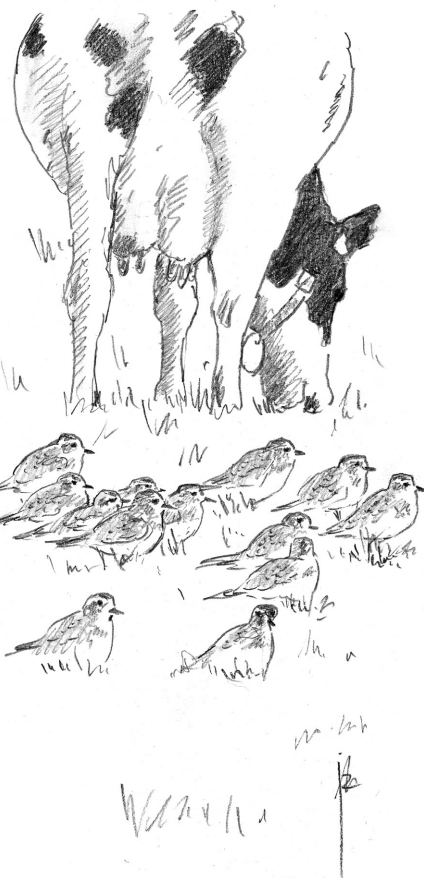
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Climate change and advanced primary moult in Eurasian Golden Plovers *Pluvialis apricaria*

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We measured primary moult scores of 1051 Eurasian Golden Plovers *Pluvialis apricaria* staging in pastures in The Netherlands from 1978 to 2011. We hypothesized that moult may have advanced due to earlier breeding resulting from global climate change. At the same time, intensification of agricultural practices has changed the environment on which the Golden Plovers depend during migration and staging, which may have affected their condition and moult schedule.

Primary moult has advanced by 8 days from 1990 to 2011, without visible changes preceding 1990. This suggests that long-term changes in weather might have caused the change in moult timing. In the absence of the variable year, the North Atlantic Oscillating (NAO) index, averaged over September–October, significantly correlated with timing of moult. However, this was a weaker relationship than that of year and timing of moult. Apparently, year correlates better with relevant weather parameters than NAO. Because moult speed at the staging areas has not changed from 1978 to 2011, the birds must have started moult earlier. Advanced breeding has been shown to have occurred in several bird species breeding in northern temperate latitudes. Golden Plovers start to moult during breeding, and therefore we think that the advancement of moult has been the result of an earlier start of breeding and not of changes in agricultural practice in The Netherlands.

Key words: wing moult, advanced breeding, staging, migratory stop-over, agricultural intensification, North Atlantic Oscillation

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Many animals living in seasonal environments move between geographically distinct breeding and non-breeding areas, tracking optimal weather or food conditions or avoiding high predation risks. It may be expected that changes in the environment will affect the timing of such events, due to altered availability of resources or simply due to changes in timing of preceding life-cycle stages (Carey 2009, Barshep *et al.* 2011). During the last few decades, the earth's climate has changed significantly (Møller *et al.* 2010). At the same time, major changes have occurred in agricultural landscapes in western Europe through the intensification of farming practices. In many cases this has come at the demise of natural values and biodiversity (Fuller *et al.* 1995; Robinson & Sutherland 2002; Wretenberg *et al.* 2006). Because the timing of life-history events is influ-

enced by environmental factors, such as weather, food availability and predation pressure, many changes may have occurred in the phenology of migratory species during the last few decades, especially those species heavily relying on agricultural areas.

We analysed timing of moult of primary feathers in Eurasian Golden Plovers *Pluvialis apricaria*, hereafter referred to as Golden Plover, systematically collected in The Netherlands during a period of 34 years. Golden Plovers depend on pastures and arable fields during migration and wintering (Jukema *et al.* 2001; Lindström 2010). They breed from south-eastern Greenland to the Khatanga River in western Siberia and those staging and wintering in The Netherlands originate mainly from Fennoscandia and NW Russia, although a significant proportion is made up of birds from further

east, up to western Siberia (Speek & Speek 1984, Jukema *et al.* 2001, Piersma *et al.* 2005). The species is monotypic and no geographically distinct populations are recognised (Byrkjedal & Thompson 1998).

The birds arrive in staging areas in north-western Europe in early August. Depending on the severity of winter, large numbers winter in those areas or move further south, mainly to northern France. In The Netherlands, numbers peak in October–November (Kleefstra *et al.* 2009) and again in March (Waarneming.nl 2012). Occasional counts, organised between 1976 and 2008, showed that numbers ranged roughly between 200,000 and 400,000 birds (Bijlsma *et al.* 2001, Kleefstra *et al.* 2014). Large numbers are present on pastures and, to a lesser extent, on arable fields (Gillings *et al.* 2007, Kleefstra *et al.* 2014), where they feed on various subterranean prey, in particular earthworms (Lumbricidae; Cramp & Simmons 1983, Thompson & Barnard 1984, Gillings & Sutherland 2007), but in the 1980s a shift seems to have occurred from inland, agricultural areas to marine coastal areas (Kleefstra *et al.* 2014). Potentially, these birds still feed inland, but only aggregate to roost on the Wadden Sea coast. Alternatively, growing numbers may feed on intertidal mudflats, but unfortunately relevant data is anecdotal (Gillings *et al.* 2006). From May until July the birds are virtually absent from The Netherlands.

Golden Plovers are exceptional, although not unique, among migratory birds in that they start wing moult during breeding to complete it in autumn in staging or wintering areas (Byrkjedal & Thompson 1998, Jukema *et al.* 2001). Birds usually do not moult flight feathers during breeding, which may either be due to the predation risks it could incur or due to the high energetic or nutritious costs of both moult and reproduction precluding their simultaneous occurrence (Hoye & Buttemer 2011). Apparently, Golden Plovers can afford to start wing moult during breeding, which may be due to low predation risks or sufficient energy reserves. Timing of breeding of Golden Plovers depends partly on spring temperature (Pearce-Higgins *et al.* 2005), and during the last few decades spring and summer temperatures have increased significantly in the northern hemisphere (Møller *et al.* 2010) while evidence is mounting that many bird species have advanced their laying dates in response to this temperature change (Dunn & Winkler 2010). We predict that the increase in temperature has advanced the timing of breeding of Golden Plovers and thereby their moult schedule. In the meantime, agricultural intensification has led to decreasing numbers of breeding meadow birds (Donald *et al.* 2001, Donald *et al.* 2006); partly

due to effects on food availability (Newton 2004, Kleijn *et al.* 2011). Many of the same factors affecting breeding meadow birds may impair foraging conditions of staging and wintering Golden Plovers. We hypothesize that this may have resulted in slower moulting of primary feathers.

METHODS

Golden Plovers were caught in pastures on the mainland of the northwest of the province of Fryslân, in the north of The Netherlands, as well as on the island of Terschelling, 50–80 km north of the mainland catching sites. Birds were caught using wilsternets – a centuries old catching technique that relies on a catcher using a flute and decoys to draw birds to a large clap net that is pulled over when birds are landing (Jukema *et al.* 2001). We analysed data from 1051 birds that were caught between 1978 and 2011 on 65 successful catching days between 2 August and 2 October. Per successful day between 2 and 81 adult birds were caught and measured. The extent of primary moult was assessed by measuring the length of each of the 10 primary feathers on an ordinal scale ranging from 0 to 5, where 0 indicates the presence of an old feather, 1 indicates the absence of a feather where an old feather has been shed to make room for a new one, and 5 the presence of a fully grown new feather (Ginn & Melville 1983). The moult score is the summed scores of the 10 primaries of one wing, therefore ranging between 0 and 50. Left and right wing moult symmetrically. Sexes cannot be distinguished based on biometrics (Jukema & Piersma 1992, Byrkjedal & Thompson 1998). Onset of primary moult can be earlier in males as Yalden & Pearce-Higgins (2002) showed in a population in the UK, but this does not seem to be a general pattern, as Byrkjedal (1978) did not detect sex differences in Norway. Birds were ringed with metal rings and immediately released after measuring. Primary moult score increases faster in the early stages of moult (Henriksen 1985), but in the range of moult scores contained in our data, scores proceeded linearly with time. All analyses were performed on adult birds of one year old or older.

Data on snow cover in the breeding areas is not available for this time span. We used the North Atlantic Oscillation (NAO) index as a covariate in our analyses because the index is correlated with weather parameters over a wide area in the northern hemisphere (Hurrell 1995, Sanz 2003). The mean index of September to November (NAO_{SON}) is correlated with

the onset and period of continuous snow cover in northern Norway, while the mean index of December to February (NAO_{DJF}) correlates with snow depth (Theakstone 2013). The index for May (NAO_M) was used because it coincides with the start of the breeding season.

Statistics

Data were analysed using Generalised Linear Models (GLMs) in SPSS (v.22, IBM Corp.). Because normality tests tend to be overly conservative with large data sets, the distributions of residual values were visually inspected and found to follow a distribution close to normality but negatively skewed. Because of this nonparametric distribution of the data, we used bootstrapping to estimate model parameters and robust estimates of the covariance matrix (also called Huber/White/sandwich estimates) which provide consistent estimates of the covariance, correcting the covariance matrix for model misspecification and sampling design. Models were compared using the Akaike Information Criterion (AIC). All statistics are shown ±1 SE.

RESULTS

Primary moult was scored for 1051 birds and scores ranged between 9 and 50 with a mean of 36.5 ± 0.2 and a median value of 37.0. We tested models with arrangements of the variables year, NAO and day number as predicting variables (Table 1). The best model included year, day and year-squared. Adding the interaction of year and day did not significantly improve the fit with moult score. Adding NAO in the

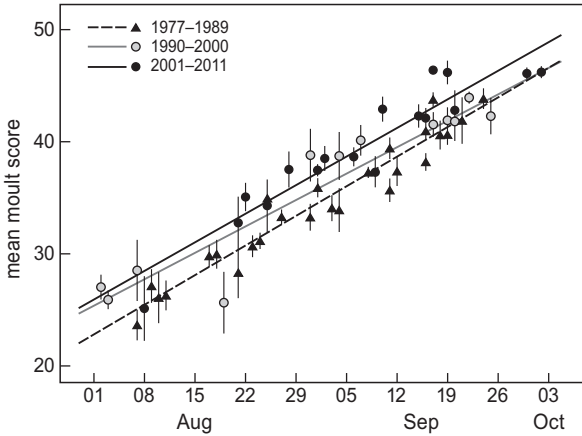


Figure 1. Average moult scores (±SE) per day in the course of a year, based on catches between 1977 and 2011.

Table 1. Results of GLM analysis relating moult score with Year, North Atlantic Oscillation indices and Day of the year, showing parameter estimates, standard errors and P-values of all significant variables after backward deletion of non-significant variables and their interaction terms. Akaike's Information Criterion (AIC) is a measure of model fit and is used to compare models.

Model	Intercept	Year	NAO (Sep-Oct)	NAO (Dec-Feb)	NAO (May)	Day	Year×Year	Year×Day	AIC
1	31.917 ± 0.335***	0.075 ± 0.014***	—	—	—	0.352 ± 0.011***	0.005 ± 0.002**	−0.002 ± 0.001 ^{ns}	6283.23
2	32.002 ± 0.336***	0.079 ± 0.013***	—	—	—	0.352 ± 0.011***	0.004 ± 0.002*	—	6284.60
3	31.649 ± 0.365***	0.080 ± 0.015***	−0.030 ± 0.246 ^{ns}	0.467 ± 0.258 ^{ns}	−0.097 ± 0.170 ^{ns}	0.356 ± 0.011***	0.006 ± 0.002**	—	6287.24
4	32.161 ± 0.230***	—	−0.641 ± 0.213**	—	—	0.364 ± 0.010***	—	—	6326.68
5	32.360 ± 0.210***	—	—	−0.321 ± 0.221 ^{ns}	—	0.360 ± 0.010***	—	—	6334.35
6	32.313 ± 0.219***	—	—	—	0.051 ± 0.149 ^{ns}	0.362 ± 0.011***	—	—	6336.35

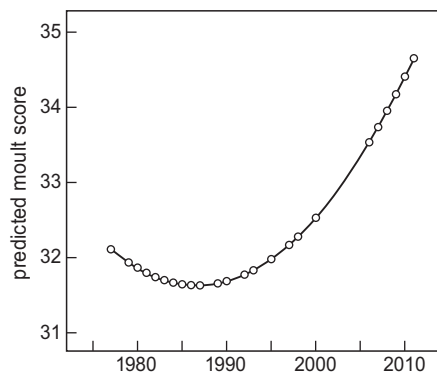


Figure 2. Predicted moult scores per year adjusted to the average catching date, i.e. 24 August, following model 2 shown in Table 1.

presence of year also did not improve estimates of moult scores and NAO without year made worse predictions of moult score. Moult scores increased by an average of 0.35 ± 0.01 per day and also increased with year: from 1977, each year moult scores were on average 0.08 ± 0.01 higher. The yearly increase was not linear but accelerating (Figure 1), as shown by the significant, positive year-squared variable (Table 1). This resulted in no discernible differences in moult scores from 1977 to 2000, but an increase with, on average, 0.25 per year during the last decade (Figure 2). Assuming that moult score increased linearly through time, start of moult – when moult score equals 0 – would be around 26 May in the first two decades and 18 May in 2011. Completion of moult – when moult score equals 50 – is estimated to be around 15 October in the first two decades and 7 October in 2011. Note that in reality moult scores do not change linearly at the start and end of moult, which introduces a bias in these estimates. Moult duration estimated in this way was 142 days and would not have changed through the years.

DISCUSSION

Primary moult in Golden Plovers caught in The Netherlands has advanced by 8 days from 1990 to 2011, while there was no change in timing of moult during the preceding 12 years (Figures 1, 2). There has not been a shift in the speed of moult and therefore we assume that the start of moult gradually shifted to an earlier date in later years. Primary moult starts in the breeding areas, even during incubation (Byrkjedal & Thompson 1998), and we hypothesize that earlier

moulting is an effect of earlier breeding. Because moult scores increase faster early during moult and because moult can be interrupted, we cannot predict the actual starting date of moult from our data. Indeed, over a wide geographical range, moulting started late June to early July (Byrkjedal 1978), which is at least a month later than the date estimated by extrapolating from our sample. This is in accordance with our estimate of moult duration, which is at least two weeks longer than what is indicated by more comprehensive analyses (Henriksen 1985; P. Machin unpubl. data).

No direct evidence is available of advanced breeding in Golden Plovers from Fennoscandia or Russia, but several findings indicate that it is likely to have occurred. During the last decades, spring snow cover has diminished in the northern hemisphere (Møller *et al.* 2010), affecting availability of nesting and feeding sites (Høye *et al.* 2007, Rakhimberdiev *et al.* 2007), and many Arctic birds arrive earlier in their breeding areas (Høye *et al.* 2007, Huntley *et al.* 2007). In Iceland, Golden Plovers arrived 0.43 d earlier each year from 1988 to 2009, and this pattern was correlated with mean local temperature (Gunnarsson & Tómasson 2011). In the period 1978–2000, spring arrival in northern Norway has advanced by almost 8 days (Barrett 2002), which suggests that the start of the breeding season has shifted likewise. In The Netherlands, south of the Golden Plovers' breeding range, another member of the Charadriidae, the Northern Lapwing *Vanellus vanellus*, advanced laying by 10 days from 1950 to 2003 in response to increasing spring temperatures (Both *et al.* 2005). Although we used NAO as an integrated measure of weather conditions in the breeding range in our analyses, correlations with weather conditions vary spatially across northern Europe (Sæther *et al.* 2003). This variation may have weakened correlations with NAO. As a case in point, in the mountains of the Scandinavian Peninsula, winter precipitation has increased leading to later snow melt and probably later breeding (Byrkjedal pers. com.).

Apart from the availability of snow-free areas for breeding and feeding, advanced breeding may also result from earlier emergence of invertebrate prey. Pearce-Higgins *et al.* (2005) showed that Golden Plovers breeding in the northern UK advanced hatching by 6 days from the 1980s to the 1990s in response to the earlier emergence of crane fly (Tipulidae) larvae. Although British birds do not migrate to The Netherlands, similar processes are likely to occur in northern Scandinavia and Russia. On the Taymir Peninsula, in the Siberian Arctic, arthropod abundance is predicted to have advanced by 7 days from 1973 to 2003 (Tulp &

Schekkerman 2008), which would lead to an earlier optimal hatching date of Arctic breeding waders. Advanced insect abundance in the breeding areas could also lead to an earlier start of moult in the absence of advanced breeding, if food availability triggers the start of moult. A functional connection between moult and breeding is therefore difficult to discern.

During the recent decades, post-breeding, staging Golden Plovers have redistributed to some degree over Europe, with higher numbers lingering on closer to the breeding areas (e.g. Sweden, Poland and Denmark; Jukkema *et al.* 2001, Kleefstra *et al.* 2014). Apart from changing temperatures, this may also have been an effect of decreasing hunting pressure (Jukkema *et al.* 2001). This would only have had an effect on the average moult stages we find in The Netherlands if birds with different timing of moult redistributed differently, and there is no indication that this occurs.

Based on the examples above, in combination with our finding of advanced wing moult, we conclude that Golden Plovers probably started breeding earlier during the last few decades in response to increasing spring temperatures, and that this has led to advanced moulting. But may the simultaneously occurring agricultural intensification in staging areas also have affected moult? During the last decades, grassland habitat has shrunk and farmers have created extensive monocultures of rye grasses *Lolium spec.*, while water tables have been lowered to enable more frequent fertilisation and mowing (Donald *et al.* 2001). While this has had strong negative effects on most bird species breeding in farmland (Newton 2004, Donald *et al.* 2006, Kleijn *et al.* 2010), effects on birds that are staging or wintering in pastures or on arable fields might be different (Lindström *et al.* 2010). Fertilisation may actually lead to increased availability of earthworms in grassland (Standen 1984, Curry *et al.* 2008), thereby positively affecting staging or wintering birds, such as Golden Plovers (Atkinson *et al.* 2005). Moult speed, however, has not changed in the staging birds, implying that changes in agricultural practises have had no effect on moult.

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SAMENVATTING

In het najaar van 1978–2011 hebben wij in de provincie Fryslân van 1051 Goudplevieren *Pluvialis apricaria* de ruiscore van de grote slagpennen bepaald (0 = alle tien slagpennen oud, 50 = alle slagpennen nieuw). De vogels foerageren hier tijdens de trek en gedurende de winter op grasland. We hebben getoetst of de timing van de rui in de loop van de jaren is veranderd en, zo ja, of dit een gevolg zou kunnen zijn van klimaatverandering of door de intensivering van de landbouw wat het biotoop van doortrekkende en overwinterende Goudplevieren heeft veranderd. Uit onze metingen blijkt dat sinds 1990 een bepaalde ruiscore van de grote slagpennen acht dagen eerder in het jaar wordt bereikt dan in de jaren hiervoor. Omdat in die jaren de snelheid waarmee de veren worden vervangen niet is veranderd, nemen we aan dat de vogels in de loop van de tijd eerder met de rui zijn begonnen. Goudplevieren beginnen al tijdens het broeden te ruïen en daarom denken we dat de vervroeging van

de rui mogelijk een gevolg is van een vroegere start van het broedseizoen sinds 1990. In de gematigde en noordelijke streken is voor verschillende soorten aangetoond dat die in de afgelopen decennia eerder zijn gaan broeden. We vonden ook een correlatie met de Noord-Atlantische Oscillatie-index (NAO), die verband houdt met grootschalige weerpatronen op het noordelijke halfrond. Dit is een aanwijzing dat lange termijn veranderingen in het weer de oorzaak zouden kunnen zijn van de vervroegde rui. Bovenop het effect van de factor 'jaar' leverde de factor 'NAO' echter geen verbetering van de voorspelling van de timing van de rui op. Blijkbaar correleert de factor 'jaar' beter met relevante weersvariabelen dan de factor 'NAO'. Omdat de snelheid van de rui niet is veranderd, zijn er geen aanwijzingen dat de intensivering van de landbouw een effect heeft gehad op het ruiproces.

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