

# Advancing breeding phenology in response to environmental change in a wild red deer population

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## Abstract

Most evidence for advances in phenology of in response to recent climate warming in wild vertebrate populations has come from long-term studies of birds. Few studies have either documented phenological advances or tested their climatic causes and demographic consequences in wild mammal systems. Using a long-term study of red deer on the Isle of Rum, Scotland, we present evidence of significant temporal trends in six phenological traits: oestrus date and parturition date in females, and antler cast date, antler clean date, rut start date and rut end date in males. These traits advanced by between 5 and 12 days across a 28-year study period. Local climate measures associated with plant growth in spring and summer (growing degree days) increased significantly over time and explained a significant amount of variation in all six phenological traits, largely accounting for temporal advances observed in some of the traits. However, there was no evidence for temporal changes in key female reproductive performance traits (offspring birth weight and offspring survival) in this population, despite significant relationships between these traits and female phenology. In males, average antler weights increased over time presumably as a result of improved resource availability and physiological condition through spring and summer. There was no evidence for any temporal change in average male annual breeding success, as might be expected if the timing of male rutting behaviour was failing to track advances in the timing of oestrus in females. Our results provide rare evidence linking phenological advances to climate warming in a wild mammal and highlight the potential complexity of relationships between climate warming, phenology and demography in wild vertebrates.

**Keywords:** climate warming, demography, mammal, phenology, plant growth, reproductive fitness, sexual selection, ungulate

Received 10 May 2010 and accepted 25 November 2010

## Introduction

Recent meta-analyses provide compelling evidence that the phenology of many temperate plant and animal populations has advanced in response to recent climate warming (Menzel & Fabian, 1999; Menzel *et al.*, 2006; Parmesan, 2007; Thackeray *et al.*, 2010). The overwhelming majority of evidence for such phenological advances in vertebrate systems comes from birds (Berteaux & Stenseth, 2006; Parmesan, 2006, 2007; Thackeray *et al.*, 2010). Long-term studies of wild birds provide rare insight into the complex interactions between local changes in climate, food availability, breeding phenology and reproductive fitness (Visser *et al.*, 1998; Both & Visser, 2001; Winkler *et al.*, 2002; Gienapp *et al.*, 2006; Charmantier *et al.*, 2008) and some of the best evidence for links between rates of phenological change and

population growth rates (Both *et al.*, 2006, 2010; Møller *et al.*, 2008). However, recent advances in our understanding of how climate change is affecting the ecological and evolutionary dynamics of avian systems serve to highlight a very notable paucity of similar studies in wild mammals (Berteaux & Stenseth, 2006; Parmesan, 2007; Thackeray *et al.*, 2010). Few studies have even documented phenological responses to climate warming in mammals, let alone investigated the wider ecological or evolutionary consequences of climatic and phenological change (although see Inouye *et al.* (2000), Adamik & Kral (2008) for examples of the former, and Réale *et al.* (2003) for an example of both in rodent populations). Long-lived mammals, such as ungulates, are typically highly polygynous and, in temperate regions, experience a long over-winter gestation period separating the mating season and the birth season. This is in stark contrast to species of passerine birds, which have been the overarching focus of studies relating phenology and climate change in wild vertebrates,

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which are typically monogamous and in temperate zones mate, lay eggs and raise young in quick succession through spring and summer. Clearly, the selective and environmental pressures on phenology are likely to differ markedly between avian and mammalian systems (Inouye *et al.*, 2000; Berteaux & Stenseth, 2006). In the present study, we document significant advances in breeding phenology in a Scottish red deer (*Cervus elaphus*) population over the last 28 years and test whether these advances can be explained by changes in climate measures associated with plant growth.

Understanding the ecological and evolutionary consequences of phenological responses to climate change hinges on the availability of longitudinal data and the ability to examine the consequences of phenological changes for reproductive fitness and demographic rates at the individual level (Visser & Both, 2005; Gienapp *et al.*, 2008; Visser, 2008). In temperate mammals, such as red deer, selective pressures on phenological traits will differ markedly between the sexes (Clutton-Brock *et al.*, 1982; Mysterud *et al.*, 2008a). Female reproductive fitness is predominantly limited by resource availability during the key periods of gestation and lactation. The reproductive consequences of climate change will depend on its effects on the timing and extent of food availability and on how well females can match energetic requirements during gestation and lactation to the availability of high quality vegetation in the spring and summer following conception (Post & Forchhammer, 2008; Mysterud *et al.*, 2008a). Advancing oestrus and parturition times could allow females to capitalize on an advancing spring flush and increase offspring survival chances and reproductive fitness (e.g. Festa-Bianchet, 1988; Coulson *et al.*, 2003; Réale *et al.*, 2003), although a failure to match breeding phenology shifts to changes in plant phenology would be expected to result in depressed reproductive performance (e.g. Post & Forchhammer, 2008). In contrast, male reproductive fitness is limited by the availability of mates and success hinges critically on how well the timing of recovery of condition after the winter period and the development of secondary sexual characters coincides with the peak in availability of oestrous females (Mysterud *et al.*, 2008a; Clements *et al.*, 2010). Male breeding phenology is likely to be highly condition-dependent and would be expected to advance if food availability increased in response to climate warming in spring and summer, although examples of such responses in males are very rare (Mysterud *et al.*, 2008a; Clements *et al.*, 2010). However, regardless of any change in average condition and competitive ability in males, a failure to track changes in the timing of oestrus in females could result in a reduction of available mates and a reduction in

average male breeding success and overall reproductive rates (Bonenfant *et al.*, 2004; Mysterud *et al.*, 2008a). Longitudinal studies linking climate, breeding phenology and reproductive performance in both sexes remain very rare in wild mammals.

Red deer are widely distributed temperate herbivores that typically exhibit an iconic harem-based breeding system (Clutton-Brock *et al.*, 1982, although see Carranza *et al.*, 1996). The annual breeding cycle of this species is characterized by an autumn mating season (or 'rut') during which males compete to control groups (or harems) of females and mate with these females as they come briefly into oestrus. Male red deer show a synchronized annual hormonal cycle that regulates antler growth and the start of rutting behaviour (Lincoln, 1992). In early spring, rising testosterone levels trigger antler shedding (or 'casting') and the immediate onset of antler growth in mature males (Lincoln, 1992). Antlers grow until July or early August, when their velvet covering dies and is cleaned off (antler 'cleaning'). In September, stags move to their traditional rutting areas where they defend harems of hinds, mating with them as they come into oestrus (Clutton-Brock *et al.*, 1982). The rut lasts from late September through to early November, although female oestrus is typically well synchronized and rutting behaviour, fights and mating are typically concentrated in a period of just a few weeks. The gestation period is around 7½ months and the majority of calves are born the following May or June. Females produce only singletons and lactate for 4–5 months until the next rut, when most mothers conceive again (Clutton-Brock *et al.*, 1982).

Although both the timing of antler growth and rutting activity in males, and oestrus and parturition dates in females, are generally synchronized within red deer populations (Guinness *et al.*, 1978; Lincoln, 1992; Bonenfant *et al.*, 2004), variation in phenological traits within populations is well documented. Studies of Scottish and Norwegian populations show that phenology is delayed in young and old individuals, and those experiencing high population densities (Clutton-Brock *et al.*, 1987; Coulson *et al.*, 2003; Langvatn *et al.*, 2004; Mysterud *et al.*, 2008a; Nussey *et al.*, 2009; Clements *et al.*, 2010). Studies of wild red deer have also linked breeding phenology to climatic variation (Coulson *et al.*, 2003; Nussey *et al.*, 2005; Clements *et al.*, 2010). However, to our knowledge, no study of wild red deer has explicitly linked temporal changes in phenology to climatic warming potentially associated with changes in plant growth phenology.

Climatic and phenological evidence suggests that, as average annual temperatures have increased, the onset of the plant growing season has advanced and its duration has lengthened across temperate Europe, as

well as in Scotland specifically, over the last few decades (Menzel & Fabian, 1999; Barnett *et al.*, 2006; Menzel *et al.*, 2006). Earlier and increased plant growth should increase food availability to herbivores at key junctures in their annual breeding cycles (Post & Stenseth, 1999; Mysterud *et al.*, 2008a). An advanced and/or increased spring flush should increase food availability for females during the last trimester of pregnancy and for males in the run-up to the antler growth period. An extended plant growth season should increase the quantity of food available across the lactation period/antler growth period and in the run-up to the autumn rut. Given aforementioned evidence of condition-dependent variation in phenology in red deer, we would predict phenological advances in response to recent changes in climate. However, evidence of such phenological responses is generally lacking for red deer and indeed mammalian herbivores in general. An analysis of neonatal traits in our study population of red deer on the Isle of Rum documented a significant advance in parturition dates between 1974 and 2000 (Coulson *et al.*, 2003). In the present study, we follow up this observation and aim to: (1) quantify rates of advance across six different phenological traits in male and female deer; (2) determine whether changes can be explained by local climate measures often used as proxies for plant growth [growing degree days (GDD)]; (3) assess whether similar temporal trends associated with changes in climate or phenology are observed in two maternal performance traits (offspring birth weight and offspring survival), male antler mass and male annual breeding success (ABS).

## Materials and methods

### Study population and data collection

The wild population of red deer in the North Block of the Isle of Rum, Scotland, has been under intensive study since the early 1970s (Clutton-Brock *et al.*, 1982). Individual deer are recognized as a result of artificial markings and natural variation, and are closely monitored throughout their lifetimes (Clutton-Brock *et al.*, 1982). Culling of the population in the 12 km<sup>2</sup> North Block study area ceased in 1972, since when the breeding phenology and reproductive performance of thousands of male and female red deer have been closely monitored (Clutton-Brock *et al.*, 1982; Coulson *et al.*, 2004). Throughout the year, censuses of the study area are undertaken to monitor the presence and location of individual deer. During the calving season, pregnant hinds are closely watched for behaviour indicating possible parturition, in order to obtain accurate times of birth. Newborn calves are captured and weighed, measured, blood sampled and uniquely marked (see Clutton-Brock *et al.*, 1982 for further details). During the autumn rut, daily censuses of the entire study area are carried

out. The identity and location of all males holding a harem are noted, as are the identities of all females within each male's harem. Females are watched intently for signs of oestrus such as being mounted and intense attention from males (Guinness *et al.*, 1971). During the winter and spring, extensive mortality and cast antler searches are undertaken in and around the study area. The males to which cast antlers belong are identified by comparing their unique structure and form to photographs taken during the rut, before casting. All cast antlers are weighed. Antler casting and cleaning dates are estimated based on regular observations of males in the field. Male ABS has been estimated using both microsatellite genotype data (from tissue, bone or antler samples collected at birth, immobilization or post-mortem, as well as from cast antlers) and behavioural data collected each rut (Pemberton *et al.*, 1992; Kruuk *et al.*, 2002; Walling *et al.*, 2010). Most mortality in the study population occurs during winter, and regular censuses and searches of the study area at this time allow us to locate the majority of carcasses and keep track of over-winter mortality (Clutton-Brock *et al.*, 1982).

The first decade of the long-term study of deer in the North Block of Rum were characterized by a pronounced increase in female population size, following the cessation of culling in 1972 (Clutton-Brock *et al.*, 1982, 2002; Coulson *et al.*, 2004). Over the first 10–15 years of the study period, the number of resident adult females in the study increased while the number of males declined (Coulson *et al.*, 2004). Early in the 1980s, the population is thought to have reached carrying capacity and the number of resident adult females using the study area has fluctuated around 200 individuals ever since (Coulson *et al.*, 2004). Previous studies on Rum have shown that parturition dates in the early part of the study became later as population density increased (Clutton-Brock *et al.*, 1987) and recent work using data from the entire study period has shown that antler casting and cleaning dates are delayed at high densities (Clements *et al.*, 2010). The apparent density-dependence of phenological traits across the entire study period seems more likely to be driven by the pronounced changes in population size over the first decade of the study, rather than by subsequent fluctuations around carrying capacity. Recently, an analysis of neonatal traits detected a significant advance in parturition dates across three decades in the North Block study population (Coulson *et al.*, 2003). To avoid potentially confounding effects of the increase in density across the first decade of the study on breeding phenology, we have restricted our analyses to the period during which the population has been at or around carrying capacity. We therefore used phenological and life history data collected on Rum between 1980 and 2007.

### Phenotypic traits

**Phenological traits.** All phenological traits analysed were expressed in Julian days since 1 January. We analysed two phenological traits in female deer (oestrus date and parturition date) and four in male deer (antler cast date, antler clean date, rut start date and rut end date). Dates of observations of behavioural signs of oestrous (e.g. being mounted or

receiving intense attention from males, see Guinness *et al.*, 1971; Clutton-Brock *et al.*, 1982) were used. If more than one oestrus event was observed for a given female across a given rut season (15 September–15 November), we took the first observed instance in the analyses presented here. The vast majority of parturition dates were known with certainty as a result of close monitoring of maternal behaviour during the calving season and any uncertain dates were excluded. As not all males were observed on a daily basis around the times of antler casting and cleaning, only instances where an individual was sighted in study area censuses around the estimated casting/cleaning date were used in analyses to ensure dates were reliable (Clements *et al.*, 2010). Male rut phenology was measured for those males that had rutted for at least 5 days during a given rutting season. A male was deemed to be rutting on a given day if he was seen holding and defending a harem of females during a daily rut census. We defined the start of a male's rut as the first day of a period of at least 5 days of harem holding, and the end of the rut was defined as the last day of harem holding. Our data for parturition and antler casting dates contained a very small number of extremely early or late events, which skewed the distributions of these traits. To ensure assumptions of normality were met, we excluded these extreme outliers from our analyses, removing parturition dates outside of the range 1 May–31 July (one observation before May and 32 observations after July: <2% of data) and antler casting dates later than 30 April (eight observations, <1% of data). Note also that data was lacking for antler casting and cleaning dates in 2003 and for oestrous dates in 2001. Ages of all deer breeding in the study area were determined through knowledge of their year of birth. As very few stags rut successfully before the age of 4 (Clutton-Brock *et al.*, 1982; Clements *et al.*, 2010), we excluded all males under this age from our analyses.

*Reproductive traits and other measures.* The measurements and definition of additional female and male reproductive performance measures used in our analyses are described in turn below.

*Offspring birth weight.* The majority of newly born calves are caught and weighed within a few days of birth. However, the age at capture does vary, so we used residual birth weight (correcting for capture age) estimated by linearly regressing weight at capture against time of weighing in hours. Based on this regression, birth weight is estimated as offspring neonatal body mass at capture  $-0.01539$  times age at capture in hours (following Clutton-Brock *et al.*, 1982).

*Offspring first-year survival.* Whether or not a calf survived until 1 May of the year after its birth, excluding all deer that were shot when venturing outside the study area (Clutton-Brock *et al.*, 1982).

*Female reproductive status.* Reproductive events in the previous year have been shown to influence female breeding phenology and performance in the study population (Clutton-Brock *et al.*, 1982; Coulson *et al.*, 2003). Five different statuses were defined (following Coulson *et al.*,

2003) as: 'naïve' – never reproduced before; 'milk' – reproduced in the previous year and the calf survived to 1<sup>st</sup> May in the next year; 'summer yield' – reproduced in the previous year but the calf died before 1 October of its first year; 'winter yield' – reproduced in the previous year but the calf died between 1 October and 1 May; 'true yield' – has reproduced previously, but not in the previous year.

*Antler weights.* Recovered cast antlers were weighed (to the nearest gram). Where both antlers were recovered, the average weight was used in analyses.

*Male ABS.* ABS was defined as the total number of calves born in a breeding season that were sired by a given male. Paternity was inferred based on a combination of genetic and behavioural data using the programs MASTERBAYES (Hadfield *et al.*, 2006) and COLONY (Wang & Santure, 2009). Full details are provided in Walling *et al.* (2010). Note that not all males that rut in our study area have been genotyped, and the proportion of rutting males genotyped has increased over time (Walling *et al.*, 2010). It was therefore necessary to control for the proportion of males genotyped in our analyses of temporal trends in ABS.

### *Environmental variables*

We used measures of GDD to provide an estimate of local climatic conditions in relation to vegetation growth (Bonhomme, 2000). GDD is estimated as the cumulative sum of the daily mean temperatures above a threshold over a set period (Barnett *et al.*, 2006). Despite the potential limitations of GDD, including the nonlinearity of the relationship between development rate and temperature (discussed in detail in Bonhomme, 2000), GDD has been used successfully in horticulture to predict flowering dates and also in agriculture to predict yield, we therefore use GDD as a proxy for vegetation growth. Here, we used a threshold of 5 °C (following Barnett *et al.*, 2006). As GDD is cumulative, it is essential to have accurate information about the mean daily temperature on every day. The maximum and minimum daily temperatures are recorded on Rum by the Met Office British Atmospheric Data Centre (2006), but there are a large number of missing records in this data series. A much more detailed and complete climatic data series has been collected on Tiree, an island approximately 70 km southwest of our study area (British Atmospheric Data Centre, 2006), for which hourly temperatures are available. The available daily temperature values recorded on Rum were very closely correlated with the maximum and minimum temperatures recorded on Tiree ( $r^2 > 0.94$ ). We calculated average daily temperatures on Rum and Tiree (as the average of minimum and maximum daily temperatures). We then used the regression slope between daily mean temperatures at the two locations to predict hourly temperatures on Rum from the available hourly temperature from Tiree. We used these predictions to estimate mean daily temperatures on Rum, by dividing the sum of the temperatures by 24. For the very few gaps in the data series that remained (a total of 34 days from 13879 between 1970 and 2007), we used the mean temperature over the previous 3 days and the subsequent 3 days.

Our aim was to test whether changes GDD across particular periods preceding key life history events across the deer annual cycle predicted variation in phenological traits. We calculated GDD over the 9 months before the autumn rut ('Jan-Sep GDD') to capture climate variation across the entire growing season preceding the rut. However, changes in GDD in early spring, at the start of the growing season and before the calving season and during the antler casting period, or in late summer, at the end of the growth season and directly before the rut, are key periods of potential food limitation for red deer (Albon & Clutton-Brock, 1988). To test whether these changes in GDD over these shorter periods of the deer annual cycle might better explain variation in phenological traits, we also calculated GDD across the 3-month period before calving (February–April: 'Feb–Apr GDD') and across the 3-month period before the rut (July–September: 'Jul–Sep GDD'). A recent report has documented increases in GDD (measured across the entire calendar year) across the whole of Scotland and in Western Scotland specifically between 1961 and 2003 (Barnett *et al.*, 2006). An increase in primary productivity would be expected over this time period in light of this change (Barnett *et al.*, 2006). To confirm these patterns in our local GDD measures for the Isle of Rum, we tested for linear trends in Jan–Sep, Feb–Apr and Jul–Sep GDD between 1980 and 2007, using a linear regression of year on each period of GDD measurement.

### Statistical analyses

We initially tested for and estimated the magnitude of temporal trends in the six phenological variables. Linear mixed-effects models (LMMs) of each trait were fitted, using maximum likelihood, with individual and year as random effects to control for repeated measures (Milner *et al.*, 1999). Phenology varies with age in both sexes in this population (Nussey *et al.*, 2009), and to control for this variation we fitted age as a fixed-effect factor in all models. Female reproductive status was also included in models of oestrus and parturition date to control for variation in female reproductive effort in the preceding year. Year was fitted as a fixed covariate to estimate temporal trends and its significance tested by comparing the explanatory power of models including and excluding the term using a likelihood ratio test (LRT; Pinheiro & Bates, 2000). Population size (measured as the number of females > 1 year old resident to the study area, following Coulson *et al.*, 1997) was never found to be a significant predictor in LMMs of phenological traits and was not considered further in our analyses (data not shown). The lack of density effects on phenology in our models including only data from 1980 onwards confirms that previously documented density-dependent delays in parturition and antler casting and cleaning dates (Clutton-Brock *et al.*, 1987; Clements *et al.*, 2010) were driven by the pronounced changes in population size in the first decade or so of the study period. There was no evidence for density-dependence in any of the analysed phenological traits when considering only the period since 1980.

We subsequently tested which, if any, of the measures of GDD on Rum over different periods best explained variation

and evident temporal trends in each phenological trait. For traits measured in autumn (oestrous, rut start and stop dates) we compared three models including one or other of Jan–Sep, Feb–Apr and Jul–Sep GDD in the same calendar year as the phenological event. For traits measured in spring or summer (parturition, antler casting and cleaning dates) we compared models including each of the Jan–Sep, Feb–Apr and Jul–Sep GDD periods over the preceding calendar year and also a model including Feb–Apr GDD in the same calendar year. Since phenological variation in these latter traits could be independently influenced by the previous year's climate conditions and conditions early in the current year, we also compared models including both Feb–Apr GDD from the current year and one of the three GDD periods from the previous year (see Table 2 for full list of models compared). It is important to note that Jan–Sep, Feb–Apr and Jul–Sep GDD measures from the same calendar year were never fitted to the same model (see Table 2).

We used the LMMs described above for each trait (including year as a covariate but no GDD variables) as our null model for comparison. GDD terms were added to the LMMs while retaining year as a covariate (following Post & Stenseth, 1999). Our aim was to test which of these periods, corresponding to times just before key junctures in the deer reproductive cycle, best explained variation in each phenological trait. However, since many of the models to be compared contained the same number of parameters (e.g. a model with Feb–Apr GDD vs. model with Jul–Sep GDD), we could not use LRTs to compare models. Instead, we selected the model with the lowest Akaike's information criteria (AIC) value as our best model. If the selected model included a GDD effect, we calculated the proportional change in the estimated temporal trend with and without the GDD term in the model, and tested whether the year effect was still significant independent of GDD effects using LRTs. To test whether observed effects of year and/or GDD terms were independent of preceding phenological events, we reran final models of each trait including all preceding phenological events and interactions between them. For example, we reran the final model of parturition date including oestrous date and the final model of rut start date with main effects and interactions between antler casting and cleaning dates and tested whether and how this changed the magnitude and significance of year and GDD terms in the models. Note that there was considerably less data available for oestrus dates than parturition dates in females, and for antler cleaning dates than other traits in males, so that models including those terms would have had substantially reduced sample size (see Table 1 for sample sizes available). Significance of all terms in these models was assessed using LRTs and all nonsignificant terms ( $P > 0.05$ ) were dropped from the LMM.

We next tested for temporal trends and GDD effects in two nonphenological reproductive traits in females (offspring birth weight and offspring first-year survival) and two in males (antler weight and ABS). We ran LMMs of the two normally distributed traits, offspring birth weight and antler weight, and generalized linear mixed-effects models (GLMMs) of offspring survival (binomial error structure with logit link) and male ABS (negative binomial error structure with log link;

	Oestrus date	Parturition date
Sample size	588 (340 females)	2139 (551 females)
<i>(A) Models of temporal trends</i>		
Random effects		
	Female = 3.93 (6%)	Female = 26.6 (20%)
	Year = 5.75 (8%)	Year = 8.4 (6%)
	Residual = 59.48 (86%)	Residual = 96.6 (73%)
	$\chi^2$	$\chi^2$
Year	10.08	20.7
Age	52.19	113.9
Status	92.18	271.2
	df	df
	1	1
	16	15
	4	4
	P	P
	<0.01	<0.001
	<0.001	<0.001
	<0.001	<0.001
	b	b
	-0.26	-0.42
	SE	SE
	0.07	0.08
<i>(B) Models including preceding phenological events</i>		
Oestrus date		
Year		
	104.6	104.6
	1	1
	<0.001	<0.001
	0.77	0.77
	-0.27	-0.27
	0.07	0.07

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**Table 2** Comparison of models of phenological traits including different periods of measurement of growth degree days. All models included age as a fixed effect (oestrous and parturition date models also included female reproductive status) and individual identity and year as random effects. The model with the lowest AIC for each trait is highlighted in bold (see text for details)

Fixed covariates				Oestrus date			Parturition date			Cast date			Clean date			Rut start date			Rut stop date		
Year	GDD			Terms	ΔAIC	AIC	Terms	ΔAIC	AIC	Terms	ΔAIC	AIC	Terms	ΔAIC	AIC	Terms	ΔAIC	AIC	Terms	ΔAIC	
	Jan-Sep*	Feb-Apr*	Jul-Sep*																		
X				4193.6	24	12.0	16321.6	24	1.9	10375.9	16	4.0	4700.2	16	9.5	8978.8	15	6.4	8687.4	15	2.4
X	X			4184.2	26	2.6	16320.2	25	0.5	10374.2	17	2.3	4700.8	17	10.1	<b>8972.4</b>	<b>16</b>	<b>0.0</b>	8685.1	16	0.1
X		X		<b>4181.6</b>	<b>26</b>	<b>0.0</b>	16321.2	25	1.5	10376.9	17	5.0	4702.0	17	11.3	8977.0	16	4.6	8689.1	16	4.1
X			X	4187.5	26	5.9	<b>16319.7</b>	<b>25</b>	<b>0.0</b>	10372.6	17	0.7	4699.5	17	8.8	8974.5	16	2.1	<b>8685.0</b>	<b>16</b>	<b>0.0</b>
X							16323.5	25	3.8	10374.0	17	2.1	<b>4690.7</b>	<b>17</b>	<b>0.0</b>						
X	X						16322.2	26	2.5	10373.4	18	1.5	4692.3	18	1.6						
X		X					16323.1	26	3.4	10375.3	18	3.4	4692.7	18	2.0						
X			X				16321.7	26	2.0	<b>10371.9</b>	<b>18</b>	<b>0.0</b>	4691.3	18	0.6						

\*For traits measured in spring or summer (parturition, casting and cleaning date) these GDD periods refer to months in the previous calendar to the phenological event, for the other traits (measured in autumn) they refer to periods in the same calendar year. The subsequent Feb–Apr period refers to the spring period in the same calendar year as spring events only.

following Nussey *et al.*, 2009). As before, individual and year were fitted as random effects and age was included as a fixed-effects factor in all models, and offspring sex and female reproductive status were fitted in all models of the two female reproductive traits (following Nussey *et al.*, 2009). To test for temporal trends, year was included as a fixed-effect covariate and, having established whether a significant temporal trend was evident, we went on to test main effects of GDD variables identified as important in previous phenological analyses. Previous studies of this population have demonstrated significant associations between parturition dates and birth weight and survival in females, and antler phenology, antler mass and ABS in males (Clutton-Brock *et al.*, 1987; Kruuk *et al.*, 2002; Coulson *et al.*, 2003; Clements *et al.*, 2010). We went on to test whether phenological traits explained significant variation in these reproductive traits and to what extent any evident temporal trends might be explained by changes in phenology. We therefore included oestrus and parturition date, as well as their interaction, in models of female offspring birth weight and offspring survival. Offspring birth weight was also added to offspring survival models and interactions between weights and oestrus and parturition dates were also tested. Effects of casting and cleaning dates on antler weight were also examined, as were effects of rut start and rut end dates on male ABS. To ensure any temporal changes in ABS were not confounded with the increase in the proportion of genotyped rutting males and thus the proportion of calves assigned a paternity over time (Walling *et al.*, 2010), we included the proportion of calves born in the subsequent spring that were assigned a father as an additional covariate in GLMMs of ABS. The significance of all fixed effects terms were tested using LRTs for LMMs or Wald's statistics for GLMMs.

All LMMs were fitted with the statistical package R, implementing the package 'LME4' (R Core Development Team, 2005). GLMMs were fitted in GenStat (VSN International, Hemel Hempstead, UK).

## Results

### Trends in GDD

All three measures of GDD increased significantly between 1980 and 2007 (Fig. 1). Jan–Sep GDD increased by an estimated 9.30 degree days per year ( $\pm 2.32$  SE,  $F_{(1,26)} = 16.10$ ,  $P < 0.001$ ). Feb–Apr GDD increased by 3.39 degree days per year ( $\pm 0.99$  SE,  $F_{(1,26)} = 11.66$ ,  $P < 0.01$ ) and Jul–Sep GDD increased by 3.28 degree days per year ( $\pm 1.37$  SE,  $F_{(1,26)} = 5.75$ ,  $P < 0.05$ ; see Fig. 1). As Jan–Sep GDD includes both Feb–Apr and Jul–Sep GDD, these measures were closely correlated ( $r = 0.83$  for Feb–Apr and Jan–Sep GDD and  $r = 0.74$  for Jul–Sep and Jan–Sep GDD), however, Feb–Apr and Jul–Sep GDD measures were less strongly positively correlated ( $r = 0.34$ ).



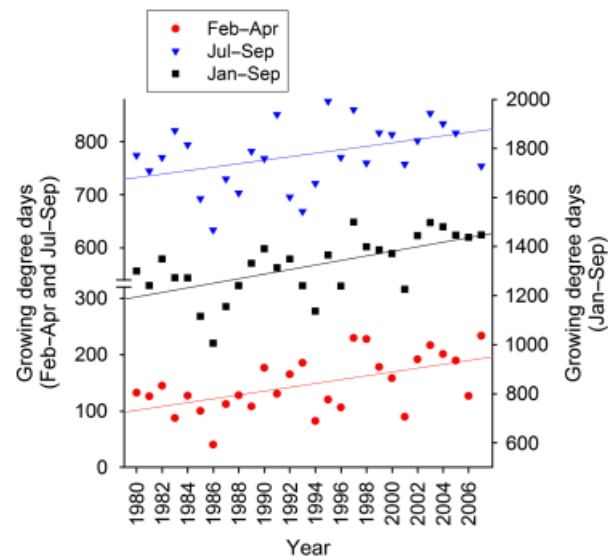
*Temporal trends in phenology*

Between 1980 and 2007, we detected significant advances in all six phenological traits (Fig. 2; Table 1). Among females, oestrus dates advanced by an estimated 0.26 days per year ( $\pm 0.07$  SE) and parturition dates by 0.42 days per year ( $\pm 0.08$  SE; Fig. 2a & Table 1). Models including only parturition dates where oestrus dates were also known estimated similar rates of

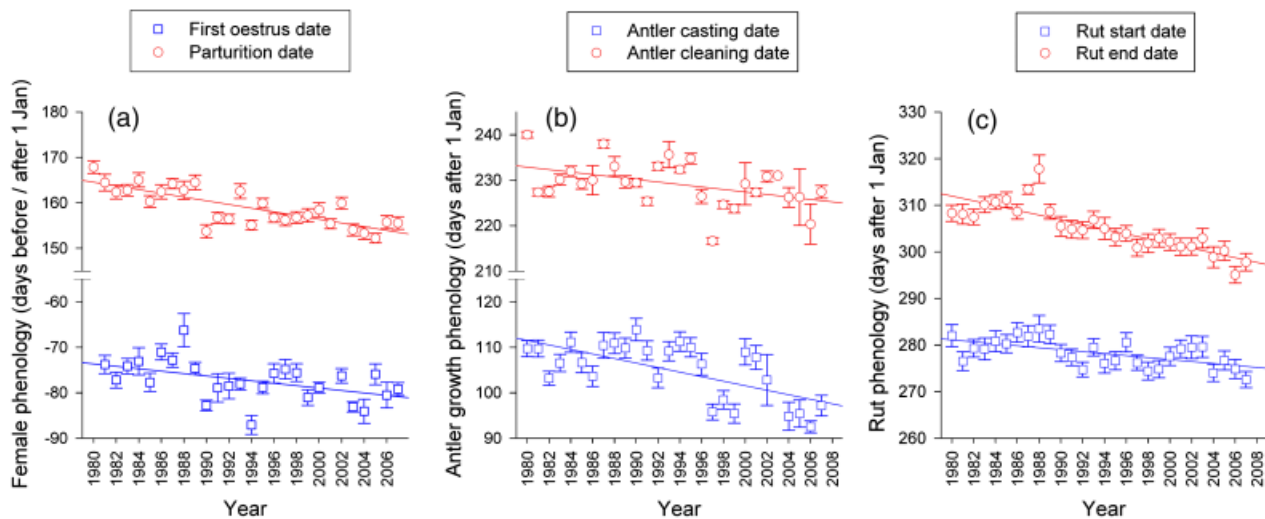
advance ( $b = -0.44 \pm 0.10$  SE,  $\chi^2_{(1)} = 13.88$ ,  $P < 0.001$ ). Oestrus date was highly significant in these models, but oestrus timing did not explain the advance in parturition dates entirely as year remained significant (Table 1).

Among males, antler casting dates advanced by 0.20 days per year ( $\pm 0.08$  SE; Table 1), while antler cleaning dates advanced by 0.26 days per year ( $\pm 0.08$  SE; Table 1; Fig. 2b). Antler casting dates significantly predicted antler cleaning date, but the temporal trend in cleaning dates remained significant and unchanged in magnitude once casting date was accounted for (Table 1). Rut start dates also became significantly earlier over the course of the study period (Table 1; Fig. 2c). Early antler cleaning dates were found to significantly predict earlier rut start dates, although there was no evidence for independent effects of either antler casting date or antler growth period (Table 1). Once cleaning date was accounted for, year was no longer significant, suggesting that the trend in rut start date was explained by advancing antler cleaning dates (Table 1). Finally, rut end dates advanced by an estimated 0.43 days per year (Table 1; Fig. 2c). Early rut start dates significantly predicted early rut end dates (Table 1), but rut end dates were not associated with main effects of antler casting or cleaning dates or interactions between these variables and rut start date (Table 1). Once effects of rut start dates were accounted for, the advance in rut end dates remained highly significant and little changed in magnitude (Table 1).

Our LMMs of phenological traits also confirmed that in females, both age and reproductive status were



**Fig. 1** Spring and summer growing degree days increased significantly between 1980 and 2007 on the Isle of Rum, Scotland. Growing degree days were measured using local weather station data as the sum of daily mean temperatures above  $5^{\circ}\text{C}$  across the months Feb–Apr (red circles, left y axis) and Jul–Sep (blue triangles, left y axis) and Jan–Sep (black squares, right y axis).



**Fig. 2** The breeding phenology of female and male red deer has advanced significantly between 1980 and 2007 in the North Block study area on the Isle of Rum. (a) Mean annual female first oestrus (blue squares) and parturition dates (red circles); (b) mean annual male antler casting (blue squares) and cleaning (red circles) dates; (c) mean annual male rut start (blue squares) and end dates (red circles). All annual means are plotted with standard error bars and a linear regression line through the means.



highly significant predictors of oestrous and parturition dates, while age was a significant predictor of all phenological traits in males (Table 1). Phenology in this population tends to be earliest in middle aged animals and is delayed in the youngest and eldest individuals (see Nussey *et al.*, 2009 for further details). Also, females that produced offspring in the previous year that survived the winter had delayed subsequent phenology, relative to females that either did not breed or bred and lost their offspring as a neonate (see Clutton-Brock *et al.*, 1982; Coulson *et al.*, 2003 for further details).

Across the 28-year study period, parturition dates in female deer were estimated to have advanced by 11.8 days while first oestrus dates advanced only 7.3 days. In males, antler casting dates and cleaning dates advanced by 5.6 and 7.3 days, respectively. Rut end dates advanced more than twice as fast as rut start dates (12.0 vs. 5.9 days, respectively) and, as a result, the average duration of a male's autumn rutting period has shortened over time (Fig. 2).

### Effects of GDD

A comparison of models including different GDD periods revealed that GDD explained significant variation in all six phenological traits (see Table 2). Increasing Feb–Apr GDD best explained variation in first oestrus dates ( $b = -0.032 \pm 0.012$  SE,  $\chi^2_{(1)} = 5.94$ ,  $P < 0.05$ ) and inclusion of this term reduced the estimated temporal trend by 36%, although the trend was still significant ( $b = -0.16 \pm 0.08$  SE,  $\chi^2_{(1)} = 4.28$ ,  $P < 0.05$ ). For parturition date, Jul–Sep GDD in the calendar year before parturition explained most variation (Table 2). Inclusion of Jul–Sep GDD ( $b = -0.020 \pm 0.010$  SE,  $\chi^2_{(1)} = 3.89$ ,  $P = 0.048$ ) reduced the estimated temporal trend by only 21% and year remained highly significant ( $b = -0.33 \pm 0.08$  SE,  $\chi^2_{(1)} = 12.76$ ,  $P < 0.001$ ). In models of parturition date including oestrus dates (for which only 588 observations were available), Jul–Sep GDD remained significant ( $b = -0.023 \pm 0.009$  SE,  $\chi^2_{(1)} = 5.70$ ,  $P < 0.05$ ) as did year, although the estimated temporal trend actually increased relative to models without the GDD term ( $b = -0.18 \pm 0.08$  SE,  $\chi^2_{(1)} = 4.67$ ,  $P < 0.05$ ).

The best-supported antler casting date model included both Feb–Apr GDD at the time of casting and Jul–Sep GDD in the previous year (Table 2). With both these GDD terms fitted, year was no longer significant in the model and the magnitude of the estimated temporal trend was reduced by 72% ( $b = -0.056 \pm 0.088$  SE,  $\chi^2_{(1)} = 0.40$ ,  $P = 0.53$ ). Without year in the model, both Feb–Apr GDD and previous Jul–Sep GDD were significantly and negatively related to antler casting date (Feb–Apr GDD:  $b = -0.024 \pm 0.011$  SE,  $\chi^2_{(1)} = 4.15$ ,  $P = 0.04$ ; previous Jul–Sep GDD:  $b = -0.021 \pm$

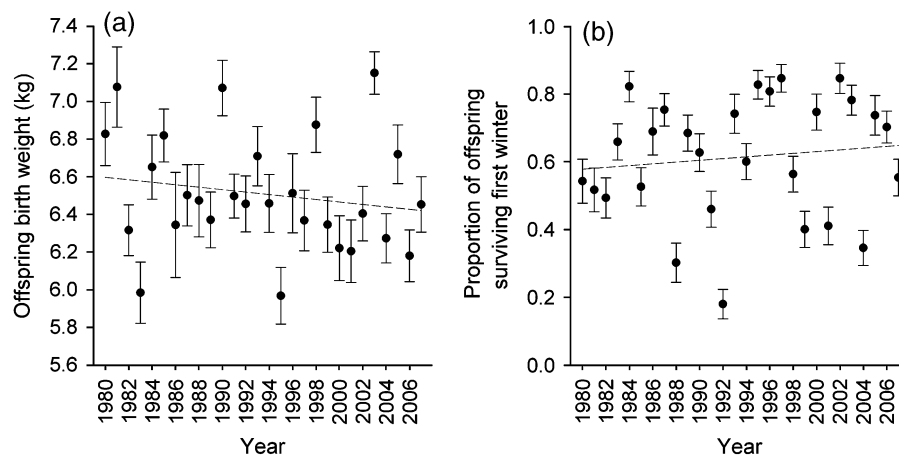
$0.009$  SE,  $\chi^2_{(1)} = 5.28$ ,  $P = 0.02$ ). This suggests that the observed advance in antler casting date over time can be largely explained by increases in GDD in the summer and spring periods preceding antler casting and regrowth.

Feb–Apr GDD in the year of antler growth was identified as the best predictor of antler cleaning dates (Table 2). As for casting date, once Feb–Apr GDD was included in the model the effect of year was no longer significant and the estimated temporal trend was reduced by 54% ( $b = -0.12 \pm 0.08$  SE,  $\chi^2_{(1)} = 2.49$ ,  $P = 0.11$ ). Unlike casting date, however, GDD in the previous summer was not a significant predictor of antler cleaning date ( $\chi^2_{(1)} = 2.41$ ,  $P = 0.12$ ). Feb–Apr GDD was highly significant ( $b = -0.042 \pm 0.010$  SE,  $\chi^2_{(1)} = 11.56$ ,  $P < 0.001$ ) and remained so when antler casting date was accounted for in the model (casting date:  $b = 0.25 \pm 0.02$  SE,  $\chi^2_{(1)} = 112.6$ ,  $P < 0.001$ ; Feb–Apr GDD:  $b = -0.046 \pm 0.008$  SE,  $\chi^2_{(1)} = 18.5$ ,  $P < 0.001$ ). Increasing GDD in the 3-month period before antler casting and growth appear to account for the observed temporal trend in antler cleaning dates.

Rut start dates were best explained by GDD across the Jan–Sep period directly preceding the rut (Table 2). Inclusion of the Jan–Sep GDD term rendered the year effect nonsignificant and reduced the magnitude of the estimated temporal trend by 60% (year:  $b = -0.083 \pm 0.077$  SE,  $\chi^2_{(1)} = 1.13$ ,  $P = 0.29$ ; Jan–Sep GDD:  $b = -0.012 \pm 0.004$  SE,  $\chi^2_{(1)} = 8.36$ ,  $P < 0.01$ ). Models described in the previous section suggest that the temporal trend in rut start dates were accounted for by changes in antler cleaning dates (Table 1) and the same was true for effects of Jan–Sep GDD (Jan–Sep GDD:  $b = -0.007 \pm 0.006$  SE,  $\chi^2_{(1)} = 1.46$ ,  $P = 0.23$ ; cleaning date:  $b = 0.48 \pm 0.10$  SE,  $\chi^2_{(1)} = 24.04$ ,  $P < 0.001$ ).

Rut end dates were best predicted by Jul–Sep GDD conditions just before the rut, although there was minimal difference in model fit if Jan–Sep GDD was used ( $\Delta AIC = +0.1$ ; Table 2). Including Jul–Sep GDD in the model reduced the estimated temporal trend by 19% but both year ( $b = -0.35 \pm 0.08$  SE,  $\chi^2_{(1)} = 14.92$ ,  $P < 0.001$ ) and Jul–Sep GDD remained significant ( $b = -0.019 \pm 0.009$  SE,  $\chi^2_{(1)} = 4.43$ ,  $P < 0.05$ ). The inclusion of rut start date in the model rendered the effect of Jul–Sep GDD marginally nonsignificant ( $b = -0.015 \pm 0.008$  SE,  $\chi^2_{(1)} = 3.13$ ,  $P = 0.08$ ), but year remained highly significant ( $b = -0.32 \pm 0.07$  SE,  $\chi^2_{(1)} = 15.32$ ,  $P < 0.001$ ).

Overall, the final model of rut end dates in males was similar to that for parturition dates in females in that GDD during the 3 months preceding the rut explained a significant but small proportion of the temporal trends in both traits. This was in contrast to oestrus dates and other male phenology traits, for which the observed temporal trends could be accounted for by increases in



**Fig. 3** Female reproductive traits downstream of parturition dates have not changed over time on Rum. (a) Mean annual offspring birth weights with standard error bars; (b) annual proportion of offspring surviving their first winter of life with proportional standard deviation bars. In both plots, the nonsignificant regression slope over time is plotted as a dashed line.

GDD in the Feb–Apr period preceding the phenological event.

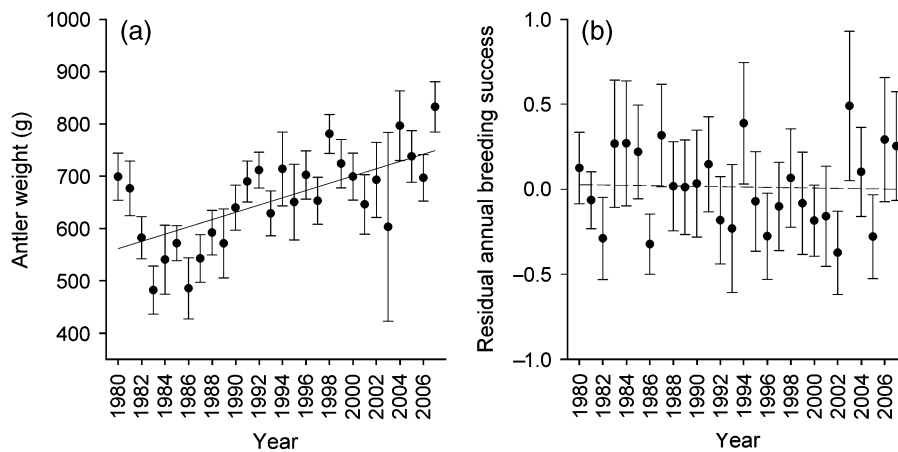
#### *Effects on other reproductive performance traits*

There was no evidence for temporal changes in average offspring birth weights or offspring over-winter survival probabilities (Fig. 3). Parturition date significantly predicted offspring birth weight: early calves are born, on average, significantly lighter ( $0.011 \text{ kg day}^{-1} \pm 0.002 \text{ SE}$ ,  $\chi^2_{(1)} = 22.52$ ,  $P < 0.001$ ; see also Coulson *et al.*, 2003). The observed advance in parturition dates would therefore lead us to expect a decrease in average offspring birth weights. However, in LMMs of offspring birth weight, either including or excluding parturition date, year was not significant (excluding parturition date:  $b = -0.006 \pm 0.007 \text{ SE}$ ,  $\chi^2_{(1)} = 0.01$ ,  $P = 0.94$ , including parturition date:  $b = 0.004 \pm 0.007 \text{ SE}$ ,  $\chi^2_{(1)} = 0.38$ ,  $P = 0.54$ ; Fig. 3a). Oestrus date, and interactions between oestrus and parturition dates, were not significant in models of offspring birth weight ( $\chi^2_{(1)} < 0.04$ ,  $P > 0.88$ ). However, offspring birth weights were significantly and positively predicted by Feb–Apr GDD just before birth ( $b = 0.003 \pm 0.001 \text{ SE}$ ,  $\chi^2_{(1)} = 7.55$ ,  $P < 0.01$ ), independent of effects of parturition date.

Both parturition date and offspring birth weight significantly predicted offspring first-winter survival probability: early- and heavy-born calves showed improved winter survival (parturition date:  $b = -0.027 \pm 0.006 \text{ SE}$ ,  $\chi^2_{(1)} = 22.88$ ,  $P < 0.001$ ; birth weight:  $b = 0.55 \pm 0.06 \text{ SE}$ ,  $\chi^2_{(1)} = 96.99$ ,  $P < 0.001$ ; see also Clutton-Brock *et al.*, 1987; Coulson *et al.*, 2003). There was no evidence for an interaction between parturition date and birth weight influencing calf sur-

vival, nor of any main effect or interactions involving oestrus dates (all tests:  $\chi^2_{(1)} < 0.5$ ,  $P > 0.50$ ). Despite the advances in parturition dates, there was no evidence of any temporal trend in offspring survival probability in models either including or excluding parturition dates (excluding parturition date: year effect:  $b = 0.013 \pm 0.021 \text{ SE}$ ,  $\chi^2_{(1)} = 0.43$ ,  $P = 0.51$ , including parturition date:  $b = 0.033 \pm 0.034 \text{ SE}$ ,  $\chi^2_{(1)} = 0.97$ ,  $P = 0.32$ ; Fig. 3b). Furthermore, neither GDD during the 3 months preceding conception (previous Jul–Sep GDD:  $\chi^2_{(1)} = 0.57$ ,  $P = 0.45$ ), nor during the 3 months preceding birth (Feb–Apr GDD:  $\chi^2_{(1)} = 0.00$ ,  $P = 0.98$ ) were significant predictors of offspring survival.

Among males, average antler weight increased significantly over time (Fig. 4a) while average ABS did not change once the increase in the proportion of calves assigned a paternity over time had been accounted for (Fig. 4b). Males that cast their previous set of antlers early in the spring grew heavier antlers over the subsequent summer (cast date effect:  $b = -2.34 \pm 0.53 \text{ SE}$ ,  $\chi^2_{(1)} = 18.3$ ,  $P < 0.001$ ), although we found no evidence for effects of antler growth period (cast  $\times$  clean date interaction:  $\chi^2_{(1)} = 0.23$ ,  $P = 0.63$ ) or independent effects of antler cleaning dates ( $\chi^2_{(1)} = 0.41$ ,  $P = 0.52$ ). Year was significant when fitted alone to models of antler weight ( $b = 3.90 \text{ grams per year} \pm 1.30 \text{ SE}$ ,  $\chi^2_{(1)} = 8.74$ ,  $P < 0.01$ ), and also when casting date was accounted for ( $b = 3.24 \pm 1.19 \text{ SE}$ ,  $\chi^2_{(1)} = 7.30$ ,  $P < 0.01$ ). There were no significant effects of either Feb–Apr or Jul–Sep GDD in the year of antler growth on antler weight ( $\chi^2_{(1)} < 1.30$ ,  $P > 0.30$ ). The effect of Jul–Sep GDD in the year before antler growth was marginally nonsignificant ( $b = 0.19 \pm 0.11 \text{ SE}$ ,  $\chi^2_{(1)} = 2.94$ ,  $P = 0.09$ ). Inclusion of this GDD term reduced the magnitude of the year



**Fig. 4** Male antler weight has increased over time on Rum, but average annual breeding success (ABS) has not. (a) Mean annual antler weight (from raw data) and (b) residual mean ABS (number of offspring sired by each rutting male having accounted for the proportion of calves born that were assigned a father), both plotted with standard error bars and linear regression slope.

effect by 19% ( $b = 2.48 \pm 1.23$  SE), although year remained narrowly significant in the model ( $\chi^2_{(1)} = 3.99$ ,  $P = 0.046$ ).

When accounting only for male's age, there was evidence for a significant temporal increase in ABS ( $b = 0.020 \pm 0.010$  SE,  $F_{(1,117)} = 4.04$ ,  $P = 0.047$ ). However, once the increase in the proportion of calves born in the study area assigned a paternity was accounted for ( $b = 1.58 \pm 0.60$  SE,  $F_{(1,33)} = 6.91$ ,  $P < 0.01$ ), the temporal trend became negligible and was no longer significant (Fig. 4b;  $b = -0.001 \pm 0.012$  SE,  $F_{(1,63)} = 0.00$ ,  $P = 0.95$ ). GDD measures were likewise nonsignificant (all:  $F < 0.80$ ,  $P > 0.49$ ). Early rut start dates were associated with increased average ABS ( $b = -0.017 \pm 0.004$  SE,  $F_{(1,1139)} = 14.97$ ,  $P < 0.001$ ), although main effects of rut end date or interactions between rut start and end dates were not significant in models of ABS (all tests:  $F < 0.80$ ,  $P > 0.35$ ).

Overall, in females there was no evidence for temporal changes in either offspring birth weights or offspring first-winter survival probabilities, despite highly significant relationships of both traits with parturition dates. In males, average antler mass increased over time, although average ABS did not show any temporal trend.

## Discussion

The breeding phenology of both female and male red deer in the North Block study area of Rum has advanced significantly over the last 28 years. Our findings provide rare evidence from a wild mammal population for phenological advances in response to recent changes in climate conditions. Both direct (i.e. thermoregulation) and indirect (i.e. plant growth and food availability) effects of temperature may have important influences

on herbivore phenology and demography (Albon & Clutton-Brock, 1988; Post & Stenseth, 1999; Myrsterud *et al.*, 2008b). The observed relationships between phenology and measures of GDD in our study population are broadly consistent with the idea that climate effects on phenology represent a condition-dependent response to an increase in food availability at key junctures in the annual breeding cycle (Myrsterud *et al.*, 2008b). Our results also reveal intriguing differences in the rate of advance in different phenological traits, and suggest that the average duration of the male rutting period is declining over time. Surprisingly, we found little evidence of improvements in other reproductive performance traits in females. There was evidence of an increase in antler size in males over time, which might be expected if there had been an increase in spring/summer resource availability and an improvement in average physiological condition of individuals across the antler growth period. Although changes in average male condition would not necessarily be expected to influence average male breeding success, there was evidence of differences in rates of phenological advance between males and females. A failure of males to track temporal changes in female timing of oestrus might be expected to result in a reduction in available mates and a drop in average male ABS. However, there was no evidence for such a decline in average male ABS.

## Seasonal effects of GDD on phenological traits

Our study population has experienced an increase in spring and summer GDD over the last three decades (Fig. 1), consistent with wider patterns of climate warming and plant growth season lengthening observed in temperate regions of the world (Menzel & Fabian, 1999;

IPCC, 2007). Advances in male phenological traits leading up to the autumn rut (antler casting and cleaning, rut start dates) were explained by changes in GDD over the preceding 9 months, most notably over the Feb–Apr period at the onset of the antler growth cycle. It is not surprising that changes in GDD over this period – which are likely to be associated with advanced and increased plant growth at the end of a food-limited winter period and the beginning of the antler shedding and regrowth cycle – would be associated with advances in highly condition-dependent phenological traits such as antler growth and the onset of harem holding behaviour in the rut. However, the additional, independent effect of GDD in the preceding summer (July–September) on antler casting dates suggests that some lagged effects of food availability before the rut preceding antler regrowth may also be important. The significant relationships between casting, cleaning and rut start dates presumably reflect the fact that they are all strongly condition-dependent traits governed by the same annual hormonal cycle (Clutton-Brock, 1982; Lincoln, 1992; Clements *et al.*, 2010). Antler weight is also expected to be highly condition-dependent and increases in average antler mass over time are likely to reflect improvements in the mean physiological state of male deer as plant growing seasons have lengthened and food availability has increased (Clements *et al.*, 2010).

Average oestrus dates in females advanced at a similar rate to male antler growth timing and rut start dates, and were also influenced by increasing GDD over the Feb–Apr period and, presumably, food availability. Average parturition dates appear to have advanced at a faster rate than oestrus dates. However, available data on oestrus timing is of considerably lower reliability and quantity compared with parturition timing data. Differences could potentially reflect a tendency for early first oestrus dates to be missed, a source of bias that could have increased as overall phenology has advanced in this population. There are also two potential biological explanations for the difference worth considering. Oestrus dates represent the first date on which a female deer was observed in oestrous, but females do not always conceive during oestrus and, on failing to do so, will typically cycle again around 18 days later (Guinness *et al.*, 1971). Thus, the advance in parturition dates not accounted for by changes in oestrus dates could potentially be due to either shortened gestation lengths or an increase in the frequency of conception at first oestrus. There is mounting evidence that gestation length may be more plastic than previously thought in cervids (e.g. Asher *et al.*, 2005; Asher, 2007; Myrsterud *et al.*, 2008a). Improved winter or spring conditions may lead to increased foetal growth rates and previous studies have suggested parturition dates are partly under off-

spring control and may be triggered upon attaining a 'target' size or weight (Asher, 2007). In this case, early attainment of a certain foetal mass may trigger early parturition through shortened gestation, with potentially no change in offspring size at birth as observed here. However, as male rutting phenology has advanced and rutting activity in late September or early October has potentially intensified, it is also entirely plausible that the probability of females conceiving at their first oestrus cycle has increased over time. In both cases, climatic factors other than GDD may also be playing an important role. The severity of winter conditions may play an important role in foetal growth and gestation lengths, and rutting activity is known to be disrupted by storms and high winds, potentially leading to oestrus females not being mating and having to recycle (Clutton-Brock *et al.*, 1982). Both the discrepancy between rates of phenological advance between oestrus and parturition dates and the fact that GDD explains only a relatively small proportion of the temporal trend in these traits (see results; Table 1) emphasize the need for further research to investigate how other climatic factors influence female breeding phenology in this population.

Although an early start predicted an early end to the rut, observed advances in end dates were not explained by changes in rut start dates and were much closer in magnitude to those observed for parturition dates than for other male phenology traits (Fig. 2). Rut end dates were predicted by Jul–Sep GDD preceding the rut, rather than Feb–Apr GDD which predicted antler growth timing and rut start dates. The obvious explanation for similarities observed between advances in rut end dates and parturition dates is simply that stags are curtailing their rutting behaviour in direct response to the end of the peak in female oestrus. This is because, once most females have been through oestrus and conceived, there is little fitness benefit in prime-condition males continuing to expend energetic resources defending harems of females. Interestingly, this explanation for the similarity in the rates of advance and climatic drivers between rut end dates and parturition dates supports the idea that females have become increasingly likely to conceive during their first oestrus over time. If the difference between rates of advance in parturition dates and oestrus dates were due to shortened gestation lengths, males would not be able to track these temporal changes as they would not be reflected by changes in patterns of oestrus.

#### *Reproductive consequences of advancing breeding phenology*

Despite observing significant associations between parturition date and both offspring birth weight and off-

spring first-winter survival, we did not observe the temporal changes in either of these two female reproductive traits. As previously documented, we found that early parturition dates predict light-born calves on Rum (Clutton-Brock *et al.*, 1982; Coulson *et al.*, 2003). Advancing parturition dates would therefore predict a decline in average offspring birth weights over time, although no such temporal trend was evident (Fig. 3a). Previous studies have shown that cohort average birth weights increase with spring temperatures on Rum: warmer conditions advance and enhance the spring flush and provide more food for females during late pregnancy, when the foetus is growing rapidly (Albon *et al.*, 1987; Albon & Clutton-Brock, 1988). We also found that GDD towards the end of pregnancy (Feb–Apr) was significantly and positively related to birth weights, independent of any effect of parturition date. The explanation for the lack of change in offspring birth weights therefore may lie in the antagonistic effects of changing parturition dates (Fig. 2a) – which should decrease birth weights – and improving spring climate and food availability (Fig. 1) – which should increase birth weights – apparently cancelling one another out.

In common with previous studies, we found that, independent of positive associations between offspring survival and offspring birth weights, earlier parturition improved offspring first-winter survival (Guinness *et al.*, 1978; Clutton-Brock *et al.*, 1987; Festa-Bianchet, 1988; Coulson *et al.*, 2003). One explanation for such associations is that late born offspring and their mothers experience declines in forage quality and food availability at an earlier stage in the lactation period, and this may reduce offspring growth and condition and increase risk of first-winter mortality (Festa-Bianchet, 1988). In our study population, while late born offspring do suffer increased mortality, survival probabilities have not increased despite advancing birth dates. Further analyses refute the idea that this lack of change in survival is because only very late born calves suffer survival costs and the proportion of these late-born calves has not changed. We found evidence that the strongest declines in offspring survival occurred among calves born in July or later (8% of births, Figure S1), but the proportion of offspring born on or after 1 July has declined significantly over the study period (GLM with binomial errors:  $b = -0.043 \pm 0.010$  SE,  $\chi^2_{(1)} = 19.51$ ,  $P < 0.001$ ). One explanation for the lack of change in calf survival is that the relationship between birth date and survival has changed over time: previous analyses have suggested that annual selection on birth date is complex and variable (Coulson *et al.*, 2003). The lack of a temporal trend in offspring survival also suggests that despite increased resource availability in spring or summer for lactating females, levels of maternal invest-

ment in offspring may have remained the same over time. It is important to bear in mind that, apart from very occasional predation of calves by golden eagles, the red deer on Rum are not predated. In many wild ungulates predation pressure is likely to represent a potent selective force on the timing of breeding, and the demographic consequences of changes in breeding phenology may differ markedly between predated and unpredated populations.

Among male deer, we found that the average mass of antlers had increased over the course of our study period (Fig. 4a). Sexually selected traits such as antlers are expected to be highly condition-dependent (Clutton-Brock, 1988; Andersson, 1994), and increases in food availability associated with local climate warming are expected to increase resources available to males for investment in antler growth. Interestingly, the increase in antler mass was not accounted for by changes in antler growth phenology or GDD measures and, while heavier antlers were predicted by earlier casting dates, the advance in the timing of the antler growth period did not explain much of the temporal trend in antler mass. Since antler mass is so strongly age-dependent, one possible explanation for the change is a shift in age structure over time in the population. Follow-up analyses did reveal that the average age of males in our study period did increase over time ( $b = 0.018 \pm 0.007$  SE,  $F_{(1,26)} = 6.71$ ,  $P = 0.016$ ). However, inclusion of the average age of the rutting population in models of antler mass did not alter the significance or magnitude of the estimated temporal increase in antler mass ( $b = 3.22 \pm 1.27$  SE,  $\chi^2_{(1)} = 6.32$ ,  $P = 0.012$ ) and the average age term itself was not a significant predictor of antler mass ( $\chi^2_{(1)} = 0.01$ ,  $P = 0.93$ ). This suggests the observed change is independent of population age structure. The mechanism responsible for the temporal change in average antler mass remains unclear, but it is certainly consistent with a condition-dependent responses to lengthening plant growth periods and warming temperatures.

There was evidence for differences in the rates of phenological advance between the sexes (Fig. 2) and, if changes in the timing of male rutting activity were failing to adequately track changes in the timing of female oestrus, we might expect this to potentially result in a reduction in available mates and a drop in average male ABS. However, once changes in the extent of paternity assignment were accounted for, there was no evidence of any change in male ABS over time (Fig. 4b). In fact, the consequences of advanced phenology and increased average condition and antler size for mating success and rut dynamics are likely to be rather more subtle and complex than the simplistic prediction described above suggests. An increase in the average

physiological state of male deer at the start of the autumn rut period could result in an increase in the intensity of intrasexual competition for control of harems and access to females. Although not reflected in any change in the average male ABS, shifts in levels of competition for mates in the rut might be better reflected in measures of annual variance or skew in male reproductive success (Clutton-Brock *et al.*, 1997). Effects of climate warming on levels of competition and the dynamics of the rut will crucially depend on how males in different states and age classes invest extra resources into competitive behaviours, and how climate changes impact on the number of females that came into oestrus and the synchrony of their oestrus cycles. Further research directed at understanding how changes in resource availability over spring and summer impacts on male behaviour during the rut and patterns of female oestrus is required to determine whether and how climate warming is actually affecting the rut dynamics and sexual selection in this population.

### Conclusions

Our results provide rare evidence linking phenological advances in a wild mammal to local climate warming. The overwhelming majority of evidence linking breeding phenology and climate change in vertebrates comes from long-term studies of birds. This study of wild red deer serves to highlight the importance of understanding the causes and consequences of changes in phenology in both sexes in polygynous mammals. Birds are typically socially monogamous and in temperate regions mate, lay eggs and raise young in quick succession in the spring and summer. In long-lived mammals, such as ungulates, the over-winter gestation period separates the mating season and the birth season. As a result, the selective and environmental pressures influencing male and female phenology are expected to differ markedly. Our findings suggest male and female phenological traits may be influenced by plant growth conditions in different seasons, perhaps reflecting differences in the period in which physiological constraints limit the onset of the breeding cycle between the sexes. Rut end dates have advanced more than twice as fast as rut start dates, and the average duration across which males hold harems of female is shortening (Fig. 2c). Importantly, we found no evidence at all to suggest that the observed changes in phenology were influencing average reproductive performance in either sex. This should encourage caution in interpreting the demographic consequences of phenological data in any system when longitudinal data on reproductive traits is not available, and highlight the potential complexity of

the relationship between climate, phenology and demography in wild vertebrates.

### Acknowledgements

We are grateful to Steve Albon, Craig Walling, Katie Stopher, Ana Bento and Mick Crawley for discussion and comments on earlier drafts of the manuscript, and Martyn Baker and many other fieldworkers on Rum. This work was supported by a National Environment Research Council (NERC) grant to TCB and LEBK, by an NERC postdoctoral fellowship awarded to DHN, and by a Royal Society university research fellowship awarded to LEBK. We also express our thanks to Scottish Natural Heritage and the Isle of Rum community for their continued support for our work on the Isle of Rum.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** The relationship between parturition date and offspring first-winter survival is non-linear. Raw data for survival and birth date are plotted along with the predicted relationship between the two variables (unbroken lines) and its standard errors (broken lines) from a generalized additive model of offspring survival fitted with binomial errors and including offspring sex and maternal status as factors and offspring birth weight as a linear covariate. The predicted curve is estimated for female calves of milk hinds with average birth weight.

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