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The timing of life-history events in a changing climate

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Although empirical and theoretical studies suggest that climate influences the timing of life-history events in animals and plants, correlations between climate and the timing of events such as egg-laying, migration or flowering do not reveal the mechanisms by which natural selection operates on life-history events. We present a general autoregressive model of the timing of life-history events in relation to variation in global climate that, like autoregressive models of population dynamics, allows for a more mechanistic understanding of the roles of climate, resources and competition. We applied the model to data on 50 years of annual dates of first flowering by three species of plants in 26 populations covering 4° of latitude in Norway. In agreement with earlier studies, plants in most populations and all three species bloomed earlier following warmer winters. Moreover, our model revealed that earlier blooming reflected increasing influences of resources and density-dependent population limitation under climatic warming. The insights available from the application of this model to phenological data in other taxa will contribute to our understanding of the roles of endogenous versus exogenous processes in the evolution of the timing of life-history events in a changing climate.

Keywords: evolution; life history; North Atlantic Oscillation (NAO); phenology

1. INTRODUCTION

An overwhelming number of recent analyses of long-term data on phenological patterns of animals and plants have reported earlier dates of migration to breeding sites, egg-laying or flowering ascribed to climatic warming (Beebee 1995; Fitter *et al.* 1995; Sparks & Carey 1995; Crick *et al.* 1997; Forchhammer *et al.* 1998*a*; Bradley *et al.* 1999; Brown *et al.* 1999; Crick & Sparks 1999; Dunn & Winkler 1999; Post & Stenseth 1999; Forchhammer & Post 2000). While these observations are valuable and provocative in that they call attention to possible large-scale ecological consequences of global warming, correlations between time or climate and phenological variables tell us little about the underlying selection pressures shaping the timing of life-history events. Nor do they provide much evolutionary basis for predicting the life-history responses of organisms to a warmer climate. This is because correlations do not allow us to discern whether earlier reproduction by animals and plants is a direct response to warmer temperatures, or a response to factors that may also vary with climate, such as reproductive resources and inter- and intraspecific competition.

To place relationships between climatic warming and phenological events in a life-history context, it is necessary to adopt an evolutionary perspective and to formulate such a perspective into a workable model (Roff 1992; Blarer *et al.* 1995). The struggle for existence envisaged by Darwin (1859) described individuals as competing with each other as well as contending with the abiotic environment in their strive to survive and reproduce. In an evolutionary context, therefore, the life-history strategies of individuals must involve outperforming their conspecific competitors in two ways: first, in terms of both number and viability of progeny (Harper 1977; Roff 1992); and, second, in terms of responding to the constraints of abiotic environmental conditions (Levins 1968; Partridge & Harvey 1988; Iwasa & Levin 1995; Brown & Brown 1998). Whereas the former is usually discussed in the context of reproductive success over the life span of an organism (Partridge & Harvey 1988; Stearns 1989), the latter may be more appropriately considered in terms of variation in strategies between years (Iwasa 1991; Iwasa & Levin 1995) in response, for example, to changes in climate (Forchhammer *et al.* 1998*a*; Post & Stenseth 1999; Forchhammer & Post 2000).

The timing of life-history events such as reproduction exerts considerable influence on the number and survival of progeny (Roff 1992; Sinervo & Doughty 1996; Olsson & Shine 1997); therefore, an evolutionarily stable strategy in many species might be to reproduce as early as possible when environmental conditions are favourable (Iwasa & Levin 1995; Stevenson & Bancroft 1995). Environmental, inter- and intraspecific constraints on earliest possible reproduction are, however, ecologically and evolutionarily plausible (Partridge & Harvey 1988; Iwasa 1991; Iwasa & Levin 1995; Klinkhamer *et al.* 1997) and several analyses have suggested that climatic warming may influence availability of resources and abundance of competitors (Callaghan & Jonasson 1995; Brooker & Callaghan 1998; Post & Stenseth 1999; Sætre *et al.* 1999).

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What remains obscure is the extent to which the long-term life-history responses of organisms to a warmer climate relate to the importance of changes in climate, resources and competition. We address this by developing an autoregressive model of the timing of life-history events that can be applied to long-term phenological data to draw inferences about the relative contributions of climate, resources and competition. With the development of this model, we attempt to fill a gap between those studies merely correlating climate and the timing of life-history events, and those short-term detailed field studies that identify specific mechanisms for the timing of life-history events but which cannot interpret the findings at the longer-term level of selection.

2. MODEL DEVELOPMENT

(a) *Definition of 'temporal dependence'*

The model framework employed is that previously used in the analysis of intertrophic-level influences on population dynamics when time-series on annual estimates of density at one trophic level are the only data available (Royama 1992; see also Stenseth *et al.* 1996; Forchhammer *et al.* 1998*b*; Forchhammer & Asferg 2000). We propose that autoregressive models of the form commonly encountered in studies of population dynamics can be suitably applied to the analysis of time-series that quantify changes in the annual timing of events. The term 'temporal dependence' is introduced in this context to denote a pattern of dependence among observed events that determines whether the timing of an event occurs earlier (negative temporal dependence) or later (positive temporal dependence) than it did in the previous one or more years. Hence, temporal dependence is an ecological phenomenon characterized by statistical autocorrelation in time-series on events that is analogous to the ecological phenomenon of density dependence as it applies to time-series on abundance. Temporal dependence may arise in two ways: either through the heritability of timing of events such as reproduction (Mitchell & Shaw 1993; Van Dijk *et al.* 1997) or through carry-over effects of density and resources on the timing of the event.

(b) *A model*

A general model of the timing of life-history events in iteroparous species in relation to variation in climate that incorporates the influences of resources and competitors (either conspecific or aspecific) is constructed for the timing of reproduction (e.g. migration, parturition, egg-laying or flowering) on the basis of empirical studies of plants and vertebrate animals. Here, in the interest of generality, our use of the term 'resources' is necessarily vague. Depending on the biology of the organism of interest, 'resources' might, to list a few examples, denote the availability and quality of forage, the physical condition of reproducing individuals, the availability and uptake of soil nutrients or the photosynthetic and meristematic activity of flowering plants, all of which could be influenced directly or indirectly by climatic variation. The generality of the model is intended to make it applicable to the analysis of the timing of life-history events in many species, including, where the assumptions are reasonable, semelparous or univoltine organisms.

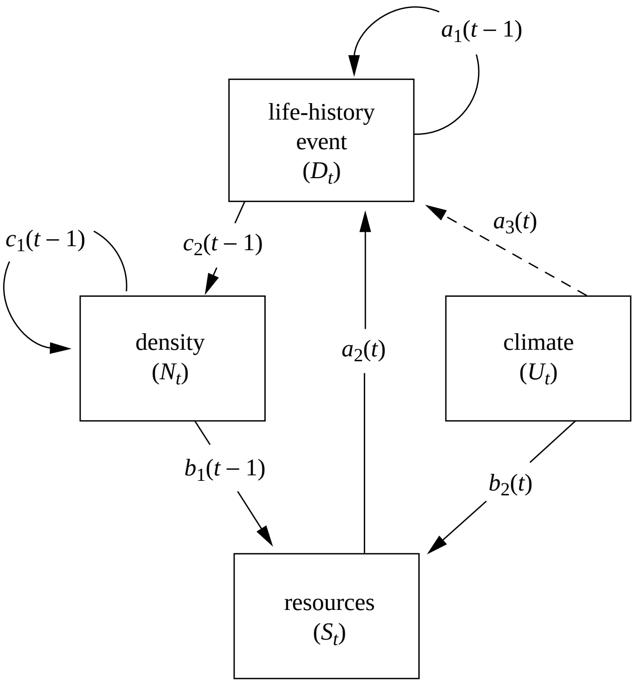

Figure 1. Conceptual model depicting relationships between the timing of a life-history event (D_t), population density (N_t), resources (S_t) and climate (U_t) that are formalized in a general statistical model of the timing of life-history events. The dashed line illustrates a potentially direct influence of climate on the life-history event that is not considered in our analysis (but see Appendix A for its implications and application).

We assume that the timing of reproduction in the current year depends on resources and the timing of reproduction in the previous year (figure 1) (Bell 1980). In large mammals and birds, for example, the annual timing of parturition and egg-laying, respectively, relate to the availability and quality of forage and, thereby, female condition, at the end of gestation (Lack 1966; Harvey *et al.* 1984; Bowyer 1991; Post & Klein 1999). In plants inhabiting seasonal environments, the timing of flowering depends on environmental control of the availability of soil nutrients and physiological processes related to the allocation of resources to reproductive tissue (Rathcke & Lacey 1985; Charlesworth & Morgan 1991; Shaver & Kummerow 1992; Galen & Stanton 1995; Molau 1996).

We further assume that resources in the current year depend on density in the previous year and climate in the current year (figure 1). For many species of animals, reproductive resources in the form of forage quality or physical condition of females during gestation are constrained by both density (Goulden & Hornig 1980; Kent 1981; Clutton-Brock *et al.* 1982, 1997) and large-scale climatic variation (Post & Stenseth 1999; Post *et al.* 1997, 1999). For plants, as well, availability of nutrients allocated to growth and reproduction can be limited by density of conspecific and aspecific competitors (Harper 1977; Wijk 1986), while soil and air temperatures constrain nutrient uptake and photosynthetic activity devoted to the accumulation of resources necessary for flowering (Shaver & Kummerow 1992; Molau 1996).

Finally, we assume that density in the current year depends on density and the timing of reproduction in the previous year (figure 1). In both animals and plants, the numbers and viability of offspring produced tend to decline as the season of production advances beyond some optimal date (Lack 1966; Schmitt 1983; Dieringer 1991; Galen & Stanton 1991; Post & Klein 1999).

Hence, in our model, climate influences the timing of reproduction through its influence on resources. Similarly, density in one year may influence the timing of reproduction in the following year through the effects of competition on resources (see, for example, Dunn & Winkler 1999). As we demonstrate in this section and in Appendix A, this can account for observations in some species of delayed effects of resources on the timing of reproduction in future years (Harper 1977; Bell 1980). Our model does not take into account potential influences of relationships between adjacent trophic levels, such as between predators and prey or between herbivores and plants (*sensu* Klinkhamer *et al.* 1997). Nor does it consider a potentially special case in which climate acts directly on the timing of reproduction without influencing resources (figure 1, dashed line; see Appendix A for a formalization of this effect). Inclusion of such an effect might be appropriate in studies of, for example, the onset of breeding in anurans that use ponds that are covered by ice during winter.

As illustrated in figure 1, interactions between the timing of reproduction, climate, resources and density-dependent population limitation can be summarized by three general functions:

$$d_t = f(d_{t-1}, s_t), \tag{1a}$$

$$s_t = g(n_{t-1}, u_t), \tag{1b}$$

$$n_t = n_{t-1} h(n_{t-1}, d_{t-1}), \tag{1c}$$

in which d_t is Julian date of reproduction, s_t is resources, n_t is density and u_t is climate, or some climatic anomaly, in year t, and where f, g and h are functions describing the date of reproduction, resources and density, respectively.

To reduce heteroscedasticity (Neter *et al.* 1990) in dates of reproduction (Forchhammer *et al.* 1998*a*; Post & Stenseth 1999) and remedy nonlinearity characteristic of temporal processes that are related to density (Gompertz 1825; May 1986) equations (1*a*) and (1*b*) can be expressed on a $\log_e$ scale. Equation (1*c*) is multiplicative and so with Taylor expansion it can be approximated as an additive function on a $\log_e$ scale. The $\log_e$ transformations give

$$D_t = a_0 + a_1 D_{t-1} + a_2 S_t, \tag{2a}$$

$$S_t = b_0 + b_1 N_{t-1} + b_2 U_t, \tag{2b}$$

$$N_t = c_0 + (1 + c_1) N_{t-1} + c_2 D_{t-1}, \tag{2c}$$

in which D_t is $\log_e(d_t)$, S_t is $\log_e(s_t)$ and N_t is $\log_e(n_t)$.

In the application of such autoregressive models to time-series data, endogenous and exogenous influences on changes in density, or in this case changes in the timing of events, can be inferred from the presence or absence of delayed autoregressive processes (Royama 1981; Turchin 1990; Stenseth 1995; Forchhammer *et al.* 1998*b*; Forchhammer & Asferg 2000). Thus, density dependence can be incorporated into resource dynamics by substituting equation (2*c*) into equation (2*b*) and solving them for S_t, which can be, in turn, substituted into equation (2*a*) (see Appendix A). This gives us a general autoregressive equation for the timing of life-history events in relation to climate that incorporates resources and density dependence (assuming additive stochasticity on a $\log_e$ scale):

$$\begin{aligned} D_t = {} & (b_1 c_0 a_2 - a_0 c_1 - c_1 a_2 b_0) + (1 + a_1 + c_1) D_{t-1} \\ & + (a_2 b_1 c_1 - a_1 - a_1 c_1) D_{t-2} + a_2 b_2 U_t \\ & + (-a_2 b_2 - c_1 a_2 b_2) U_{t-1} + \varepsilon_t, \end{aligned} \tag{3}$$

in which ε_t incorporates stochasticity and the remaining variance not included in the deterministic components of the model.

Upon examining the coefficients in equation (3), it is apparent that direct temporal dependence (the lag-one autoregressive term, D_{t-1}) may reflect influences of either (or both) the timing of reproduction in the previous year (a_1 from equation (2*a*)) or density dependence (c_1 from equation (2*c*)). As well, significant delayed temporal dependence (the lag-two autoregressive term, D_{t-2}) may reflect contributions from resources (a_2 from equation (2*a*)), density effects on resources (b_1 from equation (2*b*)), density dependence (c_1 from equation (2*c*)) or direct temporal dependence (a_1 from equation (2*a*)). A significant effect of climate in the current year (U_t in equation (3)) must reflect influences of both resources on the timing of reproduction (a_1 from equation (2*a*)) and of climate on resources (b_2 from equation (2*b*)), whereas a significant delayed effect of climate (U_{t-1}) may reflect influences of resources and climate ($a_2 b_2$) or of density dependence, resources and climate ($c_1 a_2 b_2$). By simplifying the coefficients in equation (3), we obtain the following general autoregressive model:

$$D_t = \beta_0 + (1 + \beta_1) D_{t-1} + \beta_2 D_{t-2} + \omega_1 U_t + \omega_2 U_{t-1} + \varepsilon_t. \tag{4}$$

Because the coefficient of direct temporal dependence includes 1, its statistical significance depends on difference from 1; hence negative temporal dependence results if $(1 + \beta_1) < 1$, and vice versa for positive temporal dependence.

The nature of this model allows us to draw inferences about the potential concerted effects of resources and density, as well as the concerted effects of climate, resources and density, based on the statistical significance or non-significance of the coefficients β_2 and ω_2 of the delayed temporal dependence (D_{t-2}) and climate (U_{t-1}) terms, respectively. Moreover, we can quantify the relative contributions of direct temporal dependence and density dependence if the coefficient $(1 + \beta_1)$ of the first-order autoregressive term (D_{t-1}) in equation (4) is significant (see Appendix A).

3. MATERIAL AND METHODS

(a) *A measure of global climatic variability: the North Atlantic Oscillation index*

To investigate the manner in which large-scale climatic warming influences the timing of life-history events in local populations, we incorporated the North Atlantic Oscillation (NAO) into our analyses. The NAO is an alternation in atmospheric pressures along a meridional gradient between

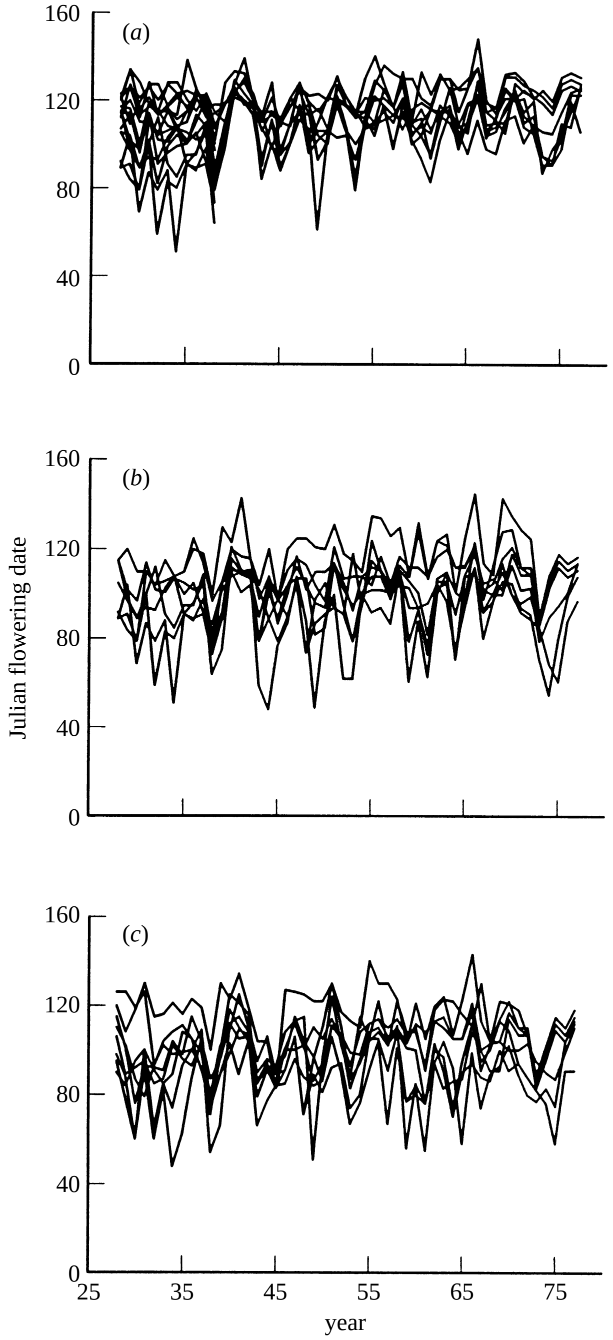

Figure 2. Annual dates of first flowering by (*a*) *Anemone nemorosa* in ten populations, (*b*) *A. hepatica* in eight populations, and (*c*) *Tussilago farfara* in eight populations in Norway from 1928 to 1977. Data are from Lauscher & Lauscher (1990).

centres over Iceland and the Azores (Lamb & Peppler 1987) that determines up to 33% of the interannual variation in winter precipitation in the Northern Hemisphere (Hurrell 1996) and up to 55% of the interannual variation in mean temperatures throughout much of the Northern Hemisphere (Schlesinger & Ramankutty 1994). The state of the NAO during winter is quantified annually as the winter NAO index, which is based on deviations from the mean difference in sea-level pressures between Iceland and the Azores for the months December–March (Hurrell 1995). Positive values of the NAO index quantify warm, wet winters in northern Europe and Scandinavia, whereas the opposite is true of negative values of the NAO index (Hurrell 1995).

(b) *Long-term data on plant phenology*

We analysed time-series on 50 years of annual dates of first flowering by three species of vascular plants (*Anemone nemorosa*, *A. hepatica* and *Tussilago farfara*) in a total of 26 populations in Norway (Lauscher & Lauscher 1990) (figure 2). We used $\log_e$-transformed dates to stabilize variances and to meet the assumptions described in the derivation of the model (equation (4)). Series were checked for stationarity by regressing $\log_e$-transformed dates against year; five out of the 26 regressions were significant and in these the term 'year' was included as an independent variable in the autoregressive models.

To assess the relative influences of temporal dependence and climatic fluctuation on timing of flowering, we set U_t in equation (4) equal to the NAO index of the current winter and U_{t-1} in equation (4) equal to the NAO index of the previous winter, then tested for the significance of these terms and the coefficients of direct and delayed temporal dependence using the AR(1) and AR(2) models in PROC AUTOREG (the autoregression procedure), SAS v. 6.12 (SAS Institute, Inc. 1996). The most parsimonious model was that with the lowest Akaike information criterion (AIC) score; we considered changes in the AIC score of less than one to represent insignificant improvement of the model (Sakamoto *et al.* 1986).

To quantify the influences of life-history traits and characteristics of the sites inhabited by the focal populations on variation in the coefficients in equation (4) (*sensu* Post & Stenseth 1999) we used forward linear, step-wise regression to model the coefficients as functions of latitude, longitude, site elevation, distance from the coast and the 50-year mean flowering date of the species at each site.

4. RESULTS

All 26 populations displayed significant, negative temporal dependence (i.e. $1 + \beta_1 < 1$), the most parsimonious dimension of which was 1, and timing of flowering in 24 of these populations was significantly related to the NAO index of the current year (table 1). None of the time-series displayed significant delayed temporal dependence or climatic effects. In nearly all populations (20 out of 26), significance of the direct temporal-dependence term (D_{t-1} from equation (4)) was attributable solely to the significance of the coefficient of density-dependent population limitation, c_1, from equation (2*c*) (table 1; see also Appendix A).

Following warm winters, plants in 24 out of 26 populations bloomed significantly earlier, and the NAO alone accounted for up to 48% of the interannual variation across populations and species (table 1). In all but one of these 24 populations, the proportion of the variance in flowering dates attributable to the NAO was at least half of the total proportion explained (table 1). The significance of the coefficient of direct climatic influence (ω_1 from equation (4)) on the timing of flowering in these 24 populations indicated significant effects of climate on resources (b_2 from equation (2*b*)) and of resources on the timing of flowering (a_2 from equation (2*a*)).

The strength of temporal dependence decreased from southern to northern sites (partial $r = 0.46$, $p = 0.01$) (figure 3*a*). Also, temporal dependence was stronger in early-blooming than in late-blooming plants (partial $r = 0.45$, $p = 0.03$) (figure 3*b*) (total model $R^2 = 0.31$, $p = 0.006$). Similarly, large-scale climatic fluctuation more

Table 1. *Coefficients* (± *s.e.m.*) *of autoregressive models of timing of flowering by plants in Norway* (*1928–1977*)

(Bold type indicates significant terms at $p < 0.05$; estimation of statistical density dependence is described in Appendix A; r^2_{NAO} indicates the amount by which the total R^2 increased with inclusion of the NAO term.)

population	temporal dependence $(1+\beta_1)$	statistical density dependence	direct climatic influence ω_1 (NAO_t)	R^2	r^2_{NAO}
Anemone nemorosa					
Trondheim	**0.34 ± 0.14**	—	**−0.012 ± 0.005**	**0.28**	**0.07**
Ranheim	**0.18 ± 0.15**	**−0.82 ± 0.15**	**−0.022 ± 0.006**	**0.25**	**0.20**
Helle	**−0.23 ± 0.14**	**−1.23 ± 0.14**	**−0.044 ± 0.008**	**0.37**	**0.36**
Notodden	**0.09 ± 0.15**	**−0.91 ± 0.15**	**−0.029 ± 0.01**	**0.17**	**0.15**
Lillehammer	**−0.01 ± 0.15**	**−1.01 ± 0.15**	−0.004 ± 0.005	0.02	0.00
Ham	**0.16 ± 0.15**	**−0.84 ± 0.15**	**−0.012 ± 0.005**	**0.14**	**0.11**
Vang	**0.21 ± 0.14**	**−0.79 ± 0.14**	**−0.020 ± 0.005**	**0.30**	**0.24**
Øksna	**0.21 ± 0.15**	—	**−0.012 ± 0.006**	**0.25**	**0.14**
Asker	**0.15 ± 0.14**	**−0.85 ± 0.14**	**−0.025 ± 0.007**	**0.24**	**0.20**
Dilling	**0.14 ± 0.15**	**−0.86 ± 0.15**	**−0.026 ± 0.008**	**0.22**	**0.19**
Anemone hepatica					
Trondheim	**0.32 ± 0.14**	—	−0.027 ± 0.01	**0.21**	**0.10**
Ranheim	**0.004 ± 0.15**	**−0.99 ± 0.15**	**−0.044 ± 0.01**	**0.24**	**0.22**
Helle	**−0.14 ± 0.15**	**−1.14 ± 0.15**	**−0.084 ± 0.027**	**0.33**	**0.32**
Lillehammer	**−0.09 ± 0.15**	**−1.09 ± 0.15**	**−0.017 ± 0.006**	**0.13**	**0.12**
Ham	**−0.07 ± 0.15**	—	**−0.024 ± 0.007**	**0.39**	**0.17**
Vang	**−0.03 ± 0.15**	**−1.03 ± 0.15**	**−0.034 ± 0.005**	**0.50**	**0.48**
Øksna	**0.06 ± 0.15**	**−0.94 ± 0.15**	**−0.032 ± 0.007**	**0.30**	**0.29**
Asker	**−0.29 ± 0.14**	**−1.29 ± 0.14**	**−0.041 ± 0.008**	**0.34**	**0.33**
Tussilago farfara					
Trondheim	**0.21 ± 0.14**	**−0.79 ± 0.14**	**−0.033 ± 0.013**	**0.17**	**0.12**
Ranheim	**−0.10 ± 0.15**	**−1.10 ± 0.15**	**−0.033 ± 0.011**	**0.15**	**0.14**
Helle	**−0.06 ± 0.15**	**−1.06 ± 0.15**	**−0.042 ± 0.013**	**0.17**	**0.15**
Lillehammer	**0.20 ± 0.15**	**−0.80 ± 0.15**	−0.01 ± 0.01	**0.06**	0.02
Ham	**0.21 ± 0.14**	—	**−0.023 ± 0.007**	**0.30**	**0.16**
Vang	**0.14 ± 0.14**	—	**−0.033 ± 0.007**	**0.39**	**0.29**
Øksna	**0.13 ± 0.15**	**−0.87 ± 0.15**	**−0.027 ± 0.008**	**0.22**	**0.19**
Dilling	**0.01 ± 0.15**	**−0.99 ± 0.15**	**−0.059 ± 0.016**	**0.23**	**0.22**

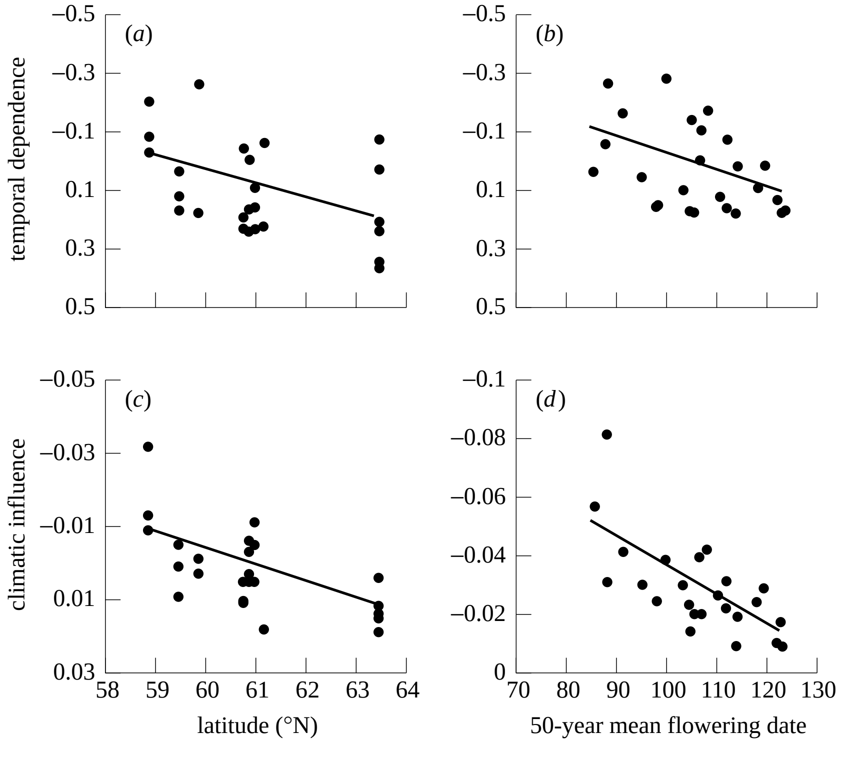

Figure 3. Variation in the strength of temporal dependence $(1+\beta_1)$ on annual dates of flowering with (*a*) latitude and (*b*) the 50-year mean flowering date of *Anemone nemorosa*, *A. hepatica* and *Tussilago farfara* at each site. Variation in the strength of the climatic influence (ω_1) (of the NAO) on annual dates of flowering with (*c*) latitude and (*d*) the 50-year mean flowering date of each population at each site. The *y*-axes are reversed to depict increasing strength from positive to negative coefficients, and the values are residuals after controlling for the significance of other variables included in the multiple regression (see § 3(b)).

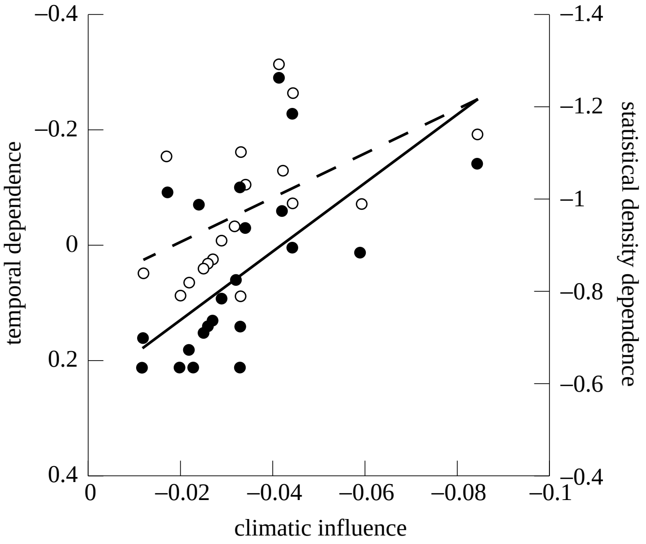

Figure 4. Increases in temporal dependence (closed circles) and statistical density dependence (open circles) with the strength of influence of large-scale climatic warming on annual timing of flowering by *Anemone nemorosa*, *A. hepatica* and *Tussilago farfara*.

strongly influenced timing of flowering at southern latitudes (partial $r = 0.46$, $p = 0.001$) (figure 3*c*) and in early-blooming plants (partial $r = 0.69$, $p < 0.001$) (figure 3*d*) (total model $R^2 = 0.68$, $p < 0.001$). Plants inhabiting southern sites in Norway, and plants that bloomed early, were thus more susceptible, or more responsive, to large-scale variation in winter climate.

A regression of the coefficients of temporal dependence against the coefficients of climatic influence on timing of flowering for all populations (table 1) revealed that temporal dependence intensified with the strength of the climatic influence across all populations (figure 4) ($r = 0.57$, $p = 0.003$). Hence, either those populations that were most strongly influenced by climate also showed a greater tendency to bloom earlier, or those populations in which there was a tendency to bloom earlier in successive years were also more responsive to winter warming. Finally, density dependence increased with the strength of the climatic influence on timing of flowering across populations (figure 4) ($r = 0.54$, $p = 0.02$).

5. DISCUSSION

Increasingly early reproduction following increasingly warm winters is a consistent observation of numerous phenological studies of diverse taxa (see § 1). The timing of reproduction influences the numbers, growth and viability of offspring (Roff 1992) and so climatic constraints on life-history events have implications for the fitness of organisms in variable environments. Hence, a mechanistic understanding of the processes underlying correlations between climate and the timing of life-history events should allow us to discern whether organisms are really responding to the alleviation of climatic constraints, or whether they are responding to changes in resources and/or competition that arise as consequences of climatic change. Furthermore, mechanistic modelling of life-history responses to climatic change with the approach developed here provides a basis for interpreting the evolutionary strategies employed by species in variable environments (Post *et al.* 2001).

Application of long-term phenological data to our model revealed patterns in the data indicating the following: first, plants across widely different regions that experienced highly variable local weather conditions bloomed earlier following warm winters; second, they did so in response to climatic influences on resources following warm winters, since coefficients a_2 and b_2 from equations (2*a*) and (2*b*), respectively, were both significant in our model (equations (3) and (4)); and, third, they did so in response to increasing density-dependent competition following warm winters (figure 4), since significant temporal dependence was related, in nearly all populations (table 1), to the significance of coefficient c_1 from equation (2*c*) (see Appendix A).

While one might expect that increasing density dependence would delay reproduction, this will only be the case if increasing density limits resources (i.e. if b_1 is significantly negative, figure 1). Such an effect would appear in the significance of coefficient β_2 of the delayed-temporal-dependence term D_{t-2}, which was not significant in any of our populations. Furthermore, our results echo a similar association in tree swallows (*Tachycineta bicolor*) throughout North America of earlier reproduction in areas of higher density (Dunn & Winkler 1999). A possible interpretation of this result is that earlier reproduction is a strategy aimed at minimizing competition for mates, food or pollinators, but see Dunn & Winkler (1999) for an alternative, though not mutually exclusive, hypothesis.

Although previous investigations of the effects of local weather conditions, especially during late-winter and spring months, have generally explained more of the variation in annual flowering dates than did our model (see, for example, Fitter *et al.* 1995; Sparks & Carey 1995), this analysis illustrates the mechanisms through which the timing of flowering may evolve in response to large-scale winter warming. In an evolutionary context, the evolutionarily stable timing of reproduction may be to reproduce as early as possible when climatic conditions are favourable (Iwasa & Levin 1995), and the presence of significant negative temporal dependence in all populations examined here suggests that plants in this analysis tended to bloom earlier in succeeding years. The strategy of earliest possible blooming may, however, incur risks, since weather conditions at the end of winter are unpredictable and snow or freezing temperatures may occur suddenly, killing flowers (Rathcke & Lacey 1985; Molau 1996; Callaghan & Carlsson 1996). Similarly, activity of pollinators may be more susceptible to changes in weather early in the flowering season (Molau 1996; Richards 1997). Nonetheless, the fitness costs of blooming late are extreme, since late-blooming individuals produce fewer and smaller seeds (Schmitt 1983; Dieringer 1991) as well as seedlings that exhibit poor survival (Galen & Stanton 1995).

In northern latitudes, the climatic constraint on timing of flowering may be more important than competition because flowering does not commence until release from snow (Rathcke & Lacey 1985; Molau 1996). In many species of flowering plants, moreover, the importance of climate to reproductive success is readily apparent. The delay in flowering induced by persistent snow cover, for example, leads to an abbreviated flowering season (Callaghan 1974; Shaver & Kummerow 1992), low seed production (Molau 1996), low seed mass and, consequently, reduced seedling survival (Galen & Stanton 1991) culminating in population-dynamical effects (Callaghan & Emanuelsson 1985; Carlsson & Callaghan 1990; Wookey *et al.* 1993).

That the magnitude of density dependence increased with the magnitude of the climatic influence on timing of flowering (figure 4) suggests, however, that competition may increase in a warmer climate. Similarly, both empirical observations and models have noted elevated rates of plant growth in response to climatic warming that are of sufficient magnitude to increase both intra- and interspecific competition (Carlsson & Callaghan 1994; Jacoby *et al.* 1996; Myneni *et al.* 1997). Additionally, because the importance of resources to the timing of flowering apparently intensified with large-scale climatic warming, we suggest that resources, for example the availability and uptake of soil nutrients or photosynthetic and meristematic activity in flowering plants, may increase in a warmer climate. Together with long-term phenological data, the model presented here may help elucidate similar mechanisms and patterns of life-history variation in other terrestrial organisms in response to climatic change.

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APPENDIX A

Isolating N_{t-1} in equation (2*b*) and inserting the resulting equation into equation (2*c*) gives an equation describing density in terms of resources, climate and the timing of reproduction:

$$N_t = c_0 + (1 + c_1)\frac{1}{b_1}(S_t - b_0 - b_2 U_t) + c_2 D_{t-1}. \tag{A1}$$

Setting $t = t - 1$ and inserting equation (A1) back into equation (2*b*) leads to a modified autoregressive equation of resource dynamics in terms of previous years' resources, climate and timing of reproduction:

$$S_t = b_0 + b_1 c_0 + (1 + c_1)(S_{t-1} - b_0 - b_2 U_{t-1}) + b_1 c_2 D_{t-2} + b_2 U_t. \tag{A2}$$

If we then solve equation (2*a*) for S_t, set $t = t-1$, and insert this into equation (A2), we obtain an equation for resource dynamics in terms of previous years' timing of reproduction and climate:

$$S_t = b_0 + b_1 c_0 + (1 + c_1)[\frac{1}{a_2}(D_{t-1} - a_0 - D_{t-2}) - b_0 - b_2 U_{t-1}] + b_1 c_2 D_{t-2} + b_2 U_t, \tag{A3}$$

in which constants b_1 and b_2 derive from the resource equation (equation (2*b*)), while constants c_1 and c_2 derive from the density equation (equation (2*c*)). To incorporate resources and density into a general model of the timing of reproduction, we then insert equation (A3) back into equation (2*a*), giving equation (3). Equation (4) results from re-designating the coefficients to simplify terms.

If, in our conceptual model, we include a direct influence of climate on the timing of the life-history event (coefficient a_3 and dashed line in figure 1), the resulting equation for resource dynamics is identical to equation (A3), except that it now includes an additional lagged climate term:

$$S_t = b_0 + b_1 c_0 + (1 + c_1)[\frac{1}{a_2}(D_{t-1} - a_0 - a_1 D_{t-2} - a_3 U_{t-1}) - b_0 - b_2 U_{t-1} + b_1 c_2 D_{t-2} + b_2 U_t. \tag{A4}$$

Insertion of this back into the alternative to equation (2*a*) that includes a direct climatic influence ($D_t = a_0 + a_1 D_{t-1} + a_2 S_t + a_3 U_t$) thus results in a model for the timing of life-history events that is identical to equation (3), except for the presence of additional direct and delayed climate terms; hence, after gathering the terms and simplifying, the coefficients of the direct and delayed climatic terms will both contain 1, and their significance must be tested on the basis of difference from 1.

The coefficient of temporal dependence $(1 + \beta_1)$ in the general model of the timing of life-history events (equation (4)) incorporates the influences of both temporal dependence and density dependence. If the coefficient of temporal dependence $(1 + \beta_1)$ in equation (4) is significant (i.e. $\neq 1$), it can be deconstructed to quantify its composition by density dependence, which will allow for quantification of the influence of density dependence on variation in D_t across years. This can be achieved as follows: if $(1 + \beta_1) \neq 1$ in equation (4), then either one or both of a_1 and c_1 are non-zero constants. The significance of a_1 can be tested in the following simple linear relationship: $D_t = a_0 + a_1 D_{t-1}$. The value of a_1 in this regression will differ from that of $(1 + \beta_1)$ in equation (4) simply because of the absence of terms quantifying direct and delayed temporal dependence and climatic effects (Neter *et al.* 1990). Thus, if a_1 in this regression is not significantly different from 0, then $(1 + \beta_1)$ in equation (4) is equal to $1 + c_1$, and the coefficient of density dependence is $c_1 = (1 + \beta_1) - 1$.

REFERENCES

Beebee, T. J. C. 1995 Amphibian breeding and climate. *Nature* **374**, 219–220.

Bell, G. 1980 The costs of reproduction and their consequences. *Am. Nat.* **116**, 45–76.

Blarer, A., Doebeli, M. & Stearns, S. C. 1995 Diagnosing senescence: inferring evolutionary causes from phenotypic patterns can be misleading. *Proc. R. Soc. Lond.* B **262**, 305–312.

Bowyer, R. T. 1991 Timing of parturition and lactation in southern mule deer. *J. Mamm.* **72**, 138–145.

Bradley, N. L., Leopold, A. C., Ross, J. & Huffaker, W. 1999 Phenological changes reflect climate change in Wisconsin. *Proc. Natl Acad. Sci. USA* **96**, 9701–9704.

Brooker, R. W. & Callaghan, T. V. 1998 The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. *Oikos* **81**, 196–206.

Brown, C. R. & Brown, M. B. 1998 Intense natural selection on body size and wing and tail asymmetry in cliff swallows during severe weather. *Evolution* **52**, 1461–1475.

Brown, J. L., Li, S.-H. & Bhagabati, N. 1999 Long-term trend toward earlier breeding in an American bird: a response to global warming? *Proc. Natl Acad. Sci. USA* **96**, 5565–5569.

Callaghan, T. V. 1974 Intraspecific variation in *Phleum alpinum* L. with special reference to polar populations. *Arctic Alpine Res.* **6**, 361–401.

Callaghan, T. V. & Carlsson, B. Å. 1996 Impacts of climate change on demographic processes and population dynamics in Arctic plants. In *Global change and arctic terrestrial ecosystems* (ed. W. C. Oechel, T. V. Callaghan, T. Gilmanov, J. I. Holten, B. Maxwell, U. Molau and B. Sveinbjörnsson), pp. 129–152. New York: Springer.

Callaghan, T. V. & Emanuelsson, U. 1985 Population structure and processes of tundra plants and vegetation. In *The population structure of vegetation* (ed. J. White), pp. 399–439. Dordrecht, The Netherlands: Junk.

Callaghan, T. V. & Jonasson, S. 1995 Arctic terrestrial ecosystems and environmental change. *Phil. Trans. R. Soc. Lond.* A **352**, 259–276.

Carlsson, B. Å. & Callaghan, T. V. 1990 Effects of flowering on the shoot dynamics of *Carex bigelowii* along an altitudinal gradient in Swedish Lapland. *J. Ecol.* **78**, 152–165.

Carlsson, B. Å. & Callaghan, T. V. 1994 Impact of climate change factors on the clonal sedge *Carex bigelowii*—implications for population growth and vegetative spread. *Ecography* **17**, 321–330.

Charlesworth, D. & Morgan, M. T. 1991 Allocation of resources to sex functions in flowering plants. *Phil. Trans. R. Soc. Lond.* B **332**, 91–102.

Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. 1982 *Red deer: ecology and behaviour of two sexes.* University of Chicago Press.

Clutton-Brock, T. H., Illius, A. W., Wilson, K., Grenfell, B. T., MacColl, A. D. C. & Albon, S. D. 1997 Stability and instability in ungulate populations: an empirical analysis. *Am. Nat.* **149**, 195–219.

Crick, H. Q. P. & Sparks, T. H. 1999 Climate change related to egg-laying trends. *Nature* **399**, 423–424.

Crick, H. Q. P., Dudley, C., Glue, D. E. & Thomson, D. L. 1997 UK birds are laying eggs earlier. *Nature* **388**, 526.

Darwin, C. 1859 *On the origin of species.* London: John Murray.

Dieringer, G. 1991 Variation in individual flowering time and reproductive success of *Agalinis strictifolia* (Scrophulariaceae). *Am. J. Bot.* **78**, 497–503.

Dunn, P. O. & Winkler, D. W. 1999 Climate change has affected the breeding date of tree swallows throughout North America. *Proc. R. Soc. Lond.* B **266**, 2487–2489.

Fitter, A. H., Fitter, R. S. R., Harris, I. T. B. & Williamson, M. H. 1995 Relationships between first flowering date and temperature in the flora of a locality in central England. *Funct. Ecol.* **9**, 55–60.

Forchhammer, M. C. & Asferg, T. 2000 Invading parasites cause a structural shift in red fox dynamics. *Proc. R. Soc. Lond.* B **267**, 779–786.

Forchhammer, M. C. & Post, E. 2000 Climatic signatures in ecology. *Trends Ecol. Evol.* **15**, 286.

Forchhammer, M. C., Post, E. & Stenseth, N. Chr. 1998*a* Breeding phenology and climate. *Nature* **391**, 29–30.

Forchhammer, M. C., Stenseth, N. Chr., Post, E. & Langvatn, R. 1998*b* Population dynamics of Norwegian red deer: density-dependence and climatic variation. *Proc. R. Soc. Lond.* B **265**, 341–350.

Galen, C. & Stanton, M. L. 1991 Consequences of emergence phenology for reproductive success in *Ranunculus adoneus* (Ranunculaceae). *Am. J. Bot.* **78**, 978–988.

Galen, C. & Stanton, M. L. 1995 Responses of snowbed plant species to changes in growing-season length. *Ecology* **76**, 1546–1557.

Gompertz, B. 1825 On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of life contingencies. *Phil. Trans. R. Soc. Lond.* B **115**, 513–585.

Goulden, C. E. & Hornig, L. L. 1980 Population oscillations and energy reserves in planktonic Cladocera and their consequences to competition. *Proc. Natl Acad. Sci. USA* **77**, 1716–1720.

Harper, J. L. 1977 *Population biology of plants*. London: Academic Press.

Harvey, P. H., Greenwood, P. J. & Campbell, B. 1984 Timing of laying by the pied flycatcher in relation to age of male and female parent. *Bird Study* **31**, 57–60.

Hurrell, J. W. 1995 Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. *Science* **269**, 676–679.

Hurrell, J. W. 1996 Influence of variations in extratropical wintertime teleconnections on Northern Hemisphere temperature. *Geophys. Res. Lett.* **23**, 665–668.

Iwasa, Y. 1991 Asynchronous pupation of univoltine insects as evolutionarily stable phenology. *Res. Popul. Ecol.* **33**, 213–227.

Iwasa, Y. & Levin, S. A. 1995 The timing of life history events. *J. Theor. Biol.* **172**, 33–42.

Jacoby, G. C., D'Arrigo, R. D. & Davaajamts, T. 1996 Mongolian tree rings and 20th-century warming. *Science* **273**, 771–773.

Kent, E. B. 1981 Life history responses to resource variation in a sessile predator, the ciliate protozoan *Tokophrya lemnarum* Stein. *Ecology* **62**, 296–302.

Klinkhamer, P. G. L., Kubo, T. & Iwasa, Y. 1997 Herbivores and the evolution of the semelparous perennial life-history of plants. *J. Evol. Biol.* **10**, 529–550.

Lack, D. 1966 *Population studies of birds.* Oxford University Press.

Lamb, P. J. & Peppler, R. A. 1987 North Atlantic Oscillation: concept and an application. *Bull. Am. Met. Soc.* **68**, 1218–1225.

Lauscher, A. & Lauscher, F. 1990 *Phänologie norwegens, teil IV.* Vienna: Eigen.

Levins, R. 1968 *Evolution in changing environments.* Princeton University Press.

May, R. M. 1986 When two and two do not make four: nonlinear phenomena in ecology. *Proc. R. Soc. Lond.* B **228**, 241–266.

Mitchell, R. J. & Shaw, R. G. 1993 Heritability of floral traits for the perennial wild flower *Penstemon centranthifolius* (Scrophulariaceae): clones and crosses. *Heredity* **71**, 185–192.

Molau, U. 1996 Climate impacts on flowering, growth, and vigour in an arctic-alpine cushion plant, *Diapensia lapponica*, under different snow cover regimes. *Ecol. Bull.* **45**, 210–219.

Myneni, R. B., Keeling, C. D., Tucker, C. J., Asrar, G. & Nemani, R. R. 1997 Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* **386**, 698–702.

Neter, J., Wasserman, W. & Kutner, M. H. 1990 *Applied linear statistical models*. Boston, MA: Irwin.

Olsson, M. & Shine, R. 1997 The seasonal timing of oviposition in sand lizards (Lacerta agilis): why early clutches are better. *J. Evol. Biol.* **10**, 369–381.

Partridge, L. & Harvey, P. H. 1988 The ecological context of life history evolution. *Science* **241**, 1449–1455.

Post, E. & Klein, D. R. 1999 Caribou calf production and seasonal range quality during a population decline. *J. Wildl. Mngmt* **63**, 335–345.

Post, E. & Stenseth, N. Chr. 1999 Climatic variability, plant phenology, and northern ungulates. *Ecology* **80**, 1322–1339.

Post, E., Stenseth, N. Chr., Langvatn, R. & Fromentin, J.-M. 1997 Global climate change and phenotypic variation among red deer cohorts. *Proc. R. Soc. Lond.* B **264**, 1317–1324.

Post, E., Langvatn, R., Forchhammer, M. C. & Stenseth, N. Chr. 1999 Environmental variation shapes sexual dimorphism in red deer. *Proc. Natl Acad. Sci. USA* **96**, 4467–4471.

Post, E., Levin, S. A., Iwasa, Y. & Stenseth, N. Chr. 2001 Reproductive asynchrony increases with environmental disturbance. *Evolution.* (In the press.)

Rathcke, B. & Lacey, E. P. 1985 Phenological patterns of terrestrial plants. *A. Rev. Ecol. Syst.* **16**, 179–214.

Richards, A. J. 1997 *Plant breeding systems*. New York: Chapman & Hall.

Roff, D. A. 1992 *The evolution of life histories*. New York: Chapman & Hall.

Royama, T. 1981 Fundamental concepts and methodology for the analysis of animal population dynamics, with particular reference to univoltine species. *Ecol. Monogr.* **51**, 473–493.

Royama, T. 1992 *Analytical population dynamics.* New York: Chapman & Hall.

Sætre, G.-P., Post, E. & Král, M. 1999 Can environmental fluctuation prevent competitive exclusion in sympatric flycatchers? *Proc. R. Soc. Lond.* B **266**, 1247–1252.

Sakamoto, Y., Ishiguro, M. & Kitagawa, G. 1986 *Akaike information criterion statistics*. Tokyo: KTK Scientific Publishers.

SAS Institute, Inc. 1996 *SAS/ETS user's guide.* Cary, NC: SAS Institute, Inc.

Schlesinger, M. E. & Ramankutty, N. 1994 An oscillation in the global climate system of period 65–70 years. *Nature* **367**, 723–726.

Schmitt, J. 1983 Individual flowering phenology, plant size, and reproductive success in *Linanthus androsaceus*, a California annual. *Oecologia* **59**, 135–140.

Shaver, G. R. & Kummerow, J. 1992 Phenology, resource allocation, and growth of arctic vascular plants. In *Arctic ecosystems in a changing climate: an ecophysiological perspective* (ed. F. S. Chapin III, R. L. Jeffries, J. F. Reynolds, G. R. Shaver, J. Svoboda & E. W. Chu), pp. 193–211. San Diego, CA: Academic Press.

Sinervo, B. & Doughty, P. 1996 Interactive effects of offspring size and timing of reproduction on offspring reproduction: experimental, maternal, and quantitative genetic aspects. *Evolution* **50**, 1314–1327.

Sparks, T. H. & Carey, P. D. 1995 The responses of species to climate over two centuries: an analysis of the Marsham phenological record, 1736–1947. *J. Ecol.* **83**, 321–329.

Stearns, S. C. 1989 Trade-offs in life-history evolution. *Funct. Ecol.* **3**, 259–268.

Stenseth, N. Chr. 1995 Snowshoe hare populations: squeezed from below and above. *Science* **269**, 1061–1062.

Stenseth, N. Chr., Bjørnstad, O. N. & Falck, W. 1996 Is spacing behaviour coupled with predation causing the microtine density cycle? A synthesis of current process-oriented and pattern-oriented studies. *Proc. R. Soc. Lond.* B **263**, 1423–1435.

Stevenson, I. R. & Bancroft, D. R. 1995 Fluctuating trade-offs favour precocial maturity in male Soay sheep. *Proc. R. Soc. Lond.* B **262**, 267–275.

Turchin, P. 1990 Rarity of density dependence or population regulation with lags? *Nature* **344**, 660–663.

Van Dijk, H., Boudry, P., McCombie, H. & Vernet, P. 1997 Flowering time in wild beet (*Beta vulgaris* ssp. *maritima*) along a latitudinal cline. *Acta Oecologica* **18**, 47–60.

Wijk, S. 1986 Performance of *Salix herbaces* in an alpine snowbed gradient. *J. Ecol.* **74**, 675–684.

Wookey, P. A., Parsons, A. N., Welker, J. M., Potter, J. A., Callaghan, T. V., Lee, J. A. & Press, M. C. 1993 Comparative responses of phenology and reproductive development to simulated environmental change in sub-arctic and high arctic plants. *Oikos* **67**, 490–502.

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