

## Seminar Module 6

### Phenological Responses to Climate Change I: Adaptation and Evidence Of Natural Selection On Phenological Traits

Alisa Hove, Brian Haggerty, and Susan Mazer  
University of California, Santa Barbara

---

#### Goals For Student Learning

This seminar module was created to help students:

- Understand the how phenological traits may evolve in response to climate change
- Understand the differences between relatively short-term phenotypically plastic responses and long-term evolutionary responses to environmental conditions.
- Understand how scientists construct and test evolutionary hypotheses regarding phenological responses to global climate change

#### Natural Selection and the Evolution of Phenological Traits

Recent and rapid climate change has influenced the phenological schedules of numerous organisms. If, however, new phenological strategies evolve in populations through the process of natural selection, then some species may persist by **adapting** to novel environmental conditions. A frequently invoked question in the debate on the biological effects of climate change is whether organisms can adapt fast enough to persist in rapidly changing environments.

In a recent review, Visser (2008) addresses this question, suggesting that measurements of evolutionary adaptation rates would help to inform and to enrich attempts to preserve biodiversity as the climate changes. He also discusses several potential responses to climate change that are not transmitted genetically from parent to offspring. He goes on to argue that long-term studies that estimate the **heritability** of phenophase expression along with the type and magnitude of selection on phenological traits are needed to understand how rapidly species can be expected to adapt to changing environmental conditions.

In plant populations where the duration of the growing season is constrained or shortened by environmental conditions, plants may evolve compressed life cycles that enable them to “make hay while the sun shines” by reproducing rapidly. In sub-alpine habitats, the duration of the growing season is limited by the timing of snowmelt and seasonal drought. For plants growing at low elevation sites, snowmelt comes early in the year. The duration of the growing season, however, may be limited by increasingly dry soils. In such habitats, individuals that delay flowering risk exposure to drought. At high-elevation sites, growing seasons are also short, but for a different reason: snowmelt often comes late in the year. Therefore, high elevation plants may have only a few weeks to reproduce between snowmelt and the onset of autumn. Stinson (2004) conducted a field study and a **common garden experiment** of a montane perennial herb, growing plants from low, intermediate, and high elevation populations in a common environment. She then estimated the strength and direction of natural selection on the **prefloration interval** in a subalpine wildflower over a three-year

period. Interestingly, she found that selection favors rapid reproduction at high and low elevations, but not at mid-elevations in her study species' range. This study provides an excellent example of how researchers study phenology and evolutionary processes in flowering plants.

### Articles To Read

Stinson, K. A. 2004. Natural selection favors rapid reproductive phenology in *Potentilla pulcherrima* (Rosaceae) at opposite ends of a subalpine snowmelt gradient. *American Journal of Botany* 91:531-539.

Visser, M. E. 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proceedings of the Royal Society B-Biological Sciences* 275:649-659.

### Suggested Discussion Questions

1. What is the difference between phenotypic plasticity and evolutionary adaptation?
2. The extent to which individuals can respond plastically to environmental conditions can vary within populations. Is it possible for natural selection to act on phenotypic plasticity?
3. Would you expect phenotypic plasticity to constrain adaptation or to promote adaptation? Upon what do you base your opinion?
4. What are four examples of plastic responses mentioned by Visser (2008)? In what taxa and/or habitats might these responses promote or ensure a population's persistence? In what taxa and/or habitats might these responses be insufficient to enable population persistence?
5. For plants growing at high elevations, what are the relative advantages and disadvantages of flowering early? Of flowering late?
6. Briefly describe the common garden experiment conducted by Stinson (2004)? Are phenological differences among the different elevations genetically based?
7. Are differences in the prefloration interval among the different elevations adaptive? Provide evidence from the article that supports your opinion.
8. Stinson (2004) did not seek evidence of climate change. But based on your current understanding of climate change and phenology, how (if at all) would you predict that the plants at Stinson's (2004) study sites would evolve in response to climate change? What evidence from the article supports your opinion?

## Glossary

- **Adaptation:** a feature that evolves in a population as the result of natural selection. Adaptations evolve over many generations because they are important for an organism's (and by extension, a population's) survival and/or reproduction.
- **Common garden experiment:** an experimental approach wherein plants from distinct environments are raised together in an identical environment. Common garden experiments are often used to determine whether differences among individuals and populations from different environments have a genetic basis.
- **Heritability:** the proportion of variation in a given phenotype that is genetically based
- **Microevolution:** change in allele frequencies over time in a single population.
- **Prefloration interval:** the number of days from snowmelt to the opening of the first flower
- **Reaction norms:** a graphical representation that shows how the phenotypes of a single genotype are expressed across a range of environmental conditions. Highly plastic genotypes typically exhibit reaction norms with steeper slopes than non-plastic genotypes.
- **Selection differential ( $s$ ):** an estimate of total (direct and indirect) phenotypic selection on a given trait.
- **Selection gradient ( $\beta$ ):** an estimate of direct phenotypic selection on a given trait.
- **Directional selection:** a type of natural selection where one phenotype is favored over other phenotypes. This causes allele frequencies to shift over time in one direction. For example, directional selection on early flowering may promote the evolution of early flowering in populations where the growing season is short or compressed.

# NATURAL SELECTION FAVORS RAPID REPRODUCTIVE PHENOLOGY IN *POTENTILLA PULCHERRIMA* (ROSACEAE) AT OPPOSITE ENDS OF A SUBALPINE SNOWMELT GRADIENT<sup>1</sup>

KRISTINA A. STINSON<sup>2</sup>

Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544 USA and Rocky Mountain Biological Laboratory (RMBL), Gothic, Colorado 81224 USA

In high altitude plants, flowering quickly ensures reproductive success within a short snow-free period, but limits maturation time and fecundity. Natural selection on prefloration intervals may therefore vary in contrasting snowmelt environments and could influence the outcome of phenological responses to climatic change. This study investigated adaptive differentiation and plasticity of prefloration intervals in the subalpine perennial *Potentilla pulcherrima*. Three years of in situ field observations were combined with phenotypic selection analyses and a common garden experiment. Plants from high, intermediate, and low altitudes expressed similar prefloration intervals and plasticity when grown at common altitude, indicating no evidence for adaptive differentiation. Selection on the prefloration interval was negative at both low and high altitudes before and after accounting for strong positive selection on size. Environmental differences between high and low altitudes indicated that long, dry seasons and short, wet seasons both favored rapid reproduction. Therefore, quicker reproduction was adaptive in response to late snowmelt, but slower reproduction in response to earlier snowmelt appeared to be maladaptive. Selection differed marginally between late snowmelt years and dry ones. Plastic responses to future precipitation patterns may therefore have positive or negative effects on fitness within a single species, depending upon altitude and year.

**Key words:** phenology; plasticity; *Potentilla pulcherrima*; reproduction; selection; snowmelt; subalpine plant.

In seasonal environments, the proper timing of reproduction is critical for maximizing fitness (Reekie and Bazzaz, 1987; Kozłowski, 1992) and is therefore likely to be influenced by natural selection. By influencing the abiotic and biotic environment in which reproduction takes place, flowering phenology can strongly influence seed number (Alatalo and Totland, 1997; Totland, 1999), pollination success (Waser, 1978; Gross and Werner, 1983; Totland, 1997; Gugerli, 1998), and the likelihood of seed predation (Gross and Werner, 1983; Brody, 1997). Quick or slow flowering also determines the allocation of resources to growth vs. reproductive output (Reekie and Bazzaz, 1987; Kozłowski, 1992; Molau, 1993). While ecotypic differentiation in flowering times is common in natural plant populations (Turesson, 1922; Clausen et al., 1948; Gross and Werner, 1983; Lacey and Pace, 1983; Kudo, 1992; Pickering, 1995; Stanton et al., 1997; Gugerli, 1998; Del Pozo et al., 2002; Fitter and Fitter, 2002), little is known about variation in the underlying developmental rates that determine the chronological timing of reproduction (Diggle, 1999). During each growing season, developmental signals to switch meristem allocation from growth to reproduction may involve both genetic and environmental cues (Geber, 1990; Stratton, 1998; Simpson and Dean, 2002; Yanovsky and Kay, 2002). The duration of

the prefloration and other intervals may therefore be plastic (Aydelotte and Diggle, 1997; Luzar, 2001) or genetically fixed (Sørensen, 1941).

Rapidly changing precipitation, temperature, and other climatic factors over the next century (Houghton et al., 1996) are likely to destabilize seasonal and genetic cues for developmental shifts between growth and reproduction each year (e.g., Inouye et al., 2002). Altered maturation rates may in turn affect reproductive output, interactions among species, and the overall functioning of ecosystems. It is therefore important to understand the extent of environmental and evolutionary processes governing variation in the prefloration interval.

Temperate mountain and polar regions may be particularly susceptible to a rapidly changing environment because of the sensitivity of plant phenology to the timing of snowmelt (e.g., Galen and Stanton, 1995; Price and Waser, 1998; De Valpine and Harte, 2001; Theurillat and Guisan, 2001; Inouye et al., 2002). Spatial and temporal patterns of snow pack, rather than photoperiod, strongly influence the date and abundance of flowering in these systems (Inouye and McGuire, 1991; Walker et al., 1995; Inouye et al., 2002). Variation among arctic and alpine species suggests that trade-offs between growth and reproduction have led to divergent strategies for ensuring reproductive success in early and late melting sites (Molau, 1993; Prock and Körner, 1996; Theurillat and Schlüssel, 2000). “Pollen-risk” species flower quickly to ensure maturation of seeds within a short growing season, but they risk reduced pollination success, small size at reproduction, and/or low seed numbers (Waser, 1978; Stenstrom and Molau, 1992; Molau, 1993; Totland, 1997; Gugerli, 1998; Totland and Eide, 1999). “Seed-risk” species mature more slowly to enhance growth and fecundity, but they may lose larger numbers of seeds if the growing season ends prior to fruit maturation (Molau, 1993; Galen and Stanton, 1995).

<sup>1</sup> Manuscript received 2 September 2003; revision accepted 4 December 2003.

The author thanks D. Stratton, H. Horn, M. Price, N. Waser, and K. Donohue for discussions on design, results, and analyses; K. Donohue, T. Seidler, A. Wilczek, K. Woods, and two anonymous reviewers for comments on the manuscript; the Rocky Mountain Biological Laboratory for logistical support; and E. Baumgartner, S. Borges, M. Carroll, M. Lett, E. Mathai, and D. Wallace-Senft for invaluable field assistance. Financial support was provided by a Doctoral Dissertation Improvement Grant from the National Science Foundation (DEB-9520859), a graduate research fellowship from Princeton University, and the Lee Snyder Scholarship for Graduate Research at RMBL.

<sup>2</sup> Present address: Harvard Forest, PO Box 68, Petersham, MA 01366 USA.

Within a species, adaptive modifications to the prefloration interval may arise from phenotypic plasticity, genetic variation, or both. While snowmelt generally occurs later with increasing altitude, environmental conditions can also change dramatically over very short distances and from year to year within a site (Sørensen, 1941; Inouye and McGuire, 1991; Galen and Stanton, 1995; Wagner and Mitterhofer, 1998; Inouye et al., 2002). Plastic phenological responses to spatial and temporal heterogeneity in snowmelt timing have been shown to increase fecundity in alpine plants (McGraw, 1987; Emery et al., 1994; Aydelotte and Diggle, 1997; Diggle, 2002). In other species, ecotypic differentiation in reproductive dates can arise along local and altitudinal snowmelt gradients, particularly if spatial separation of reproductive events precludes gene flow among altitudes (Robertson, 1895; Turesson, 1922; Clausen et al., 1948; Bliss, 1962; Gross and Werner, 1983; Waser and Price, 1985) or contrasting microsites (Bliss, 1956; Billings and Bliss, 1959; Galen and Stanton, 1993; Wagner and Mitterhofer, 1998). The magnitude and direction of natural selection on a given trait may also vary considerably among contrasting habitats (Bennington and McGraw, 1995; Caruso, 2001) and in climatically different years (Kalisz, 1986).

The extent to which plants in high altitude systems can endure climatic changes will therefore depend upon the potential for adaptive plasticity and/or genetic changes in reproductive phenology under new environmental conditions (Geber and Dawson, 1993). An initial step towards understanding evolutionary potential within extant populations is to examine relationships between size, reproductive maturation rates, and fitness under natural and experimental conditions. It is possible to infer that a trait is adaptive when there are strong correlations between that character and a fitness estimator (Lande and Arnold, 1983; Mitchell-Olds and Shaw, 1987). For instance, strong, negative relationships between prefloration times and seed numbers would indicate that quick flowering is adaptive in a given environment. Such work can greatly enhance traditional measures of phenological variation along high altitude snowmelt gradients by directly testing hypotheses about the adaptive significance of flowering quickly or slowly in different environments. However, despite their potential importance for understanding plant responses to future selective regimes, very few studies have made direct measures of phenotypic plasticity and natural selection on the reproductive phenology within high altitude species, particularly while accounting for possible relationships between size and the timing of reproduction (Stanton et al., 1997; Totland, 1999).

In this study, I used three years of field observations, phenotypic selection-regression techniques (Lande and Arnold, 1983; Mitchell-Olds and Shaw, 1987), and a classical common garden experiment to test for ecotypic differentiation and/or adaptive plasticity in the prefloration interval of the subalpine plant *Potentilla pulcherrima* Lehmann (Rosaceae). This herbaceous, long-lived perennial plant is found primarily in open, subalpine meadows in western North American mountainous regions. *Potentilla pulcherrima* is iteroparous; it flowers and fruits each year after the first year of growth, and recruitment is usually via locally dispersed seeds (personal observation). On the western slope of the Rocky Mountain range, this species is found between 2200 and 3700 m in altitude, in sites with relatively deep soils and regular accumulation of winter snow pack (Weber and Wittmann, 1996). It tends to dominate or co-dominate in mixed perennial communities, along with occasional shrubs, grasses, sedges, and other angiosperms such

as *Delphinium nuttalianum*, *Frasera speciosa*, *Ipomopsis aggregata*, *Helianthella quinquevervis*, and *Erigeron speciosus*. Within the subalpine zone, lower altitude meadows are typically released earlier from snow cover than those at higher altitudes. As altitude increases, vegetation density and temperature tend to decrease, and soil moisture tends to increase (Billings and Bliss, 1959; Ehleringer and Miller, 1975; Bell and Bliss, 1979; Bliss, 1985; Benedict, 1990). Lower altitude meadows are therefore potentially subject to late-season droughts, whereas less densely populated, higher elevation sites retain more soil moisture yet provide a shorter snow-free period. Microtopographical exposure gradients create smaller-scale variation in snowmelt timing within each altitude that may offset the general altitudinal patterns. For instance, sparse vegetation and dry conditions can predominate on early melting slopes at the lower altitudes, whereas lush vegetation may predominate in warmer, early melting sites at higher altitudes.

Utilizing the natural variation in snowmelt timing found across *P. pulcherrima*'s altitudinal range, I asked the following: (1) Does the prefloration interval differ among altitudes, and if so, is this variation due to ecotypic differentiation, phenotypic plasticity, or both? (2) Does natural selection on the prefloration interval indicate that these differences in phenology are adaptive?

## MATERIALS AND METHODS

**Field observations**—Fifteen natural populations of *P. pulcherrima* in west central Colorado, USA, were studied for three consecutive years (1994–1996). Study populations were located along an altitudinal gradient in the Gunnison National Forest in western Colorado. Five 20 × 5 m<sup>2</sup> plots were constructed within randomly selected subalpine meadows at each of three altitudes: 2600–2900 m (low), 2900–3200 m (intermediate), and 3200–3600 m (high). Plots were evenly divided into eight sections for environmental measurements. Date of snowmelt, percentage vegetative cover, soil temperature, and gravimetric soil moisture were measured at each section on a weekly basis. Soil cores were taken at 15–20 cm depth, to ensure sampling within the rooting zone.

At each plot, 25 adult *P. pulcherrima* plants were randomly selected and permanently tagged (125 per altitude) for weekly phenology censuses and size measurements. The following phenological variables were recorded in the field: date of first spring foliage appearance (emergence date), number of flowers, and number of fruits. Initial and peak reproduction dates and the number of days from emergence date to full flowering (prefloration interval) were derived from these data. Individual fitness was estimated as the total number of ripened fruits (number of fruits) harvested from each plant at each census. *Potentilla* is acrocarpous, producing a large number of distinct individual seeds (nutlets) per fruit. Final plant size was estimated in terms of maximum leaf area (leaf area), based on weekly measurements of rosette length and width. The estimator for leaf area,  $A = \pi (0.5 \text{ rosette length} \times 0.5 \text{ rosette width})$ , is strongly correlated with dry biomass (Stinson, 1998).

**Common garden experiment**—Three 12 × 15 m transplant gardens were constructed along an exposure gradient from approximately 2870 m to 3000 m in a subalpine meadow near the Rocky Mountain Biological Laboratory (RMBL), Gothic, Colorado. Snowmelt generally varies by ~5–7 d along this local gradient (personal observation). Ninety previously marked *P. pulcherrima* adults from each altitude were excavated prior to emergence from their native sites and were temporarily protected by a thin layer of snow. Thirty replicate plants from each altitude were then transplanted in a Latin-square design into each garden (3 gardens × 3 altitudes × 30 replicates per altitude per garden = 270 plants). All individuals were planted on a cool, rainy day (5 June 1996) and were identified by the altitude of origin with aluminum tags. During the second growing season after transplanting (May to August 1997), individual plants were monitored on a weekly basis to obtain emergence date, flowering date, prefloration interval, leaf area, and fecundity mea-

TABLE 1. *F* ratios from analyses of variance comparing environmental variables and plant variables, over 3 yr and among low, intermediate, and high altitude populations of *Potentilla pulcherrima* in Gunnison National Forest, Colorado, USA. \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ .

Effect	Date of snowmelt	Percentage of soil moisture	Soil temperature	Percentage of plant cover	Reproductive date (julian date)	Pre-reproductive interval (d)	Seasonal live shoot interval (d)	Leaf area (cm <sup>2</sup> )	Total fruits (number)
Year	356.73***	20.56***	2.23	51.32***	1131.809***	18356***	26.25***	33.78***	13.75***
Altitude	92.83***	1.16	4.59*	0.32	11.68**	80.67***	67.12***	30.64***	8.24*
Plot [altitude]	2.14*	3.19**	0.75	1.14	6.08***	1.54	1.56	7.28***	3.11**
Year × altitude	1.81	1.46	1.16	1.27	4.40**	2.28	16.76***	1.24	3.48*
Year × plot [altitude]	13.28***	2.36***	0.19	0.84	4.60***	4.92***	3.63***	1.46	1.66*

surements as described earlier. Snowmelt dates were recorded within each quadrant as the date of first appearance of bare ground in 1996 and 1997. Weekly gravimetric soil moisture measurements were obtained in 1997 at the rooting level at 12 designated points within each garden (three samples per quadrant).

**Data analysis**—Seasonal averages of all field observations (environmental and plant variables) were compared using an analysis of variance model with fixed main effects: year, altitude, and the year × altitude interaction term. Plot number was included as a nested, random effect in the model to control for environmental variability within altitudes. The effect of altitude was tested over the nested factor, plot. The model also included the random crossed effect of year × plot, which was used as the denominator mean square in the *F* test for effects of year and year × altitude. A repeated measures model was not used in this study because the considerable environmental variation among years precludes the assumption that responses of individual plants are parallel through time (Sokal and Rohlf, 1995, pp. 345–346). Large differences among years warrant the consideration of year × altitude and year × plot interactions as separate terms, rather than as error (Sokal and Rohlf, 1995, pp. 342–346). Tukey's HSD post-hoc analyses were applied to significant effects when comparisons between years, altitudes, and/or plots within each altitude were necessary. To test for direct effects of environmental variation on plant performance, all environmental variables differing within or among altitudes were regressed against each measured plant trait. Forward stepwise regression was used to determine the best fit model without establishing a priori relationships between the predictor and response variables (Sokal and Rohlf, 1996, pp. 654–657). Regression variables differing from zero in the final regression equations were considered to affect a given plant trait.

The three common gardens were ranked by snowmelt date (early, intermediate, and late) for analysis. To capture potential effects of among-garden variation in soil moisture, plant variables were analyzed with a two-way ANCOVA (altitude of origin × garden) using soil moisture as a covariate. Using this model, two comparisons were made in order to assess the role of ecotypic variation and plasticity. First, following classical common garden transplant designs (Turesson, 1922; Clausen et al., 1948), populations were tested for ecotypic variation by comparing the phenotypic expression of individuals from distinct habitats grown together in a common environment. With this approach, an effect of altitude on a given trait within the transplant gardens would demonstrate ecotypic differentiation, whereas no effect of altitude would indicate plasticity for that trait. A second measure of phenotypic plasticity was made possible by the inclusion of garden number in the model. This allowed for a measure of phenotypic variation as a function of local environmental heterogeneity among the different gardens. An effect of garden number on a given trait was thus interpreted as evidence for plasticity in response to local snowmelt and soil moisture conditions in early, intermediate, and late melting common gardens. In both cases, plasticity was measured in the broadest sense (population level) and not in the narrow sense (genotypic level) (e.g., Bradshaw, 1965). Differences within and among the common gardens were compared with Tukey's HSD post-hoc analyses.

Phenotypic selection regression analyses (Lande and Arnold, 1983) were conducted on both in situ and experimental plants to estimate the magnitude and direction of selection acting on the timing of reproduction, before and after accounting for selection on plant total leaf area. Standardized linear (directional) selection differentials ( $\hat{s}$ ) were estimated as the covariance be-

tween relative fitness and the standardized values for prefloration interval and leaf area. Selection differentials estimate the total selection on a trait, including both direct selection and indirect selection acting on correlated traits. Standardized linear (directional) selection coefficients ( $\beta$ ) were derived from multiple regressions of relative fitness on the prefloration interval and leaf area. Selection coefficients describe the direct selection on a trait, after accounting for selection on other traits included in the model.

Estimates of total and direct selection were obtained for in situ plants from 1994 to 1996. Selection differentials ( $\hat{s}$ ) and selection coefficients ( $\beta$ ) were calculated separately in each year and for each elevation. To measure selection within each altitude, relative fitness was calculated as the total number of fruits produced by an individual in a given altitude by the mean number of fruits produced by all individuals in that altitude. Because selection may occur at different spatial scales, relative fitness was also measured across the entire gradient. Relative fitness across all altitudes was calculated by dividing the total number of fruits produced by an individual by the mean number of fruits of all individuals from all altitudes within a given year. Heterogeneity of slopes tests (ANCOVA) were used to test whether relationships between relative fitness and the measured traits differed among altitudes and among years. Estimates of total and direct selection were also obtained as described for experimental plants. Within the common gardens,  $\hat{s}$  and  $\beta$  were calculated separately for each native altitude. The model included garden number as a fixed effect to control for environmental differences among gardens. ANCOVA models were used to test whether relationships between relative fitness and the measured traits differed among altitudes and among gardens.

## RESULTS

**Field observations**—The main environmental differences along the altitudinal gradient were date of snowmelt and soil moisture (Table 1). High altitude plots emerged from snow cover ~13 d later than intermediate altitude plots, and intermediate plots emerged ~11 d later than low altitude plots. The average dates of snow disappearance were 12 May 1994, 13 June 1995, and 15 May 1996 at low altitude; 28 May 1994, 23 June 1995, and 29 May 1996 at intermediate altitude; and 6 June 1994, 9 July 1995, and 15 June 1996 at high altitude. The 3–4 wk delay in snowmelt date at each altitude in 1995 was due to record-high snow accumulation during the preceding winter, as reported in weather records maintained by RMBL (B. Barr, RMBL, personal communication). Interannual variation in soil moisture was due to a late season drought in 1994, which reduced the percentage soil water content in each altitude by ~5% on average compared to the other two years (Turkey's HSD,  $P < 0.05$ ). Although altitude did not have a significant effect on mean soil moisture, percentage soil water content was lower and declined more rapidly in the intermediate and early altitudes compared to high altitudes in all years, as shown for 1996 (Fig. 1). Effects of plot on snowmelt timing and soil moisture were explained primarily by heterogeneity among intermediate altitude plots during 1995 and 1996. Soil temperatures ranged from ~5° to 22°C throughout the growing season, with slightly lower temperatures at high

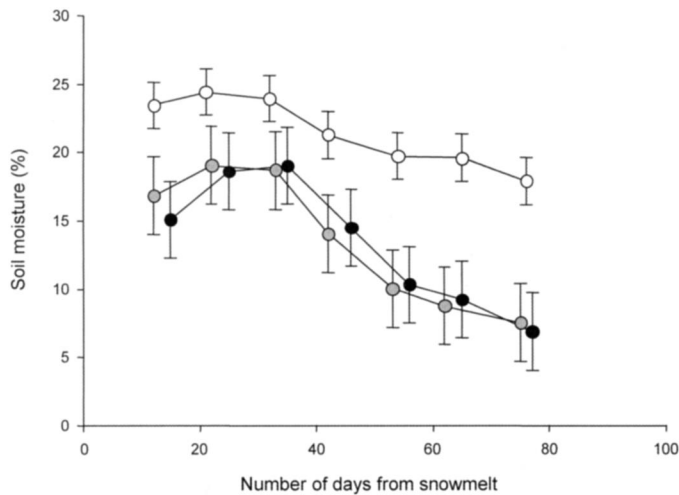


Fig. 1. Soil moisture at low, intermediate, and high altitude throughout the 1996 growing season at  $20 \times 5$  m plots in Gunnison National Forest, Colorado, USA. Mean ( $\pm 1$  SE) soil moisture is expressed as a percentage based on gravimetric data. The x-axis is the number of days from the mean snowmelt date at each altitude. Closed symbols correspond to low altitude; grey symbols correspond to intermediate altitude; open symbols correspond to high altitude.

altitude compared to the low and intermediate altitudes. Vegetative cover ranged from 60% to 100% and was similar across altitudes. A reduction of plant cover during the drought year was attributed to reduced foliage and early plant senescence at the time of measurement.

Field populations expressed interannual and altitudinal differences in all of the measured traits (Table 1). Tukey's HSD post-hoc analyses revealed differences ( $P < 0.05$ ) among altitudes and among years as follows. The prefloration interval was shorter at progressively higher altitude, and these differences were conserved from year to year (Fig. 2a). Leaf area and number of fruits declined with progressively higher altitudes (Fig. 2b, c). Plants at low altitude reduced fruit production in 1994, but increased total leaf area and number of fruits during the late snowmelt year, 1995. Dates of reproduction (Fig. 2d) were later at high altitude compared to the intermediate and low altitudes. Plants from all altitudes reproduced 3–4 wk later in 1995 than in the other two years.

There were effects of plot, year  $\times$  altitude, and the three-way interaction term on number of fruits and reproductive dates. Tukey's HSD ( $P < 0.05$ ) tests revealed that dates of reproduction differed among plots within the high altitude: earliest reproduction occurred consistently in the same two earliest melting plots every year. Plants also flowered earlier in the driest, low altitude plot compared to the other low altitude plots in 1994. The year  $\times$  altitude interaction effect on fruit number was explained by directional shifts in trait values among altitudes in the late snowmelt year: a reduction in fecundity in the intermediate and high altitudes in 1995 was accompanied by increased fecundity at low altitude.

Snowmelt date and soil moisture were the only environmental variables to affect the measured plant traits in the forward-stepwise regression analysis. Estimates for snowmelt date and soil moisture were different from zero in the final regression models for the prefloration interval and leaf area (Table 2), demonstrating that phenology and size are related to those environmental factors. Snowmelt date was the only

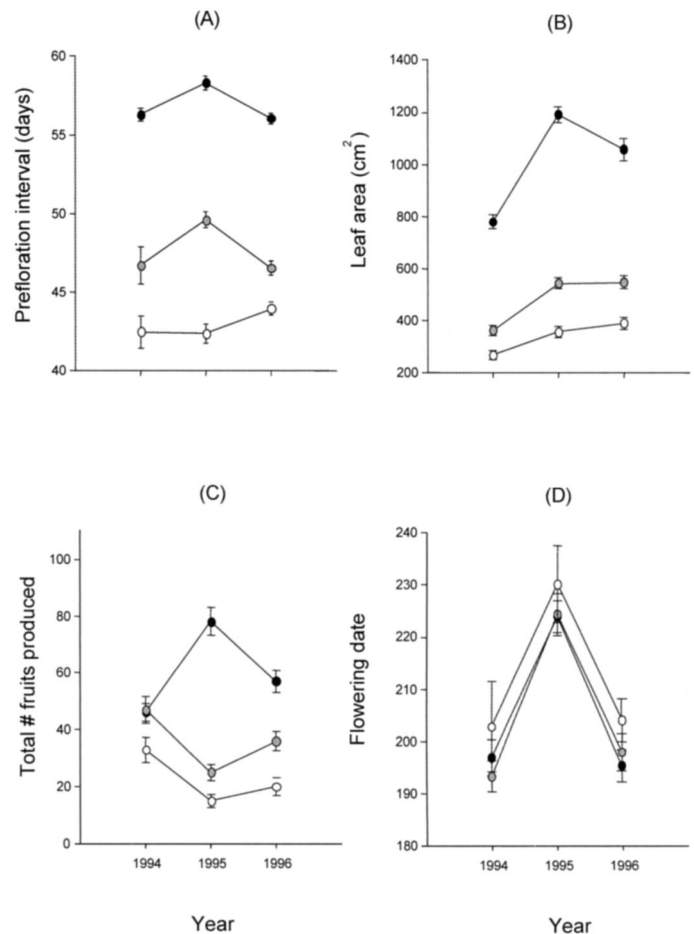


Fig. 2. Means ( $\pm 1$  SE) of plant characters for *Potentilla pulcherrima* in each year of the study. Each line connects the mean value for plants at low (closed symbols), intermediate (grey symbols), and high (open symbols) altitude. The prefloration interval (panel A) is expressed in number of days; size and fecundity are shown in panels B and C; peak flowering date (D) is expressed as day of year.

parameter to affect fruiting date. None of the regression models yielded significant parameter estimates for environmental effects on total number of fruits.

**Phenotypic selection within and among altitudes**—Phenotypic selection analyses demonstrated strong relationships between prefloration intervals, plant size, and relative fitness in the field (Table 3a). The overall directional selection coefficient and the overall selection differential were both significantly positive when all altitudes were included in the analysis. This positive relationship between prefloration interval and relative fitness was driven by longer mean reproductive intervals and higher mean fecundity at progressively lower altitudes (Fig. 2). In contrast, the separate directional selection coefficients and differentials for each altitude were negative. Thus, selection acted in the direction of longer prefloration intervals when all altitudes were included in the model, but favored shorter prefloration intervals within each altitude separately. Selection coefficients and differentials for the prefloration interval were significantly negative in the low and high altitudes, but did not differ from zero in the intermediate altitude. Selection generally acted in the direction of larger size, irrespective of altitude. Selection coefficients and differentials

TABLE 2. Variable estimates and regression results for effects of snowmelt date (calendar day) and soil moisture (gravimetric) on the traits measured in situ for field populations of *Potentilla pulcherrima* in Gunnison National Forest, Colorado, USA. Regression results are shown for best fit models resulting from forward stepwise regression of each plant trait on all environmental data (snowmelt date, soil moisture, vegetation cover, and temperature).

Plant trait	Snowmelt date		Soil moisture		R <sup>2</sup>	P
	Estimate	F	Estimate	F		
Prefloration interval	-0.28	16.91	+1.01	5.29	0.29	<0.001
Leaf area	-11.17	21.55	+45.13	8.36	0.34	<0.001
Flowering date	+0.69	97.97	63.86	1.51	0.80	<0.001
Number of fruits	—	0.049	—	0.25	—	NS

for total leaf area were positive overall and for each altitude analyzed separately, with the exception that β did not differ from zero at low altitude.

At each altitude, § and β for the prefloration interval were negative in 1995, but did not differ from zero during the drought year, 1994. A heterogeneity of slopes test on the 1994, 1995, and 1996 selection regression equations revealed nearly significant interannual effects on the relationship between prefloration interval and relative fecundity (ANCOVA for effects of prefloration interval, altitude, year, and all interaction terms:  $F_{pre-repro} = 20.41, P < 0.001$ ;  $F_{pre-repro \times year} = 2.33, P = 0.08$ ; all other effects in the model N/S). Thus, selection did not differ significantly across altitudes but was slightly different among years. Selection on size was positive at all altitudes in both the drought and late snowmelt years. Slopes of the size-fitness regression lines did not differ among years or among altitudes.

**Ecotypic variation, plasticity, and natural selection in the common gardens**—Snowmelt varied by  $5 \pm 2$  d between the earliest and latest melting gardens in both years, and the rank order for mean snowmelt dates was conserved across the two years of the study. Snowmelt varied among gardens and among quads within gardens ( $F_{garden} = 2.03, P < 0.01$ ;  $F_{quad[garden]} = 2.05, P < 0.01$ ). Soil moisture ranged from 5% to 19% in all gardens throughout the season and varied within and among gardens ( $F_{garden} = 1.58, P < 0.01$ ;  $F_{quad[garden]} = 8.16, P < 0.01$ ). Total leaf area was the only plant trait for which there was an effect of native altitude. Plants from low altitude were consistently larger than those from higher alti-

tudes in each garden ( $F_{altitude} = 3.26, P = 0.04, F_{garden} = 2.61, P = 0.08, F_{altitude \times garden} = 0.24, P = 0.24$ ), indicating that the observed in situ size differences were due to ecotypic variation among altitudes. Plants from all altitudes expressed similar prefloration intervals, dates of reproduction, and number of fruits within each garden, demonstrating no ecotypic differentiation for phenology or fecundity at the experimental altitude. Altitude  $\times$  garden interactions on number of fruits and fruiting date were nonsignificant at the  $P < 0.05$  level, further indicating no differences among populations in the level of plasticity expressed for these traits. The only trait expressing plasticity among gardens was the prefloration interval (Fig. 3). Plants in the earliest melting gardens demonstrated longer prefloration intervals than those in later melting gardens, regardless of native altitude ( $F_{garden} = 11.79, P < 0.001$ ;  $F_{altitude \times garden} = 0.15, df = 2, P = 0.96$ ). Thus, plants from all altitudes expressed similar plastic changes in the prefloration interval, in response to early, intermediate, and late snowmelt among experimental gardens.

Comparisons of directional selection coefficients in the common garden experiment revealed similar responses among plants from each altitude (Table 3b). Overall and separate directional selection coefficients and differentials were negative for the prefloration interval and positive for leaf area in all cases. Heterogeneity of slopes tests on the regression equations for each altitude and for each garden were not significant, in-

TABLE 3. Selection gradients measuring the magnitude of direct selection (β) and selection differentials measuring the magnitude of total selection (§) on the prefloration interval and leaf area of *Potentilla pulcherrima*: (a) at different altitudes in Gunnison National Forest, Colorado, USA, and (b) in common garden experiment at Rocky Mountain Biological Laboratory, Gothic, Colorado, USA. \*  $P < 0.05$ , \*\*  $P < 0.01$ .

Native altitude	Prefloration interval (d)		Leaf area (cm <sup>2</sup> )	
	(β)	(§)	(β)	(§)
<b>(a) Field observations</b>				
Low	-0.14**	-0.14**	-0.03	+0.21**
Intermediate	-0.08	-0.06	+0.31**	+0.31**
High	-0.25**	-0.22**	+0.48**	+0.12**
All	+0.25**	+0.24**	+0.01	+0.30**
<b>(b) Common garden experiment</b>				
Low	-0.27**	-0.26*	+0.13**	+0.13
Intermediate	-0.22	-0.40**	+0.56*	+0.66**
High	-0.32**	-0.44**	+0.22**	+0.38**
All	-0.28**	-0.38**	+0.34**	+0.42**

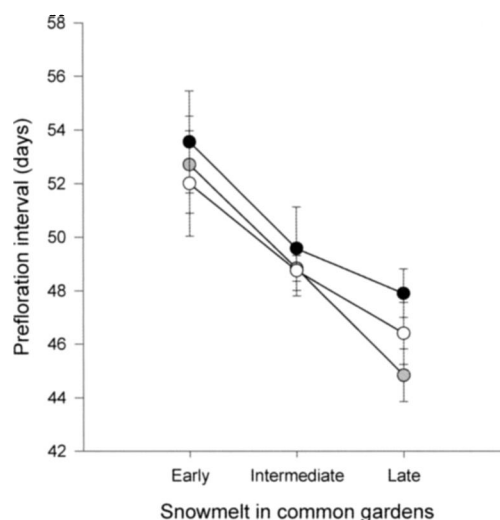


Fig. 3. Prefloration interval for *Potentilla pulcherrima* in the common garden experiment. Mean ( $\pm 1$  SE) number of days from emergence to reproduction in early-, intermediate-, and late-melting common gardens. Each line connects the mean values for populations from low (closed symbols), intermediate (gray symbols), and high (open symbols) altitude.



dicating no effects of native altitude or garden on the selection regression results. Natural selection on phenological plasticity therefore did not differ among altitudes, but rather favored shorter prefloration intervals irrespective of native or local snowmelt conditions. Compression of the prefloration interval by plants from lower altitudes at the experimental altitude may therefore be considered adaptive, while the lengthening of this interval by plants from higher altitudes appears to be a non-adaptive response.

## DISCUSSION

Although average size, prefloration interval, and fecundity were all reduced in progressively later melting sites, direct selection ( $\delta$ ) and indirect selection ( $\beta$ ) favored shorter prefloration intervals at both ends of the altitudinal gradient. Thus, there were significant fitness advantages to shorter prefloration intervals in both early and late melting sites, even after accounting for strongly positive selection on size. Because higher altitude sites are characterized by progressively later snowmelt, this negative trend between fecundity and prefloration interval length at high altitudes supports the hypothesis that rapid reproduction evolves in response to shorter growing seasons (Molau, 1993; Theurillat and Schlüssel, 2000). The common garden experiment demonstrated that accelerated reproduction in later melting sites can be attributed to phenotypic plasticity, rather than genetically determined periodicity. Negative selection on the prefloration interval in the experimental plants confirmed that this plasticity is in an adaptive direction. Previous work suggests that high-altitude populations of other alpine and subalpine species can compensate for short growing seasons by accelerating seasonal carbohydrate cycles (Mooney and Billings, 1961; Bliss, 1985; Starr et al., 2000) and by reproducing more rapidly than their lower altitude counterparts. While many studies have documented altitudinal variation in fecundity and reproductive dates (Galen and Stanton, 1991; Kudo, 1991, 1992, 1993; Galen and Stanton, 1995; Pickering, 1995; Levesque et al., 1997), whether and how plasticity in maturation rates affect the chronological sequence of development is virtually unknown in these systems (Diggle, 1999). The duration of growth and the reproductive interval have been experimentally altered in some species (Molau and Shaver, 1997; Welker et al., 1997; Price and Waser, 1998; Totland, 1999; Sandvik and Totland, 2000), whereas others express notable homeostasis regardless of habitat (Holway and Ward, 1965a) or experimental treatment (Starr et al., 2000). This study is the first to provide direct measures of both natural selection and plasticity on the prefloration interval and therefore provides an adaptive mechanism for accelerated reproductive phenology in late melting populations of a single species.

It has been suggested that rapid reproduction at higher altitudes, compared to slower reproduction at lower altitudes, represents a fitness trade-off between size at reproduction and the ability to reach maturity quickly (Clausen et al., 1948; Holway and Ward, 1965a; Kudo, 1992; Stenstrom and Molau, 1992; Molau, 1993; Levesque et al., 1997; Theurillat and Schlüssel, 2000). However, there was no evidence for divergent allocation strategies in early vs. late melting sites (Theurillat and Schlüssel, 2000). This study accounted for correlations between size and phenology by including total leaf area in the measurement of directional selection coefficients ( $\beta$ ). Whereas a directional change in  $\beta$  would indicate evolutionary

trade-offs between habitats (Mitchell-Olds and Shaw, 1987), the negative coefficients at all altitudes indicate that selection on the prefloration interval is not constrained by positive selection on size. The fact that selection differentials and coefficients were negative in the experimental gardens, regardless of positive correlations between fecundity and size, also indicates size and prefloration interval are not genetically correlated. This contrasts with theoretical predictions that cumulative allocation to growth should determine the time of reproductive maturity (Bazzaz and Ackerly, 1992; Kozłowski, 1992; Prock and Körner, 1996) and suggests instead that size-dependent fecundity does not dictate selection on the timing of reproduction in all environments (Schmid and Weiner, 1993; Callahan and Pigliucci, 2002).

Given that longer growing seasons result in higher fecundity and longer prefloration intervals in *P. pulcherrima* across its range, negative selection on the prefloration interval at the low altitude was perhaps more surprising. Even more striking was the fact that the plastic response of lengthening the prefloration interval at the experimental altitude did not appear to be adaptive, because of the consistently strong negative selection on this trait. The most likely explanation for selection on rapid reproduction in earlier melting sites is the late-season declines in soil moisture at lower altitudes. Earlier melting sites are often drier than later melting sites due to steeper soil moisture declines as the season progresses (Billings and Bliss, 1959; Holway and Ward, 1965b; Ehleringer and Miller, 1975; Isard, 1986; Friend and Woodward, 1990), and some high altitude species have been shown to reproduce earlier in drier years (Holway and Ward, 1965a). For *P. pulcherrima*, the regression of plant traits on environmental factors demonstrates that leaf area and prefloration intervals were negatively related to snowmelt date, but positively related to soil moisture. Although warmer conditions during early growth may also accelerate developmental rates (Molau, 1997; Sandvik and Totland, 2000), there was no evidence that temperature affected the prefloration interval in this system. Moreover, comparisons of phenotypic selection coefficients showed no evidence that natural selection on the prefloration interval differed between the high and low altitudes. It is therefore possible to conclude that opposing temporal constraints at the lower and upper ends of the altitudinal gradient exert similar selective pressures on this trait (Lande and Arnold, 1983; Bennington and McGraw, 1995). Long, dry seasons at lower altitudes and short, wet seasons at higher altitudes both favor the most rapidly reproducing individuals. While it is well established that annual schedules for release from snowpack can have dramatic effects on the amount of time available for growth and reproduction (Inouye and McGuire, 1991; Inouye et al., 2002; Kudo, 1991; Galen and Stanton, 1991; Walker et al., 1993), the current results underscore the importance of other factors, such as seasonal soil moisture declines, which can limit growth (Holway and Ward, 1965b; Walker et al., 1993; Price and Waser, 1998), and thereby determine the functional endpoint of the growing season. These results agree with the cautionary prediction that high altitude plant responses to climatic changes will depend upon multiple factors (Henry and Molau, 1997; Welker et al., 1997; Price and Waser, 1998; Sandvik and Totland, 2000; Starr et al., 2000). Moreover, the results demonstrate that accurately predicting the effects of altered growing season lengths will require more careful consideration of late season conditions in the subalpine zone.

Contraction of the prefloration interval in later melting gar-

dens further demonstrates that plastic changes in phenology are elicited by only a few days' difference in snowmelt timing within the subalpine zone, where both local and altitudinal heterogeneity can be quite large. This is notable, since the few studies concerned with small-spatial-scale, adaptive responses to snowmelt have focused on alpine tundra species (e.g., Galen and Stanton, 1993). Elongation of the prefloration interval in the earlier melting gardens may also be explained by small-scale and/or interannual heterogeneity in the environment. One possibility is simply that development is slowed by drought or other physiological stresses in earlier melting sites, such as fine-scale variation in temperature that were not detected here (Molau, 1997; Sandvik and Totland, 2000). Alternatively, slowing reproduction in response to early snowmelt may be favorable over the lifetime of these long-lived perennials due to unpredictable interactions between spatial and interannual variation in snowmelt (Sørensen, 1941), even though it was not adaptive in the year of the study. A major limitation in the interpretation of phenotypic selection analyses is that they assume no variation in selection from year to year. Interannual effects on selection can be as large as or larger than spatial variation in fitness (Stratton and Bennington, 1998), and altered annual precipitation patterns can have inconsistent effects on flowering times and other life history characters of high altitude plants (Inouye and McGuire, 1991; Walker et al., 1995). In this study, interannual effects on selection were marginally detectable within three years of observation and may vary considerably over the decade or longer lifespan of *Potentilla*, as well as many other subalpine perennials.

Information on genetic structure and outcrossing rates could provide additional insight into selection on prefloration intervals in *P. pulcherrima*. Because the common garden study did not test for genotype-by-environment interactions as measured by reaction norms (Bradshaw, 1965), the role of narrow sense genetic variation within and among altitudes is unclear. Genotypes may differ in size, prefloration interval, and the strength of correlation between these traits (Geber, 1990; Bennington and McGraw, 1995) and in the degree of plasticity expressed in a given environment (Sultan, 1995). Weaker selection in intermediate sites may be due to contrasting selection in microsites (Kalisz, 1986; Bennington and McGraw, 1995) or to equal fitness advantages from outcrossing with either high or low altitude populations. While many *Potentilla* species are capable of selfing, pollinator visitation and outcrossing have been shown to enhance seed set in the subarctic-subalpine species *P. nivea* and *P. crantzii* (Eriksen, 1996; Eriksen and Popp, 2000). Hence, variation in the prefloration interval of *P. pulcherrima* may also involve selection for reproductive synchrony both within and between altitudes (Galen and Stanton, 1995; Pickering, 1995; Brody, 1997).

In summary, environmental cues at relatively small spatial scales, rather than cumulative allocation to growth or genetically determined periodicity among populations, appear to control the amount of time allocated to growth prior to reproduction in *P. pulcherrima*. The adaptive nature of these responses may vary considerably within this species depending upon microsite, altitude, and year. In particular, high altitude populations may experience negative fitness consequences if lengthening of the prefloration interval accompanies predicted patterns of earlier snowmelt and drier conditions, despite a longer snow-free season in their native habitats. Predicted phenological responses to single factors, and generalizations even for a single species, should therefore be made with extreme

caution. A better understanding of environmental and genetic control over reproductive timing will be valuable for predicting longer term evolutionary responses of subalpine plants to altered and increasingly variable snowmelt patterns in this region.

## LITERATURE CITED

- ALATALO, J. M., AND O. TOTLAND. 1997. Response to simulated climatic change in an alpine and subarctic pollen-risk strategist. *Silene acaulis*. *Global Change Biology* 3, Suppl. 1: 74–79.
- AYDELOTTE, A. R., AND P. K. DIGGLE. 1997. Analysis of developmental preformation in the alpine herb *Caltha leptosepala* (Ranunculaceae). *American Journal of Botany* 84: 1646–1657.
- BAZZAZ, F. A., AND D. D. ACKERLY. 1992. Reproductive allocation and reproductive effort in plants. In M. Fenner [ed.], *Seeds: the ecology of regeneration in plant communities*. Oxon, New York, New York, USA.
- BELL, K. L., AND L. C. BLISS. 1979. Autecology of *Kobresia bellardii*: why winter snow accumulation limits local distribution. *Ecological Monographs* 49: 377–402.
- BENEDICT, J. B. 1990. Lichen mortality due to late-lying snow: results of a transplant study. *Arctic and Alpine Research* 72: 81–89.
- BENNINGTON, C. C., AND J. B. MCGRAW. 1995. Natural selection and ecotypic differentiation in *Impatiens pallida*. *Ecological Monographs* 65: 303–323.
- BILLINGS, W. D., AND L. C. BLISS. 1959. An alpine snowbank environment and its effects on vegetation, plant development and productivity. *Ecology* 40: 389–397.
- BLISS, L. C. 1956. A comparison of plant development in microenvironments of arctic and alpine tundras. *Ecological Monographs* 26: 303–337.
- BLISS, L. C. 1962. Adaptations of arctic and alpine plants to environmental conditions. *Arctic* 15: 117–144.
- BLISS, L. C. 1985. Alpine. In B. F. Chabot and H. A. Mooney [eds.], *Physiological ecology of North American plant communities*, 41–65. Chapman and Hall, New York, New York, USA.
- BRADSHAW, A. D. 1965. Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics* 13: 115–155.
- BRODY, A. K. 1997. Effects of pollinators, herbivores, and seed predators on flowering phenology. *Ecology* 78: 1624–1631.
- CALLAHAN, H. S., AND M. PIGLIUCCI. 2002. Shade-induced plasticity and its ecological significance in wild populations of *Arabidopsis thaliana*. *Ecology* 83: 1965–1980.
- CARUSO, C. M. 2001. Differential selection on floral traits of *Ipomopsis aggregata* growing in contrasting environments. *Oikos* 94: 295–302.
- CLAUSEN, J., D. KECK, AND W. HIESEY. 1948. Experimental studies on the nature of species. III. Environmental responses of climatic races of *Achillea*. Carnegie Institute of Washington Publication Number 581, Washington, D.C., USA.
- DEL POZO, A., C. OVALLE, J. ARONSON, AND J. AVENDANO. 2002. Ecotypic differentiation in *Medicago polymorpha* L. along an environmental gradient in central Chile. I. Phenology, biomass production and reproductive patterns. *Plant Ecology* 159: 119–130.
- DE VALPINE, P., AND J. HARTE. 2001. Plant responses to experimental warming in a montane meadow. *Ecology* 82: 637–648.
- DIGGLE, P. K. 1997. Extreme preformation in alpine *Polygonum viviparum*: an architectural and developmental analysis. *American Journal of Botany* 84: 154–169.
- DIGGLE, P. K. 1999. Heteroblasty and the evolution of flowering phenologies. *International Journal of Plant Sciences* 160: S123–S134.
- DIGGLE, P. K. 2002. A developmental morphologist's perspective on plasticity. *Evolutionary Ecology* 16: 267–283.
- EHLERINGER, J., AND P. C. MILLER. 1975. Water relations of selected plant species in the alpine tundra, Colorado. *Ecology* 56: 370–380.
- EMERY, R. J. N., C. C. CHINNAPPA, AND J. G. CHMIELEWSKI. 1994. Specialization, plant strategies, and phenotypic plasticity in populations of *Stellaria longipes* along an elevational gradient. *International Journal of Plant Sciences* 155: 203–219.
- ERIKSEN, B. 1996. Mating systems in two species of *Potentilla* from Alaska. *Folia Geobotanica and Phytotaxonomica* 31: 333–344.
- ERIKSEN, B., AND M. POPP. 2000. Pollen tube growth and seed set in naturally and artificially pollinated plants of *Potentilla nivea* and *P. crantzii* (Ro-

- saceae). *Scandinavian Association for Pollination Ecology honours Knut Fægri* 39: 55–65.
- FITTER, A. H., AND R. S. R. FITTER. 2002. Rapid changes in flowering time in British plants. *Science* 296: 1689–1691.
- FRIEND, A. D. 1995. Responses of snowbed plant-species to changes in growing-season length. *Ecology* 76: 1546–1557.
- FRIEND, A. D., AND F. I. WOODWARD. 1990. Evolutionary and ecophysiological responses of mountain plants to the growing season environment. *Advances in Ecological Research* 20: 59–124.
- GALEN, C., AND M. L. STANTON. 1991. Consequences of emergence phenology for reproductive success in *Ranunculus adoneus* (Ranunculaceae). *American Journal of Botany* 78: 978–988.
- GALEN, C., AND M. L. STANTON. 1993. Short-term responses of alpine buttercups to experimental manipulations of growing season length. *Ecology* 74: 1052–1058.
- GALEN, C., AND M. L. STANTON. 1995. Responses of snowbed plant species to changes in growing season length. *Ecology* 76: 1546–1557.
- GEBER, M. 1990. The cost of meristem limitation in *Polygonum arenastrum*: negative genetic correlations between fecundity and growth. *Evolution* 44: 799–819.
- GEBER, M., AND T. DAWSON. 1993. Evolutionary responses of plants to global change. In P. Kareiva, J. Kingsolver, and R. Huey [eds.], *Biotic interactions and global change*, 179–197. Sinauer, Sunderland, Massachusetts, USA.
- GROSS, R. S., AND P. A. WERNER. 1983. Relationships among flowering phenology, insect visitors, and seed-set of individuals: experimental studies on four co-occurring species of goldenrod (*Solidago*: Compositae). *Ecological Monographs* 53: 95–117.
- GUGERLI, F. 1998. Effect of elevation on sexual reproduction in alpine populations of *Saxifraga oppositifolia* (Saxifragaceae). *Oecologia* 114: 60–66.
- HENRY, G. H. R., AND U. MOLAU. 1997. Tundra plants and climate change: the International Tundra Experiment (ITEX). *Global Change Biology* 3, Suppl. 1: 1–9.
- HOLWAY, J. G., AND R. T. WARD. 1965a. Phenology of alpine plants in Northern Colorado. *Ecology* 46: 73–83.
- HOLWAY, J. G., AND R. T. WARD. 1965b. Snow and melt-water effects in an alpine area of Colorado. *American Midland Naturalist* 60: 189–197.
- HOUGHTON, J., L. FILHO, B. CALLANDER, N. HARRIS, A. KATTENBURG, AND K. MASKELL. 1996. Climate change 1995—the science of climate change. Working group I. Second assessment report of The Intergovernmental Panel on Climate Change (IPCC). Cambridge University Press, New York, New York, USA.
- INOUE, D. W., AND A. D. MCGUIRE. 1991. Effects of snow-pack on timing and abundance of flowering in *Delphinium nelsonii* (Ranunculaceae). *American Journal of Botany* 78: 997–1001.
- INOUE, D. W., M. A. MORALES, AND G. J. DODGE. 2002. Variation in timing and abundance of flowering by *Delphinium barbeyi* Huth (Ranunculaceae): the roles of snowpack, frost, and La Niña, in the context of climate change. *Oecologia* 130: 543–550.
- ISARD, S. A. 1986. Factors influencing soil moisture and plant community distribution on Niwot Ridge, Front Range, Colorado, USA. *Arctic and Alpine Research* 18: 83–96.
- KALISZ, S. 1986. Variable selection on the timing of germination in *Collinsia verna* (Scrophulariaceae). *Evolution* 40: 479–491.
- KOZŁOWSKI, J. 1992. Optimal allocation of resources to growth and reproduction: implications for age and size at maturity. *Trends in Ecology and Evolution* 7: 15–18.
- KUDO, G. 1991. Effects of snow-free period on the phenology of alpine plants inhabiting snow patches. *Arctic and Alpine Research* 23: 436–443.
- KUDO, G. 1992. Performance and phenology of alpine herbs along a snow-melting gradient. *Ecological Research* 7: 297–304.
- KUDO, G. 1993. Relationship between flowering time and fruit-set of the entomophilous alpine shrub, *Rhododendron aureum* (Ericaceae), inhabiting snow patches. *American Journal of Botany* 80: 1300–1304.
- LACEY, E. P., AND R. PACE. 1983. Effect of parental flowering and dispersal times on offspring fate in *Daucus carota* (Apiaceae). *Oecologia* 60: 274–278.
- LANDE, R., AND S. ARNOLD. 1983. The measurement of selection on correlated characters. *Evolution* 37: 1210–1226.
- LEVESQUE, E., G. H. R. HENRY, AND J. SVOBODA. 1997. Phenological and growth responses of *Papaver radicum* along altitudinal gradients in the Canadian high arctic. *Global Change Biology* 3: 125–145.
- LUZAR, N. 2001. Flower heliotropism and floral heating of five alpine plant species and the effect on flower visiting in *Ranunculus montanus* in the Austrian Alps. *Arctic Antarctic and Alpine Research* 33: 93–99.
- MCGRAW, J. B. 1987. Experimental ecology of *Dryas octopetala* ecotypes: IV. Fitness response to reciprocal transplanting in ecotypes with differing plasticity. *Oecologia* 73: 465–468.
- MITCHELL-OLDS, T., AND R. SHAW. 1987. Regression analysis of natural selection: statistical inference and biological interpretations. *Evolution* 41: 1149–1161.
- MOLAU, U. 1993. Relationships between flowering phenology and life-history strategies in tundra plants. *Arctic and Alpine Research* 25: 391–402.
- MOLAU, U. 1997. Responses to natural climatic variation and experimental warming in two tundra plant species with contrasting life forms: *Cassiope tetragona* and *Ranunculus nivalis*. *Global Change Biology* 3: 97–107.
- MOLAU, U., AND G. R. SHAVER. 1997. Controls on seed production and seed germinability in *Eriophorum vaginatum*. *Global Change Biology* 3: 80–88.
- MOONEY, H., AND W. BILLINGS. 1961. Comparative physiological ecology of arctic and alpine populations. *Ecological Monographs* 31: 1–29.
- PICKERING, C. M. 1995. Variation in flowering parameters within and among five species of Australian alpine *Ranunculus*. *Australian Journal of Botany* 43: 103–112.
- PRICE, M. V., AND N. M. WASER. 1998. Effects of experimental warming on plant reproductive phenology in a subalpine meadow. *Ecology* 79: 1261–1271.
- PROCK, S., AND C. KÖRNER. 1996. A cross-continental comparison of phenology, leaf dynamics and dry matter allocation in arctic and temperate zone herbaceous plants from contrasting altitudes. *Ecology Bulletin* 45: 93–103.
- REEKIE, E. G., AND F. A. BAZZAZ. 1987. Reproductive effort in plants. *American Naturalist* 129: 876–919.
- ROBERTSON, C. 1895. The philosophy of flower seasons, and the phenological relations of the entomophilous flora and the anthophilous insect fauna. *American Naturalist* 29: 97–117.
- SANDVIK, S. M., AND O. TOTLAND. 2000. Short-term effects of simulated environmental changes on phenology, reproduction, and growth in the late-flowering snowbed herb *Saxifraga stellaris* L. *Ecoscience* 7: 201–213.
- SCHMID, B., AND J. WEINER. 1993. Plastic relationships between reproductive and vegetative mass in *Solidago altissima*. *Evolution* 47: 61–74.
- SIMPSON, G. G., AND C. DEAN. 2002. Flowering—*Arabidopsis*, the Rosetta Stone of flowering time? *Science* 296: 285–289.
- SOKAL, R. R., AND F. J. ROHLF. 1995. *Biometry—the principles and practice of statistics in biological research*, 3rd ed. Freeman and Company, New York, New York, USA.
- SØRENSEN, T. 1941. Temperature relations and phenology of the northeast Greenland flowering plants. *Meddelelser om Grønland* 125: 1–305.
- STANTON, M. L., C. GALEN, AND J. SHORE. 1997. Population structure along a steep ecological gradient: consequences of flowering time and habitat variation in the snow buttercup, *Ranunculus adoneus*. *Evolution* 51: 79–94.
- STARR, G., S. F. OBERBAUER, AND E. W. POP. 2000. Effects of lengthened growing season and soil warming on the phenology and physiology of *Polygonum bistorta*. *Global Change Biology* 6: 357–369.
- STENSTROM, M., AND U. MOLAU. 1992. Reproductive ecology of *Saxifraga oppositifolia*—phenology, mating system, and reproductive success. *Arctic and Alpine Research* 24: 337–343.
- STINSON, K. A. 1998. Effects of snowmelt timing on three high altitude *Potentilla* species: growth, reproduction, and distribution. Ph.D. dissertation, Princeton University, Princeton, New Jersey, USA.
- STRATTON, D. A. 1998. Reaction norm functions and QTL—environment interactions for flowering time in *Arabidopsis thaliana*. *Heredity* 81: 144–155.
- STRATTON, D. A., AND C. C. BENNINGTON. 1998. Fine-grained spatial and temporal variation in selection does not maintain genetic variation in *Erigeron annuus*. *Evolution* 52: 678–691.
- SULTAN, S. E. 1995. Phenotypic plasticity and plant adaptation. *Acta Botanica Neerlandica* 44: 363–383.
- THEURILLAT, J. P., AND A. GUIGAN. 2001. Potential impact of climate change on vegetation in the European Alps: a review. *Climatic Change* 50: 77–109.
- THEURILLAT, J. P., AND A. SCHLÜSSEL. 2000. Phenology and distribution

- strategy of key plant species within the subalpine-alpine ecocline in the Valaisan Alps (Switzerland). *Phytocoenologia* 30: 439–456.
- TOTLAND, O. 1997. Limitations on reproduction in alpine *Ranunculus acris*. *Canadian Journal of Botany—Revue Canadienne De Botanique* 75: 137–144.
- TOTLAND, O. 1999. Effects of temperature on performance and phenotypic selection on plant traits in alpine *Ranunculus acris*. *Oecologia* 120: 242–251.
- TOTLAND, O., AND W. EIDE. 1999. Environmentally-dependent pollen limitation on seed production in alpine *Ranunculus acris*. *Ecoscience* 6: 173–179.
- TURESSON, G. 1922. The genotypical response of the plant species to the habitat. *Hereditas* 3: 147–236.
- WAGNER, J., AND E. MITTERHOFER. 1998. Phenology, seed development, and reproductive success of an alpine population of *Gentianella germanica* in climatically varying years. *Botanica Acta* 111: 159–166.
- WALKER, D. A., J. C. HALFPENNY, M. D. WALKER, AND C. A. WESSMAN. 1993. Long term studies of snow-vegetation interactions. *BioScience* 43: 287–301.
- WALKER, M. D., R. C. INGERSOLL, AND P. J. WEBBER. 1995. Effects of interannual climate variation on phenology and growth of two alpine forbs. *Ecology* 76: 1067–1083.
- WASER, N. M. 1978. Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. *Ecology* 59: 934–944.
- WASER, N. M., AND M. V. PRICE. 1985. Reciprocal transplant experiments with *Delphinium nelsonii* (Ranunculaceae). Evidence for local adaptation. *American Journal of Botany* 72: 1726–1732.
- WEBER, W., AND R. WITTMANN. 1996. Colorado flora: Western slope, revised ed. University Press of Colorado, Niwot, Colorado, USA.
- WELKER, J. M., U. MOLAU, A. N. PARSONS, C. H. ROBINSON, AND P. A. WOOKEY. 1997. Responses of *Dryas octopetala* to ITEX environmental manipulations: a synthesis with circumpolar comparisons. *Global Change Biology* 3, Suppl. 1:61–73.
- YANOVSKY, M. J., AND S. A. KAY. 2002. Molecular basis of seasonal time measurement in *Arabidopsis*. *Nature* 419: 308–312.

*Review*

# Keeping up with a warming world; assessing the rate of adaptation to climate change

Marcel E. Visser\*

*Netherlands Institute of Ecology, PO Box 40, 6666 ZG Heteren, The Netherlands*

The pivotal question in the debate on the ecological effects of climate change is whether species will be able to adapt fast enough to keep up with their changing environment. If we establish the maximal rate of adaptation, this will set an upper limit to the rate at which temperatures can increase without loss of biodiversity.

The rate of adaptation will primarily be set by the rate of microevolution since (i) phenotypic plasticity alone is not sufficient as reaction norms will no longer be adaptive and hence microevolution on the reaction norm is needed, (ii) learning will be favourable to the individual but cannot be passed on to the next generations, (iii) maternal effects may play a role but, as with other forms of phenotypic plasticity, the response of offspring to the maternal cues will no longer be adaptive in a changing environment, and (iv) adaptation via immigration of individuals with genotypes adapted to warmer environments also involves microevolution as these genotypes are better adapted in terms of temperature, but not in terms of, for instance, photoperiod.

Long-term studies on wild populations with individually known animals play an essential role in detecting and understanding the temporal trends in life-history traits, and to estimate the heritability of, and selection pressures on, life-history traits. However, additional measurements on other trophic levels and on the mechanisms underlying phenotypic plasticity are needed to predict the rate of microevolution, especially under changing conditions.

Using this knowledge on heritability of, and selection on, life-history traits, in combination with climate scenarios, we will be able to predict the rate of adaptation for different climate scenarios. The final step is to use ecoevolutionary dynamical models to make the link to population viability and from there to biodiversity loss for those scenarios where the rate of adaptation is insufficient.

**Keywords:** climate change; phenology; microevolution; phenotypic plasticity; intergovernmental panel on climate change; scenarios

## 1. INTRODUCTION

The world's climate is changing at an unprecedented rate and this change will continue over the following decades (IPCC 2007). There is ample evidence that climate change has ecological consequences (Walther *et al.* 2002; Parmesan & Yohe 2003; Root *et al.* 2003; Parmesan 2006). The two best recorded climate-change-induced shifts are changes in *phenology*, i.e. in timing of vegetation development (Menzel & Fabian 1999), in spawning date in frogs and toads (Beebe 1995), return date of migrant birds (Hüppop & Hüppop 2003) and butterflies (Sparks *et al.* 2005), egg hatching date in insects (Visser & Holleman 2001), laying dates in birds (Crick *et al.* 1997), etc. and in *range shifts*, in the distribution of butterflies (Parmesan *et al.* 1999), breeding range (Thomas & Lennon 1999) or overwintering range (Austin & Rehfisch 2005) of birds, etc. Less widespread documented consequences of climate change are shifts in body size (Millien *et al.* 2006; Yom-Tov *et al.* 2006) and in changes

in the strength of competition between species (Bertness & Ewanchuk 2002; Jiang & Morin 2004).

The pivotal question in the debate on the ecological effects of climate change is whether these observed shifts are sufficiently large, i.e. whether species will be able to adapt fast enough to their changing world. Establishing the maximal rate of adaptation is also of crucial importance in the general debate on climate change. The rate of temperature increase up to 2100 is not determined yet as it strongly depends on socio-economic developments worldwide. The intergovernmental panel on climate change (IPCC) predicts climate change for six of such socio-economic scenarios (IPCC 2007). It is up to biologists to predict the ecological consequences for these different IPCC scenarios, for instance, in terms of reduced population viability or loss of biodiversity. This should then, in turn, be taken into account in the discussion on which IPCC scenario the world should aim for. As the magnitude of the ecological consequences will strongly depend on the rate of adaptation of species to their changing environment, assessing this rate of adaptation will set an upper limit to the rate at which temperatures can increase without loss of population viability or biodiversity.

\*m.visser@nioo.knaw.nl

One contribution of 18 to a Special Issue 'Evolutionary dynamics of wild populations'.

In this paper, I will discuss the various mechanisms by which species can adapt to climate change and will argue that the rate of adaptation (see §2 for definitions) will be primarily set by the rate of microevolution, a rate that is estimated to be alarmingly low in vertebrates (Gienapp *et al.* 2008). I will mainly use examples from research on timing of reproduction in birds and focus mainly on the effect of climate change on temperature, rather than rainfall, etc., simply because temperature effects are the best studied. Furthermore, I will highlight the importance of long-term pedigreed population studies for this research.

## 2. ADAPTING TO A WARMING WORLD

In a warming world, species need to adapt; that is, populations need to shift their distribution of phenotypes such that the average fitness for the shifted phenotypic distribution is higher than that of the original distribution when compared within the current environment. The rate of adaptation is simply this change in the distribution of phenotypes per year. Adaptation can work via a change in the genetic composition of the population, when some genotypes increase while other genotypes, with a lower fitness, decline in frequency (microevolution). But adaptation can also work via different forms of phenotypic plasticity, and there has been ample debate on which of these two forms contribute most to the observed shifts in phenotype distribution in relation to climate change (Przybylo *et al.* 2000; Reale *et al.* 2003; Gienapp *et al.* 2008).

The effects of climate change on phenotype distributions are very apparent; it is less clear how we should interpret these shifts. Are these signs of a disruption in the ecology of species, or are these an indication that species are adapting to a changing world? This question cannot be answered without establishing whether the observed shifts are sufficiently strong. Intuitively, one would define a shift as sufficiently strong when the average fitness of a population does not decline. As shown in figure 1, this definition however does not hold. Even when the rate of adaptation matches the changes in the optimal phenotype values exactly, fitness may still decline simply owing to a decline in habitat quality (see also §4). A more accurate definition is, therefore, that the distribution of phenotypes of a species shifts at the appropriate rate when there is stabilizing selection throughout the period of the mean phenotype shift. If so, the rate of adaptation perfectly matches the rate of climate change and thus any decline in fitness is not because the distribution of phenotypes is lagging behind: the rate of adaptation is sufficient. A complication with this definition of a sufficient rate of adaptation is that in some populations for some traits there was already directional selection prior to climate change (Merilä *et al.* 2001). In such cases, the question is whether this directional selection is getting stronger.

For great tits (Visser *et al.* 1998) and pied flycatchers (Both & Visser 2001), we have shown that there is increased directional selection on laying date (c.f. figure 1*b(ii)*), and thus that the rate of adaptation is insufficient in these populations. Interestingly, in UK great tits there is not such an increased directional selection (Cresswell & McCleery 2003), and thus the rate of adaptation is sufficient for that population (see Visser & Both (2005) for further discussion).

For the analyses on increased selection, the phenotypes of individuals need to be linked to their fitness, and for many species such data are not available. In these cases, we can compare the shifts in the observed and the optimal phenotype (c.f. figure 1 the (i) panels). We can use, as a first approximation, the shift in the phenology of a species' food compared to its own shift in phenology to investigate whether the rate of adaptation has been sufficient (Visser & Both 2005). In the majority of cases, the phenology of food shifts at a different rate leading to mistimed reproduction or growth (Stenseth & Mysterud 2002; Visser *et al.* 2004). This would indicate that in many species the shifts in adaptation are insufficient to match the changes in their environment.

What is constraining the rate of adaptation? Three types of responses to climate change have been described: dispersal to suitable habitats elsewhere, change in the phenotype distribution without a change in genotypes via phenotypic plasticity, and genetic change, i.e. microevolution (Holt 1990; Davis *et al.* 2005; Gienapp *et al.* 2008). It has often been suggested that the rate of adaptation can be quite high as phenotypic plasticity works almost instantaneously: if it becomes warmer, any trait that is phenotypically plastic with respect to temperature will shift. This can be via different forms of phenotypic plasticity: the response of an individual to environmental conditions within the same year (within the individual, within the same year), via learning (within the individual, across years) or via maternal effects (across individuals). In addition, the response in the form of dispersal to suitable habitats elsewhere, or, complementary, the immigration of novel genotypes into a population (an across population mechanism), can operate on relatively short time scales. Given these different mechanisms to adapt at relatively short time scales, microevolution does not seem essential to adapt to climate change. Below I explain why this is untrue and why adaptation to climate change, also via phenotypic plasticity or immigration of novel genotypes, will involve microevolution.

### (a) *Reaction norms*

When the same genotype gives rise to different phenotypes in different environments this is termed phenotypic plasticity (Pigliucci 2001). Both traits that are expressed only once in a lifetime (non-labile traits, e.g. amphibian metamorphosis) and those that are expressed repeatedly within individual lifespan (labile traits, e.g. breeding time in iteroparous organisms) can be phenotypically plastic (Nussey *et al.* 2007). Among years, the same individual starts egg laying at different dates, hence laying date is a phenotypically plastic labile trait. The ultimate reason for this plasticity is that the optimal laying date varies from year to year, for instance, because the food abundance peaks at different times in years with different spring temperatures. If animals could measure these annual food peaks directly and produce offspring 'instantaneously' this plasticity would be perfect. But the proximate cues involved in the plasticity, i.e. the components of the environment that affect the phenotype, are often not the same variables that determine the optimal laying date. For instance, laying date is affected by temperatures much earlier in the season than when selection on laying date operates. Environmental variables are only useful as cues if they predict the future via correlations between

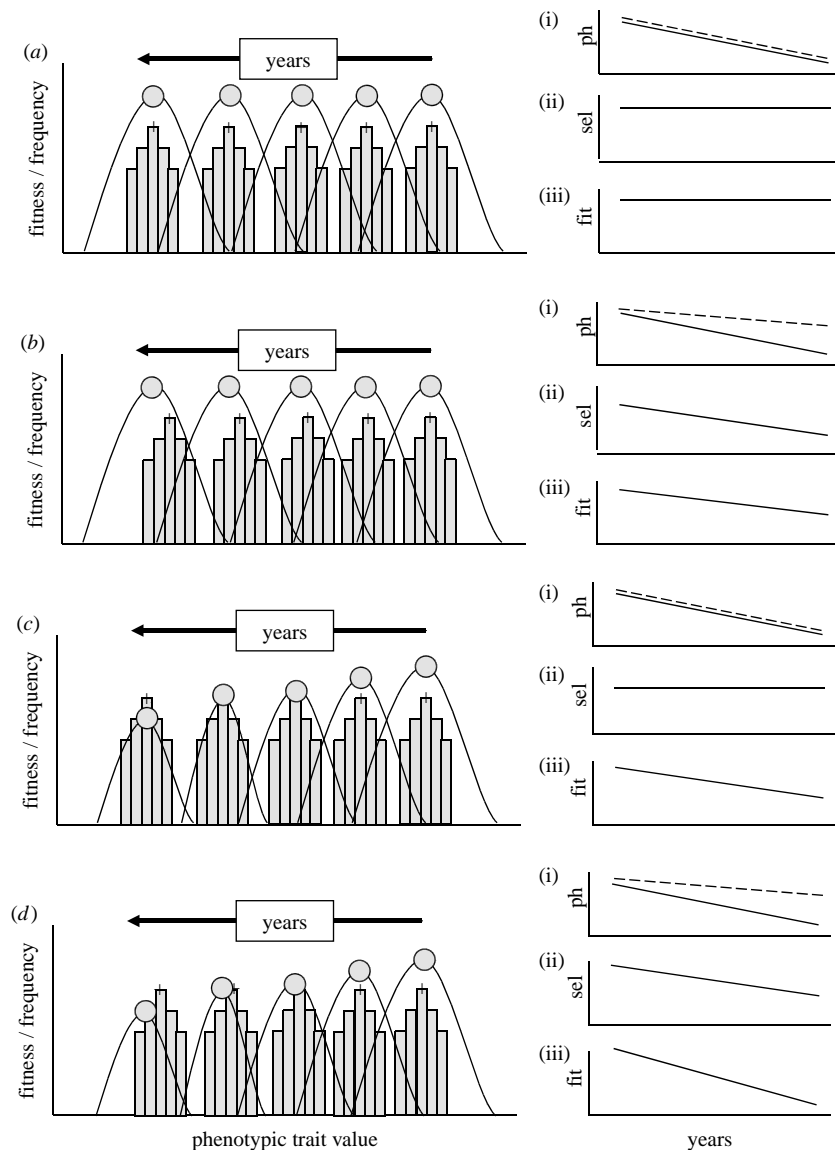


Figure 1. Over the years, due to climate change, the optimal trait value may shift as is indicated by the per year fitness curve, where the optimal trait value for that year is indicated by the dot at the highest fitness value. The actual distribution of trait values is indicated by the histogram, and the median trait value is indicated with a plus symbol. (a) There is no decline in fitness for individuals with the optimal trait value, and a perfect match between the shift in the optimal and the actual trait values. This is depicted in (a(i)) where the optimal trait value shift is indicated with a solid line and the actual trait value shift with a dashed line (ph, phenotypic trait value). In this scenario, there is no change in the selection on the trait value ((a(ii)) sd, selection differential) nor a decline in mean fitness ((a(iii)) fit, fitness). (b) There is again no decline in fitness for the optimal trait value, but the shift in the actual trait values is less than that for the optimal trait values. In this case, the lines in (b(i)) are no longer parallel, there will be increasing directional selection (b(ii)) and mean fitness will decline (b(iii)). The decline in fitness is due to an insufficient rate of adaptation. (c) There is a decline in fitness for the optimal trait values (due to, for instance, a decline in habitat quality), but a perfect match between the shift in the optimal and the actual trait values. Thus in (c(i)) the lines run parallel, and there is no increase in directional selection (c(ii)), but there is a decline in fitness (c(iii)). This decline is now not due to an insufficient rate of adaptation. (d) Finally, there is both a decline in fitness for the optimal trait values, and a shift in the actual trait values, which is less than that for the optimal trait values. Hence in (d(i)) the lines diverge, there is increasing directional selection (d(ii)) and a strong decline in fitness (d(iii)).

environmental variables that serve as proximate cues and the environmental variables that are determining selection, i.e. the covariance between phenotype and fitness (van Noordwijk & Muller 1994; Visser *et al.* 2004).

Despite the fact that animals are phenotypically plastic in response to temperature, this is not sufficient to adapt to climate change. This seems a paradox but the key insight is that reaction norms will no longer be adaptive due to the disruption of the correlation between temporally spaced environmental variables by climate change (Visser *et al.* 2004). Hence, the cues no longer accurately predict future

conditions: for instance, while in the past a certain temperature would correspond with a food peak for the offspring in 30 days, it would now correspond with a food peak in 20 days. This leads to mistimed reproduction as birds are, for instance, not sensitive enough to these cues, like temperature. As a consequence, microevolution of phenotypic plasticity is needed.

Environmental variables, like temperature or photoperiod, can be cues, i.e. they contain information about the future selective environment (Visser & Lambrechts 1999). The environment can, however, also select more

directly on reproductive decisions. For instance, in timing of reproduction there is strong selection on a close match between the offsprings' needs and the abundance of food (Visser *et al.* 2006) but as egg production is costly, both in terms of energy (Stevenson & Bryant 2000) and fitness (Visser & Lessells 2001), selection may also operate via the cost of reproduction at the egg-laying stage (harsh conditions may 'constrain' early laying, cf. Perrins 1970). If so, animals may shift their phenology to a lesser extent than the shift in phenology of the peak date in food availability (cf. Jonzen *et al.* (2007) for a similar argument). However, this will not lead to directional selection for early laying *per se* as laying too early will lead to a lower fitness via increased mortality risks for the parents due to their increased effort in the egg-laying phase. In fact, it may lead to selection of life-history traits that determine these costs of reproduction associated with egg production, like egg size. As these life-history traits will also be heritable, climate change will lead to selection on multiple life-history traits simultaneously (see also Visser *et al.* 2003; Garant *et al.* in press), and again microevolution is needed, which will affect the reaction norm of timing of reproduction. To calculate optimal reaction norms, we need to integrate the selection on all phases of the reproductive cycle, which may perhaps be possible via annual routine models (McNamara & Houston 2008). Climate change can thus affect selection on reaction norms via, for instance, higher costs of reproduction associated with egg production, but I want to stress that also in that case this is caused by the disruption of the correlation between temporally spaced environmental variables: if the phenology of the environment at the time of egg production shifts as much as that at the time of chick rearing, the cost of reproduction associated with egg production remains the same (see Visser *et al.* (1998) for further discussion).

In their simplest form, reaction norms (the curve describing the relationship between a trait and the environmental variable) have a slope (i.e. the sensitivity of the trait to the environment) and an elevation (i.e. the trait value in the average environment, Pigliucci (2001)). Both can be under selection and it is useful to make a distinction between these. However, there is often a genetic covariance between slope and elevation, which may well constrain the response to selection on the reaction norm. This genetic covariance itself may also be under selection (Sgro & Hoffmann 2004) but this discussion falls outside the scope of this review.

Selection in any particular year will operate on the phenotype expressed in that specific annual environment, and hence direct selection on reaction norms (which is the phenotypic response over a range of environments) seems difficult. However, what matters for an individual is its lifetime reproductive success and hence it has to do well in all the years it reproduces, not just in 1 year. Moreover, what matters for genotypes is their fitness over a whole range of lifetimes, which will have to do well over a wide range of environmental conditions. This does enable direct selection on reaction norms, especially in long-lived species.

#### (i) Selection on the elevation of the reaction norm

As a measure of an individual's average phenotype, much attention has been focused on the elevation of the reaction norm and the potential to respond to selection. When

these traits are heritable and under directional selection, the elevation of the reaction norm is expected to show an evolutionary change in value (Falconer & Mackay 1996). However, there are just two examples for vertebrates that have shown a response to climate change (see recent reviews Bradshaw & Holzapfel 2006; Gienapp *et al.* 2008). The genetic shift in phenology of the North American red squirrel (*Tamiasciurus hudsonicus*; Reale *et al.* 2003) has, however, been questioned (Postma 2006) while the blackcap (*Sylvia atricapilla*) for example (Berthold *et al.* 1992) may be a genetic response to environmental changes other than climate change. Gienapp *et al.* (2008) provide a set of conditions that need to be fulfilled in order to demonstrate climate change driven genetic change and conclude that studies that demonstrate such genetic change are 'conspicuously scarce'.

One of the hypotheses that is most commonly put forward to explain a lack of a response to selection is that both phenotype and fitness values are correlated to a third, unmeasured factor, like quality (Price *et al.* 1988). However, both for the great tit (*Parus major*) population of the Hoge Veluwe (The Netherlands; Gienapp *et al.* 2006) and the collared flycatcher (*Ficedula albicollis*) population of Gotland (Sweden; Sheldon *et al.* 2003) there was no statistically significant difference between the selection differential on laying date phenotype or the breeding value for laying date, indicating that breeding time and fitness are causally linked.

Another reason why evolutionary stasis on wild populations is common (see Merilä *et al.* (2001) for a complete overview of explanations) might be that the assumption that the heritability of a trait is constant over time does not hold. The annual variation in environmental conditions may mean that both selection on a trait and the additive genetic variance of that trait vary from year to year (Wilson *et al.* 2006). In Soay sheep (*Ovis aries*), selection was weaker in good environments, and there was a negative correlation between the magnitude of selection and the magnitude of the genetic variance that year, which has implications for the predicted response to selection (Wilson *et al.* 2006). This has been studied for very few species, leaving open the possibility that in other species selection and genetic variance are positively correlated, speeding up the rate of microevolution.

The simplest reason for the lack of an observed genetic response to selection is that this response is very small and therefore difficult to detect. In one of the Dutch long-term great tit populations (the Hoge Veluwe), the heritability for laying date was found to be 0.17, and the predicted response was just 1.5 days over 30 years (Gienapp *et al.* 2006). Very long time series are needed to detect such low rates of response to selection, and given that climate change started to have an impact on natural systems *ca* 1980, it may take many more years before such time series are available.

#### (ii) Selection on plasticity of the reaction norm

While under some conditions there is selection on simply being earlier in all environments (selection on main trait value), under different conditions there may be selection on the degree of plasticity (the slope of the reaction norm, i.e. on the sensitivity of the trait phenotype for the environmental variable). This would be the case if a species is still well timed in cold years but at times its reproduction is too late in warm years. Indeed, for a



Dutch great tit population, it has been shown that there is now selection on the strength of phenotypic plasticity (Nussey *et al.* 2005).

For microevolution in reaction norm slope there needs to be heritable variation in slope. For labile traits, we can often collect a number of trait values for the same individual. From that, it can be calculated whether there is variation among individuals in how they respond to their environment (I×E interactions, Nussey *et al.* 2007). Of the five examples of wild-vertebrate populations reviewed by Nussey *et al.* (2007), in four there is an I×E interaction. However, to get a response to selection genotypes need to differ in their response to the environment (G×E interactions). This has only been tested in two of these studies, in the collared flycatcher (Brommer *et al.* 2005) and the great tit (Nussey *et al.* 2005), and in a study on Soay sheep (Wilson *et al.* 2006), and in two of these three a G×E interaction was found. Clearly, we need many more studies to estimate the heritability on reaction norm slope in wild populations in general, and from there we estimate the rate of microevolution in this slope. In the great tit, for example (Nussey *et al.* 2005), no such response was detected.

In insects, the G×E interaction can be estimated by exposing relatives to different environments and measuring how their trait value depends on the environmental values (Nussey *et al.* 2007). In the timing of egg hatch of winter moths (which should be synchronized with bud burst of their host tree) there is a G×E interaction, and the reaction norm slope of egg hatch against temperature is predicted to change (van Asch *et al.* 2007). However, although there is a genetic response to selection in reaction norm elevation, no change in slope could be detected (van Asch *et al.* unpublished data). Obviously, many more studies are needed but it may be that a response to selection on reaction norm slopes is more difficult than on elevation (Wijngaarden & Brakefield 2001).

### (b) *Special cases of phenotypic plasticity*

There are two special cases of phenotypic plasticity, which have been suggested as mechanisms for species to adapt to climate change without the need for (slow) genetic changes; learning and maternal effects. Both these mechanisms can be described as reaction norms; in case of learning with the animal's past experiences as the environmental axis and for maternal effect the component of the environment affected by the mother. As in the previous section, there can be selection on both the elevation and the slope of these reaction norms.

#### (i) *Learning*

Animals can adapt to climate change if they learn from their experiences. Learning can be seen as a form of phenotypic plasticity: but instead of the current environment affecting the phenotype it is the environment experienced during earlier reproductive events by the animal. When animals reproduce too late as a first-year breeder they may shift their timing when they get older, and be better synchronized with their food source. Learning of phenology has been experimentally shown in blue tits (*Cyanistes caeruleus*), which respond to the degree in which they were mistimed in one year in their laying date in the next year (Grieco *et al.* 2002). It is unclear in how many species such learning plays a role.

Learning of timing is expected to have evolved to deal with spatial, rather than temporal, variation in seasonality. As with the phenotypic plasticity described earlier, it is essential that the environmental variables used to shape the phenotype are correlated with the environmental variables that correlate with fitness but in this case it is the environment in one year predicting the environment in the following year. For this to work, if the location where a bird breeds is early in one year, it should be early again the next year (Visser *et al.* 2006). This type of learning is not simply a carry over effect from being mistimed in one year affecting laying dates in the next year as animals that lay too late in one year will lay earlier the next year (Gienapp & Visser 2006).

Climate change may lead to selection on learning as individuals who shift their phenotype strongly to their experiences during previous reproductive attempts are likely to have a higher fitness. But this is more complicated than it looks. If a warm year is followed by another warm year, as is often the case in the last decades, animals that take past experiences into account will have a higher fitness. But if a warm year is followed by a cold year this is not so, animals may easily shift their phenotype too much. This is because this type of learning has evolved to deal with spatial variation where there is this strong year to year consistency. When 'using' this leaning to adapt to temporal variation, a single cold year in a row of warm years will select against animals with a steep reaction norm slope of laying date versus past experiences. It is therefore not probable that very strong learning will be selected for, and the optimal reaction norm slope will depend on the year to year variation in temperature.

Given that selection on learning may be affected by climate change, it would be of interest to study the heritability of the degree of learning. For this, the effect of previous experiences needs to be separated from the effects of current conditions, which can be done by using first-time breeders as a reference (Nager & Van Noordwijk 1995; Grieco *et al.* 2002). Next, using pedigreed populations, the heritability of this learning effect can be estimated. Selection may also act on the 'default trait value' for first breeders but this is just the elevation on the reaction norm described in the previous section (although we should consider that animals also use environmental cues which provide information where they are 'spatially', i.e. at an early or late site).

Will learning play a substantial role in adaptation to climate change? An obvious drawback is that this learned experience cannot be passed on to the next generation. Especially in short-lived species, where a large part of the population are first-year breeders, this will not lead to sufficient adaptation at the population level as these first-year breeders will remain mistimed.

#### (ii) *Maternal effects*

Maternal effects are modifications of offspring phenotype caused by the environment provided by the mother during development (Mousseau & Fox 1998). These can be seen as a special form of phenotypic plasticity where the trait value depends on environmental variables that are under control of the mother. This opens the possibility of adaptation without genetic change (Kirkpatrick & Lande 1989) and maternal effects, therefore, are potentially important mechanisms when adapting to climate

change. They can play a role via the environment as experienced by the offspring, such as photoperiod during the nestling period, and thus, where the maternal effect runs via the mother's timing, or maternal effects can run via direct effects provided by the mother, such as better care or yolk hormones.

An example of a maternal effect that runs via the mother's timing comes from blackcaps. In these migratory birds, the perceived photoperiod in the nestling phase affects their seasonal timing of moult and autumn migration (Coppack *et al.* 2001; Coppack & Pulido 2004): the longer the photoperiod experienced in the nestling phase, the earlier in life (i.e. at a younger age) the onset of migration. But this effect is not complete: for each later day a young bird is born, it starts migration half a day earlier in life, and thus in absolute calendar dates half a day later. Whether photoperiod during the nestling phase also affects the interval between fledging and first-time breeding is not known. In general, such an effect will be difficult to separate from genetic resemblance between mothers and daughters as early born offspring will have early reproducing parents. One way around this may be to compare the heritability in laying date for first- versus second-brood offspring (van Noordwijk 2006). These offspring are related to their mother in the same way but were raised under different photoperiodic environments. To my knowledge, not much is known about the effects of better care or maternal hormones on timing of reproduction of the offspring; although in great tits, there is an effect of female fledging mass on the clutch size she herself lays (Haywood & Perrins 1992).

Maternal effects have not evolved to cope with climate change but to cope with environmental variation that is predictable from the environment provided by the mother. Maternal effects may, under climate change, be constraining adaptation as has been suggested for the blackcap example. If laying date advances, offspring will be raised under shorter photoperiods, which in turn will lead to earlier autumn migration, perhaps too early as the growing season is prolonged under climate change (Coppack & Pulido 2004). This is a similar argument as presented earlier under the phenotypic plasticity section: if climate change leads to uncoupling of environmental variables, reaction norms, or here the maternal effects, are no longer adaptive.

The strength of maternal effects can be under selection (Kirkpatrick & Lande 1989), both at the maternal and the offspring level not only because the maternal effect themselves may have a genetic basis, i.e. determining the environment provided by the mother (maternal genes affecting the offspring phenotype), but also the response of the offspring reacting to the environment provided by the mother may be genetically determined. For the offspring, this is similar to selection on reaction norm slope and elevation. If, due to climate change, maternal effects are no longer adaptive, selection will occur and provided that the strength of the maternal effect is heritable, this will lead to microevolution in maternal effect strength. Thus, although maternal effects may play an important role in adapting to climate change, they themselves will be under selection and also here the rate of microevolution is essential for the speed at which species can adapt.

### (c) *Immigration*

One of the responses to climate change is that individuals move away to more suitable habitats (Holt 1990). I will discuss the complementary case to 'moving away', i.e. the immigration of novel genotypes into the population as this fits in better with the question of how populations adapt to climate change.

Immigration of novel genotypes into a population can potentially affect the rate of adaptation to climate change but it is a very different mechanism from the ones as discussed above. It will just supply genetic variation on which selection can act. Given that climate change has led to range expansions from more southern to northern areas (Parmesan & Yohe 2003), it may well be that current immigrants into breeding populations originate from southern populations. These animals may have genotypes that are better adapted to warmer conditions and hence dispersal may lead to more genetic variation, and hence speed up adaptation rate (Garant *et al.* 2007). The prediction is that while in the past immigrants could be preventing local adaptation (Postma & van Noordwijk 2005), and hence there was selection against such immigrants, immigrants may now promote adaptation to the changed environment, and they will now be selected for.

This scenario is, however, implicitly based on the assumption that when southern genotypes move north, they will encounter the set of environmental conditions under which they have evolved in their original range. And this is not so, it is important to realize that the climate of The Netherlands from the 1980s will not be present anywhere on the planet in 2020. There will be more northern areas that have the same mean annual temperature, but they will have a different photoperiod and probably also different rainfall patterns. Furthermore, not all species within a food chain shift north at the same rate, and thus the southern immigrants will now depend on, for instance, trees with a northern genotype, and thus the food chain this immigrants are now a part of will respond differently to climate than in the original range of these migrants.

Immigrating genotypes from southern populations will thus be better adapted in terms of temperature, but not in terms of, for instance, photoperiod. Photoperiod plays a major role in seasonal timing in vertebrates (onset of gonadal development, Gwinner (1986)) and invertebrates (diapause, Bradshaw & Holzapfel 2001). So, also for these genotypes, climate change leads to an uncoupling of environmental variables and microevolution is needed to adapt to their new range. Thus, immigration will lead to more genetic diversity and will thus speed up adaptation to climate change but these immigrants are not already fully adapted to their new environment as is often assumed (c.f. Bridle & Vines 2007).

### 3. LONG-TERM PEDIGREES

In the assessment of the rate of adaptation to climate change, long-term studies on wild populations with individually known animals play an essential role. These studies can be used to detect and understand temporal trends in life-history traits. Many of the examples of phenotypic shift due to climate change come from

such studies (Dunn & Winkler 1999; Visser *et al.* 2003; Both *et al.* 2004).

Furthermore, long-term pedigrees also can be used to estimate heritability of traits (van Noordwijk *et al.* 1981; van der Jeugd & McCleery 2002). Under climate change, heritabilities may well not be constant. When the environment changes, the additive genetic variation will change for those traits for which there is a genetic basis of among-individual variation in plasticity, i.e. an environment  $\times$  genes interaction (Hoffmann & Merilä 1999; Charmantier & Garant 2005). This is especially important if there is a correlation between the strength of selection and the amount of additive variation in a year. A negative correlation will slow down the response to selection (Wilson *et al.* 2006) while a positive correlation will speed up microevolution. As it is unlikely that the additive variance within a population will be constant over decades, and even more unlikely that it will remain constant under climate change, long-term studies can be used to detect long-term trends in heritability and to quantify any correlation between the strength of selection and the heritability.

Finally, long-term pedigrees can be used to assess the (changing) selection pressures on life-history traits. Such documentation of shifts in selection due to climate change have been few. Interestingly, even within species there are differences in how selection is affected: while in Dutch great tits there is increased selection for earlier laying (Visser *et al.* 1998; Nussey *et al.* 2005; Gienapp *et al.* 2006), in UK great tits, selection on early laying has become less intense (Cresswell & McCleery 2003). To understand intra- and interspecific differences in how selection intensity changes over time, additional measurements on other trophic levels of the food chain are needed (Visser & Both 2005). When a species shifts in phenology faster than the phenology of its prey (as may be the case in the UK great tits), this may lead to selection for a later timing of reproduction (or in the UK case less strong selection for earlier laying) while if they shift to a lesser extent than their prey (as in the case of the Dutch great tits) this will lead to stronger selection on early laying. Thus, the value of long-term pedigreed populations increases if additional measurements on their food chain are done.

A major problem with climate change is that we need to extrapolate outside the natural range, or at least outside the range that has been observed over the past decades. In that sense, even long-term data have little predictive value if the environment keeps getting warmer. To put this into perspective, the difference between very warm and very cold springs in The Netherlands is just 4°C, while some of the climate scenarios predict temperature increases of up to 6°C for 2100. Can we still extrapolate along, for instance, a linear reaction norm? To determine whether a reaction norm is nonlinear, long-term data from long-lived animals are needed. Other possibilities are to use controlled conditions (i.e. climate-controlled aviaries, etc.) or to move animals to other parts of their range (with a different climate) and study their phenotypes there (cf. genetically identical trees that are planted in botanical garden throughout Europe, Menzel (2000)).

A second major problem is that because climatic variables become uncoupled due to climate change, it

becomes very important to identify the right environmental variables that affect the phenotypes (i.e. the  $x$ -axis of the reaction norm). Ultimately, only detailed knowledge on mechanisms will inform us about this but this is a challenging task and will require close collaboration between evolutionary ecologists and physiologists (Visser *et al.* 2004; Wingfield *et al.* 2008). An alternative route is to use statistical models that correspond much better to the underlying (unknown) mechanism. For instance, while in reaction norms of timing of reproduction laying date is often regressed against the mean temperature over some specific time period of the year, it is also possible to statistically model this as a temperature-dependent daily probability of starting reproduction, using proportional hazard models, which also allows for interactions between, for instance, temperature and photoperiod (Gienapp *et al.* 2005).

To complicate matters further, there is not of course a single environmental variable that affects the phenotype, there are many. A final complication is that these multi-dimensional reaction norms are not only affected by a number of environmental variables that directly affect the genotype–phenotype relationship but also the environment experienced earlier in life (learning) and the environment as under control of the mother (maternal effects). These all need to be integrated into a single ‘response mechanism’ (Visser *et al.* 2004).

In addition, in order to understand the variation in reaction norm slopes, the environmental variables the organisms respond to need to be precisely identified. The variation in the laying date versus temperature reaction norm in great tits (Nussey *et al.* 2005) may be due to differences in the sensitivity to temperature among individuals (temperature on the  $x$ -axis). However, it could also be differences in the cost of egg production, which may enable some individuals to lay early under cold conditions, but not others (food intake on the  $x$ -axis). Yet another possibility is that there is variation in the photoperiodic sensitivity (Silverin *et al.* 1993) and some individuals are simply not ready to lay early in spring as they have not completed their gonadal development (photoperiod on the  $x$ -axis). Especially in the phenology in vertebrates, photoperiod plays an important role (Gwinner 1986). The annual pattern in photoperiod is of course not changing, leading to an uncoupling of photoperiodic and temperature patterns, and this will mean that the rate of microevolution in sensitivity to photoperiod may at some point become more important than the rate of microevolution in temperature sensitivity (Bradshaw & Holzapfel 2008).

To resolve these two problems, long-term pedigreed population studies need to be accompanied by physiological studies on the mechanisms underlying phenotypic plasticity. These mechanisms will tell us which variables actually play a role in plasticity, and what their ‘weight’ is within the response mechanism. Although it is less likely that species start using different environmental variables (cues), it is more probable that these ‘weights’ are under selection. Knowledge of the genetic variation in, and selection on, the components of the mechanism underlying plasticity is crucial to make the step towards predicting the rate of adaptation to climate change (see also Wingfield *et al.* 2008).

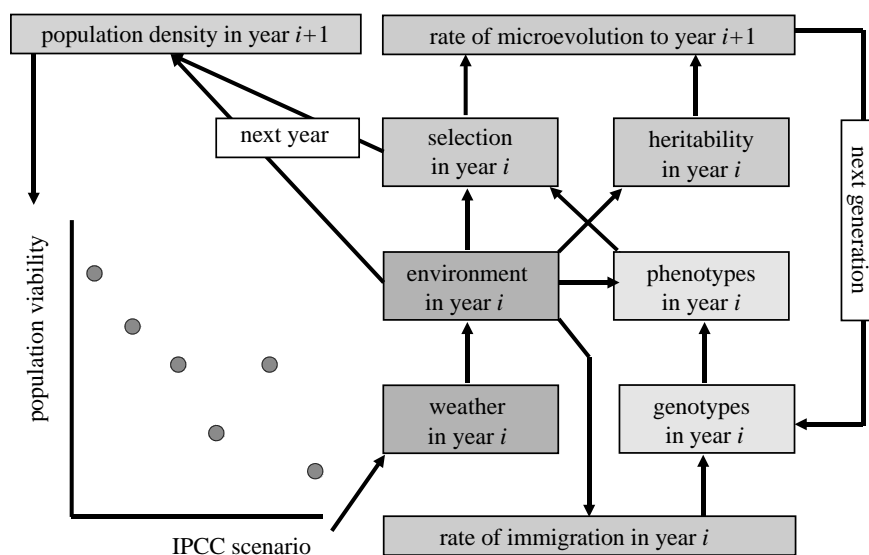


Figure 2. Diagram highlighting the importance of assessing the rate of microevolution when determining the ecological consequences of climate change, here depicted as the way population viability depends on the socio-economic development of the planet (as captured in the six scenarios of the IPCC). Each IPCC scenario predicts how the climate will change up to 2100. This will determine the weather in a specific year, which in turn will affect the biotic and abiotic environment for a species. This environment, combined with the set of genotypes, determines the set of phenotypes as these are phenotypically plastic. The environment also affects the heritability of the trait and, combined with the set of phenotypes, will determine the strength of selection on the trait. This selection and heritability determine the rate of microevolution, and thus, in combination with the immigration rate, the set of genotypes in the following year. The environment (via its (density dependent) effect on the average survival of adults and juveniles) and the strength of selection affect the population numbers in the next year, making the link to population viability. It is expected that the IPCC scenarios that will lead to a slow rate in temperature increase will have a small impact on population viability as the rate of microevolution will be sufficient for species to keep up with the warming world.

#### 4. LINKING CLIMATE SCENARIOS TO BIODIVERSITY LOSS

Climate change is threatening biodiversity (McLaughlin *et al.* 2002; Thomas *et al.* 2004) as organisms are no longer adapted to their changed environment. There are still relatively few examples that link disrupted life-history traits of organisms to their population viability or even extinction risks. One of the clear examples is the decline of pied flycatchers (*Ficedula hypoleuca*) in areas where the birds are most severely mistimed with their nestlings' food (Both *et al.* 2006). Another example is the decline of black grouse (*Tetrao tetrix*) population numbers that is linked in with mistimed reproduction (Ludwig *et al.* 2006). In, also mistimed, great tits, there is a decline in fitness (number of surviving offspring produced, Nussey *et al.* (2005)). However, there is no clear decline in population numbers, probably because population density is strongly affected by winter food in the form of beech nuts (Perdeck *et al.* 2000). The same is found in song sparrows (*Melospiza melodia*) where, despite increasing selection for early breeding, there is no effect on population numbers as numbers may be determined by juvenile survival, which is not affected by climate (Wilson & Arcese 2003). The development of a theoretical framework to link life-history traits under natural selection and population dynamics (ecoevolutionary dynamics), such as described above, has only recently been initiated (Hairston *et al.* 2005; Saccheri & Hanski 2006; Carroll *et al.* 2007; Pelletier *et al.* 2007) but is much needed to assess the ecological consequences of climate change.

The slow rate of adaptation will have large population consequences as populations will lag behind in their phenotype distribution. I want to briefly mention that climate change may also have population consequences even when the rate of adaptation is high enough

(figure 1*d*). As discussed in the introduction, the rate of adaptation can be viewed as sufficiently high if there is stabilizing selection throughout the period of the mean phenotype shift. It is important to realize that this does not necessarily mean that there is no decline in the mean reproductive output per individual or that population numbers stay stable. For instance, if climate change leads to a lower quality habitat because some prey species disappear, birds are less able to rear large broods and thus this will lead to a decline in the average clutch size via microevolution. Even if this microevolution is instantaneous, and thus there is a high rate of adaptation and there is always stabilizing selection, the reproductive output (and population numbers) will go down simply because in these poorer conditions fewer offspring can be reared to independence. But obviously, when the rate of adaptation is low, the shift in clutch size will lag behind and the impact of climate change will be even more severe.

With knowledge of both the rate of adaptation in different environments, and of the population consequences of disrupted life-history traits, we will be able to link population viability to IPCC socio-economic scenarios (IPCC 2007). From the socio-economic scenarios, emissions are calculated and from there climatic effects such as temperature and rainfall follow. From these, evolutionary ecologists need to predict the rate of genetic change in life-history traits, and as a final step, the effects on population viability for those scenarios where this rate of adaptation is insufficient. As is depicted in figure 2, we can then use these insights to link population viability to socio-economic scenarios.

In order to make this link, evolutionary ecologists will need climate predictions with a resolution of days as, especially the phenology of organisms, life-history traits

correlate with temperatures in very specific periods of the year (Visser *et al.* 2006). Climatologists use IPCC socio-economic and emission scenarios (IPCC 2007) to calculate such climate scenarios (using general circulation models like the ECHAM4 and the HadCM3, Pope *et al.* (2000)), and predict minimum/maximum temperatures, rainfall etc. on a daily basis for 1960–2100. Ideally, climatologists need to provide evolutionary biologists with three climate scenarios for each of the six IPCC emission scenarios (which in turn are based on socio-economic scenarios). This set of 18 climate scenarios can then be used to make predictions on the rate of microevolution. An example for an insect herbivore, the winter moth, for just a single climate scenario shows a microevolution rate sufficiently fast to match the climate change as predicted by that scenario (van Asch *et al.* 2007). Predicting the rate of microevolution for other emission scenarios for the winter moth was hampered by a lack of such a set of climate scenarios.

Climate change is one of the largest threats to biodiversity of our times. Only when we, as a planet, adopt a socio-economic strategy that will allow organisms to adapt in pace with the changes in their environment can we prevent severe loss of species due to global climate change. Determining the rate of climate change that populations can cope with is, therefore, information that is urgently needed. Quantitative geneticist and evolutionary ecologists, analysing long-term pedigreed datasets of wild populations, will play a crucial role in providing this key insight. We have work to do.

The author would like to thank Dan Nussey, Phillip Gienapp and three anonymous referees for their comments on a previous version of the paper and Loeske Kruuk for inviting him to contribute to this special issue, for initial discussions on the topic of the paper and for comments on all previous versions of the paper.

## REFERENCES

- Austin, G. E. & Rehfisch, M. M. 2005 Shifting nonbreeding distributions of migratory fauna in relation to climatic change. *Glob. Change Biol.* **11**, 31–38. (doi:10.1111/j.1529-8817.2003.00876.x)
- Beebee, T. J. C. 1995 Amphibian breeding and climate. *Nature* **374**, 219–220. (doi:10.1038/374219a0)
- Berthold, P., Helbig, A. J., Mohr, G. & Querner, U. 1992 Rapid microevolution of migratory behavior in a wild bird species. *Nature* **360**, 668–670. (doi:10.1038/360668a0)
- Bertness, M. D. & Ewanchuk, P. J. 2002 Latitudinal and climate-driven variation in the strength and nature of biological interactions in New England salt marshes. *Oecologia* **132**, 392–401. (doi:10.1007/s00442-002-0972-y)
- Both, C. & Visser, M. E. 2001 Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* **411**, 296–298. (doi:10.1038/35077063)
- Both, C. *et al.* 2004 Large-scale geographical variation confirms that climate change causes birds to lay earlier. *Proc. R. Soc. B* **271**, 1657–1662. (doi:10.1098/rspb.2004.2770)
- Both, C., Bouwhuis, S., Lessells, C. M. & Visser, M. E. 2006 Climate change and population declines in a long-distance migratory bird. *Nature* **441**, 81–83. (doi:10.1038/nature04539)
- Bradshaw, W. E. & Holzapfel, C. M. 2001 Genetic shift in photoperiodic response correlated with global warming. *Proc. Natl Acad. Sci. USA* **98**, 14 509–14 511. (doi:10.1073/pnas.241391498)
- Bradshaw, W. E. & Holzapfel, C. M. 2006 Evolutionary responses to rapid climate change. *Science* **312**, 1477–1478. (doi:10.1126/science.1127000)
- Bradshaw, W. E. & Holzapfel, C. M. 2008 Genetic response to rapid climate change: it's seasonal timing that matters. *Mol. Ecol.* **17**, 157–166. (doi:10.1111/j.1365-294X.2007.03509.x)
- Bridle, J. R. & Vines, T. H. 2007 Limits to evolution at range margins: when and why does adaptation fail? *Trends Ecol. Evol.* **22**, 140–147. (doi:10.1016/j.tree.2006.11.002)
- Brommer, J. E., Merilä, J., Sheldon, B. C. & Gustafsson, L. 2005 Natural selection and genetic variation for reproductive reaction norms in a wild bird population. *Evolution* **59**, 1362–1371.
- Carroll, S. P., Hendry, A. P., Reznick, D. N. & Fox, C. W. 2007 Evolution on ecological time-scales. *Funct. Ecol.* **21**, 387–393. (doi:10.1111/j.1365-2435.2007.01289.x)
- Charmantier, A. & Garant, D. 2005 Environmental quality and evolutionary potential: lessons from wild populations. *Proc. R. Soc. B* **272**, 1415–1425. (doi:10.1098/rspb.2005.3117)
- Coppack, T. & Pulido, F. 2004 Photoperiodic response and the adaptability of avian life cycles to environmental change. *Adv. Ecol. Res.* **35**, 131–150.
- Coppack, T., Pulido, F. & Berthold, P. 2001 Photoperiodic response to early hatching in a migratory bird species. *Oecologia* **128**, 181–186. (doi:10.1007/s004420100652)
- Cresswell, W. & McCleery, R. 2003 How great tits maintain synchronization of their hatch date with food supply in response to long-term variability in temperature. *J. Anim. Ecol.* **72**, 356–366. (doi:10.1046/j.1365-2656.2003.00701.x)
- Crick, H. Q. P., Dudley, C., Glue, D. E. & Thomson, D. L. 1997 UK birds are laying eggs earlier. *Nature* **388**, 526. (doi:10.1038/41453)
- Davis, M. B., Shaw, R. G. & Etterson, J. R. 2005 Evolutionary responses to changing climate. *Ecology* **86**, 1704–1714. (doi:10.1890/03-0788)
- Dunn, P. O. & Winkler, D. W. 1999 Climate change has affected the breeding date of tree swallows throughout North America. *Proc. R. Soc. B* **266**, 2487–2490. (doi:10.1098/rspb.1999.0950)
- Falconer, D. S. & Mackay, T. F. C. 1996 *Introduction to quantitative genetics*. New York, NY: Longman.
- Garant, D., Forde, S. E. & Hendry, A. P. 2007 The multifarious effects of dispersal and gene flow on contemporary adaptation. *Funct. Ecol.* **21**, 434–443. (doi:10.1111/j.1365-2435.2006.01228.x)
- Garant, D., Hadfield, J. D., Kruuk, L. E. B. & Sheldon, B. C. In press. Stability of genetic variance and covariance for reproductive characters in the face of climate change in a wild bird population. *Mol. Ecol.*
- Gienapp, P. & Visser, M. E. 2006 Possible fitness consequences of experimentally advanced laying dates in great tits: differences between populations in different habitats. *Funct. Ecol.* **20**, 180–185. (doi:10.1111/j.1365-2435.2006.01079.x)
- Gienapp, P., Hemerik, L. & Visser, M. E. 2005 A new statistical tool to predict phenology under climate change scenarios. *Glob. Change Biol.* **11**, 600–606. (doi:10.1111/j.1365-2486.2005.00925.x)
- Gienapp, P., Postma, E. & Visser, M. E. 2006 Why breeding time has not responded to selection for earlier breeding in a songbird population. *Evolution* **60**, 2381–2388.

- Gienapp, P., Teplitsky, C., Alho, J. S., Mills, J. A. & Merilä, J. 2008 Climate change and evolution: disentangling environmental and genetic responses. *Mol. Ecol.* **17**, 167–178. (doi:10.1111/j.1365-294X.2007.03413.x)
- Grieco, F., van Noordwijk, A. J. & Visser, M. E. 2002 Evidence for the effect of learning on timing of reproduction in blue tits. *Science* **296**, 136–138. (doi:10.1126/science.1068287)
- Gwinner, E. 1986 *Circannual rhythms*. Berlin, Germany: Springer.
- Hairston, N. G., Ellner, S. P., Geber, M. A., Yoshida, T. & Fox, J. A. 2005 Rapid evolution and the convergence of ecological and evolutionary time. *Ecol. Lett.* **8**, 1114–1127. (doi:10.1111/j.1461-0248.2005.00812.x)
- Haywood, S. & Perrins, C. M. 1992 Is clutch size in birds affected by environmental-conditions during growth? *Proc. R. Soc. B* **249**, 195–197. (doi:10.1098/rspb.1992.0103)
- Hoffmann, A. A. & Merilä, J. 1999 Heritable variation and evolution under favourable and unfavourable conditions. *Trends Ecol. Evol.* **14**, 96–101. (doi:10.1016/S0169-5347(99)01595-5)
- Holt, R. D. 1990 The microevolutionary consequences of climate change. *Trends Ecol. Evol.* **5**, 311–315. (doi:10.1016/0169-5347(90)90088-U)
- Hüppop, O. & Hüppop, K. 2003 North Atlantic oscillation and timing of spring migration in birds. *Proc. R. Soc. B* **270**, 233–240. (doi:10.1098/rspb.2002.2236)
- IPCC 2007 Summary for policymakers. In *Climate change 2007: the physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change* (eds S. Solomon, D. Qin, M. Manning, Z. Chen & M. Marquis), pp. 1–18. Cambridge, UK: Cambridge University Press.
- Jiang, L. & Morin, P. J. 2004 Temperature-dependent interactions explain unexpected responses to environmental warming in communities of competitors. *J. Anim. Ecol.* **73**, 569–576. (doi:10.1111/j.0021-8790.2004.00830.x)
- Jonzen, N., Hedenstrom, A. & Lundberg, P. 2007 Climate change and the optimal arrival of migratory birds. *Proc. R. Soc. B* **274**, 269–274. (doi:10.1098/rspb.2006.3719)
- Kirkpatrick, M. & Lande, R. 1989 The evolution of maternal characters. *Evolution* **43**, 485–503. (doi:10.2307/2409054)
- Ludwig, G. X., Alatalo, R. V., Helle, P., Linden, H., Lindstrom, J. & Siitari, H. 2006 Short- and long-term population dynamical consequences of asymmetric climate change in black grouse. *Proc. R. Soc. B* **273**, 2009–2016. (doi:10.1098/rspb.2006.3538)
- McLaughlin, J. F., Hellmann, J. J., Boggs, C. L. & Ehrlich, P. R. 2002 Climate change hastens population extinctions. *Proc. Natl Acad. Sci. USA* **99**, 6070–6074. (doi:10.1073/pnas.052131199)
- McNamara, J. M. & Houston, A. I. 2008 Optimal annual routines: behaviour in the context of physiology and ecology. *Phil. Trans. R. Soc. B* **363**, 301–319. (doi:10.1098/rstb.2007.2141)
- Menzel, A. 2000 Trends in phenological phases in Europe between 1951 and 1996. *Int. J. Biometeorol.* **44**, 76–81. (doi:10.1007/s004840000054)
- Menzel, A. & Fabian, P. 1999 Growing season extended in Europe. *Nature* **397**, 659. (doi:10.1038/17709)
- Merilä, J., Sheldon, B. C. & Kruuk, L. E. B. 2001 Explaining stasis: microevolutionary studies in natural populations. *Genetica* **112**, 199–222. (doi:10.1023/A:1013391806317)
- Millien, V., Lyons, S. K., Olson, L., Smith, F. A., Wilson, A. B. & Yom-Tov, Y. 2006 Ecotypic variation in the context of global climate change: revisiting the rules. *Ecol. Lett.* **9**, 853–869. (doi:10.1111/j.1461-0248.2006.00928.x)
- Mousseau, T. A. & Fox, C. W. 1998 *Maternal effects as adaptations*. New York, NY: Oxford University Press.
- Nager, R. G. & Van Noordwijk, A. J. 1995 Proximate and ultimate aspects of phenotypic plasticity in timing of great tit breeding in a heterogeneous environment. *Am. Nat.* **146**, 454–474. (doi:10.1086/285809)
- Nussey, D. H., Postma, E., Gienapp, P. & Visser, M. E. 2005 Selection on heritable phenotypic plasticity in a wild bird population. *Science* **310**, 304–306. (doi:10.1126/science.1117004)
- Nussey, D. H., Wilson, A. J. & Brommer, J. E. 2007 The evolutionary ecology of individual phenotypic plasticity in wild populations. *J. Evol. Biol.* **20**, 831–844. (doi:10.1111/j.1420-9101.2007.01300.x)
- Parnesan, C. 2006 Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* **37**, 637–669. (doi:10.1146/annurev.ecolsys.37.091305.110100)
- Parnesan, C. & Yohe, G. 2003 A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42. (doi:10.1038/nature01286)
- Parnesan, C. *et al.* 1999 Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* **399**, 579–583. (doi:10.1038/21181)
- Pelletier, F., Clutton-Brock, T., Pemberton, J., Tuljapurkar, S. & Coulson, T. 2007 The evolutionary demography of ecological change: linking trait variation and population growth. *Science* **315**, 1571–1574. (doi:10.1126/science.1139024)
- Perdeck, A. C., Visser, M. E. & Van Balen, J. H. 2000 Great tit *Parus major* survival, and the beech-crop cycle. *Ardea* **88**, 99–108.
- Perrins, C. M. 1970 The timing of birds' breeding season. *Ibis* **112**, 242–255.
- Pigliucci, M. 2001 *Phenotypic plasticity; beyond nature and nurture. Syntheses in ecology and evolution*. Baltimore, MD: John Hopkins University Press.
- Pope, V. D., Gallani, M. L., Rowntree, P. R. & Stratton, R. A. 2000 The impact of new physical parametrizations in the Hadley Centre climate model: HadAM3. *Clim. Dyn.* **16**, 123–146. (doi:10.1007/s003820050009)
- Postma, E. 2006 Implications of the difference between true and predicted breeding values for the study of natural selection and micro-evolution. *J. Evol. Biol.* **19**, 309–320. (doi:10.1111/j.1420-9101.2005.01007.x)
- Postma, E. & van Noordwijk, A. J. 2005 Gene flow maintains a large genetic difference in clutch size at a small spatial scale. *Nature* **433**, 65–68. (doi:10.1038/nature03083)
- Price, T., Kirkpatrick, M. & Arnold, S. J. 1988 Directional selection and the evolution of breeding date in birds. *Science* **240**, 798–799. (doi:10.1126/science.3363360)
- Przybylo, R., Sheldon, B. C. & Merila, J. 2000 Climatic effects on breeding and morphology: evidence for phenotypic plasticity. *J. Anim. Ecol.* **69**, 395–403. (doi:10.1046/j.1365-2656.2000.00401.x)
- Reale, D., McAdam, A. G., Boutin, S. & Berteaux, D. 2003 Genetic and plastic responses of a northern mammal to climate change. *Proc. R. Soc. B* **270**, 591–596. (doi:10.1098/rspb.2002.2224)
- Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C. & Pounds, J. A. 2003 Fingerprints of global warming on wild animals and plants. *Nature* **421**, 57–60. (doi:10.1038/nature01333)
- Saccheri, I. & Hanski, I. 2006 Natural selection and population dynamics. *Trends Ecol. Evol.* **21**, 341–347. (doi:10.1016/j.tree.2006.03.018)
- Sgro, C. M. & Hoffmann, A. A. 2004 Genetic correlations, tradeoffs and environmental variation. *Heredity* **93**, 241–248. (doi:10.1038/sj.hdy.6800532)

- Sheldon, B. C., Kruuk, L. E. B. & Merila, J. 2003 Natural selection and inheritance of breeding time and clutch size in the collared flycatcher. *Evolution* **57**, 406–420.
- Silverin, B., Massa, R. & Stokkan, K. A. 1993 Photoperiodic adaptation to breeding at different latitudes in great tits. *Gen. Comp. Endocrinol.* **90**, 14–22. (doi:10.1006/gcen.1993.1055)
- Sparks, T. H., Roy, D. B. & Dennis, R. L. H. 2005 The influence of temperature on migration of Lepidoptera into Britain. *Glob. Change Biol.* **11**, 507–514. (doi:10.1111/j.1365-2486.2005.00910.x)
- Stenseth, N. C. & Mysterud, A. 2002 Climate, changing phenology, and other life history and traits: nonlinearity and match–mismatch to the environment. *Proc. Natl Acad. Sci. USA* **99**, 13 379–13 381. (doi:10.1073/pnas.212519399)
- Stevenson, I. R. & Bryant, D. M. 2000 Climate change and constraints on breeding. *Nature* **406**, 366–367. (doi:10.1038/35019151)
- Thomas, C. D. & Lennon, J. J. 1999 Birds extend their ranges northwards. *Nature* **399**, 213. (doi:10.1038/20335)
- Thomas, C. D. *et al.* 2004 Extinction risk from climate change. *Nature* **427**, 145–148. (doi:10.1038/nature02121)
- van Asch, M., van Tienderen, P. H., Holleman, L. J. M. & Visser, M. E. 2007 Predicting shifts in phenology in response to climate change, an insect herbivore example. *Glob. Change Biol.* **13**, 1596–1604. (doi:10.1111/j.1365-2486.2007.01400.x)
- van der Jeugd, H. P. & McCleery, R. 2002 Effects of spatial autocorrelation, natal philopatry and phenotypic plasticity on the heritability of laying date. *J. Evol. Biol.* **15**, 380–387. (doi:10.1046/j.1420-9101.2002.00411.x)
- van Noordwijk, A. J. 2006 Are unseen effects of early environment negligible? Three examples in great tits (*Parus major*). *Acta Zool. Sin.* **52**(Suppl.), 675–677.
- van Noordwijk, A. J. & Muller, C. B. 1994 On adaptive plasticity in reproductive traits, illustrated with laydate in the great tit and colony inception in a bumble bee. In *Animal societies individuals, interactions and organization* (eds P. Jarman & A. Rossiter), pp. 180–194. Kyoto, Japan: Kyoto University Press.
- van Noordwijk, A. J., van Balen, J. H. & Scharloo, W. 1981 Genetic variation in the timing of reproduction in the great tit. *Oecologia* **49**, 158–166. (doi:10.1007/BF00349183)
- Visser, M. E. & Both, C. 2005 Shifts in phenology due to global climate change: the need for a yardstick. *Proc. R. Soc. B* **272**, 2561–2569. (doi:10.1098/rspb.2005.3356)
- Visser, M. E. & Holleman, L. J. M. 2001 Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proc. R. Soc. B* **268**, 289–294. (doi:10.1098/rspb.2000.1363)
- Visser, M. E. & Lambrechts, M. M. 1999 Information constraints in the timing of reproduction in temperate zone birds: great and blue tits. In *Proc. 22nd Int. Ornithol. Congr. Durban* (eds N. J. Adams & R. H. Slotow), pp. 249–264. Johannesburg, South Africa: BirdLife.
- Visser, M. E. & Lessells, C. M. 2001 The costs of egg production and incubation in great tits (*Parus major*). *Proc. R. Soc. B* **268**, 1271–1277. (doi:10.1098/rspb.2001.1661)
- Visser, M. E., van Noordwijk, A. J., Tinbergen, J. M. & Lessells, C. M. 1998 Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proc. R. Soc. B* **265**, 1867–1870. (doi:10.1098/rspb.1998.0514)
- Visser, M. E. *et al.* 2003 Variable responses to large-scale climate change in European *Parus* populations. *Proc. R. Soc. B* **270**, 367–372. (doi:10.1098/rspb.2002.2244)
- Visser, M. E., Both, C. & Lambrechts, M. M. 2004 Global climate change leads to mistimed avian reproduction. *Adv. Ecol. Res.* **35**, 89–110.
- Visser, M. E., Holleman, L. J. M. & Gienapp, P. 2006 Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia* **147**, 164–172. (doi:10.1007/s00442-005-0299-6)
- Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J. M., Hoegh-Guldberg, O. & Bairlein, F. 2002 Ecological responses to recent climate change. *Nature* **416**, 389–395. (doi:10.1038/416389a)
- Wijngaarden, P. J. & Brakefield, P. M. 2001 Lack of response to artificial selection on the slope of reaction norms for seasonal polyphenism in the butterfly *Bicyclus anynana*. *Heredity* **87**, 410–420. (doi:10.1046/j.1365-2540.2001.00933.x)
- Wilson, S. & Arcese, P. 2003 El Nino drives timing of breeding but not population growth in the song sparrow (*Melospiza melodia*). *Proc. Natl Acad. Sci. USA* **100**, 11 139–11 142. (doi:10.1073/pnas.1931407100)
- Wilson, A. J., Pemberton, J. M., Pilkington, J. G., Coltman, D. W., Mifsud, D. V., Clutton-Brock, T. H. & Kruuk, L. E. B. 2006 Environmental coupling of selection and heritability limits evolution. *PLoS Biol.* **4**, 1270–1275. (doi:10.1371/journal.pbio.0040216)
- Wingfield, J. C., Visser, M. E. & Williams, T. D. 2008 Integration of ecology and endocrinology in avian reproduction: a new synthesis. *Phil. Trans. R. Soc. B* **363**, 425–441. (doi:10.1098/rstb.2007.2149)
- Yom-Tov, Y., Yom-Tov, S., Wright, J., Thorne, C. J. R. & Du Feu, R. 2006 Recent changes in body weight and wing length among some British passerine birds. *Oikos* **112**, 91–101. (doi:10.1111/j.0030-1299.2006.14183.x)