ECOLOGY LETTERS

*Ecology Letters*, (2012) **15**: 502–508 doi: 10.1111/j.1461-0248.2012.01766.x

LETTER

# A single climate driver has direct and indirect effects on insect population dynamics

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## Abstract

Weather drives population dynamics directly, through effects on vital rates, or indirectly, through effects on the population's competitors, predators or prey and thence on vital rates. Indirect effects may include non-additive interactions with density dependence. Detection of climate drivers is critical to predicting climate change effects, but identification of potential drivers may depend on knowing the underlying mechanisms. For the butterfly *Speyeria mormonia*, one climate driver, snow melt date, has multiple effects on population growth. Snow melt date in year t has density-dependent indirect effects. Through frost effects, early snow melt decreases floral resources, thence per-capita nectar availability, which determines fecundity in the lab. Snow melt date in year t + 1 has density-independent direct effects. These effects explain 84% of the variation in population growth rate. One climate parameter thus has multiple effects on the dynamics of a species with non-overlapping generations, with one effect not detectable without understanding the underlying mechanism.

## Keywords

Climate, density-dependent indirect effects, *Erigeron*, flower phenology, frost, Lepidoptera, pollinator, snow melt timing, *Speyeria*, weather.

*Ecology Letters* (2012) **15**: 502–508

## INTRODUCTION

On-going climate change makes it increasingly urgent that we understand the operation of weather as a driver of population dynamics. Much of our current knowledge derives from a long-standing debate among ecologists (e.g. Nicholson & Bailey 1935; Andrewartha & Birch 1954; reviewed by Murray 1982): what is the relative role of extrinsic versus intrinsic factors in determining population dynamics? Recently, the debate has diversified to include whether environmental drivers can be understood or even detected without mechanistic hypotheses, based on a species' biology, that relate potential drivers to vital rates (e.g. Benton *et al.* 2006; Krebs & Berteaux 2006; Månsson & Lundberg 2006). We address this question here, with an example showing that a single climate driver may have both readily detectable and more cryptic effects whose detection requires a mechanistic hypothesis about the effects on a vital rate. Our study also suggests a class of climate effects on population dynamics that may be difficult to detect without an understanding of underlying mechanisms.

A second critical question is the mode of operation of environmental drivers. What is the relative importance of direct or indirect effects on population dynamics? In the simplest case, weather or composite climate metrics are treated as direct density-independent drivers in the analysis of time-series data. Choice of weather metrics to be tested is often determined by exploratory data analysis (e.g. Forister *et al.* 2011; Knape & de Valpine 2011), the weather metrics focused on in climate change studies (reviewed in Stenseth *et al.* 2002; Wallis DeVries *et al.* 2011), or available weather data sets (e.g. humidity is rarely available or considered, but see Goulson *et al.* 2005). In some cases, density may be included as a co-variate along with weather variables (e.g. Portier *et al.*1998).

In contrast, weather may have indirect effects on populations, through effects on other species in the community (see White 2008). Commonly proposed indirect effects operate on the food resource base of a population, although effects via predators or competitors have also been proposed (e.g. Jonzén *et al.* 2005; reviewed by Sibly & Hone 2002). For indirect effects via the food resource base, the impact on population dynamics depends on the per capita food resource base (a density-dependent effect) as translated into birth and death rates. Analyses looking only for effects of weather will miss this density-dependent indirect effect. Furthermore, appropriate hypotheses about the density-dependent indirect effects of weather depend on a functional understanding of the effects of resource constraints on vital rates, along with an understanding of the effects of weather on the resource itself. Documentation of such 'cryptic' indirect density-dependent effects of weather on population dynamics exists for only three species, to our knowledge (Belovsky & Slade 1995; Hone & Clutton-Brock 2007; Prevital *et al.* 2009). Each of these cases was made possible by a functional understanding of the pathway through which the indirect effect operates. We show that both direct and indirect effects may result from a single climate parameter and add a fourth example of a density-dependent indirect effect to the literature.

Aside from the mode of operation of weather drivers on population dynamics, the interaction of drivers with population age structure can make it difficult to detect effects of weather without a deeper understanding of the focal species' biology (e.g. Benton *et al.* 2006). In essence, time lags in weather effects may result if weather has different effects at different life stages. This has been studied in organisms with

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overlapping generations (e.g. Coulson *et al.* 2001), but effects of a single weather driver on multiple life stages have not been documented for a species with a simple life cycle and non-overlapping generations.

Here we study how one climate parameter determines population dynamics for a univoltine butterfly species with non-overlapping generations. Fecundity is directly related to nectar intake in this species (Boggs & Ross 1993), providing the functional understanding needed to translate weather effects into vital rates. First, we document *Erigeron speciosus* (Asteraceae) as the preferred floral nectar host of our focal butterfly, *Speyeria mormonia* (Lepidoptera: Nymphalidae), and show that flower head number is affected by timing of spring snow melt. Second, we develop and test the hypothesis that snow melt timing has density-dependent indirect and density-independent direct effects on butterfly population dynamics. Confirmation of this hypothesis shows, first, the importance of understanding mechanisms for detecting weather drivers of population dynamics; second, the multiple ways in which one driver can operate to affect dynamics; and third, that even an organism with a simple life cycle and non-overlapping generations can experience multiple effects of a single driver.

## STUDY SYSTEM AND PREDICTIONS

The focal species, *S. mormonia*, is a univoltine, montane butterfly, distributed throughout the North American Rocky Mountains, Great Basin Ranges and the Sierra Nevada in open, moist meadows. Adults feed on nectar and young males feed from mud, dung and carrion (Boggs & Jackson 1991). Females generally mate once (Boggs 1986), and eggs are laid singly in the litter near larval host plants in year t. Larvae over-winter as unfed first instars, feeding on *Viola* species after snow melt in year t + 1 and developing to adults in about 6 weeks.

Previous laboratory studies of adult food restriction showed that female fecundity declines linearly with declines in adult food intake, such that half *ad libitum* feeding results in fecundity that is half that under *ad libitum* feeding (Boggs & Ross 1993). *S. mormonia*'s eggs have a high C:N ratio relative to those of other butterfly species, and up to 80% of egg carbon derives from sugars eaten by adults, based on radiotracer and stable isotope studies (Boggs 1997; O'Brien *et al.* 2004). Food deprivation has no effect on female or male longevity, or on egg weight (Boggs & Ross 1993)

*Erigeron speciosus* was identified in the course of our study as the primary nectar source for *S. mormonia*. Because of this, its per capita flower availability should be a broad indicator of nectar availability to the butterfly. We therefore predicted that the per capita amount of nectar available, approximated as per capita flower availability, should be a determinant of butterfly population growth, if fecundity is a limiting factor.

Frosts occurring early in the growing season often kill developing flower buds (Inouye 2008), resulting in fewer flower heads, so that variation in weather affects variation in flower (hence nectar) availability in this system. We also postulate that such frosts kill post-diapause butterfly larvae or pupae. We chose day of year of first bare ground as the winter's snow melts as the surrogate measure for the probability of exposure to early season frosts, occurring after plant and butterfly development starts at the end of winter.

Based on this phenology and an understanding of the physiological underpinnings of butterfly life history, we first predicted that snow melt timing in a given year t affects butterfly fecundity through indirect effects on the per capita flower abundance of their preferred adult nectar hosts (a delayed density-dependent indirect effect). Second, we predicted that snow melt timing in year t + 1 directly affects developing larvae, possibly through mortality due to exposure to early growing season frosts in years with early snow melt (a density-independent direct effect).

## METHODS

Our study sites were located near the Rocky Mountain Biological Laboratory (latitude N 38º 57.48′, longitude W 106° 59.35′, ~ 2940 m asl), in the Elk Mountains of Colorado, USA.

### Floral preferences

To determine the floral nectar host preferences of *S. mormonia*, we recorded flower species fed on by nectaring butterflies captured in the course of mark-release-recapture (MRR) or behavioural studies in 1980 ($n$ = 464 observations), 1985 ($n$ = 381), 1986 ($n$ = 483), 1988 ($n$ = 165) and 1989 ($n$ = 241). The square roots of the proportions of visits by males and by females to *E. speciosus* were each normally distributed. We then regressed the proportion of visits to *E. speciosus* against the peak density of *E. speciosus* flowers (see Floral density), in order to examine floral preference as a function of relative *E. speciosus* flower density across years.

We also examined the visitation proportions to other floral species, to document relative use.

### Floral density

We used seven 2 × 2-m permanent plots in rocky meadows with shallow soil and relatively sparse vegetation that ranged in altitude from 2941 to 2988 m, and nine plots in meadows with deep soil and dense herbaceous vegetation that were at 2886 m. The closest plots were located within 250 m of the butterfly study site.

The number of *E. speciosus* capitula in bloom was counted every other day in each plot every year from 1975 to 2009 except 1990. Peak number of flowers was calculated by summing the peak number recorded in each plot (which occurred across a range of dates). An estimate for 1990 was calculated by regressing 34 years of *E. speciosus* flowering on that of *Helianthella quinquenervis* (another composite that flowers at about the same time and is also susceptible to early summer frosts, and for which data were recorded in 1990) ($y = 221.69 + 0.18x$, $r^2 = 0.35$, $F_{1,32} = 17.41$, $P = 0.001$).

Flowering data were also collected in these same plots for *Dugaldia hoopsii, Pyrrocoma crocea,* and *Heliomeris multiflora* (Asteraceae). These three species are secondarily visited by *S. mormonia*. We examined correlations between peak flower number for each of these species and peak number of *E. speciosus*. Peak numbers were ln-transformed to achieve normality.

### Butterfly density

We used standard MRR techniques (e.g. Boggs 1987). Butterflies were caught, a number written on both hind wings with an indelible marker, and the date, sex and number recorded. The butterfly was then released at the capture site. We carried out MRR throughout the flight season in 1980–1982, 1985–1991, 1999 and 2005, and at the peak of the male flight season in 1998 and 2004. We recorded data every day

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to every third day, depending on the year, except on days with continuous clouds and rain. MRR was done for 6–12 person hours/day, with the time consistent within a year. Using site numbers in Boggs (1987), sites 1–3 were used in 1980–1982, with an area of 1.65 ha; sites 1–10 were used in 1985–1989, with an area of 4.85 ha; and sites 4–10 were used in 1990–1991, 1998–1999 and 2004–2005, with an area of 3.2 ha. Areas were measured using a Trimble GPS unit (Trimble GeoXT; Trimble Navigation, Sunnyvale, CA), with differential correction using a base station, and hence differ from those used in Boggs (1987), which had been estimated from USGS maps.

We used annual estimates of male butterfly population densities. Male recapture rates are higher than female recapture rates (Boggs 1987). In the present data set, only 5 of 14 years have more than 15 female recaptures and female recapture rates of 8% or better. For many years, it is not possible to make even messy estimates of female population density. However, for those 5 years, female population density is positively correlated with male population density ($r = 0.89$, 4 d.f., $P = 0.04$). Thus, population density estimates for males are more reliable, and reflect female density.

For all years except 1998 and 2004, we used Cook's method (Cook *et al.* 1967) to calculate total annual male population sizes, based on known and interpolated daily estimates plus daily residence rates. Raw MRR data were analysed using POPSTRUC (Watt *et al.* 1977). This program estimates daily population size using Jolly techniques. We used recapture-decay curves to estimate daily residence rates, because our marking effort was evenly distributed through the flight season (Boggs 1987). Annual population size estimates were divided by study site area to obtain density estimates.

For 1998 and 2004, we first estimated male population size per hectare at peak flight during the season using a Lincoln Index. We used that value to estimate total male population size per hectare, based on a regression of total male population size per hectare on peak male population size per hectare for 11 years' data between 1980 and 2005 ($y = 22.97 + 2.39x$, $F_{1,9} = 104.21$, $P < 0.001$, adjusted $r^2 = 0.91$). The ln-transformation of male population density was normally distributed.

Both Jolly's method and the Lincoln Index equate birth and death with immigration and emigration, respectively, and assume that an individual does not migrate out of and into a site during the season. *S. mormonia*'s habitat is quite large, and our study sites covered a small fraction of the overall population. Our smallest study area, 1.65 ha, is on the order of a Wrightian neighbourhood, based on dispersal distances previously reported (Boggs 1987). Some butterflies thus migrated in and/or out of the site within a season.

However, we are interested in the ratio of interannual population sizes, not in absolute population size. Migration in and out of the site within a season does not affect this ratio if dispersal rates are constant across the years that are compared. The proportion of males dispersing within a site did not differ significantly among years in 1980–1982 for sites with equal shape and area ($G = 0.68$, 2 d.f., ns), although it differed significantly for sites with differing shapes and areas (Boggs 1987). We therefore assumed that dispersal rates in and out of the site were equal across years when the same study site was used. This allowed us to compare density estimates among years for which the same study site was monitored. The only contiguous years thus excluded from the analysis were 1989/1990, when the study site was reduced from 4.85 to 3.2 ha. When included in the analysis presented in the results, 1989/1990 growth rate was also a significant outlier (studentised residual = 4.35, 7 d.f., $P < 0.05$). Population growth rates used in the analysis thus came from nine pairs of sequential years.

Flower number was divided by male density to yield flowers per butterfly/ha. Data were ln-transformed to achieve normality for analysis.

### Snowmelt timing

Snowmelt timing was recorded at a 10 m × 10 m site within 0.6–1.0 km of the butterfly and flower plots. Snowmelt date was defined as the first date on which more than one half the site is bare. The site melts relatively uniformly, so in most years the entire site is first bare on the same date (W. Barr, pers. comm. 7 Dec 2011). Data were normally distributed. We examined temporal auto-correlation with a lag of 1 year in snow melt date between pairs of years used in the population growth analysis and in the 33-year snow melt data set.

### Population growth analysis

We used a multivariate form of the Ricker population growth equation (Dennis *et al.* 1998). The modelled butterfly growth rate depended on flowers per capita in year t and snow melt date in year t + 1:

$$N_{t+1} = N_t e^{(a + b*\ln(\text{flowers}_t/N_t) + c*\text{snowmeltdate}_{t+1})} \quad (1)$$

With re-arrangement:

$$\ln N_{t+1} - \ln N_t = a + b * \ln(\text{flowers}_t/N_t) + c * \text{snow melt date}_{t+1} \quad (2)$$

where $N_t$ is the male population density in year t.

Effects of nectar availability on population growth rate might be captured by $\ln(\text{flowers}_t)$ or snow melt $\text{date}_t$. Likewise, an effect of butterfly density alone in year t might be captured by $\ln N_t$. We therefore substituted these parameters for $\ln(\text{flowers}_t/N_t)$ in preliminary analyses. We also tested the combination of snow melt $\text{date}_t$ and $\ln N_t$. Both significance of the parameters and AIC were used to evaluate these preliminary results.

All regression analyses were done using Systat 12 (Systat Software, Inc.).

Educational copies of Figs 1 and 3a in presentation format can be found in online Supporting Information (Appendix S1).

## RESULTS

### Butterfly floral preference

*Erigeron speciosus* was the preferred nectar plant for *S. mormonia* in our study site. The plant flowers from mid-late July to mid-late August, during the peak of the male and female butterfly flight seasons. The square root of the proportion of all floral visits to *E. speciosus* by nectaring butterflies in each of five studied years was log linearly related to the number of blooming flowers (Fig. 1), but not significantly related to the number of flowers per butterfly. For years with 300 or more flowers present in the survey plots (23 of 35 years recorded, or 66%), we estimate that 70–90% of all nectaring visits by females and 60–90% by males were to *E. speciosus* during the blooming period (approximately 3 weeks) for that plant in our study site (Figs 1 and 2). In 75% of all recorded years at least 155 flowers were present, yielding an estimated > 50% of all nectaring visits to *E. speciosus*.

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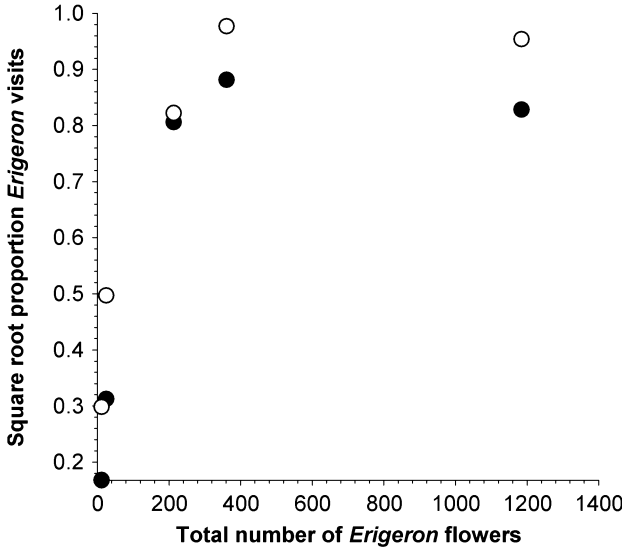


**Figure 1** The square root proportion of visits by *Speyeria mormonia* to *Erigeron speciosus* is log-linearly related to the peak number of blooming flowers. Data are from 1980, 1985, 1986, 1988 and 1989. Females (open circles): $y = -0.02 + 0.15 \ln x$, adjusted $r^2 = 0.90$, $F_{1,3} = 38.84$, $P = 0.008$. Males (closed circles): $y = -0.19 + 0.16 \ln x$, adjusted $r^2 = 0.86$, $F_{1,3} = 24.61$, $P = 0.016$.

Among other floral species, only *Dugaldia hoopsii, Pyrrocoma croceus,* and *Heliomeris multiflora* had average visitation rates of greater than 1%. *D. hoopsii* was ranked second behind *E. speciosus* in 1980, 1985 and 1989, while *P. croceus* was ranked second in 1986, and *H. multiflora* was second in 1988 (Table 1).

### Floral and butterfly densities

The peak number of *E. speciosus* flower heads increased monotonically with snow melt date (Inouye 2008; Fig. 2). Thus, snow melt date directly affected floral density and overall nectar availability in any given year.

The ln peak number of *E. speciosus* flower heads was significantly positively correlated with ln peak flower head number of *H. multiflora* ($r = 0.47$, 31 d.f., $P = 0.007$) and *P. croceus* ($r = 0.35$, 33 d.f., $P = 0.04$), but not *D. hoopsii* ($r = -0.15$, 35 d.f., $P = 0.39$).

Estimated butterfly population densities covered two orders of magnitude, ranging between 28 and 4492 males/ha over the course of the study (Fig. 3a). The drop in males/ha in 1985 was associated with a severe late June snow storm and freeze, occurring later than most early growing season freezes.

**Table 1** Proportion of visits by *Speyeria mormonia* to the second, third and fourth ranked floral species after *Erigeron speciosus* in the context of peak maximum number of *E. speciosus* flower heads

| | Peak # | Proportion visits | | |
|---|---|---|---|---|
| Year | *E. speciosus* | *Dugaldia hoopsii* | *Pyrrocoma croceus* | *Heliomeris multiflora* |
| 1980 | 1185 | 0.06 | 0.02 | 0.02 |
| 1985 | 12 | 0.52 | 0.23 | 0.15 |
| 1986 | 361 | 0.01 | 0.10 | 0.05 |
| 1988 | 213 | 0.11 | 0.08 | 0.12 |
| 1989 | 25 | 0.41 | 0.32 | 0.08 |

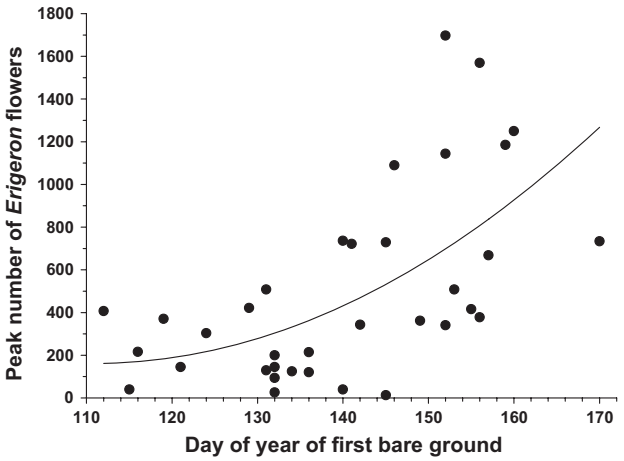


**Figure 2** Day of year of first bare ground determines peak flower number in *Erigeron speciosus* that same year. Maximum number of flowers = 3803.633 − (66.318 * First bare ground) + (0.302 * First bare ground^2), $r^2 = 0.36$, $F_{1,33} = 8.671$, $P = 0.006$.

### Snow melt timing

Date of snow melt showed a negative temporal autocorrelation with a 1 year lag for the nine pairs of years used in the analysis of butterfly population growth (snow $melt_{t+1} = 224.54–0.62$*snow $melt_t$; $F_{1,7} = 6.21$, $P = 0.04$). However, for the 37-year database from 1975 to 2011, date of snow melt shows no temporal autocorrelation ($r = 0.08$, 36 d.f., n.s.).

### Butterfly population growth

Per capita flower availability in year t and snow melt date in year t + 1 provided the best fit and explained 84% of the variance in butterfly population growth rate (Table 2; Fig. 3b,c). Thus, together with the effect of early snow melt on floral numbers, early snow melt affects *S. mormonia* population dynamics through: (a) a decrease in flowers per capita, which decreases fecundity and (b) a postulated decrease in offspring survival as larvae or pupae the next season.

We used $\ln(flower_t/N_t)$ to capture the density-dependent indirect effects of weather on fecundity, hence population growth. Neither flowers alone (no density-dependence) nor snow melt date in year t (the root weather effect) were significant (Table 2). Likewise, pure density dependence and the combination of density dependence and snow melt date in year t did not provide a better fit than per capita flower availability (Table 2). Understanding the underlying physiology was thus crucial to successful identification of population growth drivers and predictions of their effects on population size.

## DISCUSSION

We found that timing of snow melt affects the population dynamics of the butterfly *S. mormonia* both directly and through density-dependent indirect effects on flower availability. This is among the first demonstrations of density-dependent indirect effects, and documents multiple effects of a single weather parameter on population dynamics in a species with non-overlapping generations. These results argue that, while we can account for a very large amount of variation in population growth, functional hypotheses are important to a full understanding of population dynamics and the effects of climate

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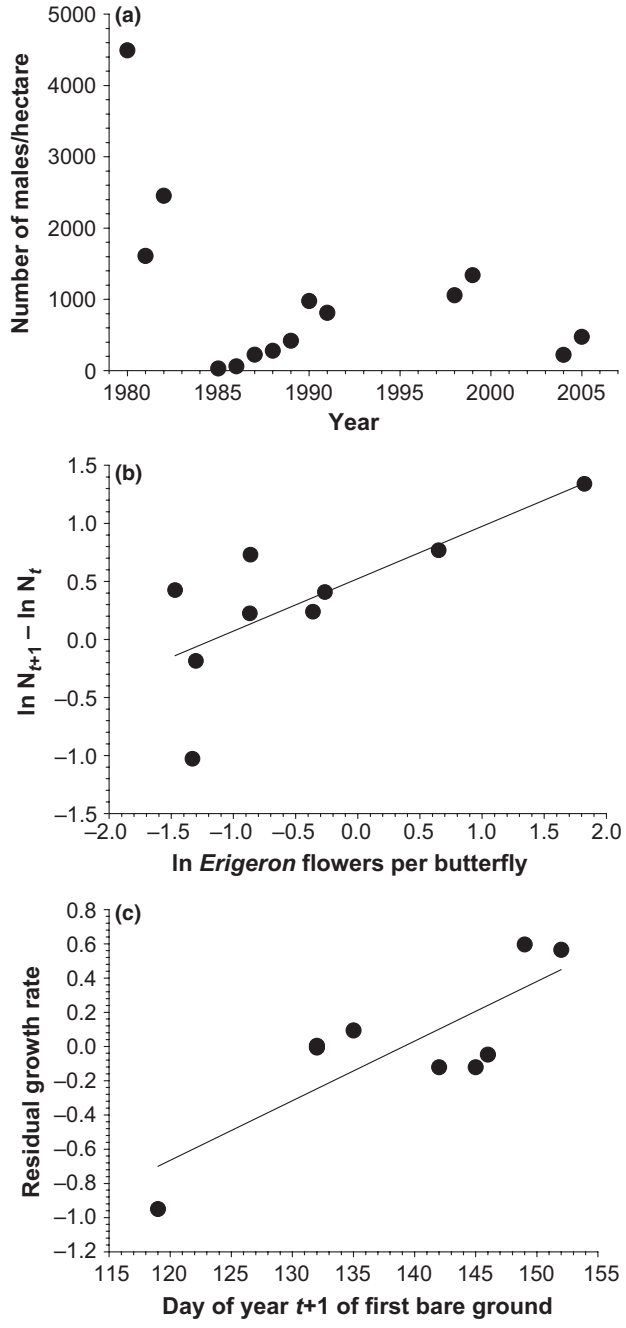


**Figure 3** Population dynamics of male *Speyeria mormonia*. (a) Male *S. mormonia* butterfly population numbers between 1980 and 2005. (b) Ln flowers per capita in year t affects male butterfly population growth between years t and t + 1. (c) Day of year of first bare ground in year t + 1 affects the residual of male butterfly population growth rate between years t and t + 1 vs. ln flowers per capita. The residual growth rate is shown because the effect in year t + 1 occurs after the effect in year t.

variability and change. Also, age-structure cannot be neglected for univoltine species.

The only three other examples of density-dependent indirect effects of weather on population dynamics also operated through resource limitation and resulting competition for those resources (Belovsky & Slade 1995; Hone & Clutton-Brock 2007; Prevital *et al.* 2009). In combination with our results, these examples suggest that the operation of weather drivers through density-dependent resource limitation is one class of scenarios for which a functional understanding is critical to understanding population dynamics. The effects may be diluted if the focal population uses multiple resource types, not all of which are equally affected by weather. In our case, the identity of secondary floral species varied from year to year, and the abundance of two of the three species was correlated with that of the primary floral species, likely enhancing our ability to detect the indirect weather effect.

The extent to which specific biological knowledge is needed has follow-on implications for the development of population models for species' range shifts in response to climate change (e.g. Wallis DeVries *et al.* 2011), among other analyses. Most long-term databases on population dynamics (e.g. NERC Centre for Population Biology, Imperial College 2010) contain only time-series data, which by themselves cannot yield insight into mechanism (Benton *et al.* 2006; Knape & de Valpine 2011).

The diverse effects of a single weather driver seen here are particularly impressive given that the butterfly in question has an annual life cycle. We are not dealing with a demographic cohort effect, in which effects on one age- or stage-class (cohort) at one point in time affect the population dynamics over subsequent time intervals in a population with demographic structure and overlapping generations, as the cohort moves through subsequent age or stage classes(Coulson *et al.* 2001; Saether *et al.* 2005). Our findings argue that even simple systems may show complex responses to future changes in climate means, variances and autocorrelation patterns.

The focal butterfly may be an important pollinator for *E. speciosus*, given the butterfly's degree of specialisation on the plant. If so, multiple effects of snow melt date on both pollinator and plant may increase the among-year variance in flowers per butterfly and hence flower visitation rates. In general, the overall plant-pollinator community at our site is being influenced by climate change effects on species' co-flowering patterns (Forrest *et al.* 2010; Aldridge *et al.* 2011) and what appears to be an increasing frequency of frost effects on sensitive species (Inouye 2008; Miller-Rushing & Inouye 2009; Lambert *et al.* 2010). In light of the present study, this suggests that understanding species interactions, particularly mutualistic interactions, in the face of climate variation requires an understanding of the functional relationships and how they influence population dynamics.

Other authors have advocated use of climate parameters that capture regional- to continental-scale coordinated changes in weather, rather than individual weather parameters. Such holistic parameters are based on atmosphere-ocean large-scale interactions and measured by sea surface temperature anomalies (SSTAs). Examples include the El Niño – Southern Oscillation or the Pacific Decadal Oscillation. SSTAs have been used successfully in studies of population dynamics (Stenseth *et al.* 2002; Hallett *et al.* 2004; Halkka *et al.* 2006) or population outbreaks resulting in migration (Vandenbosch 2003; Srygley *et al.* 2010). In our region, effects on temperature and precipitation appear to be driven independently by combinations of decadal and multidecadal SSTAs (McCabe *et al.* 2007; Schoennagel *et al.* 2007). While snow melt timing captured the relevant weather conditions in our case, it is possible that a principal components analysis including SSTAs could be fruitful over longer time scales.

Our finding of sequential effects of a single weather parameter on population dynamics raises the question of the role of temporal autocorrelation of population drivers. While we did not detect autocorrelation in the longer snow melt time series, it was present in the shorter series. A positive autocorrelation may amplify population

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**Table 2** Regression models predicting population growth rates of *S. mormonia* from year t to t + 1. Corrected AIC = Akaike Information Criteria corrected for small sample size

| Parameter | Coefficient | *P* | F | d.f. | *P* | Corrected AIC |
|---|---|---|---|---|---|---|
| Constant | −2.37 | n.s. (0.56) | 1.11 | 2,6 | n.s. (.39) | 32.24 |
| Ln flowers$_t$ | −0.12 | n.s. (0.55) | | | | |
| Snow melt$_{t+1}$ | 0.02 | n.s. (0.35) | | | | |
| Constant | −4.13 | n.s. (0.61) | 0.86 | 2,6 | n.s. (0.47) | 32.8 |
| snow melt$_t$ | 0.001 | n.s. (0.97) | | | | |
| snow melt$_{t+1}$ | 0.03 | n.s. (0.36) | | | | |
| Constant | −0.43 | n.s. (0.85) | 8.02 | 2,6 | 0.02 | 23.36 |
| ln N$_t$ | −0.3 | 0.02 | | | | |
| snow melt$_{t+1}$ | 0.02 | n.s. (0.24) | | | | |
| Constant | 3.84 | n.s. (0.48) | 5.51 | 2,6 | 0.05 | 33.93 |
| ln N$_t$ | −0.33 | 0.02 | | | | |
| snow melt$_t$ | −0.02 | n.s. (0.40) | | | | |
| snow melt$_{t+1}$ | 0.005 | n.s. (0.82) | | | | |
| Constant | −4.36 | 0.02 | 16.39 | 2,6 | 0.004 | 18.27 |
| ln flowers/N$_t$ | 0.49 | 0.003 | | | | |
| snow melt$_{t+1}$ | 0.04 | 0.01 | | | | |

responses, increasing the variance in population numbers, while a negative autocorrelation may depress responses. However, this information is not captured by simple use of time-lagged weather variables, because the density dependence of the driver differs in the two time intervals. Yet again, a functional hypothesis is important in understanding population dynamics.

## ACKNOWLEDGEMENTS

Collection and analysis of the floral data were supported by the US National Science Foundation DEB 75-15422, DEB 78-07784, BSR 81-08387, DEB 94-08382, IBN-98-14509, DEB-0238331, and DEB 0922080 and Earthwatch grants to DWI. Collection and analysis of butterfly data was partially supported by grants from the National Academy of Sciences, the Roosevelt Fund, the American Philosophical Society, the Whitehall Foundation, Stanford University's Biology Field Studies Program and the US National Science Foundation IOS-0923411 to CLB. The D. Bench, A. Enders, J. Tuttle families and Trampe Ranches permitted us to work on their land. A. Lerner, N. Bonoff, J. Bowsher, J. Delgado, E. Forwand, T. Karasov, C. Lemire, R. Loveland, E. Maxwell, C. Meister, K. Middleton, L. Nordby, R. O'Keefe, D. Price, E. Paul, D. Reeder, J. Richmond, C. Ross, S. Sabin, E. Shortwell, S. Simonson, S. Sonnad, K. Tomalty and A. Woods helped with the butterfly MRR study. M. Mayfield helped with data entry. W. Barr provided snow melt data. M. Nakajima, K. Niitepõld, W.B Watt and three referees commented on the manuscript. The authors declare no conflict of interest.

## AUTHORSHIP

CLB and DWI designed the research; DWI collected and analysed the plant data; CLB collected and analysed the pollinator data; CLB did the final statistical analysis and wrote the first draft of the manuscript, and CLB and DWI contributed substantially to the revisions.

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Editor, Jane Hill
Manuscript received 9 November 2011
First decision made 7 December 2011
Manuscript accepted 23 February 2012

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