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Demographic consequences of increased winter births in a large aseasonally breeding mammal (*Bos taurus*) in response to climate change

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Running headline: Increased winter births in response to climate

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Summary

1. Studies examining changes in the scheduling of breeding in response to climate change have focused on species with well-defined breeding seasons. Species exhibiting year-round breeding have received little attention and the magnitudes of any responses are unknown.
2. We investigated phenological data for an enclosed feral population of cattle (*Bos taurus* L.) in northern England exhibiting year-round breeding. This population is relatively free of human interference.
3. We assessed whether the timing of births had changed over the last sixty years, in response to increasing winter and spring temperatures, changes in herd density, and a regime of lime fertilization.
4. Median birth date became earlier by 1.0 days per year. Analyses of the seasonal distribution of calving dates showed that significantly fewer calves were born in summer (decline from 44% of total births to 20%) and significantly more in winter (increase from 12% to 30%) over the study period. The most pronounced changes occurred in winter, with significant increases in both the proportion and number of births. Winter births arise from conceptions in the previous spring and we considered models that investigated climate and weather variables associated with the winter preceding and the spring of conceptions.
5. The proportion of winter births was higher when the onset of the plant growing season was earlier during the spring of conceptions. This relationship was much weaker during years when the site had been fertilised with lime, suggesting that increased forage biomass was overriding the impacts of changing plant phenology. When the onset of the growing season was late, winter births increased with female density.
6. Recruitment estimates from a stage-structured state-space population model were significantly negatively correlated with the proportion of births in the preceding winter, suggesting that calves born in winter are less likely to survive than those born in other seasons.
7. This is one of the first studies to document changes in the phenology of a year-round breeder, suggesting that the impact of climate on the scheduling of biological events may be more extensive than previously thought and that impacts may be negative, even for species with relatively flexible breeding strategies.

Keywords

Aseasonal, Breeding season, Chillingham cattle, state space model, ungulate

Introduction

Phenology is a crucial structuring factor in many areas of ecology and evolution, comprising the temporal intersection between key biological events and an organism's environment (Forrest & Miller-Rushing 2010). Recent climate warming has significantly advanced the phenology of a wide-range of taxa in many ecosystems (Root *et al.* 2003; Parmesan 2007; Thackeray *et al.* 2010), with change progressing at an unprecedented rate and predicted to continue (IPCC 2007). Therefore, there is an urgent need to determine how different species respond to climate change. However, the majority of studies have investigated changes in birds and insects, with comparatively few on mammals (Parmesan 2007; Bronson 2009; but see: Inouye *et al.* 2000; Sinclair, Mduma & Arcese 2000; Coulson *et al.* 2003; Réale *et al.* 2003; Durant *et al.* 2005; Post & Forchhammer 2008; Ozgul *et al.* 2010; Moyes *et al.* 2011). Moreover, studies have focused on species exhibiting clear seasonality in breeding, and here we focus on evaluating phenological responses of an animal that breeds year-round.

Phenology and synchrony of births comprise a vital component of a species' overall reproductive strategy that has been selected to optimise production of surviving offspring (Stearns 1992). Ungulate reproduction varies in timing between rigidly seasonal and continuous, depending primarily on the seasonality of climate and food availability and quality (Bronson 1989). In general, seasonality is more pronounced at higher latitudes due to greater annual variation in temperature; but can also occur in the tropics due to strongly seasonal rainfall, both of which influence seasonal patterns of primary production (Bronson 1989; Sinclair, Mduma & Arcese 2000). For example, deer from the genus *Odocoileus* exhibit highly seasonal breeding at northern latitudes, asynchronous breeding with a pronounced spring peak in Florida, but breed year round at their extreme southern range in Venezuela (Richter & Labisky 1985; Brokx 1972). Lactation is known to be the most energetically demanding period of the annual reproductive cycle in female ungulates, and females that match this to the peak of newly emergent forage plant tissue with high digestibility and nutritional value have been shown to have higher fitness (Robbins 1983; Festa-Bianchet 1988; Clutton-Brock 1991). Variation in birth phenology within an ungulate species is also known to be linked to climate. Calving dates of red deer, *Cervus elaphus*, were delayed following years of high autumn rainfall (Nussey *et al.* 2005). Moyes *et al.* (2011) found that six phenological traits in red deer advanced temporally, correlated with timing of local plant growth. Other factors also constrain the seasonality and the degree of synchrony of mammalian reproduction: inter- and intra-specific (density) competition for resources; predation avoidance by adjusting birth synchrony; and dietary strategy, with generalists being less vulnerable to seasonal changes in specific food types (Sinclair, Mduma & Arcese 2000; Loe *et al.* 2005; Bronson 1989).

Feral herbivores have been shown to differ from their wild counterparts in the seasonality of their reproductive cycles (Setchell 1992). Domesticated modern pigs breed year round, unlike their European wild boar, *Sus scrofa*, ancestors which have strongly seasonal breeding patterns (Eckstein & Zuckerman 1956; Bronson 1989), while Soay sheep, *Ovis aries*, and mouflon cross-bred with domestic sheep (*Ovis gmelini musimon* × *Ovis* sp) exhibit earlier age at first reproduction and higher twinning rates than their wild counterparts (Clutton-Brock & Pemberton 2004; Garel *et al.* 2005). Such differences are a consequence of artificial selection during domestication which aims to maximise reproductive performance, via selection for traits accelerating the onset of reproductive maturity and improved fecundity. Despite the fact that feral ungulates are increasingly important components of ecosystems (Grange *et al.* 2009), relatively little is known about the potential impacts of environmental change on their reproductive

phenology.

Currently, there are few studies evaluating whether species are shifting their phenology sufficiently to match changes in the environment by evaluating fitness consequences of such shifts and population growth trajectories (Visser & Both 2005). Herbivores have been shown to exhibit both negative and positive fitness consequences to climate change. Large herbivores in the high arctic exhibiting highly seasonal reproduction, timed to coincide with the peak plant growing season (Post *et al.* 2003), have become increasingly mismatched in the timing of their breeding from the onset in forage plant growth, resulting in increased offspring mortality and reduced production (Post & Forchhammer 2008). Conversely, in systems where trophic mismatch is not apparent, climate warming can have a positive effect, with birth weights of red deer being heavier following warmer springs with corresponding increased survival rates (Albon *et al.* 1987). Moyes *et al.* (2011) found no temporal changes in offspring survival of red deer, despite significant advances in breeding phenology. However, feral populations that have been selectively bred to maximise reproductive output, are predicted to be more elastic in their phenological response to climate change and to show different responses from their wild counterparts. Selection for maximal reproductive output and elastic responses in phenology have also been shown to have negative fitness consequences (reduced population growth rates). Feral Camargue prime-aged female horses, *Equus caballus*, maintained high levels of fecundity at high population densities, despite depleting food resources, at the expense of their survival probabilities (Grange *et al.* 2009). Cattle are also predicted to experience negative impacts of climate change via reduced nutritional quality of grassland forage associated with increased temperature (Craine *et al.* 2010).

Here we evaluate changing phenology in Chillingham cattle, a previously husbanded herbivore living in an unmanaged state since at least the 16th century (termed feral hereafter). This herd exhibits year-round breeding (Hall & Hall 1988), despite its environment showing strong seasonality in climate and vegetation dynamics (Armstrong *et al.* 1997). Historical domestication of Chillingham cattle is predicted to have influenced their phenology, leading to aseasonal reproduction, and contrasting responses to environmental change from those expected in wild ungulates. In this paper we use a sixty year dataset of cattle birth dates to test five hypotheses (Table 1) to evaluate how breeding phenology has changed over time, the environmental correlates of these changes and whether such changes are impacting on population demography.

Materials and methods

The Study System

Chillingham cattle have been kept enclosed in a 143 ha park of woodland and permanent, relatively infertile upland grassland at Chillingham, north-east England (55° 31' N, 2° 54' W; 153m altitude) since at least 1646 (Hall & Hall 1988). Apart from the provision of hay each winter and addition of lime (36 tonnes/year; R.G.H Bunce & S.J.G. Hall unpublished) to improve herbage production and quality between 1980 and 2004, cattle are completely free from human interference. Age and sex-specific herd density has been estimated annually since 1946 on 31st December for: young <1 year of age; young between 1 and 2 years of age; 2 year olds; and adults (>2 years old). Birth dates and the deaths of calves <30 days of age have also been recorded during daily checks. Cattle are not uniquely marked, and hence individual level data are not available.

Calves are born in all months of the year (Hall & Hall 1988). The average gestation period of 280 days is similar to that of husbanded cattle (Hammond 1927), cows give birth to a single calf, and lactation potentially continues until the birth of the next calf. Approximately 50% of

calves die before reaching maturity, with the highest mortality occurring during the first year (Hall & Hall 1988).

Analysis of median birth dates (Hypothesis 1 (H1))

Standard approaches to the investigation of changes in phenology use linear regression to estimate the relationship between year and the first or median day of calving (usually taken relative to 1st January). There are two generic statistical difficulties, both of which apply in the case of Chillingham cattle: (a) “day of year” is a circular variable and cannot be normally distributed. For seasonal breeders this can be partially overcome by calculating breeding dates relative to a time of year when breeding never occurs; clearly problematic for species with year-round breeding; (b) changes over time in the number of births per year could lead to the estimation of biased and potentially spurious trends in birthing dates, which could violate the assumption of constant variance when looking at trends in median day of calving. Analyses of trends in first birth date are completely omitted, since trends in this quantity are impossible to interpret when the number of births per year is changing over time (Miller-Rushing, Inouye & Primack 2008). However, linear regression was used to estimate trends in annual median birth date, to facilitate comparison with published studies of phenology trends and to address H1 (see Table 1). Median birth dates were estimated relative to the start of the month in which fewest births occurred (November) and (for the purposes of comparison with studies from other taxa) relative to 1st January.

Analysis of changing birth seasonality (H2, H3 and H4)

The main analysis used multinomial and binomial logistic regression (“MASS” and “nnet” packages in R; Venables & Ripley 2002, R Development Core Team, 2009) to investigate whether the proportion of births occurring in each season had changed over time, and binomial regression to assess whether such changes were associated with changes in environmental conditions and demographic characteristics of the herd. Winter, spring, summer and autumn were each defined as three month periods starting on the 1st December, 1st March, 1st June and 1st September respectively. Similar results were obtained if these seasonal definitions were shifted by one month in either direction (not presented).

The proportions of births in each season were first modelled as a multinomial and binomial GLM against year, and the count of births in each season were modelled as a Poisson GLM against year to look for evidence of temporal trends. Finally, as the proportion of winter births showed the most change during the study period (the only season to show significant changes in both the proportion and total number of births), and as the multinomial model can be difficult to interpret, analyses were concentrated on investigating factors influencing the proportion of winter births. As winter births arise from spring conceptions nine months previously, we considered climate and demographic variables in the winter and spring months prior to and during spring conceptions that would influence female condition and the probability of successful conception. Thus we assumed that if the proportion and number of observed births in the winter had increased, the corresponding proportion and number of conceptions in the spring nine months previously (lagged⁻¹ spring period) would also have increased and focused our analyses on this period. This makes the assumption that the gestation period remained constant and there were no systematic changes in abortion rates.

We fitted a number of environmental and demographic variables:

1. ***Density*** Adult female density was fitted because all potential demographic density

covariates (total herd, adult, adult female, adult male density and proportion of adult females) were highly correlated. We then refitted models with alternative demographic measures to check that this did not improve the model fit.

2. **Lime** A binary variable that indicated whether or not lime fertilisation occurred in any given year was also included. To confirm that lime treatment was not confounded with other explanatory variables, analysis of the proportion of winter births was repeated using only data from 1947-1979 (the period before lime treatment).
3. **North Atlantic Oscillation** As large-scale seasonal measures of climate have been found to be useful predictors of ecological processes (Hallett *et al.* 2004; Stenseth & Mysterud 2005), we considered winter (wNAO; <http://www.cgd.ucar.edu/cas/jhurrell/indices.html>) indices for the winter prior to spring conceptions.
4. **Growing Degree Days (GDD)** As temperature is one of the main determinants of plant production in the British uplands (Grace 1988), we considered three different measures of plant phenology, based on GDD with a 5.5°C threshold: “winterGDD” was the summed GDD in the winter prior to spring conceptions; “earlyGDD” was summed GDD between December and April, prior to and during spring conceptions; and “onset of growing season” was calculated as the Julian date on which 60 cumulative GDDs had been accumulated (this value was selected because it fell between the late winter/early spring period between February and May; see Sparks *et al.* (2005)). As other published studies had used a threshold of 200 GDDs, which is often used as a measure of when to apply nitrogen to pasture (Sparks *et al.* 2005), we also fitted models with this alternative measure (which produced dates falling between late April and mid-June).
5. **Local temperature** Average minimum temperatures in the winter preceding and the spring of conceptions based on monthly summaries from Durham, 94 km from Chillingham (UK Meteorological Office; <http://www.metoffice.gov.uk/climate/uk/stationdata/>). Temperature data were also available from Chillingham Barns 2 km from the study site for 1998-2008, and hence were not used. Data from Chillingham Barns and Durham were highly correlated ($R^2=97.2\%$).
6. **Local rainfall** Rainfall data were available for Chillingham Barns for 1961-2008, so were not used in analyses. Rainfall data were not highly correlated between Durham and Chillingham ($R^2=47.3\%$). Hall and Hall (1988) found that Chillingham cattle conceptions were not correlated with local monthly rainfall. However, in order to confirm that rainfall was not influencing the proportion of births in winter, model selection was also undertaken on a shorter data set for which local rainfall data were available (results presented as online supplementary information).
7. **Year** Spurious relationships between an explanatory variable and the response variable could potentially arise if both are correlated with a third variable, particularly time (Grosbois *et al.*, 2008). We investigated this possibility by fitting modified versions of our binomial regression models in which “year” is forced to be an explanatory variable within all models (to account for possible trends within the response variable) and in which those continuous explanatory variables that show evidence of trend are de-trended (see supplementary information for further details).

Weather and demographic variables that were lagged by one year were considered, and therefore analysis was restricted to 1947-2008. As some of the weather variables, the wNAO index and plant phenology measures were highly correlated these were not fitted in the same model (see Supplementary Information for details on correlations). Interactive terms between

density, climate variables and lime treatment were considered. Interactions with lime were included as there is *a priori* evidence that fertilisation may increase the carrying capacity of the population by altering available forage biomass (Tallowin *et al.* 1990,), thus potentially masking effects of changing plant phenology.

Models were compared using Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham & Anderson 2002; Hurvich & Tsai 1989) with models evaluated by calculating the difference (Δ AICc) between the AICc of alternative models relative to the "best" model with the lowest AICc. Models with a Δ AICc of two or less are generally considered similar to the "best" model in their ability to describe the properties of the data in an accurate and parsimonious way (Sakamoto, Ishiguro & Kitagawa 1986). Models with a Δ AICc value of ten or greater are considered to have virtually no empirical support. See supplementary information for full model results. Model selection was performed within the context of both the original and "de-trended" analyses. There was no evidence to support the inclusion of "year" as an explanatory variable within our models. AICc values for the top twenty models were always higher in models that contained "year" than in equivalent models that did not (see supplementary information), and the final model within the de-trended analysis contained the same explanatory variables as the final model in the original analysis. We therefore report results from the non-detrended models in the main text and include model tables for both non-detrended and detrended data in the supplementary information.

The scale parameter was fixed at one for the purposes of model selection, but was subsequently estimated for the final model in order to check for evidence of over- or underdispersion.

Population modelling (H5)

Recruitment, defined as the number of calves produced per cow of 2 years age or older that survive to their first census, was modelled in a state-space modelling framework (e.g., Calder *et al.* 2003; Newman *et al.* 2006). A discrete time, stage-structured model described the dynamics of six age and sex classes of cattle: female calves (class 1); male calves (class 2); female yearlings (class 3); male yearlings (class 4); females ≥ 2 yr (class 5); and males ≥ 2 yr (class 6). A set of possible candidate models, based on the variables found to be affecting the proportion of winter births (density, onset of the growing season and lime treatment), were considered for the effects of population density and climate variables upon the recruitment rate, assuming that the logit-transformed recruitment rate is a linear function of the explanatory variables (see supplementary information for full details).

The relationship between the proportion of births occurring in the winter and the estimates of recruitment to the subsequent census (based on the population model with lowest DIC) was examined using a binomial logistic regression model.

Results

Temporal changes in birth phenology and seasonality (H1 and H2)

Four-hundred and eighty-seven births were recorded during the study, with births occurring in every month of the year (average proportion of births per season: spring= 0.346, summer= 0.314, autumn=0.136, winter=0.204; see Figure 1 for running averages). However, there was evidence for a shift in the timing of births with median date advancing by 1.0 days per year (S.E. = 0.360, $p = 0.008$; assuming 1st January as start of year; predicted values equate to an

advance from the 2nd July in 1947 to the 1st May in 2008), an overall shift of just over two months over the 60 year study period. Similar results of 1.2 days per year were obtained using 1st November as the start date (S.E. = 0.332, $p = 0.001$).

The multinomial analysis also indicated a significant overall change in the seasonality of births over time ($p = 0.004$, likelihood ratio test comparing a model with “year” against an intercept-only model), with parameter estimates suggesting that the relative proportions of winter births increased (0.013) while the relative proportions of summer and autumn births decreased (-0.016 and -0.005 respectively) relative to a spring slope. Effects were strongest for winter and summer births (proportion of winter births increased from 18.3% to 30.2%, and summer births declined from 43.9% to 20.2%) and separate binomial analyses in each of the four seasons indicated that the increase in the proportion of winter births and decrease in the proportion of summer births were statistically significant (winter: $Z = 2.573$, S.E. = 0.007, $p = 0.010$; summer $Z = -2.913$, S.E. = 0.006, $p = 0.004$; p -values are significant even if the threshold for significance is adjusted to account for multiple testing) whilst spring and autumn were not (spring: $Z = 1.323$, S.E. = 0.006, $p = 0.186$; autumn: $Z = -1.049$, S.E. = 0.008, $p = 0.294$). The total number of births occurring in winter and spring showed a significant increase over time (Figure 1: winter: $Z = 4.930$, S.E. = 0.006, $p < 0.001$; spring: $Z = 4.710$, S.E. = 0.004, $p < 0.001$) but there was no change in summer or autumn births (summer: $Z = 1.374$, S.E. = 0.005, $p = 0.169$; autumn: $Z = 1.561$, S.E. = 0.007, $p = 0.119$; Figure 1). Therefore, winter was the only season showing a significant increase in both the proportion and total numbers of births over time.

Drivers of spring conceptions (H3 and H4)

Several extrinsic and intrinsic variables changed over the study period including climatic and demographic variables, indices of plant phenology, and land management (lime fertilisation). Total herd size varied between thirteen and seventy individuals, increasing over the study period. Mean minimum temperatures in spring and winter increased significantly by 0.017°C ($t = 3.642$, S.E. = 0.005, $p < 0.001$) and 0.017°C per year ($t = 2.326$, S.E. = 0.008, $p = 0.023$) respectively, while the wNAO index generally became more positive by 0.039 per year ($t = 2.707$, S.E. = 0.014, $P = 0.009$) and early GDD showed a decrease of 0.770°C per year, mainly due to several warm early years at the beginning of the period (early GDD: $t = -2.375$, S.E. = 0.324, $p = 0.021$). However, there was no significant trend in the alternative measures of plant phenology (winter GDD: $t = -0.825$, S.E. = 0.161, $p = 0.413$; Julian GDD date: $t = 1.085$, S.E. = 0.137, $p = 0.282$).

Due to high levels of correlation between adult female density in the current year and in the previous year (0.921) models were fitted with current female density. Refitting the best model (by AICc) with alternative cattle population density data did not improve the fit (?AICc value of 7.169 for a model with total adult current density; and ?AICc of 8.167 for a model with total herd density). Refitting the models with female density lagged by one year was not as well supported (?AICc value of 2.613).

The binomial model of the proportion of winter births with the lowest AICc included a two-way interaction between growing season onset and female density, and a two-way interaction between lime treatment and the onset of the growing season (Table 2 & 3; see supplementary information for full model results). Odds ratio associated with the onset of the growing season getting earlier by 10 days are large (2.744 95% CI 1.694- 4.445), indicating a strong negative relationship in absolute terms between the onset of the growing season and the proportion of winter births. In years without lime treatment there was evidence that the proportion of winter

births was inversely related to the start date of the growing season, with higher proportions of winter births when the growing season was early (regardless of herd density). However, when the onset of the growing season was later, the proportion of winter births increased in relation to herd density, such that the lowest predicted proportion of winter births occurred in years of late onset of the growing season and low herd density. However, in years with lime treatment the relationship with the onset of the growing season was much less pronounced, again with the lowest predicted proportions occurring in years of late onset of the growing season and low herd density (Figure 2 and 3). There was no evidence for overdispersion in this model (dispersion parameter 1.053). Fitting the model with an alternative measure of the onset of the growing season based on a threshold of 200 GDDs resulted in similar model estimates but was not better supported by AICc (not presented). Analysis of the shorter time-series with local rainfall data did not find strong support for a correlation between rainfall and the proportion of winter births (supplementary information) and the same variables were selected when the analysis was repeated on the data-set for years without lime treatment (results not presented).

Correlations between recruitment and the proportion of winter births (H5)

The best supported Bayesian population model by DIC contained only the date of onset of the growing season. We detected a negative effect of the onset of the growing season on recruitment in the population, with lower recruitment following years when the onset of the growing season was early. Recruitment estimates from this best model were negatively correlated to the proportion of births occurring in the preceding winter months (estimate -5.945; S.E. 2.934; Z-value 2.026; $p=0.043$; Figure 4). Moreover, modelling of the binomial proportion of winter births on recruitment within the state space framework indicated that winter births negatively affected recruitment (see supplementary information for full model results).

Furthermore, chi squared tests using the raw birth data found evidence of a survival cost to winter births in the second half of the study, when the proportion of winter births increased. More calves born in winter died before reaching 30 days of age than for those born in other seasons. This result was not statistically significant for the complete time series or the first half of the time series (overall $\chi^2=1.981$; d.f.=1; $p=0.159$; 1948-1979 $\chi^2=1.323$; d.f.=1; $p=0.250$), but was highly significant in the second half of the study ($\chi^2=9.932$; d.f.=1; $p=0.002$). The percentages of calves dying before 30 days of age were: 1948-1979 (spring= 24.24; summer=21.05; autumn= 19.44; winter=31.25); 1980-2008 (spring= 13.08; summer= 1.49; autumn= 3.12; winter= 15.19). The other seasons showed no significant differences in the proportions dying relative to the remaining three seasons for the overall and the first half of the study period (spring: $\chi^2=1.981$; d.f.=1; $p=0.159$; summer: $\chi^2=2.059$; d.f.=1; $p=0.151$; autumn: $\chi^2=0.862$; d.f.=1; $p=0.353$). However, there were significantly fewer of the summer births between 1980 and 2008 that died early ($\chi^2=6.864$; d.f.=1; $p=0.009$)

Discussion

Temporal changes in birth phenology and seasonality (H1 and H2)

The frequency of winter births has significantly increased in Chillingham cattle between 1947 and 2008, resulting in an apparent shift in phenology towards earlier breeding and a significant rescheduling of the annual cycle of breeding. Median birth dates advanced by 1.1 days per year, corresponding to an overall shift of just over two months over the 60 year study period, but it is important to stress the difficulties of using changes in median birth date (or first birth

date) to estimate changes in phenology for species that breed in all seasons, or for which the number of births varies substantially.

This estimate of 1.1 days per year is similar to published studies of seasonal breeding mammals and hence does not provide strong support for H1 that feral populations exhibit greater flexibility in responding to changing environmental conditions. Advancement in median or average birth dates (days/year) of 0.3 in Caribou (*Rangifer tarandus*; Post & Forchhammer 2008); 0.71 in harbour seals (*Phoca vitulina*; Reijnders, Brasseur & Meesters 2010); 1.8 in red squirrels (*Tamiasciurus hudsonicus*; Réale *et al.* 2003); and 0.42 for red deer (Moyes *et al.* 2011) have been reported previously. It should, however, be noted that the Chillingham data span 60 years, the longest available time series for any mammal, and hence includes decades with negligible climate change. Plasticity in timing of breeding has also been observed in wild ungulates. Norwegian reindeer (*R. tarandus*) introduced to South Georgia completely reversed their annual reproductive cycle by six months within two years, in response to the reversal of day length variation from the northern to southern hemisphere (Leader-Williams 1988). We predict that some wild species may also broaden their breeding seasonality in the future and recommend that this be investigated further.

Our study reveals that even aseasonal breeders are exhibiting changing phenology in response to climate change, and highlights the value of long-term studies in detecting such changes. In support of H2 (see Table 1), we found that the number of births in winter and spring, the seasons of the year showing significant warming, increased significantly. However, only the winter season showed significant changes in both the number and proportion of births.

Drivers of spring conceptions (H3 and H4)

The proportion of winter births was higher in years when the onset of the plant growing season in the preceding spring, the period when winter born calves would be conceived (Hammond 1927), was earlier, and increased with increasing density of adult female cattle at mid-range and latest dates of the onset of the growing season (supporting H3 and H4; see Table 1). Although the mechanism leading to increased winter births cannot be elucidated from this correlative analysis, we suggest that winter and spring warming has shifted the onset of plant seasonal growth and enabled female cattle to reach a suitable breeding condition earlier in the year, leading to earlier calf births. Temperature and rainfall are known to be the major factors influencing plant growth, with temperature the strongest driver at northern latitudes. Large-scale satellite-derived information has shown that spring vegetation growth in the northern hemisphere starts earlier in response to recent warmer temperatures (Zhou *et al.* 2001). Unlike red deer (Nussey *et al.* 2005), we found no evidence that rainfall affected the seasonality of breeding in Chillingham cattle, suggesting that rainfall is unlikely to be limiting in this system. Similarly, Hall & Hall (1988) found no evidence that rainfall correlated with the probability of conceptions in Chillingham cattle.

We found that climate was not the only driver of changing seasonality in Chillingham cattle. There was evidence that winter births were more likely when female herd density was high in years when the onset of the growing season in the preceding spring was later. This supports H4 (see Table 1) and is in line with evidence from other feral populations including Soay sheep (Clutton-Brock *et al.* 1992; Forchhammer *et al.* 2001) that high winter density led to poorer quality and earlier born young. Clearly, simple analyses of shifting phenology that do not account for changing population size can be misleading.

There was some evidence that the correlation between the earlier onset of the growing season in the preceding spring and the proportion of winter births was less clear in years when lime fertilisation occurred, suggesting that liming increased the availability or quality of forage such that cattle were in better condition and less responsive to the onset of the growing season. Moreover, fertilisation may have increased the carrying capacity of this grassland site for cattle. Lime fertilisation increased the cover of productive herbage species (R.G.H. Bunce & S.J.G. Hall unpublished) but quantitative data are not available to indicate whether liming increased forage biomass or altered plant phenology. Without experimental manipulation it is not possible to fully discount a degree of confounding between liming and the effects of climate change and demography. However, the shift to higher numbers of winter births precedes the onset of liming in 1980 (Figure 1), there is much inter-annual variation in winter births, and the effects of the key climatic and demographic variables were similar when the analysis was restricted to 1947-1979 that pre-dated lime treatment.

Correlations between recruitment and the proportion of winter births (H5)

Changing seasonality to having a higher proportion of births in the winter incurs a negative cost to recruitment in Chillingham cattle, thus providing support for H5 (see Table 1). There was a significant correlation between recruitment estimates and the proportion of winter births in the preceding year; and also evidence that winter born calves were more likely to die before the age of 30 days during the latter half of the study period. Hall and Hall (1988) also found that early phenology incurred a cost, with calves that survived to one year of age having a median birth date that was a month later than those that did not survive. Winter has been shown to be the period of highest juvenile mortality in other ungulate species, for example Soay sheep (Clutton-Brock & Coulson 2002). Moreover, in many holarctic ungulates growth and fecundity are positively related to winter temperatures (Clutton-Brock & Albon 1983; Mech *et al.* 1987), with effects of winter weather operating on the condition of the breeding females and the effects on offspring development persisting through adult life (Post *et al.* 1997; Gaillard *et al.* 2003). Therefore it appears that although winter and spring temperatures are showing evidence of climate warming, and cattle are responding to this by conceiving earlier in the spring, winter born calves are more likely to die than those born at other times of the year, and hence there may be a mismatch between conditions determining conception timing and the resulting increased mortality because such conceptions lead to winter births. Despite this fitness cost of winter births, cattle show no indication of reverting to a wild-type seasonal breeding pattern and we hypothesise that selection during the process of domestication has led to Chillingham cattle becoming physiologically constrained from exhibiting seasonal breeding.

In summary, our study is one of the first to document changes in the phenology of a year-round breeder, shedding new light on how environmental change may be significantly altering the pattern of the timing of breeding, and suggesting that the impact of climate on the scheduling of biological events may be more extensive than previously thought. Bronson (2009) predicts that the mammals that will be most severely affected by climate change will be long-lived species at mid to high latitudes whose reproduction is rigidly controlled by photoperiod. There is a current lack of studies of phenology in species without a clearly defined breeding season, hindering general conclusions as to whether or how such species shift their timing of breeding in response to climate change, but we predict that other feral populations may also be negatively affected by climate change. Although feral ungulates may respond plastically to climate and environmental

change due to previous selection for reproductive output, our study shows that such shifts in seasonality may have negative consequences due to young being increasingly born in sub-optimal months. Furthermore, closed feral populations such as Chillingham cattle with reduced genetic variation due to inbreeding (Visscher *et al.* 2001) may be less able to adapt in the long-term to changing environmental regimes. Chillingham cattle are showing no evidence of reverting back to a wild phenotype and exhibiting seasonal breeding, despite evidence that increased frequency of winter births is negatively impacting recruitment. Thus, we conclude that the impacts of climate change on ungulates may be operating more subtly than simply being due to trophic mismatch in timing of peak energetic demands and peak forage availability leading to fitness costs, as has been found in wild ungulates with seasonal breeding, for example caribou (Post & Forchhammer 2008). Further studies are needed to investigate whether other aseasonal breeders are also responding to climate change and whether such responses may be affecting trophic interactions and community structure.

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Table 1: Hypotheses tested in order to evaluate how the phenology of winter births has changed over time in a year-round breeding population of cattle.

	Hypothesis	Rationale	Supporting references
H1	Median birth phenology has advanced over time in cattle at a greater rate to that reported for other wild taxa.	Feral ungulates show enhanced reproductive output and different seasonal breeding patterns compared to their wild ungulate counterparts. We therefore predict that feral populations will show greater elasticity in phenological response than wild ungulates owing to previous selection for enhanced reproductive output.	Eckstein & Zuckerman 1956; Bronson 1989; Setchell 1992; Clutton-Brock & Pemberton 2004; Garel et al. 2005
H2	The proportion of births in winter and spring show the greatest change (increase) over time.	Winter and spring months show the greatest evidence of climate warming in the Northern Hemisphere, driving a significant advance in the forage plant growing season	Schwartz, Ahas & Aasa 2006.
H3	Conditions (winter/spring temperatures or onset of plant growth) immediately prior to or during spring are negatively correlated with spring conceptions (hence winter births).	There is much evidence from ungulates that poor forage conditions prior to conceptions result in females being in poor condition and unable to or delaying conception.	Chapman, Furlong & Harris 1997; Langvatn et al. 2004; Griffiths et al. 2010
H4	The proportion of spring conceptions (hence winter births) is positively associated with herd density.	There is evidence from Soay sheep and red deer that high winter density leads to poorer quality young (lower body weight) and to earlier born young.	Clutton-Brock et al. 1992; Forchhammer et al. 2001; Coulson, Milner-Gulland & Clutton-Brock 2000; Coulson et al. 2003
H5	Cattle recruitment (defined as the number of calves produced per adult female that survive to their first census) is negatively associated with breeding phenology (proportion of winter births).	Historical artificial selection for fecundity leads to high reproductive output, even when conditions are not optimal (for example high herd density or births during winter when conditions are relatively harsh) and at the expense of survival of breeding females or young.	Clutton-Brock et al. 1992; Grange et al. 2009

Table 2: Parameter estimates for the proportion of winter births between 1947 and 2008 based on the best supported (by AICc) binomial model on the non-detrended data. The best model included an interaction between the density of adult females and the onset of the plant growing season (date on which cumulative GDD reached a threshold of 60 during the spring of conceptions), and an interaction between lime (binary variable indicating years when the site was treated with lime) and the onset of the growing season.

Parameter	Estimate	Standard Error	Z statistic	P value
Intercept	6.558	2.196	2.987	0.003
Female density	-0.178	0.137	-1.298	0.194
Onset of growing season (Julian date)	-0.101	0.024	-4.185	<0.001
Lime	-3.971	1.733	-2.291	0.022
Female density * onset of growing season	0.003	0.001	2.031	0.042
Onset of growing season * lime	0.043	0.017	2.585	0.010

Table 3: The ten best supported models (by AICc) that were identified by the model selection procedure when using binomial logistic regression to investigate the proportion of winter cattle births. “Female density” is defined as the total number of adult females (>2 years of age) on the 31st December; “lime” is a binary variable indicating years when the pasture was treated with lime; “onset of growing season” is the Julian date on which cumulative GDD reached a threshold of 60; “winter GDD” is the cumulative GDDs over a threshold value of 5.5°C for December to February in the winter prior to spring of conceptions; “early GDD” is the cumulative GDDs over a threshold value of 5.5°C for December to May in the winter prior to and spring of conceptions; “wNAO” is winter NAO in the winter before spring conceptions.

Model	k	ΔAICc	AICc weight
Female density * onset of growing season + onset of growing season * lime	6	0.000	0.427
Female density + onset of growing season * lime	5	1.811	0.173
Female density * onset of growing season * lime	8	2.385	0.130
Female density * winter GDD + winter GDD * lime	6	3.906	0.061
Female density * onset of growing season + lime	5	4.542	0.044
Female density * onset of growing season	4	4.908	0.037
Female density + wNAO * lime	5	5.989	0.021
Female density * onset of growing season + female density * lime	6	6.448	0.017
Female density + winter GDD * lime	5	6.485	0.017
Female density + early GDD * lime	5	6.841	0.014

Figure 1: The proportion of births occurring in each season per year during the 62 year study period (years in which the total number of births was ≤ 3 are omitted). The period during which lime fertilization occurred at Chilligham is indicated by the grey rectangles. The bold black line shows the seven year mean proportion of total births per season).

Figure 2: Predicted probability of winter births for years when the site was not fertilised (upper panel) and years with lime fertilisation (lower panel) for the most supported model by AICc. This model included an interaction between female density and the onset of the growing season in the spring of conceptions and an interaction between lime and the onset of the growing season. The legend in the upper panel shows the predicted probability associated with each colour, with red indicating the highest probability of winter births.

Figure 3: Observed (hatched grey line) and predicted (solid black line) number of winter births based on the best model (by AICc). This model included an interaction between female density and the onset of the growing season in the spring of conceptions and an interaction between lime and the onset of the growing season.

Figure 4: Predicted relationship from a binomial logistic regression between recruitment (number of calves produced per cow of 2 years age or older that survive to their first census) estimates from the population model and the proportion of winter births (with 95% confidence limits). This model is weighted according to individual sample sizes. The pale grey points show the raw proportions of winter births against recruitment.

Figure 1

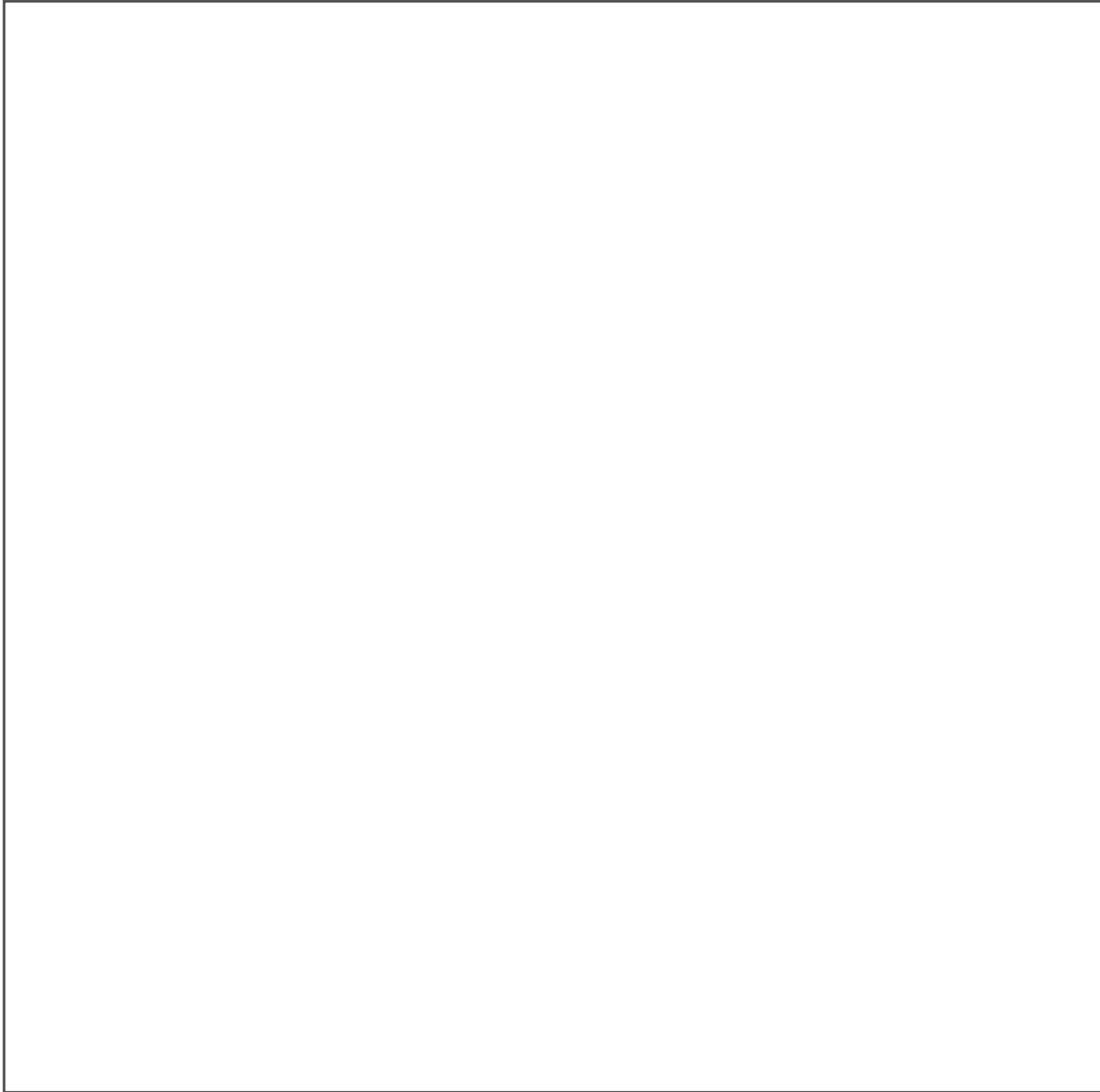


Figure 2

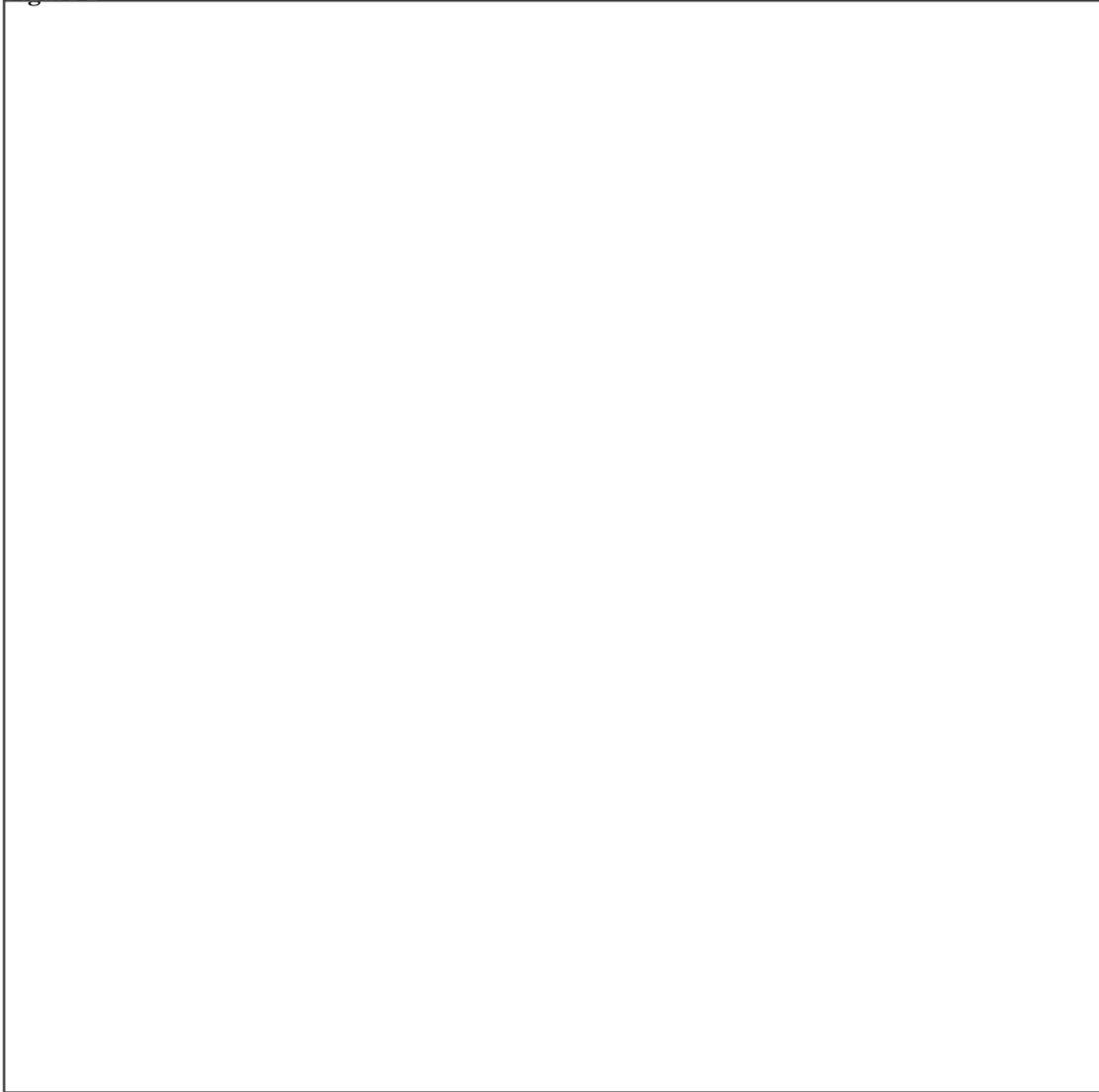


Figure 3

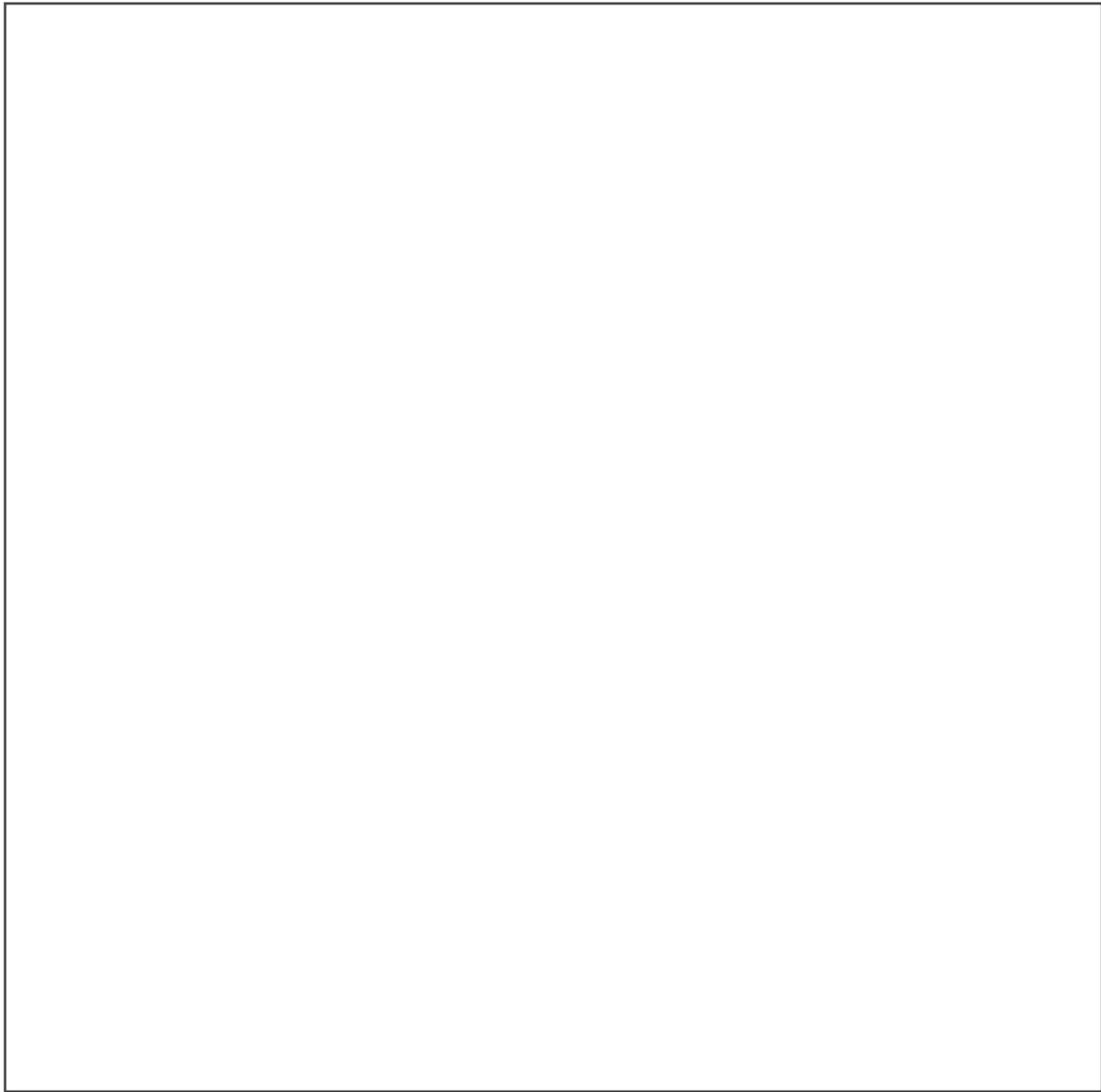
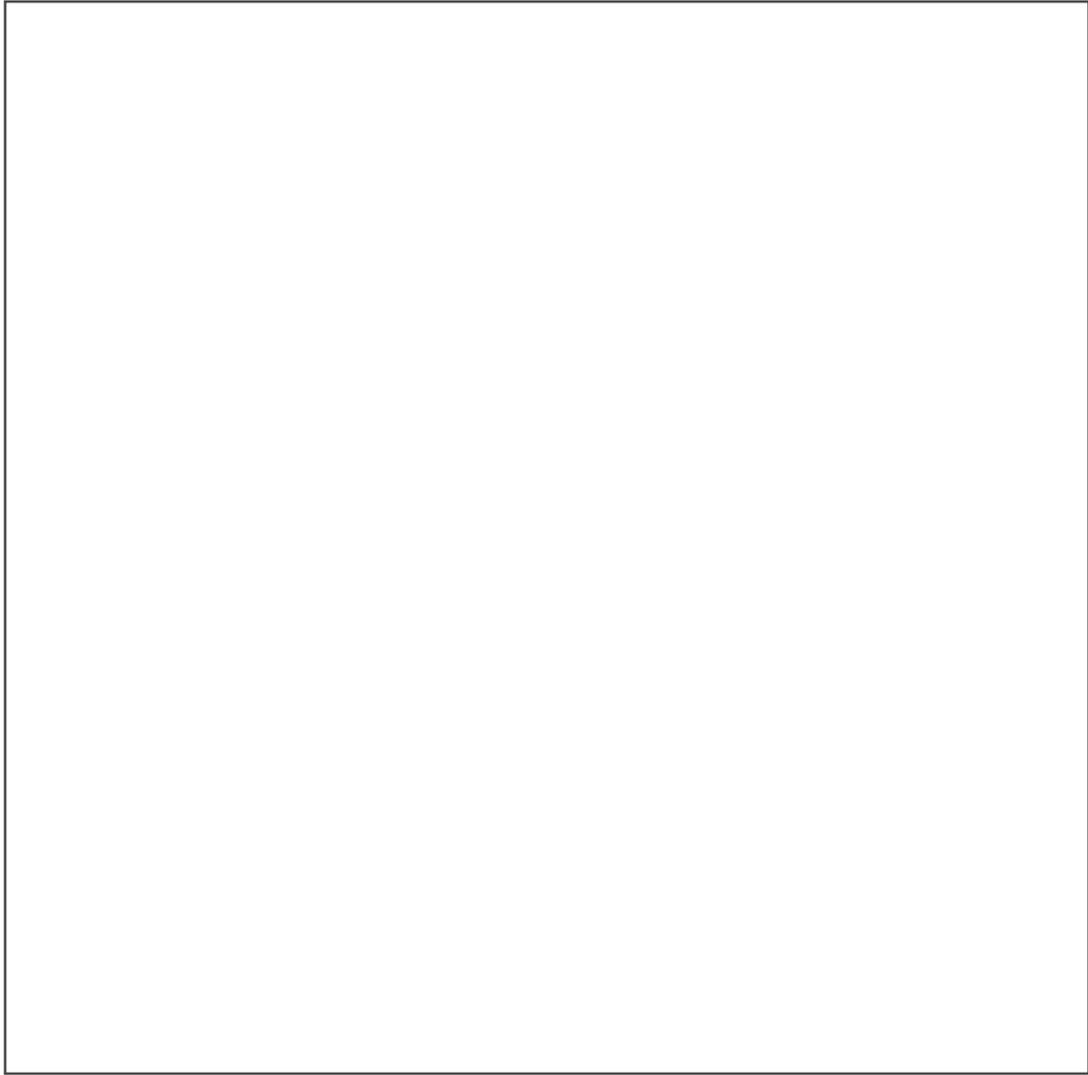


Figure 4



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The following Supporting Information is available for this article online:

Appendix S1 provides further details of the binomial modelling of the proportion of winter births and Appendix S2 provides details of the state space modelling of recruitment.