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Warmer springs advance the breeding phenology of golden plovers *Pluvialis apricaria* and their prey (Tipulidae)

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Abstract Most studies of climate-driven changes in avian breeding phenology have focused on temperate passerines, yet the consequences of such environmental change may be more deleterious for other avian taxa, such as arctic and sub-arctic waders (Charadrii). We therefore examine large-scale climatic correlates of the breeding phenology of one such species (golden plover *Pluvialis apricaria*), and the timing of emergence of their adult tipulid prey, to assess the potential for climate change to disrupt breeding performance. Golden plover first-laying dates were negatively correlated with both March and April temperature, the mean laying date of first clutches was additionally negatively correlated with March rainfall. The timing of final laying dates were negatively correlated with April temperature only. The timing of tipulid emergence was negatively correlated with May temperature. In combination with historical climatic data, these models suggest a 9-day advancement of golden plover first-laying dates occurred during the 1990s, although this remains within the range of natural variation for the twentieth century. The magnitudes of predicted changes in mean and final laying dates, and the timing of tipulid emergence, were smaller. Climate predictions for 2070–2099 suggest potential advances in first-laying dates by 25 days, whilst the timings of mean and final laying dates are predicted to change by 18 days and 13 days, and tipulid emergence by 12 days. Given

the importance of adult tipulids to young golden plover chicks, these changes may result in a mismatch between the timing of first-laying dates and tipulid emergence, so reducing the success of early breeding attempts. Modelling suggests that these changes could reduce breeding success in a South Pennines population by about 11%.

Keywords Breeding biology · Climate change · Craneflies · Moorland · Temperature · Waders

Introduction

Rising spring temperatures, in recent years, have led to earlier breeding for a range of bird species (e.g. Brown et al. 1999; Crick and Sparks 1999; Winkler et al. 2002; Sanz 2003). The magnitudes of these changes are greatest among species or populations breeding at higher latitudes (Root et al. 2003; Sanz 2003), and for species that winter in the Northern Hemisphere rather than long-distance migrants (Forchhammer et al. 2002; Jonzen et al. 2002). As the timing of avian reproduction affects both survival and reproductive performance (Lack 1968), there is concern that these shifts in breeding phenology will change life-history parameters and so alter population size. In particular, the synchrony of timing of bird breeding and peaks in abundance of food during the breeding season may be decoupled, although this has been rarely studied (Visser et al. 1998, 2003; Cresswell and McCleery 2003; Strode 2003).

Most existing studies of avian breeding phenology have considered temperate passerines (e.g. Crick and Sparks 1999; Forchhammer et al. 2002; Winkler et al. 2002; Cotton 2003; Strode 2003). These are species that may ameliorate some of the influences of climate on breeding phenology through alteration of clutch size or incubation period, or by varying the number of breeding attempts in a season (Cresswell and McCleery 2003; Visser et al. 2003). Species with more northerly distributions and conservative breeding behaviours, such as

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arctic and sub-arctic waders (Charadrii), might suffer more from future climate change. To examine the sensitivities of such a species to climate change, we model the breeding phenology of golden plovers *Pluvialis apricaria*.

Golden plovers have an upland and northern distribution, breeding in a range of open habitats (Byrkjedal and Thompson 1998), and are almost exclusively single brooded (Byrkjedal and Thompson 1998; Pearce-Higgins 1998). In the United Kingdom, golden plovers lay their first clutches in late March and April (Parr 1980; Pearce-Higgins and Yalden 2003), and produce second clutches only in response to nest loss 12–41 days later (Parr 1980; Nethersole-Thompson and Nethersole-Thompson 1986). The hatching of first clutches roughly coincides with the synchronised emergence of adult tipulids (Whittingham et al. 2001; Pearce-Higgins and Yalden 2004), an important prey, whose abundance correlates with the growth and survival of young chicks (Pearce-Higgins and Yalden 2004).

In order to assess whether changes in avian breeding phenology are likely to influence population size, it is important also to assess the potential for alterations in the phenology of peaks in prey abundance. We do this for golden plovers by examining the phenology of moorland tipulids, which generally follow an annual life-cycle (Coulson 1962; Coulson et al. 1976; Todd 1996). The adults emerge in late May and early June and survive for a few days to lay their eggs, producing a 2- to 3-week peak of abundance (Coulson 1962; Pearce-Higgins and Yalden 2004). We test the hypothesis that climate change will result in a loss of synchrony between the timing of golden plover breeding, and the emergence of their prey. As adult tipulids are a key food source for a variety of upland breeding birds (e.g. Butterfield and Coulson 1975; Coulson and Whittaker 1978), many of which are of conservation concern (Thompson et al. 1995), this work has a wider relevance for our ability to predict future changes in the functioning of upland ecosystems as a result of climate change.

Materials and methods

Unlike existing studies of changes in avian breeding phenology (e.g. Crick and Sparks 1999; Visser et al. 2003), there are insufficient long-term data-sets to simply examine temporal trends in the timing of golden plover breeding. Instead, we model annual variation in the timing of breeding using climatic variables, and apply these models to long-term climate data-sets to assess the likely magnitude of phenological changes over recent decades, and predict changes that may occur under future climate scenarios. Data on the timing of golden plover reproduction were collated from studies within the United Kingdom that cover at least 2 years (Table 1). Although data were summarised in different ways for different studies, in all cases the date of completing the first clutch and final clutch were obtained directly, or by back-calculating from hatching dates, assuming a 30-day incubation period (Ratcliffe 1976; Pearce-Higgins and Yalden 2003). Additionally, the mean date of completion of first clutches was determined (apart from for Parr 1980), and probably provides the most accurate measure of phenology because it is unaffected by sample size and relaying following nest-failure. These measures are subsequently termed first, final and mean laying dates, respectively.

Data on the timing of tipulid emergence were obtained from studies of moorland and blanket bog habitats (hereafter termed moorland) within the United Kingdom (Table 1) that again spanned a minimum of 2 years. The methods used to assess tipulid abundance varied widely between studies, from sticky traps (Coulson 1962) and pitfall traps (Robson 1998) to line-transects (Whittingham et al. 2001; Pearce-Higgins and Yalden 2004), whilst the survey interval varied from daily (Pearce-Higgins and Yalden 2004) to weekly (Whittingham et al. 2001). To correct for these differences, the mean date of emergence for each year of a given study was calculated by multiplying the mid-point

Table 1 Locality, duration and source of studies used in the analysis

Location	References for data	No. years study	
		Golden plover	Tipulid
Tailbridge Hill (NY80), Cumbria	D. Lloyd, unpublished report (1976, in litt.)	3	–
Kerloch Hill (NO68), Aberdeenshire	Parr (1980)	5	–
Moorfoots (NT34), Borders	Campbell (1978)	2	–
Widdybank Fell and Chapel Fell (NY83), Co. Durham	Whittingham et al. (2001)	4	3
Snake Summit (SK09), Derbyshire	Yalden and Yalden (1989); Pearce-Higgins and Yalden (2003, 2004)	6	4
Torside (SK09), Derbyshire	P. A. Anderson, unpublished (1986)	–	2
Monk's Moor (NY83), Co. Durham	Robson (1998)	–	2
Loch nan Clar & Badanloch (NC73), Caithness	Downie et al. (1996)	–	2
Moor House (NY 73), Cumbria ^a	Coulson (1962); Butterfield and Coulson (1975)	–	4

Four-figure OS grid references are provided in parenthesis

^a To make the data comparable between the two studies, only counts relating to *T. subnodicornis* were used for this locations

date of each survey period by the proportion of tipulids from that year recorded in that period, and summing these values across all periods in that year. This is, in effect, an average of emergence dates, weighted by the number of tipulids emerging on that date.

Measures of annual mean monthly temperature and rainfall for 1900–2000 were obtained for the United Kingdom from the TYN CY 1.1 data-set (Mitchell et al. 2002). These data are derived from a high-resolution (0.5°) climate grid based on an interpolation of monthly climate data from a network of meteorological stations (New et al. 2002), and aggregated into country-specific values using mean values from each grid cell, weighted by surface area (Mitchell et al. 2002). Because we are interested in large-scale climate change, the use of a national assessment of climate as a broad indicator of temperature was a more useful measure than data from separate weather stations within close proximity to each study area. In addition, these data are directly compatible with the TYN CY 3.0 data (Mitchell et al. 2002; T. D. Mitchell et al., unpublished) that provide outputs for 16 climate models for 2070–2099 for the United Kingdom (McCarthy et al. 2001). Both TYN CY1.1 and 3.0 data-sets are available from <http://www.cru.uea.ac.uk/cru/data/hrg.htm>.

Analyses of first and mean laying dates were conducted in relation to both March and April climate measures. Final laying dates were in late May and early June, so May temperature and rainfall were included as additional covariates for this analysis. Because of the potential influence of survey effort on first and final laying dates, the number of nests found was also included as a covariate in these analyses. Due to the timing of moorland tipulid emergence, being late-May and early-June (Coulson 1962; Pearce-Higgins and Yalden 2004), measures of April and May temperature and rainfall were used to assess variation in emergence in relation to climate.

Analyses were conducted using generalised linear models (GLMs) with study location as a fixed factor to account for spatial variation in phenology, and the relevant climatic variables as covariates. All data were normally distributed. Variable selection was by backwards deletion of terms not significant at $P < 0.05$ from a full model incorporating all relevant climate measures (see above), to produce a minimum adequate model (MAM). To assess the potential for bias in this model selection procedure (Burnham and Anderson 2002), we also examined the significance of terms in the full models. No additional predictor variables were significant and each of the predictor variables in the MAMs remained significant in the full models, apart from one case where $P = 0.08$. Additionally, the coefficients of the significant terms were highly correlated between the two model approaches ($r = 0.872$); therefore, we can be confident that the MAMs presented are relatively unbiased by the model selection procedure used. Further, the degree of collinearity between the predictor variables was low, with only one of the 15 pairs of

variables being significantly correlated, and that only weakly (May temperature and rainfall, $r = -0.30$).

To test the likely ability of each MAM to produce robust predictions, data were sequentially removed from each study area, and the remaining data were used to recalculate the parameter estimates of terms in the MAM and predict the missing values. The accuracy of these predictions was tested by simple correlation between predicted and observed values (cf. Green 1996). Model building was conducted in Minitab 13.1 (Minitab 2000) using the General Linear Model command.

Results

Having accounted for study location, there were significant correlations between temperature and the measures of golden plover laying phenology (Table 2). First-laying dates were negatively correlated with March and April temperature, whilst final laying dates were negatively correlated with April temperature only. Mean laying date was negatively correlated with March and April (Fig. 1) temperature, and March rainfall. These relationships accounted for 72, 27 and 87% of the residual error (assessed from the sum of squares) in first, final and mean laying dates, respectively, having accounted for study location. Thus, golden plover lay earlier in warm, and to a lesser extent, wet, springs. Models of first ($r = 0.48$, $n = 20$, $P = 0.034$) and mean ($r = 0.80$, $n = 15$, $P < 0.001$) laying dates produced robust predictions, as tested by sequentially removing data from each study area, recalculating the model parameters, and correlating the predictions against the removed data. The model of final laying dates had limited predictive power ($r = 0.26$, $n = 20$, $P = 0.27$). As might be

Table 2 Minimum adequate models describing annual variation in the phenology of golden plover laying dates and tipulid emergence in relation to mean monthly temperature and rainfall across the United Kingdom. Laying dates are assessed as days since 1 March, and tipulid dates as days since 1 May

	Coefficient	SE	<i>F</i>	<i>P</i>
First-laying date				
Intercept	121.35	13.16		
Location			$F_{4,13} = 1.85$	0.18
March temperature	-4.94	1.26	$F_{1,13} = 22.54$	< 0.001
April temperature	-7.23	1.52	$F_{1,13} = 15.47$	0.002
Mean laying date				
Intercept	91.38	9.77		
Location			$F_{3,7} = 1.04$	0.43
March temperature	-2.16	0.75	$F_{1,7} = 8.36$	0.02
April temperature	-6.70	0.97	$F_{1,7} = 47.33$	< 0.001
March rainfall	-0.068	0.028	$F_{1,7} = 5.94$	0.041
Final laying date				
Intercept	135.97	19.73		
Location			$F_{4,14} = 8.10$	0.001
April temperature	-6.63	2.91	$F_{1,14} = 5.18$	0.039
Mean tipulid emergence				
Intercept	89.03	17.07		
Location			$F_{5,10} = 1.27$	0.35
May temperature	-6.60	1.74	$F_{1,10} = 14.41$	0.004

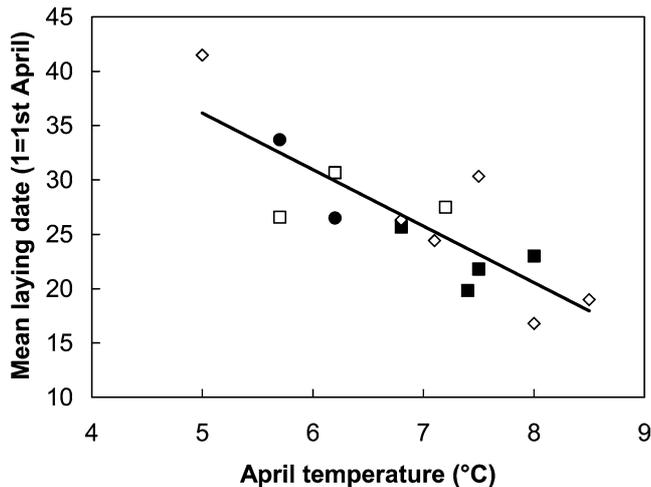


Fig. 1 Correlation between mean first-clutch golden plover laying date and mean April temperature in the United Kingdom. *Symbols* relate to individual studies (see Table 1)

expected from the different responses to temperature of first and final laying dates, the overall length of the breeding season (number of days between first and final laying dates) was positively correlated with March temperature ($F_{1,14}=17.73$, $P=0.001$), accounting for 48% of the residual error after allowing for study location ($F_{4,14}=10.63$, $P<0.001$).

The timing of tipulid emergence was strongly negatively correlated with May temperature. Having accounted for study location in the model (Table 1), this explained an additional 59% of the residual error. The rate of change was such that for every 1°C increase in temperature, the mean date of tipulid emergence was 7 days earlier (Fig. 2). The correlation between observed and predicted dates of emergence following the

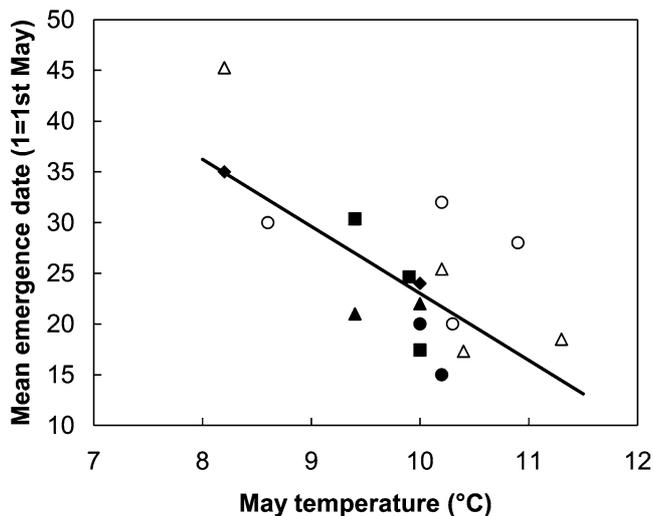


Fig. 2 Correlation between mean date of tipulid emergence and mean May temperature in the United Kingdom. *Symbols* relate to individual studies (see Table 1). The equation for the line of best fit is given in Table 2

sequential removal of data approached statistical significance ($r=0.477$, $n=17$, $P=0.053$).

Annual mean monthly temperature data from 1900–2000 were used to estimate the phenology of golden plover breeding and tipulid emergence through the twentieth century, through application of the phenological models (Fig. 3). To better assess the degree of synchrony between the appearance of young golden plover chicks and peaks of tipulid emergence, the timing of golden plover breeding was summarised for this analysis as hatch dates rather than laying dates, assuming a 30-day incubation period (see Materials and methods). These predictions suggest that the golden plover breeding season advanced during the first half of the century, prior to a subsequent reversal and period of stability from the 1960s to 1980s. First-hatch dates during the 1990s are predicted to have been about 9 days earlier than the 1960–1990, 30-year mean (but match those of the 1940s), whilst mean and final-hatch dates appear to have advanced from the 30-year mean by about 6 days and 4 days, respectively. Predicted fluctuations in the timing of tipulid emergence showed less variation, apart from a gradual trend for earlier emergence over the last three decades.

Application of the models in Table 2 to future climate predictions suggest that by 2070–2099, golden plover breeding will be considerably earlier. The current first, mean and final-hatch dates of 17 May, 28 May and 29 June, estimated from the (1960–1990) 30 year means, are predicted to be advanced to 22 April, 10 May and 16 June, respectively. These respective changes of 25, 18 and 13 days will increase the length of the breeding season by 12 days. The timing of tipulid emergence is

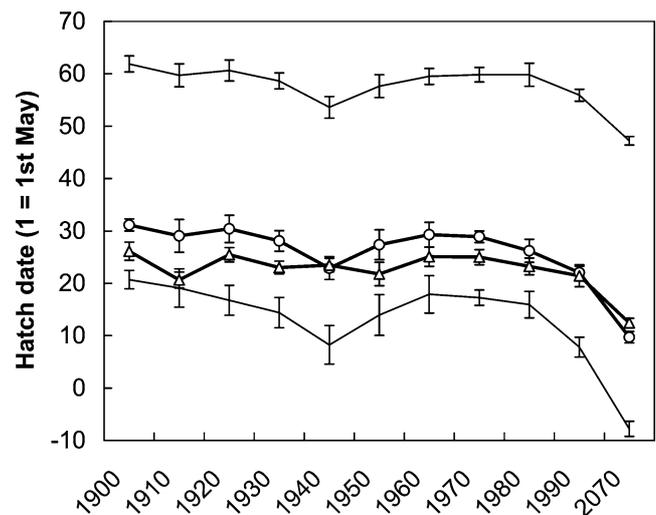


Fig. 3 Variation in predicted golden plover hatch dates (first and last hatch dates, *thin lines*; mean first-clutch hatch date, *circles and line*) through the twentieth century, summarised as decadal means (\pm SE). Predicted peak of tipulid emergence is plotted in the same manner by *triangles and line*. Estimates for 2070–2099 averaged across 16 climate scenarios (\pm SE) are presented as the last point in each sequence

predicted to become 12 days earlier, on average, than the current date of 24 May. As a result, the predicted differences for 2070–2099 between either first or mean golden plover hatch dates and date of mean tipulid emergence are outside the range of mean values for each decade estimated for the twentieth century (One-sample t -test, $t_{10}=9.77$, $P<0.001$ and $t_{10}=8.32$, $P<0.001$ respectively) and may therefore be biologically significant.

Discussion

Most existing studies of the impacts of climate change are dependent upon long-term data-sets to show specifically how demographic or phenological parameters have changed in recent years (e.g. Crick and Sparks 1999; Winkler et al. 2002; Cotton 2003; Strode 2003). However, this restricts such analysis to common and well-studied species. To gain a similar assessment for rarer and less well-studied taxa, which may be more susceptible to future change, ecologists are restricted to make predictions based on correlating annual variation in the parameters of interest with relevant climate variables (cf. McCleery and Perrins 1998); i.e. the approach used here. Although we cannot validate the conclusions from this method, the predicted changes in golden plover breeding phenology match the magnitude of change from other studies (Winkler et al. 2002; Root et al. 2003; Visser et al. 2003), whilst the models also appear largely spatially robust. The use of such regression modelling also allows predictions to be made of the magnitude of change in the parameters of interest under different climate scenarios, although we accept the limitations of extrapolating phenomenological models beyond the data on which they are based.

Golden plover laying dates were negatively correlated with large-scale measures of spring temperature: birds bred earlier during milder springs. This effect was strongest for first-laying dates, presumably because the timing of final laying dates was additionally influenced by rates of nest loss and the frequency of relaying (cf. Pearce-Higgins and Yalden 2003). Previous studies have linked the timing of golden plover breeding to the absence of snow cover at individual localities (Byrkjedal 1980; Parr 1980). However, such climatic measures are only of local relevance, so it is valuable for us to link breeding phenology with large-scale measures of climate, and this effect seems to be robust even though most populations covered in this study were from areas where such snow cover is rare. A broad-scale analysis of nest-record card data across the United Kingdom (Crick 1992) highlighted similar, albeit weak, effects of temperature on golden plover laying dates, and stronger negative effects of rainfall, that contrasted with our finding that plovers nested earlier in wetter springs. However, Crick (1992) did not attempt to take account of variation in coverage and effort between locations. By restricting our analysis to data from study sites with intensive fieldwork over multiple years, the potential for

such confounding effects has been minimised. A similar correlation between April soil temperature and Green-shank *Tringa nebularia* laying dates (Thompson et al. 1986) suggests that the breeding phenology of moorland waders in general may be governed by similar climatic cues.

The emergence of adult tipulids on moorland is synchronised at the end of May and beginning of June (Coulson 1962; Pearce-Higgins and Yalden 2004); the precise timing varies with May temperature. Despite the coarse nature of much of the data on timing of emergence, and the lumping of different tipulid species in most studies, we were still able to detect a significant effect of temperature. The observed relationship between date of emergence and May temperature is probably attributable to the effect of temperature on pupal development (cf. Lantsov 2003). We could not examine the impact of climate upon tipulid abundance, largely because different studies measured abundance using a range of different methods (Table 1). However, it is likely that the magnitude of emergence will be related to temperature during the larval growing season (Todd 1996) and soil moisture (Coulson 1962; McCracken et al. 1995). With additional data, it should be possible to model annual variation in abundance in a similar manner to that achieved for pastoral systems (Blackshaw and Perry 1994).

Correlations with temperature suggest that during the 1990s, the timing of golden plover laying has advanced from the 30-year means from 1960 to 1990, although currently still remains within the range of natural variation predicted through the last century (Fig. 3). Predicted changes in the phenology of tipulid emergence suggest an advancement by 3 days during the 1990s, also well within the previous range. Under future climate scenarios for 2070–2099 (McCarthy et al. 2001), first-laying dates could advance by 25 days, resulting in a potential lengthening of the breeding season by 12 days; mean and final laying dates and the timing of tipulid emergence are each predicted to change by 18, 13 and 12 days, respectively. Although such predictions are tentative¹, they do suggest that first-laying dates may advance more quickly than tipulid emergence.

To illustrate how these changes might affect golden plovers at the population level, we use data from the well-studied Snake Summit population in the South Pennines (Pearce-Higgins and Yalden 2003). The timing of first clutches is described by data from 1996 to 1998, assuming clutches laid after 4 May are relays (Pearce-Higgins and Yalden 2003), whilst the standard deviation (SD) of laying dates from each year was averaged to

¹Predicted first-laying dates for 2070–2099 are in March, yet the model includes April temperature. To counter any error this may introduce, future changes in first-laying dates were also estimated by substituting February for March temperature and March for April temperature in the current model. This produced similar predictions to the original calculation, suggesting advancement in first-laying dates of 27 days, supporting the validity of our conclusions.

describe the temporal spread of laying. The timing and spread of tipulid emergence was similarly determined using data from the same site and years (Pearce-Higgins and Yalden 2004). We constructed a model population of 100 breeding pairs, with a temporal spread of first clutches normally distributed around an average hatch date of 19 May (SD 11.14). Temporal variation in tipulid abundance was modelled by distributing total annual abundance, averaged across the 3 years, along a normal distribution around an average emergence date of 29 May (SD 7.37). The effect of the overlap between hatching dates and tipulid emergence upon breeding success was calculated by modelling the daily survival rate of young (<9 days) chicks as a function of daily tipulid abundance, using the following equation (Pearce-Higgins and Yalden 2004):

Daily survival rate

$$= \frac{1}{1 + (1/\exp(0.223 + 5.222\sqrt{\text{daily tipulid abundance}}))}$$

Assuming a nest survival rate of 61% and 54% survival of older chicks (Pearce-Higgins and Yalden 2003), and allowing that 50% of nest failures precipitate relaying (Parr 1980), an average of 0.87 fledglings per pair was predicted from the 1990s data. These calculations predict a decline from 0.91 fledglings per pair from the likely phenologies from 1960 to 1989 (calculated from the 30 year climatic means) to 0.81 in 2070–2099 (calculated from the future predictions of climate); a loss of 11% as a result of the 6-day advancement of mean first-laying dates relative to tipulid emergence.

These results indicate that in some situations, future climate change may reduce golden plover breeding success by disrupting the synchrony between hatching and the emergence of their prey. It is possible that such negative changes may be countered by a positive effect of increased temperature on chick growth (Pearce-Higgins and Yalden 2002). Chicks may also be able to compensate for any reductions in tipulid availability by selecting other prey (cf. Pearce-Higgins and Yalden 2004), although the superabundance of emerged tipulids in May is unlikely to be completely replaced by other taxa; the condition of breeding Dotterel *Charadrius morinellus* declines in years with low tipulid abundance (Holt et al. 2002). Further work is required to account for the direct impacts of altered climate on prey abundance. It is interesting that for this South Pennines population the timing of golden plover hatching relative to tipulid emergence was earlier than the UK average (cf. Fig. 3), suggesting such edge-of-range populations may be the most vulnerable to change. More work is clearly required to assess the relatively magnitude of likely changes in breeding success as a result of climate change in different parts of the range (cf. Visser et al. 2003).

To conclude, this work has shown that increased spring temperatures in the last decade appear to have advanced golden plover laying dates, matching the pattern observed in temperate passerines, although the

range of this change so far remains within that observed during the twentieth century. This pattern of advancement is most pronounced for first-laying dates, resulting in a likely increase in the length of the breeding season, which may reduce the overall synchrony of breeding. A general warming also appears to have resulted in earlier emergence of tipulids, but at a slower rate than the change in golden plover first-laying dates. As a result, the earliest golden plover broods may experience reduced survival if exposed to lower tipulid densities when they hatch, and this is supported by modelling the changes in the breeding success of a well-studied population. The United Kingdom is globally important for the moorland habitats it supports, and the assemblage of plants and animals associated with this ecosystem (Thompson et al. 1995). Given the importance of tipulids in the diets of other moorland breeding birds (e.g. Meadow Pipits *Anthus pratensis*, Red Grouse *Lagopus lagopus*, Greenshank; Butterfield and Coulson 1975; Coulson and Whittaker 1978; Thompson et al. 1986), this study suggests that other species will also be sensitive to detrimental effects of future climate change. The approach taken in this study should therefore be extended to other species. Better monitoring of breeding phenology, combined with a study of its variation with respect to climate would be needed to assess the validity of any predictions. It would be relatively easy to combine this with extensive monitoring of tipulid abundance and phenology on moorlands, using a simple line-transect method (cf. Pearce-Higgins and Yalden 2004).

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