

## Seminar Module 4

### Animal-Climate Interactions

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#### Goals For Student Learning

This seminar module was created to help students:

- Understand how researchers study phenological responses of birds and mammals to climate change
- Understand how phenological schedules in animal populations and communities are influenced by climate and may be affected by ongoing or predicted climate change

#### Animal-Climate Interactions

Many (but not all) plant species exhibit strong phenotypically plastic responses to climate change. The magnitude and direction of phenological responses in animals, however, can be quite variable and have been documented to a much lesser extent than those of plants. This seminar module provides an introduction to research on mammalian and avian phenological responses to climate change, and ensuing **demographic** outcomes.

Several recently published studies rely on long-term phenological monitoring efforts to detect the effects of climate change on animal populations. For example, in Møller et al.'s (2008) evaluation of 100 European bird species, the scientists take advantage of the fact that spring migration times and demographic trends of their focal species have been closely monitored for over 50 years.

A recently published article by Moyes et al. (2011) shows that advances in the key breeding phenophases of male and female red deer in Scotland are strongly correlated with increases in the number of **growing degree-days**, a measure of climate often used as a proxy for the duration of conditions that promote plant growth. Another recent study on yellow-bellied marmots in the Colorado Rockies highlights the relationship between phenological shifts and demographic parameters. Ozgul et al. (2011) describe how early emergence from hibernation and early weaning have prompted larger average body sizes and have led to a sharp increase in the marmot population over the past 32 years. While this population boom may be beneficial in the short term, the authors note that marmots are adapted to colder climates, and that prolonged warm summers may ultimately decrease growth rates in juveniles.

#### Articles To Read

Møller, A. P., D. Rubolini, and E. Lehikoinen. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proceedings of the National Academy of Sciences of the United States of America* 105:16195-16200.

Moyes, K., D. H. Nussey, M. N. Clements, F. E. Guinness, A. Morris, S. Morris, J. M. Pemberton, L. E. B. Kruuk, and T. H. Clutton-Brock. 2011. Advancing breeding phenology in response to environmental change in a wild red deer population. *Global Change Biology* 17:2455-2469.

Ozgul, A., D. Z. Childs, M. K. Oli, K. B. Armitage, D. T. Blumstein, L. E. Olson, S. Tuljapurkar, and T. Coulson. 2010. Coupled dynamics of body mass and population growth in response to environmental change. *Nature* 466:482-485.

### Suggested Discussion Questions

1. How, in general, are the bird and mammal populations observed in these studies responding to recent climate change?
2. Møller et al. (2008) concluded that bird species whose phenological schedule did not track recent climate change were in decline. But what are some other potential factors that could have influenced how species respond phenologically to climate change? How did the investigators take those other factors into account in these studies?
3. Table 1 in Møller et al. (2008) presents the results of three multiple regression analyses, each of which focused on a different response variable. The three different response variables that the researchers analyzed were:
  - Avian population trend from 1970-1990
  - Avian population trend between 1990-2000
  - Avian population trend between 1960-2006

According to Møller et al.'s (2008) analyses, which causative variables (e.g., migration distance, body mass, etc.) best explain variation in each of the response variables listed above?

4. What are the major red deer phenophases that were recorded by Moyes et al. (2011)? How did male phenophases respond to the increase in growing degree-days (GDD) in comparison to female phenophases? Did the effects observed depend on GDD during a certain time of the year?
5. How did the researchers measure male breeding success? How (if at all) did breeding success change over the 28 years of the study?
6. Moyes et al. (2011) found that offspring weights and offspring survival rates have not changed over time. What does this suggest about how the advancement of certain phenophases might influence population demography in the future?

7. What demographic parameters did Ozgul et al. (2011) record? How have these parameters changed over time? What marmot phenophases did the researchers observe? How have they changed over time?
8. How have changes in individual body mass mediated demographic change in the marmot population?
9. After the Ozgul et al. (2011) study was published, popular news stories with headlines such as “Fat Marmot Population Explodes” and “Is Climate Change Leading to Super-Marmots?” were quite prevalent. Do you think that climate change might lead to a huge super-marmot population in the long-term? What evidence from the peer-reviewed primary source supports your view?

## Glossary

- **Demography:** the study of how populations change in size, composition, and distribution over time and in response to biological processes such as birth, death, immigration, and emigration.
- **Growing degree days (GDD):** a measure of heat accumulation that phenologists, farmers, and other scientists use to evaluate and predict plant growth

$$GDD = \frac{T_{max} - T_{min}}{2} - T_{base}$$

- Where:  $T_{max}$  = the maximum daily temperature,  $T_{min}$  is the minimum daily temperature, and  $T_{base}$  = base temperature for the plant
- **Parturition:** the act or the process of giving birth
- **Oestrus (estrus):** The periodic readiness to mate that occurs in most female mammals. It immediately precedes ovulation.
- **Weaning:** the process of introducing mammalian offspring to its adult food source and gradually reducing its consumption of its mother’s milk

# Populations of migratory bird species that did not show a phenological response to climate change are declining

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Recent rapid climatic changes are associated with dramatic changes in phenology of plants and animals, with optimal timing of reproduction advancing considerably in the northern hemisphere. However, some species may not have advanced their timing of breeding sufficiently to continue reproducing optimally relative to the occurrence of peak food availability, thus becoming mismatched compared with their food sources. The degree of mismatch may differ among species, and species with greater mismatch may be characterized by declining populations. Here we relate changes in spring migration timing by 100 European bird species since 1960, considered as an index of the phenological response of bird species to recent climate change, to their population trends. Species that declined in the period 1990–2000 did not advance their spring migration, whereas those with stable or increasing populations advanced their migration considerably. On the other hand, population trends during 1970–1990 were predicted by breeding habitat type, northernmost breeding latitude, and winter range (with species of agricultural habitat, breeding at northern latitudes, and wintering in Africa showing an unfavorable conservation status), but not by change in migration timing. The association between population trend in 1990–2000 and change in migration phenology was not confounded by any of the previously identified predictors of population trends in birds, or by similarity in phenotype among taxa due to common descent. Our findings imply that ecological factors affecting population trends can change over time and suggest that ongoing climatic changes will increasingly threaten vulnerable migratory bird species, augmenting their extinction risk.

conservation | extinction risk | migration phenology | population trends

Climate change during the second half of the twentieth century has resulted in a mean increase in global temperatures by 0.6°C, with particularly large changes during spring in temperate and Arctic regions of the world (1). Plants and animals have responded to this change by markedly advancing their annual cycles, including timing of reproduction (2–4).

While the phenology of plants and insects has advanced with increases in spring temperature (2–4), many consumers of plants and insects and higher-level predators have responded to a lesser extent or not at all, thus causing a mistiming in reproduction relative to peak availability of food (5, 6). The consequences of such mistiming in reproduction are reduced reproductive output, with diminished recruitment rate and ultimately a decline in population size (7), which possibly can affect the risk of extinction.

Previous studies of migratory birds have shown rapid advances in timing of spring migration during the last 4 decades, associated with advancement of spring and warming of spring weather (8). Considerable heterogeneity in advancement in timing of spring migration among species (8, 9) may be due in part to spatial heterogeneity in climate change across Europe, with spring temperatures increasing in some regions but not in others (10).

However, despite such heterogeneity, spring phenological responses to climate change are species-specific and consistent in different populations, making an investigation of predictors of species-specific variation in change in migration timing, considered as an indicator of the phenological response to climate change, meaningful (9).

The ability of many species to respond to climate change has been a major concern, because species unable to advance their annual cycle will suffer from increased mistiming of reproduction, with potential consequences for the risk of extinction (11). To date, however, there have been no attempts to assess how a phenological response to climate change relates to bird population trends, although previous studies have identified farmland breeding habitat, migration distance, body mass, northernmost distribution limit, ecological specialization, number of broods, thermal maximum (i.e., temperature at the hot edge of the species-specific climate envelope), natal dispersal, and relative brain size as significant predictors of interspecific differences in breeding population trends (12–19).

In this comparative study, we related changes in mean/median (“mean” hereinafter) timing of spring migration of 100 European migratory bird species since 1960, which was considered a cue as to the ability of a given species to show a phenological response to recent climate warming, to their population trends during two separate periods, 1970–1990 and 1990–2000 (20). We predicted that migratory bird species that did not anticipate timing of spring migration (i.e., that did not show a phenological response to climate change) should demonstrate declining populations, while taking into account several variables previously shown to be associated with population trends (see above and 12–19) or response to climate change. Among variables potentially affecting the phenological response to climate change, we considered migration distance, intensity of sexual selection, and total population size; a small population size, and thus lack of genetic variation, potentially could explain lack of response to climate change (8, 9, 21, 22). All analyses were performed while accounting for phylogenetic relatedness among species by using phylogenetically independent linear contrasts (23).

Population trends of European birds were obtained from a qualitative assessment conducted by BirdLife International, expressed on a seven-point scale ranging from a large population decline to a large population increase (20). We deliberately avoided using change in first arrival dates as a cue to phenology.

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**Table 1. Minimal adequate multiple regression models of population trend of migratory birds during 1970–1990, population trend of migratory birds during 1990–2000, and change in mean spring migration date of migratory birds 1960–2006, obtained by step-down removal of nonsignificant predictors (see *Methods*)**

Variables	F	df	P	Estimate (SE)
Population trend during 1970–1990				
Species-specific values				
Body mass	21.13	1,95	<0.001	0.724 (0.157)
Farmland habitat	5.19	1,95	0.025	−0.886 (0.389)
Independent contrasts				
Body mass	8.36	1,92	0.005	1.263 (0.437)
Farmland habitat	8.80	1,92	0.004	−1.164 (0.393)
Northernmost breeding latitude	5.54	1,92	0.021	−0.081 (0.035)
Population trend during 1990–2000				
Species-specific values				
Change in migration date	27.19	1,96	<0.001	−2.801 (0.537)
Independent contrasts				
Change in migration date	31.48	1,94	<0.001	−2.656 (0.473)
Change in migration date, 1960–2006				
Species-specific values				
Population trends 1990–2000	21.84	1,92	<0.001	−0.069 (0.015)
Migration distance	7.70	1,92	0.007	0.111 (0.040)
Number of broods	5.21	1,92	0.025	−0.052 (0.023)
Independent contrasts				
Population trends 1990–2000	23.33	1,90	<0.001	−0.079 (0.016)
Migration distance	5.00	1,90	0.028	0.110 (0.049)
Number of broods	5.69	1,90	0.019	−0.072 (0.030)

Statistics for excluded terms are reported in [Table S1](#).

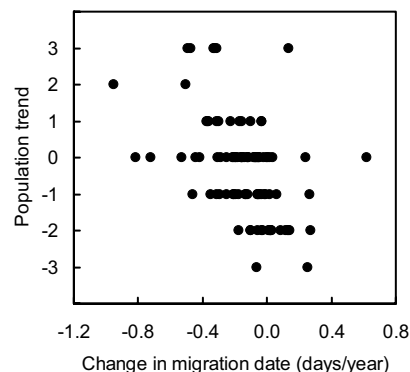
ical response to climate change, because this phenological datum is strongly dependent on sampling effort and may be affected by changes in population size (8, 9).

## Results

The analysis of population trends during 1970–1990 based on species-specific values identified body mass and farmland breeding habitat as main predictors of population trends, whereas the effects of other variables were not significant [Table 1 and [supporting information \(SI\) Table S1](#)]. Specifically, population trends of large species and those not breeding in agricultural habitats were more favorable than those of small species breeding mainly in farmland (Table 1). The additional effects of habitat specialization [−0.321 (standard error [SE], 0.468),  $F_{1,34} = 0.47$ ,  $P = 0.50$ ] and thermal maximum [−0.178 (0.189),  $F_{1,34} = 0.89$ ,  $P = 0.35$ ] were not significant, neither were those of relative brain size [1.069 (1.377 SE),  $F_{1,60} = 0.60$ ,  $P = 0.44$ ] and natal dispersal [0.162 (0.383 SE),  $F_{1,41} = 0.18$ ,  $P = 0.67$ ]. The inclusion in the initial model of a categorical predictor identifying species wintering in Africa versus other species (instead of migration distance; see *Materials and Methods*) further showed that species wintering in Africa declined more in this period compared with other species [−0.621 (0.275 SE),  $F_{1,94} = 5.11$ ,  $P = 0.026$ ; [Table S2](#)]. The analyses based on phylogenetically independent contrasts, besides confirming the significant effects of body mass and breeding habitat, revealed that species extending their breeding ranges to more northern latitudes showed the largest population declines (Table 1). The effects of habitat specialization [0.145 (0.090 SE),  $F_{1,33} = 2.56$ ,  $P = 0.12$ ] and thermal maximum [−0.023 (0.041 SE),  $F_{1,33} = 0.31$ ,  $P = 0.58$ ] were not significant, neither were those of relative brain size [0.308 (0.349 SE),  $F_{1,57} = 0.78$ ,  $P = 0.38$ ] and natal dispersal [−0.019 (0.086 SE),  $F_{1,38} = 0.05$ ,  $P = 0.82$ ]. Inclusion of a variable reflecting wintering in Africa in the initial model instead of migration distance confirmed that species wintering in Africa

suffered larger declines compared with other species [−0.781 (0.339 SE),  $F_{1,91} = 5.29$ ,  $P = 0.024$ ; [Table S2](#)].

In contrast, change in migration date was the only predictor of population trends during 1990–2000 (Table 1, Fig. 1). This analysis also revealed an additional effect of habitat specialization, with habitat specialists declining more than habitat generalists [effect of habitat specialization, −0.889 (0.341 SE),  $F_{1,35} = 6.80$ ,  $P = 0.013$ ]. However, the inclusion of habitat specialization did not affect the relationship between population trend and change in migration date [−2.425 (0.504 SE),  $F_{1,35} = 23.12$ ,  $P < 0.001$ ]. Thermal maximum [0.261 (0.150 SE),  $F_{1,35} = 3.05$ ,  $P = 0.09$ ], relative brain size [2.344 (1.387 SE),  $F_{1,61} = 2.86$ ,  $P = 0.10$ ],



**Fig. 1.** Recent population trends of European migratory bird species (1990–2000) (negative values: decline; positive values: increase; see *Materials and Methods* and ref. 20) in relation to change in mean spring migration date (days/year) in the period 1960–2006 (9). Change in mean spring migration date for each species was estimated as least square means after accounting for among-sites variance, geographical coordinates and initial year of time series in mixed models (see *Materials and Methods* and ref. 9).



and natal dispersal [0.593 (0.366 SE),  $F_{1,41} = 2.64$ ,  $P = 0.11$ ] did not significantly predict population trends. The analyses based on contrasts confirmed the significant relationship between population trend and change in migration date (Table 1) but showed no additional effects of habitat specialization [0.003 (0.093 SE),  $F_{1,31} = 0.00$ ,  $P = 0.98$ ], thermal maximum [0.025 (0.038 SE),  $F_{1,31} = 0.46$ ,  $P = 0.50$ ], relative brain size [0.390 (0.321 SE),  $F_{1,56} = 1.48$ ,  $P = 0.23$ ], and natal dispersal [−0.028 (0.081 SE),  $F_{1,40} = 0.12$ ,  $P = 0.73$ ] did not significantly predict population trends. Inclusion of a variable reflecting wintering in Africa instead of migration distance in initial models did not affect the conclusions for both species-specific and contrast-based analyses (Table S2).

We tested whether the relationship between population trends and the significant predictors of population trends identified by the regression models (see above and Table 1) differed between the two time periods (1970–1990 vs. 1990–2000) by using a mixed model analysis in which population trend was the dependent variable and time period was considered a fixed-effect factor, with change in migration date, farmland breeding habitat, wintering in Africa, northernmost breeding latitude and body mass as covariates. Species identity was considered a random-effect factor, to account for replication of species-specific values between periods. The model was subjected to sequential removal of nonsignificant predictors (see *Materials and Methods*). The interaction term between period and change in migration date was statistically significant ( $F_{1,93,8} = 10.29$ ,  $P = 0.002$ ), implying that the slope of the relationship between population trend and change in migration date differed between the two periods [1970–1990, estimate = −0.558 (0.610 SE),  $t = -0.91$ ,  $P = 0.36$ ; 1990–2000, estimate = −2.772 (0.607 SE),  $t = -4.57$ ,  $P < 0.001$ ]. Similarly, the effect of wintering in Africa on population trends differed between periods [ $F_{1,94,5} = 7.96$ ,  $P = 0.006$ ; 1970–1990, estimate = −0.637 (0.294 SE),  $t = -2.16$ ,  $P = 0.032$ ; 1990–2000, estimate = 0.270 (0.294 SE),  $t = 0.92$ ,  $P = 0.36$ ]. In contrast, the effects of northernmost breeding latitude, farmland breeding habitat, and body mass on population trends did not differ between periods (time period × northernmost breeding latitude,  $F_{1,92,1} = 0.99$ ,  $P = 0.32$ ; time period × farmland habitat,  $F_{1,91,4} = 1.01$ ,  $P = 0.32$ ; time period × body mass,  $F_{1,94,3} = 3.66$ ,  $P = 0.06$ ). The overall effect of northernmost breeding latitude was not significant ( $F_{1,92,5} = 2.79$ ,  $P = 0.10$ ), similar to the analysis of species-specific values reported in Table 1. Moreover, population trends showed a significant decline between 1970–1990 and 1990–2000, suggesting deterioration of the conservation status of European migratory bird species over the past 30 years (least squares means (SE), 1970–1990: 0.15 (0.12); 1990–2000: −0.32 (0.12);  $F_{1,94,9} = 10.99$ ,  $P < 0.001$ ), and the overall effect of farmland habitat on population trends was weakly, but not significantly, negative [−0.597 (0.310 SE),  $F_{1,92,7} = 3.70$ ,  $P = 0.057$ ].

A potential confounding factor of the relationship between population trends during 1990–2000 and change in migration date is that some species included in the present study had resident populations that contributed to the overall population trend (20, 24) but did not contribute to a change in migration phenology. Consequently, we created a binary variable, migration status, with strictly migratory species (i.e., long-distance migrants migrating more than 24° latitude) coded as 1 and all other species, including those with resident populations in Europe, coded as 0. We then tested the effect of the interaction between migration status and change in migration date on population trend. The effects of the interaction [0.915 (1.423 SE),  $F_{1,94} = 0.41$ ,  $P = 0.52$ ] and migration status [0.043 (0.292 SE),  $F_{1,94} = 0.02$ ,  $P = 0.88$ ] were not significant, whereas the effect of change in migration date on the 1990–2000 population trend remained significant [−3.015 (0.701 SE),  $F_{1,94} = 12.90$ ,  $P < 0.001$ ]. Therefore, our conclusions were not confounded by

including in the analyses species that had both resident and migratory populations in Europe.

The analysis of factors affecting long-term phenological trends, besides confirming the relationship between population trends during 1990–2000 and phenological response to climate change, revealed that change in migration date was predicted by migration distance, with short-distance migrants advancing the most, and by number of broods, with species laying more broods advancing migration date the most (Table 1) (see also 9). The results for contrast-based analyses were similar (Table 1). The additional effects of ecological specialization, thermal maximum, relative brain size, and natal dispersal were not significant in analyses based on both species-specific values or contrasts (all  $P$  values  $> 0.11$  and  $> 0.20$ , respectively; details not shown). Including wintering in Africa instead of migration distance in initial models did not qualitatively affect any conclusion (Table S2).

## Discussion

Our study clearly showed that European migratory bird species with declining breeding populations in Europe in the last decades (1990–2000) responded the least to recent climate change as reflected by the temporal trend in spring migration phenology, or even delayed their timing of spring migration, whereas species with stable or increasing populations advanced migration. This conclusion was independent of potentially confounding variables previously found to predict population trends in a range of extensive studies of this scientific problem and was not confounded by phylogenetic relatedness among species. Interestingly, change in migration date did not predict population trends of migrants in an earlier period (1970–1990), implying that the relevance of climate-mediated phenological changes on population trends could have increased in recent years.

Obviously, future studies may identify other potentially confounding variables, although we consider this possibility unlikely given the extent of research on population trends of birds dating back more than 2 decades and the number of potentially confounding variables that we have taken into account in our analyses. We can exclude the alternative hypothesis that species were simply less easy to detect when their populations declined, because neither body mass nor population size predicted change in migration date (Table S1), although body mass positively predicted population trends during 1970–1990 (see also below). Likewise, we can exclude the hypothesis that it is advantageous to arrive earlier when populations are increasing and less advantageous when they are declining, due to differences in level of competition and hence degree of protandry (25, 26). In fact, sexual dichromatism has been shown to predict protandry (27), but sexual dichromatism did not predict change in migration date or population trend (Table S1). The ability to adjust migration date to changing climatic conditions also may depend on the concomitant variation in winter habitat quality, because of carryover effects (28, 29). If certain winter habitats degraded more than others during the twentieth century [e.g., farmland habitats in Europe, African forests, and open dry savannahs in the Sahel (30, 31)], then variation in the ability to advance migration date among species wintering in different habitats might be expected. Similarly, the breeding population of migrants can be regulated by ecological conditions in winter quarters, and thus population trends may vary according to winter habitat, provided that ecological conditions have changed differentially according to habitat type (31, 32). However, change in migration date or population trends during both periods did not vary in relation to the main wintering habitat (see Table S3) for species wintering or not wintering in Africa (analysis of variance on species-specific values: species not wintering in Africa, all  $P > 0.10$ ; species wintering in Africa, all  $P > 0.18$ ). This also could be the case because, for example,

habitat changes may negatively impact certain species but not others wintering in the same habitat (31). In any case, this result implies that the relationship between population trends during 1990–2000 and change in migration date was not confounded by variation in wintering habitat among species.

Other interesting findings emerge from this study. First, species breeding in farmland habitats declined more than other species during 1970–1990 but not during 1990–2000. This pattern could have been expected, because the effects of agricultural intensification on farmland breeding birds were more severe in the earlier period compared with the subsequent period (12, 20, 33). Alternatively, agricultural intensification during the second half of the twentieth century depleted populations of farmland species to an extent that any additional change in agricultural practices had no further impact on population trends of migrants. Unfortunately, the lack of a differential effect of farmland habitats on population trends between periods, as revealed by the mixed model analysis, complicates the interpretation of this finding.

Second, species wintering in Africa declined more during 1970–1990 compared with 1990–2000. The differential effect of wintering in Africa on population trends during the two periods, a finding confirmed by the mixed model analysis, could be related to the occurrence of prolonged droughts in sub-Saharan Africa during the 1970s, which strongly and negatively affected the breeding populations of several trans-Saharan migrants (31).

Third, species with more northern distributions exhibited larger population declines than those with a more southern distribution during 1970–1990, after controlling for phylogenetic effects. This result is consistent with previous findings (16), and it can be reconciled with the observed stronger effects of climate change on biological diversity at northern latitudes in the boreal region (1, 2). Thus, northern breeding migratory bird species could be more sensitive to climate warming, because of altered environmental conditions and community composition resulting from changes in climate [e.g., suffering increased competition from resident breeding species (34)]. The multiple regression analyses also showed that population trends of larger species were more favorable than those of smaller species during 1970–1990, although we consider this finding to be either a sampling artifact (a few large, unrelated species that increased considerably during 1970–1990 were driving this relationship, see Table S3) or a consequence of the easier detectability of larger species during population increases. This latter explanation is unlikely, however; if it was true, then a similar trend should have been detected in the subsequent period as well.

Overall, our findings indicate that factors affecting population declines of European bird species varied temporally in the second half of the twentieth century. Specifically, farmland breeding habitat, wintering in Africa, and northern breeding latitudes were associated with population declines during 1970–1990, whereas climate-driven change in spring migration phenology was the only significant predictor of population trends in more recent decades. Therefore, an important message of this study is that factors affecting population trends and extinction risk of birds appear to be dynamic over time, and this fact should be taken into account in evaluations of conservation priorities for declining species.

Finally, our analyses also identified ecological and life-history correlates of phenological response of migratory birds to climate change. While controlling for the effect of population trend during 1990–2000, which strongly predicted change in migration timing, we found that long-distance migrants advanced spring migration date the least, and that species laying a greater number of clutches showed a stronger advance in timing of spring migration. A stronger advance in timing of spring migration in short-distance versus long-distance migrants is in accordance with most previous studies [e.g., (8, 9), but see (35)]. This pattern

is indeed to be expected, because short-distance migrants spend the winter closer to the breeding areas compared with long-distance migrants, which may allow such species to better tune the timing of spring migration to concomitant weather conditions (8, 9), and the timing of migration of short-distance migrants may have a stronger environmental component compared with long-distance migrants (8, 36). On the other hand, a greater advance of timing of spring migration in species raising a greater number of broods could occur because spring climate warming (leading to a progressively longer breeding season) may have relaxed constraints affecting interclutch intervals in multi-brooded species. Such a relaxation could have resulted in greater plasticity in migration schedules, and thus in increased ability to adjust the timing of spring migration to climate change in multibrooded versus single-brooded species. Interestingly, warming of spring between 1971 and 2005 resulted in increased interval between clutches in a migratory songbird (37).

The underlying mechanisms responsible for long-term changes in timing of migration remain unknown, although phenotypic plasticity, gene flow, and microevolutionary response constitute the three possibilities (38). Total population size, which may reflect the amount of genetic variation (22), did not explain the relationship between phenological response in mean timing of spring migration and population trends, suggesting that reduced genetic variability did not affect population declines and did not explain lack of changes in migration timing. A possibility is that poor environmental conditions that particularly affect threatened species translate into poor body condition, resulting in reduced maternal effects that may represent important determinants of the phenotype of the next generation. Early maternal effects may have long-lasting consequences for the ability to respond phenotypically to changing environmental conditions (39–41). We hypothesize that such an unavoidable maternal legacy may affect the ability to adjust the timing of spring migration to climate change.

Our findings have important implications for future evaluations of conservation status and for attempts to manage populations of declining species. If migratory bird species do not advance their timing of migration, they may arrive later relative to the phenologically optimal timing of reproduction, because the phenology of primary producers and prey species can advance more rapidly. Mistiming of reproduction results in reduced reproductive output (7), with the reduction in output assumed to increase with increasing degree of mistiming. Therefore, we predict that, under current climate change scenarios, species with a threatened population status and declining breeding populations will suffer further losses. Our findings highlight the importance of investigating heterogeneity among species in response to climate change, while also allowing the identification of a suite of species that is likely to become particularly threatened during the next decades.

## Materials and Methods

**Change in Migration Dates.** We collected 289 estimates of change in mean/median spring migration dates of migratory birds with a minimum duration of 15 years from Europe (west of the Ural Mountains) during 1960–2006, mainly from bird observatories with multiple populations passing during migration (8, 9, 42, 43). Most of these observatories are located in central Europe and southern Fennoscandia, and intercept populations of migratory birds on the way to their breeding grounds (9). This fact prevented us from quantifying change in migration phenology in relation to local climate, because climate during any part of the migratory path could potentially affect change in phenology (44, 45). Therefore, we analyzed change in phenology over time, assuming that such change was due to change in climate, as has been done in other studies (8, 9, 21, 35, 46, 47). Changes in migration dates were the slope of the simple linear regression of migration date on year, expressed as days/year.

We developed mixed models (restricted maximum likelihood method) to quantify variation in change in migration date among species and sites, while

statistically assessing differences related to latitude, longitude, and initial year of time series [see (9) for details]. The data used as the response variable in the present study were species-specific least squares means derived from the model concerning mean/median migration dates presented in table 3 of Rubolini *et al.* (9).

**Population Trends.** We obtained estimates of European population trends of breeding birds during two separate periods, 1970–1990 and 1990–2000, using an assessment by BirdLife International (20) on a seven-point scale: large decline (–3), moderate decline (–2), small decline (–1), stable (0), small increase (+1), moderate increase (+2), and large increase (+3). The categories “small decrease” and “small increase” were not available for the period 1970–1990 (20). These qualitative assessments were available for a much larger number of species than quantitative estimates of population trends during 1980–2005, estimated as the change in population size from an initial index value of 100, with the European population index based on national indices weighted by the relative size of different national populations (see <http://www.ebcc.info/index.php?ID=148>). However, for the 58 species in our sample that were common to the two data sets, we found a strong positive relationship ( $r = 0.77$ ;  $P < 0.001$ ) between qualitative and quantitative estimates. We used the qualitative rather than the quantitative estimate of population trend as a predictor in the analyses, because this is available for a greater number of species and is representative of all of Europe west of the Urals (20), whereas quantitative estimates are based on long-term data from a limited fraction of European countries. Qualitative population trend estimates for 1990–2000 were significantly, although weakly, correlated with trends of the previous period (1970–1990) ( $r_s = 0.38$ ,  $P < 0.001$ ,  $n = 96$  species). Although population trends were expressed on an interval scale, all conclusions remained unaltered when we instead based the analyses on nonparametric rank order correlations or regressions of ranks in the analyses of contrasts (details not shown).

**Potential Predictors of Population Trends and Phenological Response.** Previous studies indicated that breeding in farmland habitats (12, 48), migration distance (13, 14, 32), northern distribution limit (4, 15, 16), relative brain mass (17), degree of ecological specialization, thermal maximum, number of broods (16, 18), and body mass (19) predicted population trends of common breeding birds. We extracted information on farmland breeding habitat (0 = population mainly breeding in habitats other than farmland; 1 = population mainly breeding in farmland) from appendix 4 of BirdLife International (20). We determined the global northernmost and southernmost latitudes of the breeding and the wintering distributions, respectively, to the nearest tenth of a degree of all species, based on information on breeding and wintering ranges shown on maps by Cramp and Perrins (24). Migration distance was estimated as the mean of the two latitudes during breeding minus the mean of the two latitudes during winter (expressed in absolute values). We also considered a categorical covariate, wintering in Africa (0 = not wintering in Africa; 1 = wintering in Africa) (24, 32), and coded the main wintering habitats of all species according to Cramp and Perrins (24) (see the details of the coding in Table S3).

Information on brain mass was obtained from Garamszegi *et al.* (49), Iwaniuk and Nelson (50), and Mlíkovský (51). Information on ecological specialization and thermal maximum was derived from Jiguet *et al.* (18). In addition, information on natal dispersal was derived from Jiguet *et al.* (18) and Wernham *et al.* (52). Body mass and number of broods (maximum number of broods laid per season) of all species were recorded from Cramp and Perrins (24). Finally, total population size in the western Palearctic (20) also was included in the analyses, because larger populations may give rise to a larger number of heterozygous loci (22, 53, 54), which may facilitate phenological

response to climate change. Information on sexual dichromatism was derived from a standard field guide (55), with all species with a visible sexual difference in coloration receiving a score of 1 and all others receiving a score of 0.

The entire data set is reported in Table S3.

**Comparative and Statistical Analyses.** Species cannot be treated as statistically independent observations in comparative analyses, because apparent phenotypic correlations may result from species sharing a common ancestor rather than convergent evolution. We controlled for similarity in phenotype among species due to common phylogenetic descent by calculating standardized independent linear contrasts (23), using the CAIC software (56), assuming a gradual evolution model (see *SI Methods* for additional details). The composite phylogeny used for the contrast analyses (Fig. S1) was based on Sibley and Ahlquist (57), combined with several other sources (see *SI Methods* for details).

We log<sub>10</sub>-transformed migration distance, body mass, total population size, and natal dispersal (by adding 1 to the migration distance). We used farmland habitat, wintering in Africa, and sexual dichromatism as continuous variables, because using dichotomous variables as continuous predictors is similar to using a dummy variable in standard regression analyses (58). The variable wintering in Africa was strongly positively correlated with log (migration distance) ( $r = 0.79$ ,  $P < 0.001$ ), and thus we ran each analysis with either one variable or the other, to avoid collinearity among predictors. To avoid biases in the calculation of relative brain size due to the particular set of species included in the study, we adopted the following procedure. Relative brain size was expressed as the residuals of a linear regression, where the slope was obtained from a log-log phylogenetically corrected regression of brain size on body mass of a large set of 567 bird species for which we were able to retrieve information on the two phenotypic traits (49–51) and to code the phylogeny (details not shown). The slope of this regression (based on phylogenetically independent contrasts) was  $\log(\text{brain size}) = 0.581 (0.010 \text{ SE}) \log(\text{body mass})$  ( $F_{1,494} = 35.20$ ,  $P < 0.0001$ ; contrasts with standardized residuals  $> 1.96$  were excluded from the regression analysis). The same procedure was adopted for contrast analyses. In this case, we first calculated contrasts of log (brain size) on log (body mass) for the set of species included in this study, and then calculated the residuals of these contrasts from the aforementioned phylogenetically corrected regression equation.

We used multiple regression to find the minimal adequate model, using the JMP software (59). The minimal adequate model was obtained by step-down removal of nonsignificant predictors (60). We conducted two sets of analyses. In the first set, population trend (during either 1970–1990 or 1990–2000) was the dependent variable, whereas change in migration date was a predictor, thereby hypothesizing that population trends could be affected by change in migration date. In the second set, change in migration date was the dependent variable, and population trends (during both 1970–1990 and 1990–2000) were included as predictors, because it could be argued that this variable has changed more recently than population trend, and we aimed to identify traits of species that could possibly predict the response to climate change.

Besides change in migration date and population trend, in these models we tested the effects of several other variables (i.e., farmland breeding habitat, migration distance or wintering in Africa, northernmost breeding latitude, sexual dichromatism, body mass, European breeding population size, maximum number of broods; see above). The effects of ecological specialization and thermal maximum (18), relative brain size, and natal dispersal were analyzed by adding these variables in turn to the minimal adequate models identified above. This was done because values for these variables were available for only a limited subset of species (see Table S3).

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# Supporting Information

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Supporting Information corrected 10/21/2008

## SI Methods

**Comparative Analyses and Phylogeny.** We tested the statistical and evolutionary assumptions of comparative analyses (1) by regressing the absolute standardized contrasts against their standard deviations. To test for effects of problems of heterogeneity in variance, we excluded outliers (contrasts with Studentized residuals  $>3$ ) in a second series of analyses (2), and repeated analyses with the independent variables expressed in ranks. In neither case did these analyses change any of the main conclusions, and thus we do not report them here.

The composite phylogeny used in the contrast analyses (Fig. S1) was based mainly on Sibley and Ahlquist (3), combined with other sources (4–16). Because information for the composite phylogeny originated from different studies using different molecular and phylogenetic methods, branch lengths were transformed assuming a gradual model of evolution, with branch lengths being proportional to the number of species contained within a clade, as implemented by the CAIC software (17). However, a second set of analyses based on similar branch length produced qualitatively similar results to those reported here (details not shown).

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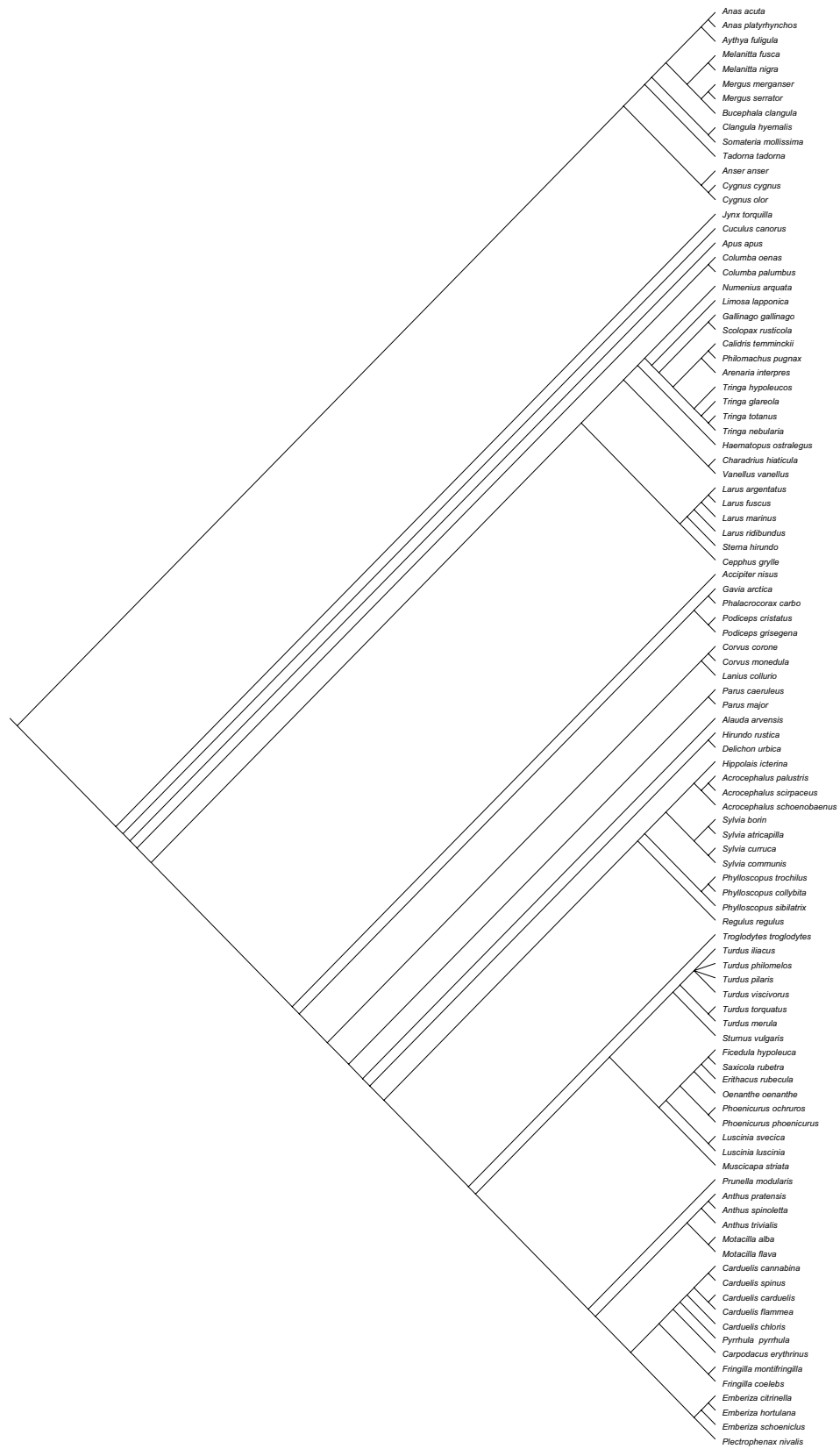


Fig. S1. Phylogenetic relationships between the species with information on change in mean migration date.

**Table S1. Statistics for excluded terms in multiple regression models of population trend of migratory birds during 1970–1990, population trend during 1990–2000, and change in mean migration date, 1960–2006**

Variables	<i>F</i>	<i>df</i>	<i>P</i>	Estimate (SE)
Population trend during 1970–1990				
Species-specific values				
Northernmost breeding latitude	3.29	1, 94	.07	−0.058 (0.032)
Change in migration date	2.59	1, 93	.11	−0.902 (0.561)
Population size	1.12	1, 92	.29	0.218 (0.206)
Number of broods	0.34	1, 91	.56	−0.107 (0.184)
Migration distance	0.19	1, 90	.66	−0.134 (0.301)
Sexual dichromatism	0.26	1, 89	.61	−0.138 (0.269)
Independent contrasts				
Change in migration date	1.66	1, 91	.20	−0.779 (0.606)
Population size	2.06	1, 90	.15	0.359 (0.249)
Number of broods	0.34	1, 89	.56	−0.126 (0.214)
Migration distance	0.21	1, 88	.65	−0.168 (0.368)
Sexual dichromatism	0.21	1, 87	.64	0.171 (0.367)
Population trend during 1990–2000				
Species-specific values				
Body mass	2.55	1, 95	.11	0.349 (0.150)
Farmland habitat	1.06	1, 94	.31	−0.380 (0.369)
Northernmost breeding latitude	0.68	1, 93	.41	−0.026 (0.031)
Sexual dichromatism	0.46	1, 92	.50	−0.167 (0.247)
Migration distance	0.35	1, 91	.56	−0.161 (0.273)
Number of broods	0.09	1, 90	.76	−0.058 (0.186)
Population size	0.01	1, 89	.94	0.016 (0.216)
Independent contrasts				
Migration distance	1.14	1, 93	.29	−0.298 (0.278)
Population size	1.51	1, 92	.22	−0.230 (0.187)
Sexual dichromatism	0.22	1, 91	.64	−0.125 (0.267)
Number of broods	0.26	1, 90	.61	−0.094 (0.185)
Northernmost breeding latitude	0.15	1, 89	.70	0.012 (0.030)
Farmland habitat	0.00	1, 88	.95	−0.026 (0.381)
Body mass	0.00	1, 87	.98	−0.011 (0.388)
Change in migration date, 1960–2006				
Species-specific values				
Body mass	2.17	1, 91	.14	−0.043 (0.029)
Northernmost breeding latitude	0.56	1, 90	.46	−0.004 (0.005)
Population size	0.22	1, 89	.64	−0.015 (0.033)
Farmland habitat	0.21	1, 88	.65	0.029 (0.062)
Sexual dichromatism	0.17	1, 87	.68	−0.017 (0.041)
Population trends 1970–1990	0.11	1, 86	.92	0.002 (0.017)
Independent contrasts				
Body mass	1.83	1, 89	.18	−0.087 (0.064)
Farmland habitat	1.07	1, 88	.30	0.061 (0.059)
Northernmost breeding latitude	0.28	1, 87	.06	−0.003 (0.005)
Sexual dichromatism	0.12	1, 86	.73	−0.018 (0.053)
Population trends 1970–1990	0.04	1, 85	.84	0.003 (0.016)
Population size	0.01	1, 84	.93	−0.003 (0.039)

Excluded terms are shown in the order of removal from the model (first to be removed are shown at the bottom).



**Table S2. Minimal adequate multiple regression models of population trend of migratory birds during 1970–1990, population trend of migratory birds during 1990–2000, and change in mean spring migration date of migratory birds 1960–2006, obtained by step-down removal of nonsignificant predictors (see *Methods*), where the effect of wintering in Africa has been included in initial models instead of migration distance (see *Methods*).**

Variables	<i>F</i>	df	<i>P</i>	Estimate (SE)
Population trend during 1970–1990				
Species-specific values				
Body mass	13.17	1, 94	<.001	0.569 (0.164)
Wintering in Africa	5.11	1, 94	.026	−0.621 (0.275)
Farmland habitat	4.79	1, 94	.031	−0.834 (0.381)
Independent contrasts				
Farmland habitat	7.09	1, 91	.009	−1.087 (0.408)
Northernmost breeding latitude	5.90	1, 91	.017	−0.082 (0.034)
Wintering in Africa	5.29	1, 91	.024	−0.781 (0.339)
Body mass	4.72	1, 91	.033	0.958 (0.441)
Population trend during 1990–2000				
Species-specific values				
Change in migration date	27.19	1, 96	<.001	−2.801 (0.537)
Independent contrasts				
Change in migration date	31.48	1, 94	<.001	−2.656 (0.473)
Change in migration date, 1960–2006				
Species-specific values				
Population trends 1990–2000	22.28	1, 92	<.001	−0.068 (0.014)
Migration distance	11.19	1, 92	.001	0.136 (0.041)
Number of broods	5.52	1, 92	.021	−0.052 (0.022)
Independent contrasts				
Population trends 1990–2000	24.62	1, 90	<.001	−0.078 (0.016)
Wintering in Africa	10.65	1, 90	.002	0.157 (0.048)
Number of broods	5.88	1, 90	.017	−0.070 (0.029)

Table S3. Complete dataset used in analyses

Species	Trend in migration date	Population trend 1970–1990	Population trend 1990–2000	No. of broods	Natal dispersal	Farmland breeding habitat	Habitat specialization	Thermal maximum	Migration distance	Wintering in Africa	Winter habitat	Northern-most breeding latitude	Sexual dichromatism	Brain mass (g)	Body mass (g)	European breeding population
																(pairs × 10 <sup>5</sup> )
<i>Accipiter nisus</i>	-0.032	3	1	1	15.6	0	-	-	12.79	0	1	70.00	1	2.92	204.0	3.95
<i>Acrocephalus palustris</i>	-0.157	0	0	1	-	0	-	-	66.84	1	3	63.93	0	0.52	12.0	50.00
<i>Acrocephalus schoenobaenus</i>	-0.060	0	0	2	40.4	0	-	-	62.10	1	3	70.63	0	-	11.9	59.00
<i>Acrocephalus scirpaceus</i>	-0.116	0	0	1	47.0	0	-	-	44.60	1	3	64.64	0	0.58	11.8	38.50
<i>Alauda arvensis</i>	-0.291	-3	-1	4	5.5	1	1.32	20.08	13.01	0	2	71.16	0	0.97	36.4	600.00
<i>Anas acuta</i>	-0.099	-3	-2	1	-	0	-	-	26.72	1	4	70.63	1	-	917.0	3.40
<i>Anas platyrhynchos</i>	-0.461	0	-1	1	19.9	0	-	-	8.12	0	3	71.09	1	5.82	1119.0	42.00
<i>Anser anser</i>	0.136	3	3	1	-	0	-	-	12.28	0	3	71.11	0	11.91	3464.5	1.55
<i>Anthus pratensis</i>	-0.346	0	-1	3	0.9	0	0.69	16.97	15.64	0	2	71.17	0	0.36	19.2	115.00
<i>Anthus (spinoletta) petrosus</i>	-0.312	0	-1	2	-	0	-	-	21.27	0	3	75.00	0	0.58	21.5	15.20
<i>Anthus trivialis</i>	-0.130	0	-1	3	-	0	0.46	19.55	47.07	1	1	70.50	0	0.68	23.4	345.00
<i>Apus apus</i>	-0.049	0	-1	1	36.8	0	-	-	59.39	1	5	70.00	0	0.69	39.6	119.50
<i>Arenaria interpres</i>	-0.050	0	0	1	-	0	-	-	63.88	1	4	83.33	1	-	107.5	0.58
<i>Aythya fuligula</i>	-0.056	0	-2	1	-	0	-	-	17.08	0	3	70.16	1	4.36	656.5	8.05
<i>Bucephala clangula</i>	-0.154	2	1	1	-	0	-	-	9.66	0	3	70.31	1	-	840.3	5.40
<i>Calidris temminckii</i>	0.034	0	0	1	-	0	-	-	43.12	1	3	71.25	0	-	26.1	2.53
<i>Carduelis cannabina</i>	0.116	0	-2	3	4.4	0	0.63	20.54	4.11	0	2	66.00	1	0.67	18.9	190.00
<i>Carduelis carduelis</i>	-0.368	0	1	3	11.1	0	0.56	20.59	1.16	0	2	63.57	1	0.59	15.6	205.00
<i>Carduelis chloris</i>	-0.286	0	0	2	4.2	0	0.52	20.51	1.34	0	5	70.31	1	0.89	27.6	230.00
<i>Carduelis flammea</i>	-0.178	0	-	2	22.7	0	-	-	9.46	0	2	76.00	1	0.59	13.1	139.00
<i>Carduelis spinus</i>	-0.253	0	-	2	-	0	-	-	6.83	0	1	70.00	1	0.56	13.8	140.00
<i>Carpodacus erythrinus</i>	0.238	0	0	1	-	0	-	-	24.22	0	1	67.67	1	-	23.4	45.50
<i>Cephus grylle</i>	0.006	-2	0	1	-	0	-	-	0.70	0	4	81.75	0	-	394.5	2.15
<i>Charadrius hiaticula</i>	-0.193	0	-1	3	-	0	-	-	2.56	0	4	83.33	0	-	63.2	1.70
<i>Clangula hyemalis</i>	-0.440	0	0	1	-	0	-	-	15.78	0	4	82.22	1	-	722.5	7.20
<i>Columba oenas</i>	-0.954	3	2	4	10.4	0	0.68	19.24	3.45	0	1	65.00	0	2.27	314.5	6.25
<i>Columba palumbus</i>	-0.360	0	1	3	10.7	1	0.19	20.26	2.03	0	1	67.33	0	2.38	494.5	130.00
<i>Corvus corone</i>	-0.215	3	0	1	9.9	0	0.32	20.46	5.71	0	2	71.17	0	8.14	544.5	120.00
<i>Corvus monedula</i>	-0.816	0	0	1	8.6	0	0.55	20.40	0.29	0	2	66.36	0	4.69	249.0	101.00
<i>Cuculus canorus</i>	0.266	0	-1	1	-	0	0.27	20.46	49.38	1	1	70.47	0	2.24	120.5	64.00
<i>Cygnus cygnus</i>	-0.474	3	3	1	-	0	-	-	9.29	0	3	70.00	0	-	11375.0	0.19
<i>Cygnus olor</i>	-0.325	2	3	1	34.3	0	-	-	1.08	0	3	62.41	1	-	10750.0	1.03
<i>Delichon urbica</i>	0.026	0	-2	2	10.4	0	0.89	20.55	44.25	1	5	70.33	0	0.59	19.5	169.50
<i>Emberiza citrinella</i>	-0.205	0	-1	3	8.4	1	0.54	19.35	4.72	0	2	70.44	1	0.82	26.8	245.00
<i>Emberiza hortulana</i>	0.063	-3	-1	1	-	1	-	-	36.48	1	2	67.50	1	-	20.6	106.00
<i>Emberiza schoeniclus</i>	-0.249	0	-1	2	5.4	0	-	-	10.52	0	3	71.18	1	0.68	18.8	68.00
<i>Erethacus rubecula</i>	-0.302	0	1	3	6.0	0	0.25	20.42	5.00	0	5	70.00	0	0.66	16.4	630.00
<i>Ficedula hypoleuca</i>	-0.118	0	-1	1	20.6	0	-	-	43.00	1	1	70.67	1	0.45	14.3	160.00
<i>Fringilla coelebs</i>	-0.140	0	0	2	3.6	0	0.51	20.57	5.54	0	2	71.25	1	0.77	24.2	1850.00
<i>Fringilla montifringilla</i>	-0.156	0	0	2	-	0	-	-	13.75	0	1	71.25	1	0.78	22.6	175.00
<i>Gallinago gallinago</i>	0.009	0	-2	1	-	0	-	-	7.05	0	3	71.25	0	1.35	106.5	14.15
<i>Gavia arctica</i>	0.251	-3	-3	1	-	0	-	-	10.57	0	4	73.28	0	-	2804.5	0.72
<i>Haematopus ostralegus</i>	-0.033	3	-2	1	-	0	-	-	21.39	0	4	71.25	0	-	531.0	3.75
<i>Hippolais icterina</i>	-0.033	0	-1	1	-	0	-	-	71.34	1	2	70.00	0	0.54	13.3	53.00
<i>Hirundo rustica</i>	-0.174	-2	-1	3	14.1	1	0.88	20.52	42.34	1	5	70.38	1	0.58	19.1	260.00
<i>Jynx torquilla</i>	0.141	-2	-2	3	-	0	-	-	35.20	1	5	69.50	0	-	37.3	9.40
<i>Lanius collurio</i>	-0.010	-2	-1	1	-	1	0.67	20.20	64.72	1	2	66.33	1	1.00	30.7	96.50
<i>Larus argentatus</i>	-0.502	3	2	1	-	0	-	-	22.14	0	4	71.25	0	6.43	895.0	15.25
<i>Larus fuscus</i>	-0.333	3	3	1	28.2	0	-	-	34.34	1	4	71.25	0	-	817.5	3.25
<i>Larus marinus</i>	-0.492	0	3	1	-	0	-	-	7.28	0	4	79.31	0	-	1599.5	1.45
<i>Larus ridibundus</i>	0.129	3	-2	1	47.0	0	-	-	23.50	0	4	68.00	0	2.88	280.5	18.50
<i>Limosa lapponica</i>	-0.018	0	0	1	-	0	-	-	59.92	1	4	70.31	0	-	301.0	0.04
<i>Luscinia luscinia</i>	-0.084	0	0	1	-	0	-	-	63.10	1	1	65.00	0	-	25.0	53.00
<i>Luscinia svecica</i>	-0.045	0	0	2	-	0	-	-	25.50	1	3	71.17	1	-	18.2	61.50
<i>Melanitta fusca</i>	0.028	0	-2	1	-	0	-	-	2.55	0	4	70.63	1	-	1587.5	0.93

Species	Trend in migration date	Population trend 1970–1990	Population trend 1990–2000	No. of broods	Natal dispersal	Farmland breeding habitat	Habitat specialization	Thermal maximum	Migration distance	Wintering in Africa	Winter habitat	Northernmost breeding latitude	Sexual dichromatism	Brain mass (g)	Body mass (g)	European breeding population
																(pairs × 10 <sup>5</sup> )
<i>Melanitta nigra</i>	-0.532	0	0	1	-	0	-	-	16.10	0	4	74.53	1	-	1306.5	1.15
<i>Mergus merganser</i>	-0.130	2	-1	1	-	0	-	-	4.89	0	3	71.25	1	-	1641.5	0.61
<i>Mergus serrator</i>	-0.208	0	-1	1	-	0	-	-	11.05	0	4	73.20	1	-	1090.5	0.97
<i>Motacilla alba</i>	-0.075	0	0	3	16.1	0	0.47	20.24	18.12	0	2	71.17	1	0.58	20.8	195.00
<i>Motacilla flava</i>	-0.014	0	-1	2	12.5	1	-	-	40.98	1	2	70.67	1	0.47	17.4	109.50
<i>Muscicapa striata</i>	-0.056	-2	-1	2	12.8	0	-	-	64.40	1	1	70.50	0	0.53	15.5	180.00
<i>Numenius arquata</i>	0.023	-	-2	1	-	0	-	-	44.67	0	4	70.63	0	3.68	725.0	2.90
<i>Oenanthe oenanthe</i>	0.021	0	-2	2	18.9	0	-	-	38.17	1	2	71.17	1	0.72	24.0	88.00
<i>Parus caeruleus</i>	-0.069	0	0	2	5.3	0	0.44	20.57	0.00	0	1	67.33	1	0.65	11.8	320.00
<i>Parus major</i>	-0.252	0	0	2	5.3	0	0.36	20.47	0.00	0	1	70.67	1	0.85	18.5	685.00
<i>Phalacrocorax carbo</i>	-0.313	3	3	1	-	0	-	-	2.63	0	3	71.27	0	-	2254.0	3.40
<i>Philomachus pugnax</i>	0.019	0	-2	1	-	0	-	-	52.20	1	3	71.25	1	-	140.5	3.55
<i>Phoenicurus ochruros</i>	-0.377	0	1	3	-	0	0.89	19.93	15.83	0	5	60.36	1	0.61	16.0	64.00
<i>Phoenicurus phoenicurus</i>	-0.068	-3	0	2	12.2	0	0.78	19.70	33.93	1	1	70.50	1	0.54	15.9	114.00
<i>Phylloscopus collybita</i>	-0.180	0	0	2	-	0	0.41	19.87	22.55	0	1	70.29	0	0.38	7.7	454.45
<i>Phylloscopus sibilatrix</i>	0.272	0	-2	2	20.0	0	2.09	18.92	52.74	1	1	68.33	0	-	9.1	180.00
<i>Phylloscopus trochilus</i>	-0.048	0	-1	2	20.8	0	0.65	17.70	68.09	1	1	71.18	0	0.31	9.3	780.00
<i>Plectrophenax nivalis</i>	-0.722	0	0	2	-	0	-	-	20.49	0	2	83.00	1	-	37.4	11.90
<i>Podiceps cristatus</i>	-0.098	3	-2	2	-	0	-	-	4.40	0	4	66.00	0	-	875.0	3.75
<i>Podiceps grisegena</i>	-0.060	0	-1	2	-	0	-	-	7.87	0	4	67.67	0	-	829.8	0.44
<i>Prunella modularis</i>	-0.153	0	0	3	2.1	0	0.38	19.05	9.23	0	2	70.67	0	0.71	19.0	190.00
<i>Pyrrhula pyrrhula</i>	-0.303	0	0	3	4.6	0	0.71	18.87	0.00	0	1	70.31	1	0.89	31.0	106.50
<i>Regulus regulus</i>	-0.156	0	0	2	-	0	1.09	18.86	0.00	0	1	70.29	1	0.38	5.8	270.00
<i>Saxicola rubetra</i>	0.015	0	-1	2	0.5	1	0.79	19.44	34.84	1	2	70.00	1	0.67	16.6	77.00
<i>Scolopax rusticola</i>	-0.176	-	-2	1	-	0	-	-	14.32	0	1	70.16	1	2.47	309.5	42.00
<i>Somateria mollissima</i>	-0.030	3	1	1	-	0	-	-	3.34	0	4	80.83	1	7.92	2066.5	10.20
<i>Sterna hirundo</i>	0.622	0	0	1	-	0	-	-	52.75	1	4	71.25	0	-	125.0	4.20
<i>Sturnus vulgaris</i>	0.085	0	-2	2	9.5	1	0.40	19.96	2.63	0	2	71.25	1	1.70	80.5	395.00
<i>Sylvia atricapilla</i>	-0.167	0	1	2	41.2	0	0.32	20.49	19.63	0	1	70.10	1	0.67	18.9	370.00
<i>Sylvia borin</i>	0.016	0	0	2	-	0	0.34	19.39	63.25	1	1	70.31	0	0.62	19.0	240.00
<i>Sylvia communis</i>	-0.102	0	1	2	14.4	1	0.54	20.35	53.05	1	2	69.33	1	0.56	14.5	195.00
<i>Sylvia curruca</i>	-0.119	0	0	2	32.3	0	0.51	19.71	27.79	1	2	69.67	0	0.53	12.4	63.00
<i>Tadorna tadorna</i>	-0.118	2	0	1	-	0	-	-	9.35	0	4	66.17	1	4.74	1152.0	0.54
<i>Tringa glareola</i>	0.000	-2	0	1	-	0	-	-	62.89	1	3	70.78	0	-	67.5	7.75
<i>Tringa hypoleucos</i>	0.134	0	-2	1	-	0	-	-	44.39	1	3	71.25	0	-	47.8	11.60
<i>Tringa nebularia</i>	-0.194	0	0	1	-	0	-	-	49.16	1	3	70.31	0	-	173.5	1.18
<i>Tringa totanus</i>	-0.024	-2	-2	1	-	0	-	-	35.28	1	3	71.09	0	1.42	112.0	4.45
<i>Troglodytes troglodytes</i>	-0.228	0	1	2	8.9	0	0.41	20.40	1.34	0	1	69.33	0	0.50	8.9	315.00
<i>Turdus iliacus</i>	-0.208	0	0	2	-	0	-	-	10.77	0	1	71.17	0	1.45	62.8	185.00
<i>Turdus merula</i>	-0.314	0	1	4	3.3	0	0.21	20.52	3.98	0	5	71.17	1	1.92	95.8	610.00
<i>Turdus philomelos</i>	-0.192	0	0	4	7.0	0	0.40	19.69	14.65	0	1	70.33	0	1.59	70.5	280.00
<i>Turdus pilaris</i>	-0.050	0	0	2	-	1	-	-	10.77	0	2	71.17	0	1.85	92.1	190.00
<i>Turdus torquatus</i>	-0.061	0	0	2	-	0	-	-	14.13	0	2	71.17	1	1.87	117.0	4.90
<i>Turdus viscivorus</i>	-0.415	0	0	3	8.3	0	0.44	20.09	4.36	0	2	69.00	0	2.21	117.8	52.00
<i>Vanellus vanellus</i>	-0.061	0	-3	1	-	1	-	-	12.08	0	2	70.16	1	2.16	218.5	22.50

Information on trend in mean migration date (days/year) (see *Methods*), breeding population trend [large decline (-3), moderate decline (-2), small decline (-1), stable (0), small increase (+1), moderate increase (+2) to large increase (+3); scores were not given for species classified as "fluctuating" [see (18)], number of broods, natal dispersal, farmland breeding habitat [0 = no; 1 = yes; from code 7, "agricultural and grassland habitats," in appendix 4 of BirdLife International (18)], habitat specialization, thermal maximum, migration distance (° latitude), wintering in Africa (0 = no; 1 = yes), main wintering habitat (1 = woodland, forest, or wooded savannah; 2 = farmland and grassland, dry savannah, grassland, or other dry open habitats; 3 = wetlands and inland waters; 4 = sea and coastal areas; 5 = all terrestrial habitats), northernmost breeding latitude, brain mass (g), body mass (g), and size of the European breeding population size (pairs × 10<sup>5</sup>). See *Methods* for details and data sources.

# 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

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## 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 (Bertheaux & 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 (Bertheaux & 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 oestrus (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 13 879 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;



**Table 1** Linear mixed-effects models to test for and quantify temporal trends in six phenological traits in female and male red deer. (A) Upper parts of table for each trait shows random and fixed effects terms included in initial models to test for temporal trends. Models include year and age as fixed effects (and female reproductive status for oestrus date and parturition date models). (B) Lower parts of table for each trait shows models run subsequent to models in (A) to test whether temporal trends are independent of preceding phenological events. All models include same terms as model above (under A) but only year and any significant preceding phenological traits fitted to model are shown, whilst non-significant phenological effects fitted and then dropped are listed below. Statistical significance was assessed using likelihood ratio tests (see text)

	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%) Year = 5.75 (8%) Residual = 59.48 (86%)	Female = 26.6 (20%) Year = 8.4 (6%) Residual = 96.6 (73%)					
Year	$\chi^2$ 10.08 df 1 P <0.01	$\chi^2$ 20.7 df 1 P <0.001	SE 0.07	b -0.26	P <0.001	b -0.42	SE 0.08
Age	$\chi^2$ 52.19 df 16 P <0.001	$\chi^2$ 113.9 df 15 P <0.001					
Status	$\chi^2$ 92.18 df 4 P <0.001	$\chi^2$ 271.2 df 4 P <0.001					
<i>(B) Models including preceding phenological events</i>							
Oestrus date		104.6			<0.001	0.77	0.07
Year		10.2			<0.01	-0.27	0.07
<i>(A) Models of temporal trends</i>							
Sample size	1491 (374 males)	1181 (360 males)					
Random effects	Male = 39.5 (45%) Year = 7.7 (9%) Residual = 40.7 (46%)	Male = 47.8 (35%) Year = 3.3 (2%) Residual = 83.7 (62%)					
Year	$\chi^2$ 5.87 df 1 P <0.05	$\chi^2$ 8.03 df 1 P <0.001	SE 0.08	b -0.26	P <0.001	b -0.21	SE 0.07
Age	$\chi^2$ 2170.8 df 11 P <0.001	$\chi^2$ 353.7 df 10 P <0.001					
<i>(B) Models including preceding phenological events</i>							
Casting date		112.8		0.25	<0.001	0.50	0.02
Cleaning date		7.91		-0.24	<0.01	-0.15	0.10
Start date		29.9		0.12	<0.001	0.12	0.09
Year		2.42		0.08	<0.01	0.10	0.02
<i>Nonsignificant phenological effects dropped from model</i>							
Start × clean × cast							
Start × cast						0.00	1
Start × clean						1.77	1
Cast × clean						1.85	1
Cast						0.75	1
Clean						1.45	1
						2.66	1

**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	GDD	GDD	Terms	ΔAIC	AIC	Terms	ΔAIC	AIC	Terms	ΔAIC	AIC	Terms	ΔAIC	AIC	Terms	ΔAIC	AIC			
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			X				16323.5	25	3.8	10374.0	17	2.1	<b>4690.7</b>	<b>17</b>	<b>0.0</b>						
X	X		X				16322.2	26	2.5	10373.4	18	1.5	4692.3	18	1.6						
X		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 Hempsted, 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

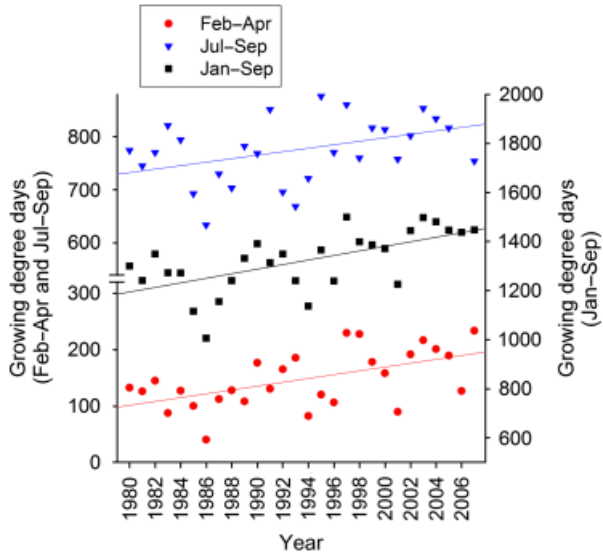


Fig. 1 Spring and summer growing degree days increased significantly between 1980 and 2007 on the Isle of Rum, Scotland. Growing degree days were measured using local weather station data as the sum of daily mean temperatures above 5 °C across the months Feb–Apr (red circles, left y axis) and Jul–Sep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

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

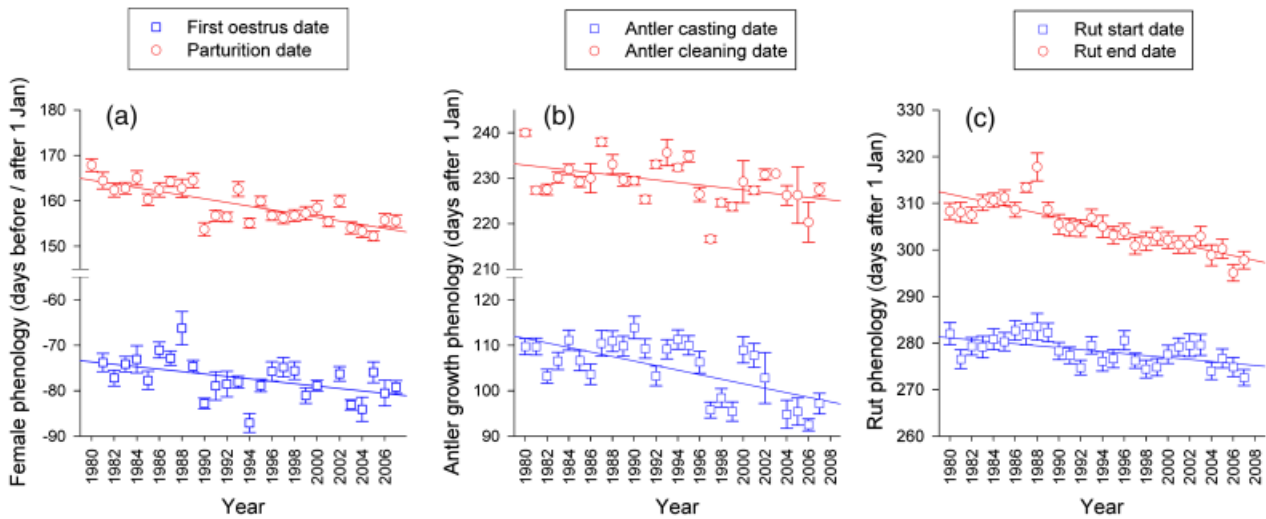


Fig. 2 The breeding phenology of female and male red deer has advanced significantly between 1980 and 2007 in the North Block study area on the Isle of Rum. (a) Mean annual female first oestrus (blue squares) and parturition dates (red circles); (b) mean annual male antler casting (blue squares) and 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 oestrous 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 oestrous 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 oestrous 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.

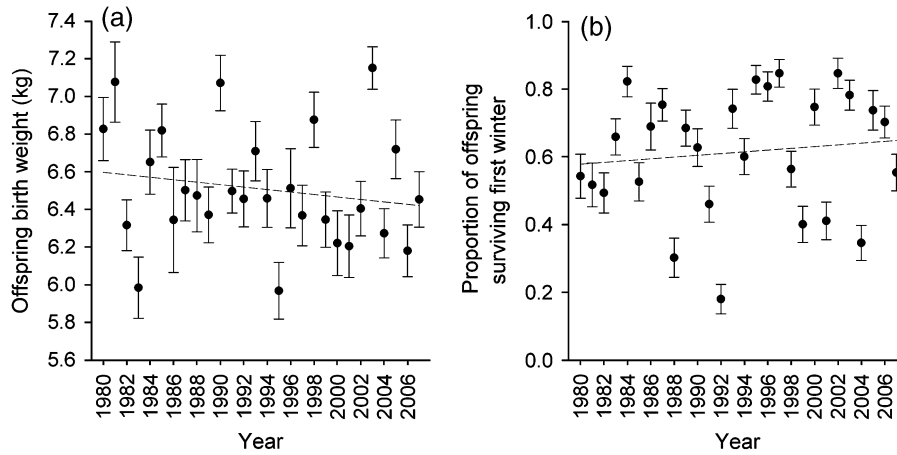
Feb–Apr GDD in the year of antler growth was identified as the best predictor of antler cleaning dates (Table 2). As for casting date, once Feb–Apr GDD was included in the model the effect of year was no longer significant and the estimated temporal trend was reduced by 54% ( $b = -0.12 \pm 0.08$  SE,  $\chi^2_{(1)} = 2.49$ ,  $P = 0.11$ ). 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 oestrous 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.

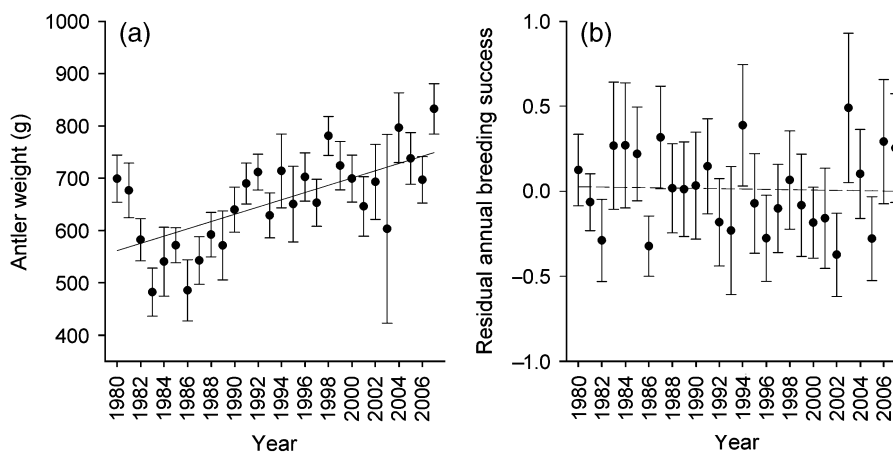
#### *Effects on other reproductive performance traits*

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; Mysterud *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 (Mysterud *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; Mysterud *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.

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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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## LETTERS

# Coupled dynamics of body mass and population growth in response to environmental change

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Environmental change has altered the phenology, morphological traits and population dynamics of many species<sup>1,2</sup>. However, the links underlying these joint responses remain largely unknown owing to a paucity of long-term data and the lack of an appropriate analytical framework<sup>3</sup>. Here we investigate the link between phenotypic and demographic responses to environmental change using a new methodology and a long-term (1976–2008) data set from a hibernating mammal (the yellow-bellied marmot) inhabiting a dynamic subalpine habitat. We demonstrate how earlier emergence from hibernation and earlier weaning of young has led to a longer growing season and larger body masses before hibernation. The resulting shift in both the phenotype and the relationship between phenotype and fitness components led to a decline in adult mortality, which in turn triggered an abrupt increase in population size in recent years. Direct and trait-mediated effects of environmental change made comparable contributions to the observed marked increase in population growth. Our results help explain how a shift in phenology can cause simultaneous phenotypic and demographic changes, and highlight the need for a theory integrating ecological and evolutionary dynamics in stochastic environments<sup>4,5</sup>.

Rapid environmental change, largely attributed to anthropogenic influences, is occurring at an unprecedented rate<sup>6,7</sup>. Concurrent with environmental change, there have been changes in the phenology<sup>8</sup>, geographic distribution<sup>9</sup>, phenotypic trait distributions and population dynamics<sup>10</sup> of wildlife species, particularly those living in extreme environments including high altitude or latitude ecosystems<sup>2,11</sup>. However, the proximate causes that generate such change are rarely identified, and most analyses are phenomenological<sup>2</sup>. Population-level responses to environmental change can be of several types: genetic changes occur as a result of directional selection on heritable traits or drift<sup>12,13</sup>; life-history and quantitative traits can shift as a result of both a plastic response to environmental change<sup>14,15</sup> and changing selection pressures<sup>16–18</sup>; and population size can change with changing demographic rates<sup>19,20</sup>. Each of these processes depends on the association between phenotypic traits and survival, reproduction, trait development among survivors and the distribution of traits among newborns<sup>21</sup>. Understanding the effects of environmental change on populations consequently requires insight into how phenotype–demography relationships are altered and how these changes affect the distribution of phenotypic traits, life history and population growth<sup>22,23</sup>.

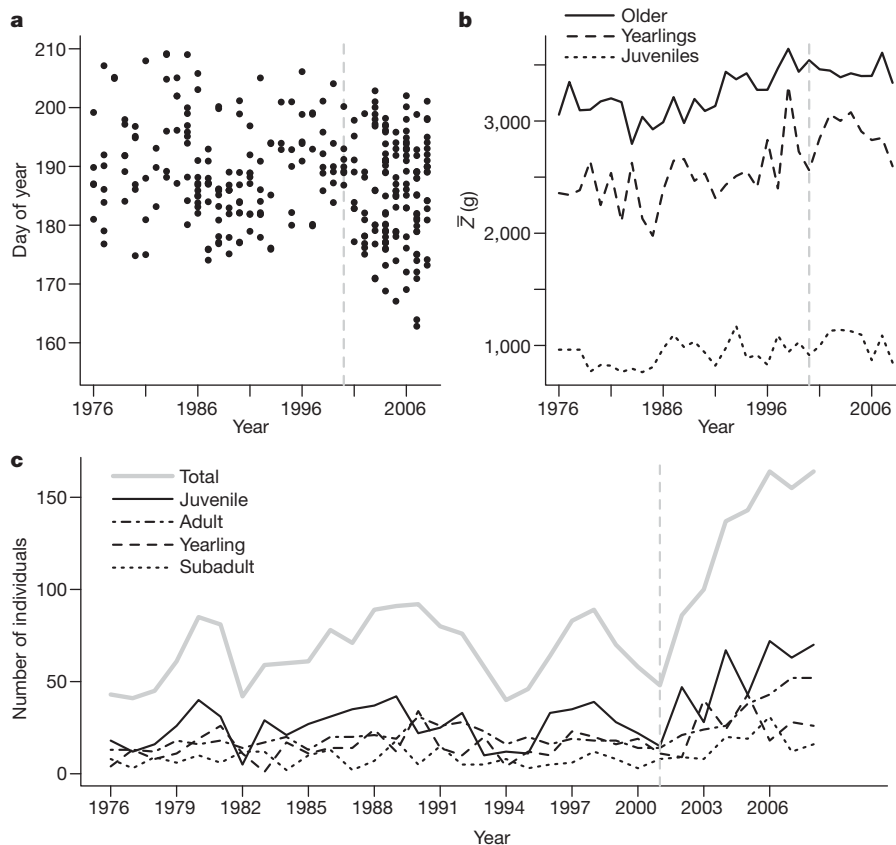
In this study, we use a long-term data set from a hibernating sciurid rodent inhabiting a subalpine habitat to investigate how environmental change has affected phenotypic traits and population dynamics (Supplementary Fig. 1). We used 33 years (1976–2008) of

individual-based life-history and body-mass data collected from a yellow-bellied marmot (*Marmota flaviventris*) population located in the Upper East River Valley, Colorado, USA. We used data only from the female segment of the population because maternity, unlike paternity, is known with confidence for each pup and most males disperse by the end of their second year. We focus on body mass as the focal phenotypic trait because marmot life history, particularly survival during hibernation and reproduction on emergence, is heavily dependent on this trait<sup>24,25</sup>.

Environmental change has influenced several aspects of marmot phenology<sup>8</sup>. Marmots have been emerging earlier from hibernation<sup>8</sup> and giving birth earlier in the season (Fig. 1a), which allows individuals more time to grow until immergence into hibernation. Using body-mass measurements from repeated captures during each summer and mixed-effects models, we estimated body mass on 1 August for each individual in the population in each year (Supplementary Fig. 2). Despite annual fluctuations, there has been a shift in the mean body mass in older age classes; for example, the mean body mass for 2-year-old and older adults increased from 3,094.4 g (standard error of the mean (s.e.m.) = 28.9) during the first half of the study to 3,433.0 g (s.e.m. = 28.0) during the second half (Fig. 1b). Meanwhile, population size fluctuated around a stable equilibrium until 2001, followed by a steady increase over the last seven years (Fig. 1c). A nonlinear (weighted) least-squares analysis indicated a break-point in population dynamics at year 2000.9 (s.e.m. = 1.12,  $P < 0.001$ ). The regression slopes from this analysis reveal that the population size increased on average by 0.56 (s.e.m. = 0.45,  $P = 0.22$ ) marmots per year between 1976 and 2001 and by 14.2 marmots per year subsequently (s.e.m. = 3.17,  $P < 0.01$ ), indicating a major shift in the population dynamics. To examine these demographic and phenotypic changes, we compared body-mass–demography associations between pre-2000 and post-2000 years. We included a one-year lag because body condition is expected to influence population size (through survival and reproduction) one year later. It is notable that the change in population growth rate occurred more suddenly than the change in mean body mass (Fig. 1b, c). Nonetheless, the majority of the highest mean body masses were observed during the last decade, particularly for adults, indicating that gradual changes in the environment may have passed a threshold leading to a gradual shift in the body mass and an abrupt shift in the demographic regime. Interestingly, other aspects of marmot habitat, including flowering rates of tall bluebells (*Mertensia ciliata*), also changed around 2000 (Supplementary Fig. 3).

Our next objective was to understand why these joint changes were observed. We used mark–recapture methods<sup>26</sup> and generalized linear and additive models<sup>27</sup> to identify the most parsimonious functions

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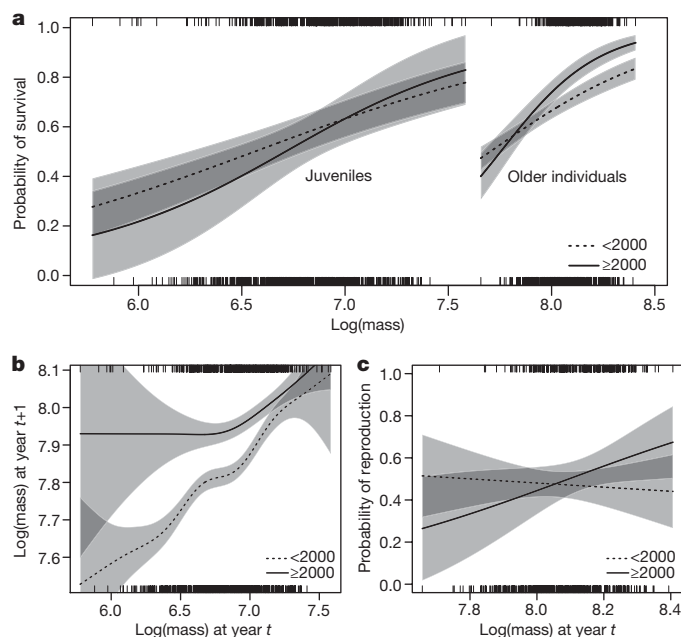


**Figure 1 | Trends in the phenology, mean phenotypic trait and demography for females of the yellow-bellied marmot population.** **a–c**, Time of weaning ( $-0.17$  days per year,  $P < 0.01$ ) (**a**), mean 1 August mass ( $\bar{Z}$ ) (**b**), and abundance in each age class (**c**). The four age classes are juvenile ( $<1$  yr),

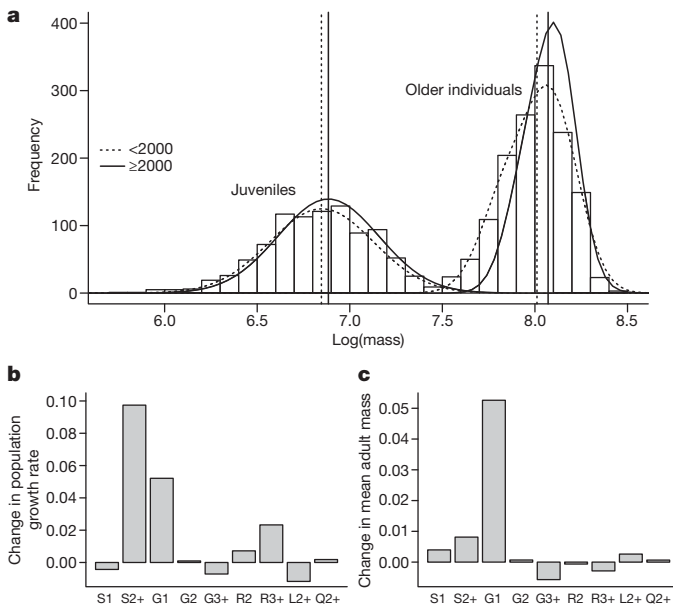
yearling (1 yr-old), subadult (2 yrs-old) and adult ( $\geq 3$  yrs-old). Subadult and adult masses are combined (older) in **b**. Vertical dotted lines delineate different phases of population dynamics.

describing associations between body-mass and demographic (survival, reproduction probability and litter size) and trait-transition (growth and offspring body mass) rates. We also tested for the effects of age class and study period on these rates. Body mass had a significant positive influence on most rates in both periods (Supplementary Figs 4–7). Moreover, the form of some of the body-mass–rate functions also changed over time. Heavier marmots, particularly adults, survived better in later years (Fig. 2a). Both mean juvenile growth (from the first to second August of life) and the dependence of growth on mass increased in later years (Fig. 2b); the resulting increase in growth was much greater among smaller juveniles. In addition, heavier females had a higher chance of reproducing in later years (Fig. 2c).

To understand the population dynamic and phenotypic consequences of these changes, we used a recently developed method, an integral projection model (IPM)<sup>28,29</sup>, which projects the distribution of a continuous trait based on demographic and trait transition functions. Using the fitted functions relating body mass to each rate, we parameterized two IPMs, one for the pre-2000 period and one for after 2000. Eigenanalysis of the two IPMs captured the observed change in the dynamics: the annual asymptotic population growth rate ( $\lambda$ ) increased from an approximately stable ( $\lambda = 1.02$ ) in the earlier period to a rapidly increasing ( $\lambda = 1.18$ ) in the later period (Fig. 1c). The stable mass distributions for each of the periods captured the observed increase in body mass in both juveniles (38.2 g, 4.2%) and older age classes (166.7 g, 5.8%) (Fig. 3a). To identify which demographic or trait transition function had contributed most to the observed increase in population growth rate, we performed a retrospective perturbation analysis of the two IPMs. The observed increase in population growth rate was predominantly due to changes in the adult survival and juvenile growth functions (Fig. 3b).



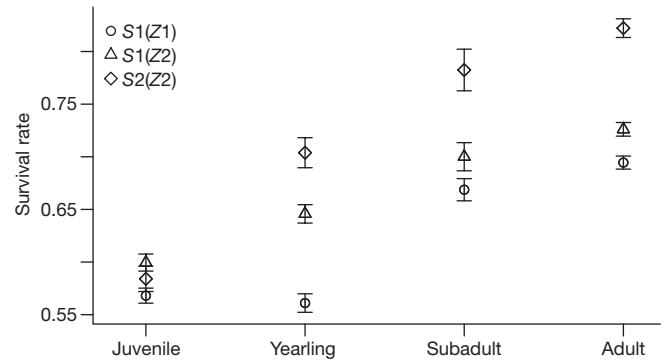
**Figure 2 | The relationship between body mass and demographic and trait transition rates.** **a–c**, Effect of body mass on survival (**a**), juvenile growth (**b**) and adult reproduction (**c**) for pre-2000 ( $<2000$ ) and post-2000 ( $\geq 2000$ ) years. Shaded areas indicate the 95% confidence intervals, and rugs below and above the graph represent the distribution of the body mass data for  $<2000$  and  $\geq 2000$ , respectively.



**Figure 3 | Trait-based analysis of the population dynamics.** **a**, Stable August log-body-mass distributions (lines) for juveniles and older individuals for  $<2000$  and  $\geq 2000$ . Vertical lines show the mean body masses. Bars indicate the actual observed distribution over the entire study period. **b**, **c**, Retrospective perturbation analysis of the integral projection model gives the relative contribution of each function to population growth (**b**) and to change in mean adult body mass (**c**) from the  $<2000$  to the  $\geq 2000$  period (G, growth; L, litter size; Q, offspring mass; R, reproduction probability; S, survival; numbers indicate the age classes).

The increase in mean adult survival was the key demographic factor underlying the observed shift in population dynamics between the two periods. It could have been caused by two non-mutually exclusive processes: a change in the relationship between August mass and survival, and a change in mean August mass in each age class. To understand the relative contributions of these two processes, we estimated three mean survival rates for each age class using: (1) the earlier period's survival curve and trait distribution,  $S_1(Z_1)$ ; (2) the earlier period's survival curve and the later period's trait distribution,  $S_1(Z_2)$ ; and (3), the later period's survival curve and trait distribution,  $S_2(Z_2)$ . The difference between (2) and (1) versus the difference between (3) and (2) indicates the contributions of the change in mean mass versus the change in survival curve. The juvenile survival did not change substantially, yet the observed small increase was caused by a change in the mass distribution. For older marmots, both processes made comparable contributions to the increase in survival (Fig. 4). The change in the mass distribution contributed slightly more to the increase in yearling survival, whereas the change in the survival curve contributed more to the increase in subadult and adult survival. As the increase in the survival of older individuals is the prominent cause of the observed population increase, both the faster growth of marmots and the change in the relationship between August mass and survival must have had an important role in the observed shift in population dynamics.

Finally, to understand the processes underlying the observed phenotypic change, we decomposed the change in mean body mass,  $\Delta \bar{Z}$ , into contributions from selection and other processes using the recently developed age-structured Price equation<sup>21</sup> (Supplementary Fig. 8A). The mean annual growth of juveniles increased from  $1,523.7 \text{ g year}^{-1}$  (s.e.m. = 45.1) for years before 2000 to  $1,847.4 \text{ g year}^{-1}$  (s.e.m. = 78.1) for those after 2000 ( $P < 0.01$ ). This faster growth from the first to the second August of life resulted in higher mean body masses in the older age classes, as also demonstrated by the retrospective perturbation analysis of the IPMs (Fig. 3c). The temporal change in mean body mass for the whole



**Figure 4 | Contributions of the changes in mean mass ( $Z_1$  to  $Z_2$ ) and mass-survival relationship ( $S_1$  to  $S_2$ ) to the increase in mean survival from  $<2000$  to  $\geq 2000$ .** The proximity of the triangle ( $S_1(Z_2)$ ) to the circle ( $S_1(Z_1)$ ) versus to the diamond ( $S_2(Z_2)$ ) indicates the contributions of the change in mean mass versus the change in survival curve for each age class. Confidence intervals indicate the process variation estimated using the particular mass distribution and survival function.

population over the 33 years was predominantly explained by changes in the mean growth rate contributions (52%), with selection-related terms contributing only 3% (Supplementary Fig. 8B), indicating that the change in body mass is not the result of a change in selection operating on the trait.

How can we interpret these results? The population-level response to environmental change was mediated to a large extent through environmental influences on body mass. The increase in the length of the growing season has altered the phenology; marmots are now born earlier and they have more time to grow until the next hibernation. This increase in juvenile growth has caused an increase in body mass in all age classes. Yet, most of this change was an ecological (plastic) rather than an evolutionary response to environmental change as also seen in Soay sheep on St Kilda<sup>22</sup>. This increase in body mass and the length of the growing season has also altered the functional dependence of vital rates on body mass. Heavier marmots now survive and reproduce better than they once did, and this has led to a rapid increase in population size in recent years.

A simultaneous response to environmental change in phenology, phenotypic traits and population dynamics seems to be commonplace in nature<sup>2</sup>. We have demonstrated how such joint dynamics can be investigated, and have shown how changes in phenotypic traits and population dynamics can be intimately linked. If we are to understand the biological consequences of environmental change it will prove necessary to gain further insight into these linkages. Despite this, we do not completely understand why the body-mass–demography associations changed as markedly as we observe. This means that predicting future change will prove more challenging than characterizing past change. We suspect that the observed increase in marmot survival is likely to be a short-term response to the lengthening growing season. Longer-term consequences may depend on whether long, dry summers become more frequent, as this would decrease growth rates and increase mortality rates. Characterizing observed interactions between environment, phenotypic traits and demography is challenging; accurately predicting how they may change in the future will almost certainly require a mechanistic understanding of how environmental change impacts resource availability as well as individual energy budgets<sup>30</sup>.

## METHODS SUMMARY

This study was conducted in the Upper East River Valley near the Rocky Mountain Biological Laboratory, Gothic, Colorado ( $38^\circ 57' \text{ N}$ ,  $106^\circ 59' \text{ W}$ , approximately 2,950 m elevation). We used data from 1,190 live-trapped females from 1976 to 2008. The body-mass data were collected from each individual at several captures during May–September. We used a generalized mixed model for each age class to estimate the 1 August (214th day-of-year) body masses accounting for the random

effects of year, site and individual identity. For the analysis of stage-specific survival functions, we used a multistate mark–recapture model where we tested for the individual and interaction effects of body mass (as a time-varying individual covariate) and the study period. We used generalized linear and additive models for the rest of the demographic and transition functions and tested for linear, nonlinear and interaction effects of body mass, age class and study period. Using the most parsimonious functions relating body mass to each demographic and trait-transition rate, we parameterized two  $400 \times 400$  stage- and mass-structured integral projection matrices (one for the pre-2000 period and one for after 2000), each consisting of 4 stages and 100 mass intervals. For the retrospective perturbation analysis, we created 512 IPMs representing all possible combinations of change among the nine functions and estimated the corresponding change in  $\lambda$ . The same method was used to estimate the contribution of each functional change to the change in mean adult mass. Using the age-structured Price equation, we decomposed the observed change in mean body mass into exact contributions from selection and other processes.

**Full Methods** and any associated references are available in the online version of the paper at [www.nature.com/nature](http://www.nature.com/nature).

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**Supplementary Information** is linked to the online version of the paper at [www.nature.com/nature](http://www.nature.com/nature).

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## METHODS

**The study system.** The yellow-bellied marmot is a large, diurnal, burrow-dwelling rodent, occupying montane regions of western North America<sup>25,31</sup>. The species hibernates from September or October to April or May, during which time individuals lose approximately 40% of their body mass<sup>25</sup>. The need to mobilize energy for reproduction and then prepare for hibernation in a short time period accounts for the energy conservative physiology of this species<sup>32,33</sup>. The critical factor determining winter survival and subsequent reproductive success is the amount of fat accumulated before hibernation<sup>34,35</sup>. On emergence all age classes start gaining mass at the rate of about 12–14 g day<sup>-1</sup>. The annual cycle is a major constraint on population dynamics. The need to satisfy the energy requirements for hibernation limits reproduction to a single annual event occurring immediately after emergence. The short active season combined with large body size delays reproductive maturity until two years of age<sup>36</sup>.

This study was conducted in the Upper East River Valley near the Rocky Mountain Biological Laboratory, Gothic, Colorado (38° 57' N, 106° 59' W). Data were collected from 17 distinct sites within the study area<sup>37,38</sup>. From 1962 to 2008, yellow-bellied marmots were live-trapped at each site throughout the active season (May–September) and individually marked using numbered ear tags<sup>39</sup>. Animal identification number, sex, mass and reproductive condition were recorded at each capture. Ages for females that were captured as juveniles were known, whereas ages for other females were estimated based on body mass ( $\leq 2$  kg = yearling,  $> 2$  kg = adult)<sup>24</sup>. In this study, we omitted the years before 1976 owing to lower sampling effort.

Survival and reproduction are affected by the length of the active season, which varies from year to year as a consequence of variation in the onset and/or termination of snow cover<sup>40,41</sup>. The length of the growing season also varies among marmot sites over a distance of 4.8 km in the Upper East River Valley where the greatest difference in elevation between colonies is 165 m. The biology of yellow-bellied marmots in Colorado is described in further detail elsewhere<sup>25,39</sup>.

**Estimation of 1 August body mass.** Marmot life history is tightly related to the circannual rhythm<sup>25</sup>. As marmots lose approximately 40% of their body mass during hibernation<sup>25</sup> and females give birth in late May, the mean body mass changes substantially over the active season and among age classes. Furthermore, the study area includes several sites with different elevations and aspects and the environmental conditions vary among years, causing variation in mean body mass among sites and years at a given date. In this study, we focus on the estimated 1 August body mass as it provides the best trade-off between data availability and biological significance. The trapping data until mid-August is sufficient to provide a good estimate of body mass, from which point on the data become sparse in most years (Supplementary Fig. 2). August mass is biologically significant for several reasons: (1) it is beyond the influence of the previous hibernation, particularly for non-reproductive stages; (2) marmots are weaned no later than mid-July and there is no reproductive activity until the following spring so 1 August mass is not confounded by pregnancy; (3) as the plant mass growth peaks in mid-July<sup>33,42</sup>, growth plateaus in early August for non-reproductive adults, mid-August for juveniles and late August for reproductive females<sup>25,43,44</sup>. Therefore, it covers most of the critical period for individual growth.

The body-mass data were collected from each individual at several captures throughout the active season. Individuals were captured an average of 3.12 times in a given year with a maximum of 7.45 captures in 2003. We grouped individuals into four age classes (*a*): juvenile (*a* = 1, year 0–1), yearling (*a* = 2, year 1–2), subadult (*a* = 3, year 2–3), and adult (*a* = 4, year  $> 3$ ). To estimate the 1 August body mass for each individual per year, we constructed a general linear mixed model including the fixed effect of day of year on body mass, and the random effects of year, site and individual identity. Models were fitted with the lme4 package<sup>45</sup>. A separate model was fitted to each age class and random deviations were incorporated in both the intercept and the (linear) day-of-year term for all three random effects. Because it includes several ages ( $\geq 3$  yrs old), the adult model also incorporates a random 'observation age' term (nested within individual) to accommodate individual level variation in size among successive observation years. We did not attempt to determine whether specific variance components were significantly different from zero. This is unnecessary when the goal of modelling is prediction; negligible sources of variation are simply estimated to be near zero and thus to contribute little to predicted values. For all four age classes we compared a set of nested models for the fixed effects structure, which incorporated up to third-order polynomial terms for day of year. The set of models constructed for adults also considered models with a fixed effect of age and the interaction of age with day of year. Fixed effect structures were compared using likelihood ratio tests<sup>46</sup>. Some caution is required when applying likelihood ratio tests to examine the significance of fixed effects as these

are known to be anticonservative. Fortunately, all of the results we report were highly significant.

The most parsimonious models included second-order polynomial terms for day of year in juveniles and yearlings, and only the linear effect in subadults and adults (Supplementary Fig. 2). The most parsimonious adult model also included an age effect but not the interaction term with day of year. For example, in juveniles and yearlings the expected mass of an individual at observation *i* is given by:

$$E[\mu_i] = (\beta_0 + u_{fm(i),0} + v_{yr(i),0} + w_{st(i),0}) + (\beta_1 + u_{fm(i),1} + v_{yr(i),1} + w_{st(i),1})D + \beta_2 D^2$$

where *D* is the day of year; *u*, *v* and *w* refer to the random female, year and site effects, respectively;  $\beta_1$  and  $\beta_2$  are the linear and quadratic fixed effect terms for day of year, respectively; and  $\beta_0$  is the global intercept. In the random terms, the first subscript (for example, *yr*(*i*)) can be viewed as a mapping function referencing the appropriate random effect level for observation *i*, and the second subscript references the random intercept or slope term as appropriate. Using the fitted models, we predicted the 1 August (214th day-of-year) mass for each individual conditional on the predicted random effects given by the best linear unbiased predictors (BLUPs). We used these estimated 1 August masses for the rest of the analyses.

### Relationship between body mass and demographic and trait transition rates.

To understand the link between phenotypic dynamics and population dynamics, we examined the relationship between body mass and each of the five demographic and trait transition rates using the long-term individual-based data. The demographic rates are, (1) the survival from one year to the next (0 or 1), (2) reproducing the following year conditional on survival (0 or 1), and (3) litter size conditional on reproduction ( $\geq 1$ ); whereas the trait-transition rates are, (4) the ontogenic growth from one August to the next, and (5) the average 1 August body mass of the offspring (that is, juvenile) produced to the next year. It is important to note that most of the juvenile growth (from its first to second August of life) occurs after individuals emerge from their first hibernation as yearlings; similarly, most of the yearling growth (from its second to third August of life) occurs after individuals emerge from their second hibernation as subadults.

For the analysis of survival rates, we used a multistate mark-recapture model<sup>26</sup> implemented using Program MARK<sup>47</sup> with the RMark interface<sup>48</sup>, where we tested for the effect of body mass (as a time-varying individual covariate) on stage-specific survival rates. For the rest of the rates, the functions were characterized using generalized linear and additive models (GAMs)<sup>27</sup>, as the associations between quantitative traits and demographic rates could be nonlinear<sup>49,50</sup>. For each rate, the number of demographic classes was determined by comparing models with different stage structures using Akaike's information criterion<sup>51</sup>.

We next tested for linear, nonlinear, and two-way interaction effects of the current August body mass, age class and study period. All rates, except for litter size and offspring mass, showed significant changes from the earlier to the later period (Supplementary Table 1), and body mass had a significant influence on all rates during both periods. Moreover, the relationship between body mass and some of the demographic and trait-transition rates significantly differed between the two periods (Supplementary Figs 4–7). The general models describing the demographic and trait-transition rates are summarized in Supplementary Table 1.

**Construction of the integral projection models.** The analysis of demographic and trait-transition rates described earlier showed that individual fates are influenced by their body mass and age class. To accommodate both factors in an efficient manner we constructed a stage- and mass-structured IPM. General IPMs project the distribution of discrete and continuous trait-structured population in discrete time. Their main advantage is that they allow parsimonious modelling of changes in both the phenotypic distribution and population growth rate based on easily estimated demographic and trait-transition functions<sup>28</sup>. Theory for general IPMs in a constant environment and an example application of an age- and size-structured model can be found in refs 29 and 52, respectively. Using the most parsimonious functions relating body mass to each demographic and trait-transition rate, we parameterized two IPMs, one for earlier ( $< 2000$ ) and one for later ( $\geq 2000$ ) years.

The two main elements of an IPM are the projected trait distributions for each stage class and the projection kernel components. Our IPM tracks the distribution of body mass in juvenile (*a* = 1), yearling (*a* = 2), subadult (*a* = 3) and adult (*a* = 4) stages. For a general stage class *a*, the number of individuals in the mass range  $[x, x + dx]$  at time *t* is denoted by  $n_a(x, t)$ . The dynamics of  $n_a(x, t)$  are governed by a set of coupled integral equations:

$$n_1(y, t+1) = \sum_{a=2}^4 \int_{\Omega} F_a(y, x) n_a(x, t) dx$$

$$n_{a+1}(y, t+1) = \int_{\Omega} P_a(y, x) n_a(x, t) dx \quad (\text{for } a=1, 2, 3)$$

$$n_4(y, t+1) = \int_{\Omega} P_3(y, x) n_3(x, t) dx + \int_{\Omega} P_4(y, x) n_4(x, t) dx$$

where  $\Omega$  is a closed interval characterizing the mass domain,  $F_a(y, x)$  are recruitment kernels that determine the contribution of juvenile, subadult and adult stages to the next generation, and  $P_a(y, x)$  are survival-growth kernels that determine the transitions among (or in the case of adults, within) the four life stages.

These kernels are implied directly by the statistical analysis of the data; the necessary functions are already parameterized for the two periods and summarized in Supplementary Table 1. The survival-growth kernel for individuals of age  $a$  is given by:

$$P_a(y, x) = S_a(x) G'_a(y, x)$$

An individual that remains in the population must survive over winter and grow. The prime notation in the growth kernel is present to highlight that this function is not the same object as the corresponding demographic growth model in Supplementary Table 1, but rather it is the conditional distribution of  $y$  given  $x$  (which is easily derived from the demographic growth model). The recruitment kernels are given by:

$$F_a(y, x) = S_a(x) R_a(x) L_a(x) Q'_a(y, x)$$

Reading from left to right, we see that to contribute a juvenile to the population in the following summer, a current individual with mass  $x$  must survive over winter and successfully reproduce in the following summer, giving rise to female recruits with mass  $y$ , the number and size of which depends on the reproducing adults' size. The prime notation present in the identifier of the offspring mass kernel serves the same purpose as that in the adult growth kernel above. The model only accounts for females, thus  $L_a(x)$  is the number of female offspring. Having specified the survival-growth and fecundity kernels, the model is now complete.

Sequential iteration of the IPM entails repeated numerical integration. To achieve this, we used a simple method called the midpoint rule. This method constructs a discrete approximation of the IPM on a set of 'mesh points' and then uses matrix multiplication to iterate the model. Similarly, computation of the asymptotic growth rate and stable age  $\times$  mass distribution is achieved by following the common procedures for a matrix projection model<sup>53</sup>. A detailed explanation of the midpoint rule has been previously given<sup>29</sup>. The accuracy of the method depends on the size of the mesh; increasing this improves the numerical accuracy of the approximation. We chose to divide the body mass interval into 50 mass classes, as this ensures that the population growth rate calculations are accurate to at least three decimal places.

**Retrospective perturbation analysis of the IPM.** To identify which one of the nine demographic and trait transition functions (Supplementary Table 1) contributed the most to the observed increase in  $\lambda$  from the earlier to the later period, we performed a retrospective perturbation analysis of the two IPMs. We first created a design matrix with nine columns representing all the functions (Supplementary Table 1) and 512 rows representing all possible combinations of change among these nine functions. The entries of the design matrix are 0 or 1, indicating whether the function was parameterized using  $<2000$  or  $\geq 2000$  data, respectively. Next, for each combination, we created an IPM and estimated the corresponding  $\lambda$ . Using the dummy coding for each of the nine functions as binary explanatory variables and  $\lambda$  as the response variable, we tested for the main effects of and two-way interactions between each of the nine functions. The main-effects model explained a substantial amount of the variation in  $\lambda$  ( $R^2 = 98.7\%$ ); therefore, we ignored the two-way interactions. The resulting regression effect sizes denote the change in  $\lambda$  contributed by the change in each of the nine demographic and trait transition components. Similarly, we estimated the contribution of each functional change to the mean adult mass by estimating a mean adult mass from the stable size distribution (right eigenvector) for each combination and applying the same methodology outlined above.

**The age-structured Price equation.** To understand the processes underlying the observed phenotypic change, we decomposed the change in mean body mass,

$\Delta \bar{Z}$ , into contributions from selection and other processes using the age-structured Price equation<sup>21,22</sup>. The exact change in mean value of a trait over a time step,  $\Delta \bar{Z}(t) = \bar{Z}(t+1) - \bar{Z}(t)$ , is decomposed into seven contributions. The mathematical details have been previously provided<sup>21,22</sup>. Here we provide further details on the interpretation of terms in Supplementary Fig. 8A. The *DCs* term describes change in  $\bar{Z}$  resulting from changes in demographic composition owing to ageing, whereas the *DCr* term describes the change in  $\bar{Z}$  resulting from the addition of new individuals owing to birth. The *VS* term is the viability selection differential on  $Z$  across all individuals; it describes how selective removal of individuals through mortality alters  $\bar{Z}$ . The contribution to  $\bar{Z}$  from age-specific trait development (growth or reversion) among individuals that survive is captured in the *GR* term. The *FS* term is the reproductive selection differential, which describes how  $\bar{Z}$  differs between parents and the unselected population. The *OMD* term represents the contribution of differences between offspring and parental trait values to  $\bar{Z}$ . The *ODC* term describes the contribution from any covariance between *OMD* and number of offspring produced by each individual. Each of these terms is weighted by demographic sensitivities, which describe how survival or reproduction in an age class contributes to population growth.

All analyses in this study were performed using the statistical and programming package, R (ref. 54).

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