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PHENOLOGICAL SEQUENCES REVEAL AGGREGATE LIFE HISTORY RESPONSE TO CLIMATIC WARMING

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Abstract. Climatic warming is associated with organisms breeding earlier in the season than is typical for their species. In some species, however, response to warming is more complex than a simple advance in the timing of all life history events preceding reproduction. Disparities in the extent to which different components of the reproductive phenology of organisms vary with climatic warming indicate that not all life history events are equally responsive to environmental variation. Here, we propose that our understanding of phenological response to climate change can be improved by considering entire sequences of events comprising the aggregate life histories of organisms preceding reproduction. We present results of a two-year warming experiment conducted on 33 individuals of three plant species inhabiting a low-arctic site. Analysis of phenological sequences of three key events for each species revealed how the aggregate life histories preceding reproduction responded to warming, and which individual events exerted the greatest influence on aggregate life history variation. For alpine chickweed (*Cerastium alpinum*), warming elicited a shortening of the duration of the emergence stage by 2.5 days on average, but the aggregate life history did not differ between warmed and ambient plots. For gray willow (*Salix glauca*), however, all phenological events monitored occurred earlier on warmed than on ambient plots, and warming reduced the aggregate life history of this species by 22 days on average. Similarly, in dwarf birch (*Betula nana*), warming advanced flower bud set, blooming, and fruit set and reduced the aggregate life history by 27 days on average. Our approach provides important insight into life history responses of many organisms to climate change and other forms of environmental variation. Such insight may be compromised by considering changes in individual phenological events in isolation.

Key words: *arctic;* Betula nana; Cerastium alpinum; *climate change; global warming; phenology;* Salix glauca.

Introduction

The annual timing of reproduction by organisms inhabiting seasonal environments is characterized by a sequence of phenological events that constitute the individual's life history as it relates to offspring production. In temporally varying environments, natural selection has shaped the timing of these events and relationships among them through their influences on offspring production, survival, and lifetime reproductive success (Primack 1987, Stearns 1992). Any of the life history events preceding and including offspring production may be constrained by a variety of factors, including density-dependent resource limitation, competition, herbivory, and abiotic conditions (Cole 1954, Silvertown et al. 1997, Post et al. 2001). Because of the consequences for offspring production and survival of variation in the timing of reproduction, individuals can be expected to adjust their reproductive phenology according to variation in the magnitude and importance of such constraints from year to year. Phenological responses to climatic variation and change represent some of the clearest examples of this environmental tracking by reproducing individuals, as Miller-Rushing and Primack (2008) have documented for data on hundreds of plant taxa spanning over a century.

Because evolution in one trait rarely, if ever, proceeds independently of other associated traits (Williams 1966, Maynard Smith 1993), individuals might experience constraints on the extent of phenotypic plasticity they display in response to density-dependent resource limitation or environmental variation and change. As a consequence, organisms may display greater adaptive responses in some components of their life history to environmental change, such as changes attributable to climate warming, than in others. For instance, many recent studies have documented shifts in timing of key life history events related to reproduction, such as timing of arrival at breeding grounds by migratory birds

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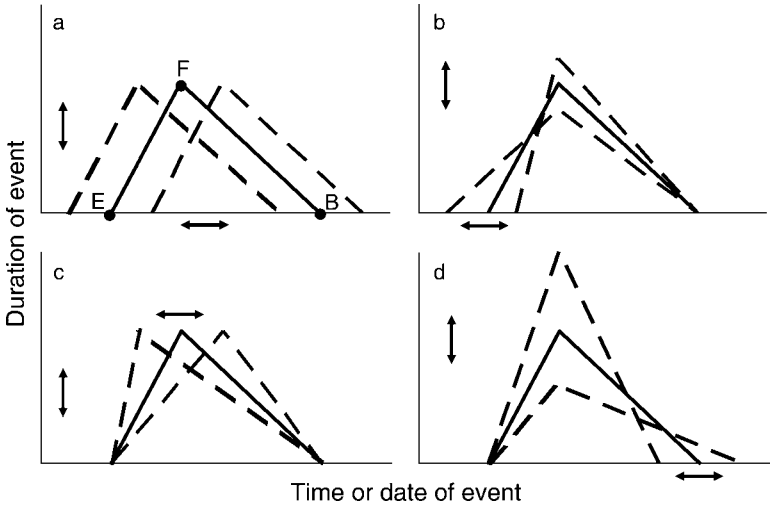

FIG. 1. Hypothetical changes in the timing of a sequence of phenological events constituting an aggregate life history. In this example, E denotes the timing of emergence of a plant, F denotes the timing of flower set, and B denotes the timing of first blooming. The *x*-axis represents the timing or date of the life history events in the sequence, and the *y*-axis represents the duration of each individual event. The area under the polygon quantifies the aggregate life history, that is, the total amount of time devoted to the aggregate life history preceding offspring production. Solid lines delineate the baseline life history in each panel. Dashed lines delineate aggregate life histories as they would be modified by shifts in E, F, or B. The aggregate life history and its shape may vary in four ways: (a) earlier or later occurrence of all phenological events; (b) earlier or later occurrence of the first event only; (c) earlier or later occurrence of the second event only; or (d) earlier or later occurrence of the last event only (all indicated with horizontal arrows). Moreover, the shape of the aggregate life history may be influenced by changes in the duration of any individual event or all events, as indicated with the vertical arrows. The dates of key life history events might also include, e.g., for birds, arrival at breeding grounds, nesting, egg-laying, hatching, and so on.

(Forchhammer et al. 1998, 2002, Root et al. 2003), but comparatively minor shifts in other life history events such as egg-laying (Both and Visser 2001, 2005). Hence, to improve our understanding of the manner in which organisms respond to climate change, it is important to begin to think in terms of the individual's aggregate life history response, rather than changes in single events in isolation. For this more comprehensive approach, it is beneficial to consider the sequence of phenological events constituting the life history of an organism leading up to and including reproduction, and the timing of successive events in relation to one another. Such a perspective enables us to understand better organismal response to rapid environmental change as well as its potential demographic and fitness consequences (sensu Lewontin 1965).

We advocate an aggregate life history approach to understanding organism response to climate change because the timing of individual life history events may be independently advanced, delayed, or unchanged by warming. As an example, consider a series of life history events leading up to reproduction, which, in plants, might comprise emergence, flower set (the first appearance of a flower bud in the current growing season), and blooming. Any number of events comprising an aggregate life history may be considered, but the simplest case, and the one we will pursue for illustrative purposes, is a sequence of three events. Climatic warming could influence this phenological sequence in several ways, advancing or delaying the timing of all of the events together (Fig. 1a), or advancing or delaying individual events while leaving others unchanged (Fig. 1b–d). Warming might also influence changes in the timing of individual events in the sequence to different extents. Moreover, the duration of each life history event may increase, decrease, or remain constant with climatic warming (*y*-axis shifts in Fig. 1). Taking changes in both into account will give a more informative picture of where the greatest or least flexibility in life history response to warming occurs in the life cycle of organisms. Using this approach, we can observe sequences of life history events related to reproduction, and ask whether the aggregate life history of an organism has responded to warming.

Because natural selection favors precocity (Cole 1954, Williams 1966), we should expect alleviation of environmental constraints on early development to promote accelerated progression to reproduction. Indeed, according to Williams (1966), rapid development should always be favored by natural selection because the more quickly an organism matures to a given critical size for successful reproduction the less likely it is to perish before reproducing (see also Primack 1987). As well, if adult survivorship sets the limit on reproductive success, then investment in early reproduction should be favored (Sibly 1997). Similarly, we should expect the aggregate life history of an organism (the period encompassing development to reproduction) not only to shift toward earlier reproduction, but also to be minimized if existing constraints are lifted.

Organisms may also experience tradeoffs between adjustment of one life history event to climatic change and the timing of the subsequent life history event preceding reproduction. Such tradeoffs may determine the manner in which both the timing and duration of successive life history events respond to climate change. In migratory birds, for example, changes in the timing of arrival at breeding sites in response to climatic warming may alter the length of the interval between the timing of arrival and the timing of egg-laying (Both and Visser 2005). Similarly, changes in early stages of plant phenology in response to climatic warming may alter the interval between emergence and flowering or between flowering and fruit production or seed dispersal. As a consequence of variation in both the timing and duration of successive life history events, the organism's aggregate life history may change. Alternatively, if only the timing but not the duration of life history events responds to climatic warming, the organism's aggregate life history may remain unaltered despite shifting temporally (sensu Fig. 1a).

By recording the timing and duration of successive life history events related to, for example, reproduction, and their changes over time in response to climatic warming, or by comparing their differences between warmed and control plots in an experimental setting, we can quantify the aggregate life history response to climatic warming. An advantage of this approach lies in its ability to inform us of whether an organism's investment of time in development preceding and including reproduction may be altered by climatic change. Furthermore, it allows us to determine whether the so-called aggregate life history of an organism remains constant despite shifts in response to warming, whether it changes but does not shift in response to warming, or whether it changes due to a shift in the timing of one or more life history events. Such information has the potential to furnish vital insights into species' differences in their life history responses (or lack thereof) to climate change that may have consequences for reproductive success and population behavior.

Methods

To test the hypothesis that an organism's aggregate life history may change in response to climatic warming, we conducted a controlled warming experiment in a low-arctic plant community near Kangerlussuaq, West Greenland (67°6′48″ N, 50°20′ W). The area is characterized by non-carbonate mountain complexes dominated by low-shrub tundra (Circum-Arctic Vegetation Map Team 2003; see also Post et al. 2003). Beginning in June 2002, as part of a larger experiment designed to quantify the influences of herbivory and warming on primary productivity and plant community dynamics, we erected six 800-m^2 exclosures in a remote site utilized by caribou (*Rangifer tarandus*) and muskoxen (*Ovibos moschatus*). The exclosures were circular, and constructed of steel t-posts and woven-wire fence measuring 120 cm high. From 14–15 May 2003, we erected four open-topped passive warming chambers (OTCs) inside each of three of the exclosures. The OTCs were constructed of UV-neutral glazing material in 1 mm thickness (Sun-Lite HP, Solar Components Corporation, Manchester, New Hampshire, USA) according to the protocol of the International Tundra Experiment (ITEX); they were cone-shaped, with a 60° side angle, and measured approximately 150 cm in diameter at the base and stood approximately 40 cm high (Marion et al. 1997). The OTCs are designed to elevate passively near-surface temperatures while minimizing unwanted side effects, such as interfering with gas exchange and evaporation and precipitation (Molau and Mølgaard 1996). In addition to elevating temperature, they may, however, alter the relative humidity at the soil surface within the chamber, in addition to reducing surface wind speed (Molau and Mølgaard 1996). However, the suitability of OTCs as an analogue of climatic warming has been experimentally validated (Hollister and Webber 2000), and so we assume that elevated temperature was the predominantly important abiotic alteration on our plots.

Upon erection of the OTCs, we also demarcated an adjacent control plot for each treatment plot. Within each exclosure, control and treatment plots were separated by a minimum of 3 m. We placed surface thermometers and hygrometers inside treatment and control plots. Although there was a thin cover ($\leq$1 cm) of patchy snow on the ground at the time the OTCs were erected on 14 May 2003, we recorded all visible species present and their phenological states at that time. We revisited the field site on 3 June 2003, when all snow was melted, and remained on-site until termination of the experiment on 19 June 2003, when all OTCs were taken down. The experiment resumed on 18 May 2004, when we revisited the field site and replaced all OTCs, thermometers, and hygrometers. As in 2003, there was a trace of snow on the ground upon reinitiation of the experiment in 2004, and we recorded all species present and their phenological states at that time. Observations in 2004 recommenced on 4 June and terminated on 20 June, following the procedures used in 2003. We visited all plots on a daily or near-daily basis, and recorded the phenological stages of all species present in each plot, as well as surface temperature and humidity. Average daily temperature on our plots was quantified as the mean of the minimum and maximum temperatures recorded on each plot within a 24-hour period. For each year, we compared mean minimum daily temperature, mean maximum daily temperature, and mean average daily temperature between treatment and control plots using an ANOVA with "treatment" as a fixed factor and "date" as a random factor.

To the best of our knowledge, all plots contained a single individual of the clonal gray willow (*Salix glauca*; Salicaceae) and/or a single individual of dwarf birch (*Betula nana*; Betulaceae), as well as one to several

individuals of many forb species (see Post et al. 2003). We recognize, however, that what we identified as individuals may be more accurately described as ramets rather than as genets. Therefore, we restricted our analyses to data on a single individual of each species for each plot. We were able to track phenological progression through at least three stages of development in individual willow, birch, and a single forb species, alpine chickweed (*Cerastium alpinum*). In both years of the experiment, however, chickweed emerged during our absence between erection of OTCs and recommencement of our observations in early June.

To quantify the aggregate life history of an organism, we may define it as a function of both the timing of key life history events related to reproduction and their duration. As well, as a result of selection on an organism's fecundity schedule (Lewontin 1965), we can expect the duration of any particular life history event, or the total duration of all observed life history events, to be related to the timing of onset for any sequence of life history events. Hence, the aggregate life history of an organism may be quantified as the area of the polygon delineated in parameter space by the points representing, in our case, the duration of each phenological event plotted against the dates on which those events occurred, as in Fig. 1. It is the area of such a polygon that we will denote as the organism's aggregate life history.

To derive polygons on which to base our analyses of changes in the aggregate life histories of the study organisms in response to warming, we plotted, for each individual, the date of each observed phenological event on the *x*-axis in Fig. 1, and the duration of each event on the *y*-axis. Because our observations concluded with the third phenological event observed for each species, its duration was recorded as zero; however, its actual duration could also have been included in the estimation of the aggregate life history if it had been observed. We then quantified, for each individual, the area of the polygon anchored by these points and extending downward to the *x*-axis, thereby estimating the aggregate life history (ALH) of the organism preceding production of offspring. Polygon areas were calculated by separating each polygon into a trapezoid and a triangle, calculating their respective areas, and summing them. In other applications of this approach, the method for quantifying the area of the polygon representing an organism's ALH would, of course, vary according to the shape of the polygon. For each species, we then compared the mean ALH on warmed vs. ambient plots using a univariate ANOVA. It is important to stress that, in this approach, we are not analyzing the relationship between the *y*-axis variable (duration) and the *x*-axis variable (date), because, of course, the duration of any phenological interval is dependent upon the dates of the events defining the beginning and end of the interval. Rather, this approach is used as a means of depicting and quantifying the ALH as a two-dimensional polygon defined by the timing and duration of a series of phenological events (sensu Fig. 1).

For each species, we used the earliest observed phenological events as the start of the ALH, and the latest observed events as the end of the ALH preceding offspring production. These varied slightly among the three species observed because of differences in their phenological progression. The events comprising the ALH preceding offspring production in the three species were as follows: for alpine chickweed, emergence of vegetation, flower set (the date of first appearance of flower buds), and first bloom; for gray willow, opening of leaf buds, flower set (the date on which the catkin reached ~1 mm in size), and first bloom; and for dwarf birch, flower set (the date on which the catkin reached ~1 mm in size), bloom, and fruit set (the date on which more half of the visible stigmas had withered and initial swelling of the ovary was apparent). Because the phenological events observed differed among species, direct comparisons among them of their responses to warming are not possible. Nonetheless, the same events were observed within species on treatment and control plots, facilitating species-specific analyses of ALH response to warming.

Aggregate life histories were estimated for three and two chickweed individuals on treatment and control plots, respectively, in 2003, and three and three chickweed individuals on treatment and control plots, respectively, in 2004; five and five gray willow individuals on treatment and control plots, respectively, in 2003; and seven and five dwarf birch individuals on treatment and control plots, respectively, in 2003. Chickweeds observed in 2003 and 2004 were not the same individuals, and data were pooled between years. All individuals were observed on different plots. Because we observed only 11 individual chickweed plants, 10 individual willows, and 12 individual dwarf birch, we urge caution in the interpretation of our results, but have no reason to believe that the plants we observed were not representative of the larger populations.

Results

Mean daily average temperature was significantly higher on treatment than on control plots by 2.02°C in 2003, and 1.4°C in 2004 (both P values = 0.001; Table 1). In 2003, the mean daily minimum temperature recorded on our plots was 0.63°C warmer on treatment than on control plots ($P = 0.002$), whereas, in 2004, mean daily minimum temperature did not differ significantly between treatment and control plots ($P = 0.25$). In 2003, mean daily maximum temperature was higher on treatment than on control plots by 3.9°C, whereas, in 2004, this difference was only 2.6°C (both P values $<$ 0.001). We are unable to explain the differences in treatment means between years as being due to different ambient environmental conditions. Daily temperatures recorded by the Danish Meteorological Institute at Kangerlussuaq Airport were higher in 2004 than in 2003

TABLE 1. Temperatures (mean ± SE) on treatment vs. control plots in the study site, and ambient environmental temperatures during the study as measured at Kangerlussuaq International Airport, Greenland, ~20 km from the study site.

Conditions	Mean daily temperature (°C)		
	Average	Minimum	Maximum
2003			
Treatment	$10.8^{a} \pm 0.17$	$-2.25^{a} \pm 0.16$	$23.1^{a} \pm 0.20$
Control	$8.78^{b} \pm 0.18$	$-2.88^{b} \pm 0.16$	$19.2^{b} \pm 0.20$
Ambient	8.54 ± 0.11	2.63 ± 0.09	14.5 ± 0.13
2004			
Treatment	$12.0^{a} \pm 0.16$	$3.18^{a} \pm 0.13$	$20.8^{a} \pm 0.26$
Control	$10.6^{b} \pm 0.17$	$3.07^{a} \pm 0.13$	$18.2^{b} \pm 0.26$
Ambient	9.95 ± 0.06	4.62 ± 0.06	15.3 ± 0.09

Notes: Within columns, and within years, lowercase letters denote comparisons between means on treatment and control plots. Different letters denote means that differ significantly ($P < 0.05$).

(Table 1); however, this weather station lies approximately 20 km from our study site at the end of a fjord, and may not represent weather conditions at our site, which is adjacent to the Inland Ice. One possible explanation for the differences between years on our plots is that average daily wind speed was higher in 2004 than in 2003, because the main mechanism of warming induced by OTCs is wind blockage. Average daily relative humidity was ~9% lower on treatment than on control plots in both years, but this difference was not significant in either year (both P values > 0.05).

For chickweed, the mean timing of emergence between treatment and control plots did not differ, presumably because individuals on both plots were emergent upon the first observation in June of each year. However, the duration of emergence (i.e., the number of days from the occurrence of emergence to the date of flower set) was shorter on warmed than on control plots because flower set occurred on average 2.5 days earlier on warmed than on control plots ($F_{1,9} = 11.1$, $P < 0.01$; Fig. 2a). The duration of flower bud set did not differ between warmed and control plots ($F_{1,9} = 0.004$, $P = 0.95$). Blooming in chickweed did not occur significantly earlier on warmed than on control plots ($F_{1,9} = 1.55$, $P = 0.25$). Despite alteration of the duration of emergence and the timing of flower set by the warming treatment, the aggregate life history of chickweed was not significantly shorter on warmed (25.2 ± 9.0 days) than on control (37.4 ± 9.9 days) plots ($F_{1,9} = 0.78$, $P = 0.40$). Hence, this species, while displaying a slight developmental shift suggestive of an advance in response to warming of phenological events preceding offspring production (Fig. 2a), similar to a rigid translation of the fecundity schedule (Fig. 1a), did not adjust its aggregate life history in response to warming. These results, may, however, have been influenced by the lack of observations of actual dates of emergence.

In gray willow, leaf opening occurred 3 days earlier on warmed than on control plots ($F_{1,8} = 13.2$, $P < 0.01$; Fig. 2b). As well, the duration of the leaf opening phase was shorter by 4 days on warmed than on control plots ($F_{1,8} = 6.95$, $P = 0.03$) because flower bud set occurred earlier by 7 days on warmed than on control plots ($F_{1,8} = 10.6$, $P = 0.01$; Fig. 2b). However, the duration of flower bud set did not differ between warmed and control plots ($F_{1,8} = 0.18$, $P = 0.68$). Nonetheless, blooming occurred 7 days earlier on warmed than on control plots ($F_{1,8} = 10.1$, $P = 0.01$). As a result, the aggregate life history of gray willow was not only advanced by warming, it was

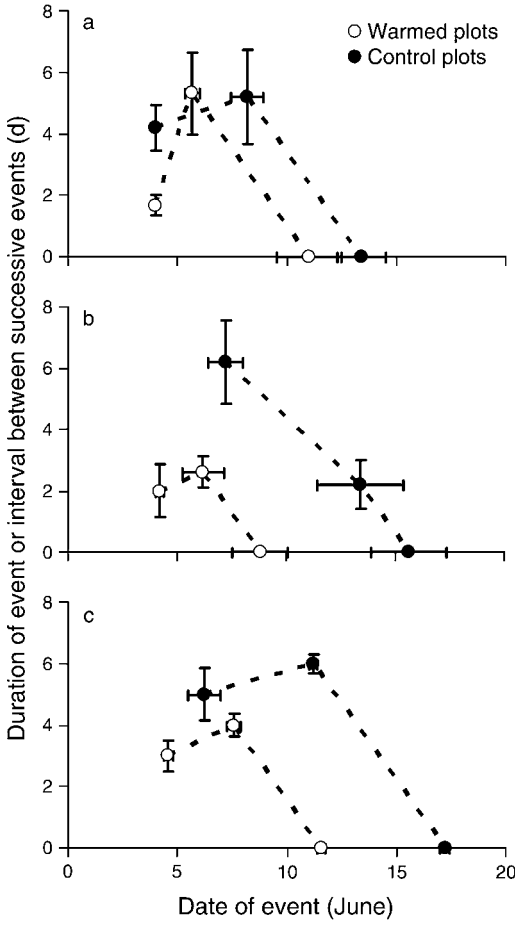

FIG. 2. Mean aggregate life history responses of multiple individuals of (a) alpine chickweed (*Cerastium alpinum*), (b) gray willow (*Salix glauca*), and (c) dwarf birch (*Betula nana*) to experimental warming in Kangerlussuaq, West Greenland, during the growing seasons in 2003 and 2004. For each species, each point represents the mean (±SE) timing of a phenological event in the sequence comprising the total observed life history preceding seed production, against which is plotted the mean (±SE) duration of that event. In chronological order from left to right, these were, for chickweed, emergence, flower set, blooming; for willow, leaf opening, flower set, blooming; for birch, flower set, blooming, fruit set. Dashed lines delineate boundaries of the polygons anchored by the means plotted in each panel; these polygons represent the mean aggregate life history of each species on warmed and ambient (control) plots.

also reduced significantly on warmed (10.3 ± 6.6 days) compared to control (32.3 ± 6.7 days) plots ($F_{1,8} = 5.47$, $P = 0.048$; Fig. 2b).

Flower bud set in dwarf birch occurred on average 1.6 days earlier on warmed than on control plots ($F_{1,10} = 6.18$, $P = 0.03$; Fig. 2c). The duration of flower bud set in dwarf birch was on average 2 days shorter on warmed than on control plots, though this difference was only marginally significant ($F_{1,10} = 6.18$, $P = 0.052$). Blooming, in contrast, occurred nearly 4 days earlier ($F_{1,10} = 85.1$, $P < 0.001$) and was shorter in duration by 2 days on warmed than on control plots ($F_{1,10} = 14.6$, $P = 0.003$). Fruit set in dwarf birch occurred on average nearly 6 days earlier on warmed than on control plots ($F_{1,10} = 367.5$, $P < 0.001$). Hence, dwarf birch responded to warming by advancing all life history events monitored, as well as reducing the intervals between them. As a result, the aggregate life history of dwarf birch on warmed plots (20.4 ± 3.6 days) was less than half of that on control plots (47.0 ± 4.2 days; $F_{1,10} = 22.9$, $P = 0.001$).

Discussion

Differences in responses of the individual life history events within each species studied here to experimental warming might be indicative of the extent to which phenological phases differ in their plasticity with respect to environmental constraints. In a long-term experiment conducted in a subalpine meadow, Price and Waser (1998) observed that warming advanced timing of reproduction in four of 10 forb species studied, whereas warming altered the duration of reproduction in only one of those species. Our study emphasizes that, when considered in sequence, differences in the timing and duration of individual events reveal which events are key to variation in the aggregate life history response to climatic warming. For example, even though the duration of emergence in chickweed was reduced by warming (Fig. 2a), its aggregate life history remained unchanged by warming (with the caveat that emergence was not observed and is assumed to have shifted in parallel to timing of flower set). In gray willow, by contrast, the reduction in the aggregate life history of individuals on warmed plots compared to ambient plots apparently related mainly to a reduction in the length of time spent in the leaf opening stage (Fig. 2b). In dwarf birch, however, the reduction of the aggregate life history by warming appeared to be driven mainly by a reduction in the length of time spent in the blooming stage (Fig. 2c). Similar analyses of sequential life history events in other species, or in similar species in different environments, may reveal not only the extent to which the total life histories of other organisms respond to climatic warming, but also which individual phenological events are key to such changes.

Each of the examples in this study reveals a shortening of at least one component of the aggregate life history in response to warming. In far northern or alpine environments, where early warming may also be followed by frost events, hastening development through at least one stage of the phenological sequence in response to warming may also reflect a strategy aimed at minimizing risk of floral tissue loss in highly variable environments. Inouye (2008), for instance, documented that earlier snowmelt in an alpine environment led to earlier blooming by many forb species, but also greater flower bud loss to frost kill. In some species, such as aspen sunflower (*Helianthella quinquenervis*), annual bud loss can be as high as 100%. Under such intense selection in highly seasonal environments where freezing occurs during the growing season, acceleration through the blooming stage should be favored, as we documented in dwarf birch (Fig. 2c).

The life history responses to warming observed in this study may have fitness consequences for reproducing individuals that extend beyond phenological dynamics. A meta-analysis of long-term warming manipulations across the Arctic and sub-Arctic revealed, for instance, increases in reproductive success of forbs but reductions in reproductive success of deciduous shrubs, including *B. nana* and *Salix* spp., following warming with OTCs (Arft et al. 1999). Moreover, experimental manipulation of germination timing in *Arabidopsis thaliana* influenced multiple life history characters related to reproduction, including rosette size, numbers of leaves, timing of flowering, and over winter mortality (Donohue 2003). Early-germinating individuals had more leaves and were larger at the time of reproduction than later germinants, whereas the interval between bolting and flowering was not related to germination timing, resulting in earlier flowering in early germinants (Donohue 2003). As well, Inouye (2008) reported an interesting threshold effect in the relationship between flower production and date of snowmelt that has implications for demography and reproductive success. In years with late snowmelt, there is a positive relation between flowering date (which is determined by snow melt) and numbers of flowers produced; however, this relationship is absent in years with early snowmelt, suggesting greater loss of flower heads to frost by plants that bloom later in such years (Inouye 2000, 2008).

Whether the abbreviated aggregate life histories we observed in relation to experimental warming will be characteristic of the response of arctic plants to climate change is difficult to foresee. The main limitation of our study was the low numbers of individuals within each species studied. Furthermore, our experiment lasted only two years. Longer-term warming experiments have revealed disparate results. In one four-year manipulation in a subalpine meadow in Norway, the duration of flowering in *Cerastium* sp. was unaltered by warming (Totland and Schulte-Herbruggen 2003). As well, in other arctic sites, phenological responses of *B. nana* to experimental warming appear to attenuate after the first two years of warming (Arft et al. 1999), although productivity responses persist (Wahren et al. 2005).

Further insights into the manner in which the aggregate life history may vary with differential responses of individual phenological events to climatic warming may be gained by examining recent research on migratory birds. Many species of migratory birds are arriving earlier on breeding grounds, and initiating egg-laying earlier, in response to spring warming (Forchhammer et al. 1998, 2002, Walther et al. 2002, Root et al. 2003). Throughout Europe, for instance, flycatchers (*Ficedula* sp.) have advanced their laying dates in response to increases in local temperatures, and the magnitude of the advance in laying date scales with the increase in local temperatures (Both et al. 2004). Similar continental-scale analyses of breeding phenology of North American species have revealed that Tree Swallows (*Tachycineta bicolor*) advanced their laying date by nine days over a 32-year period in response to increasing temperatures (Dunn and Winkler 1999), though clutch sizes did not vary with advances in laying date (Winkler et al. 2002). The shift toward earlier egg-laying has not, however, matched the shift in arrival on breeding grounds in at least one population, suggesting a translation of Lewontin's (1965) fecundity schedule similar to that depicted in Fig. 1b. Flycatchers in the Netherlands, despite having advanced their laying dates, have not advanced their arrival dates at breeding grounds (Both and Visser 2001). This disparity in the response of different phenological events to warming suggests that the interval between them has declined, as has, perhaps the aggregate life history of Flycatchers related to nesting. Moreover, in years when Pied Flycatchers (*F. hypoleuca*) nest late relative to the peak in abundance of their prime food source, caterpillars, they reduce the interval between laying and hatching by initiating incubation earlier (Both and Visser 2005). Such an adjustment in the second event in the phenological sequence related to reproduction in flycatchers, and a consequent reduction in the interval between successive events in that sequence, is reminiscent of the response to warming shown by willows in this study (Fig. 2b), which led to a reduction in the individuals' aggregate life histories.

Continental-scale analyses of plant phenology also indicate disparities in the response of distinct life history events to climatic warming. Across Europe, for instance, early phenological events such as leaf unfolding have advanced by several days while late events such as leaf senescence have been delayed by several days (Menzel and Fabian 1999). At individual sites in Germany, there is evidence that advances in early phenological events are mirrored by changes in later events, though early events appear to have advanced to a greater degree than later events (Menzel et al. 2001), again suggestive of the form of change shown in Fig. 1b. Similarly, in an analysis of plant phenology spanning 97 populations in Norway, four of 11 species showed an increase in the duration of flowering, in addition to flowering earlier, in response to climatic warming (Post and Stenseth 1999). Although these studies relate patterns observed at the landscape scale, rather than changes in the life histories of individuals, they are nonetheless indicative of the flexibility and inequity displayed by the response of different life history events to warming.

Conclusion

Phenological responses of plants and animals to experimental warming or observed climate change have typically been studied in isolation. By considering changes in the sequence of key phenological events that comprise the life histories of organisms, and interactions among them, we may gain a better understanding of the implications of climate change for life history variation and its demographic consequences than is possible by considering only changes in isolated events. The approach we have developed and applied here is a first step in this direction. Although we were able to monitor responses to warming of just a few individuals and species over two growing seasons, the consequences of phenological shifts for aggregate life histories were clear. We urge the application of this approach, or at least the incorporation of this aggregate perspective, in future studies.

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Literature Cited

Arft, A., et al. 1999. Responses of tundra plants to experimental warming: meta-analysis of the International Tundra Experiment. Ecological Monographs 69:491–511.

Both, C., et al. 2004. Large-scale geographical variation confirms that climate change causes birds to lay earlier. Proceedings of the Royal Society B 271:1657–1662.

Both, C., and M. E. Visser. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature 411:296–298.

Both, C., and M. E. Visser. 2005. The effect of climate change on the correlation between avian life-history traits. Global Change Biology 11:1606–1613.

Circum-Arctic Vegetation Map Team. 2003. Circumpolar arctic vegetation map. Scale 1:7,500,000. U. S. Fish and Wildlife Service, Anchorage, Alaska.

Cole, L. 1954. The population consequences of life history phenomena. Quarterly Review of Biology 29:103–137.

Donohue, K. 2003. Germination timing influences natural selection on life-history characters in *Arabidopsis thaliana*. Ecology 83:1006–1016.

Dunn, P. O., and D. W. Winkler. 1999. Climate change has affected the breeding date of Tree Swallows throughout North America. Proceedings of the Royal Society of London B 266:2487–2490.

Forchhammer, M. C., E. Post, and N. C. Stenseth. 1998. Breeding phenology and climate. Nature 391:29–30.

Forchhammer, M. C., E. Post, and N. C. Stenseth. 2002. North Atlantic Oscillation timing of long- and short-distance migration. Journal of Animal Ecology 71:1002–1014.

Hollister, R. D., and P. J. Webber. 2000. Biotic validation of small open-top chambers in a tundra ecosystem. Global Change Biology 6:835–842.

Inouye, D. W. 2000. The ecological and evolutionary significance of frost in the context of climate change. Ecology Letters 3:457–463.

Inouye, D. W. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. Ecology 89:353–362.

Lewontin, R. C. 1965. Selection for colonizing ability. Pages 79–94 *in* H. G. Baker and G. L. Stebbins, editors. The genetics of colonizing species. Academic Press, New York, New York, USA.

Marion, G. M., G. H. R. Henry, D. W. Freckman, J. Johnstone, G. Jones, M. H. Jones, E. Levesque, U. Molau, P. Mølgaard, A. N. Parsons, J. Svoboda, and R. A. Virginia. 1997. Open-top designs for manipulating field temperature in high-latitude ecosystems. Global Change Biology 3(Supplement 1):20–32.

Maynard Smith, J. 1993. The theory of evolution. Cambridge University Press, Cambridge, UK.

Menzel, A., N. Estrella, and P. Fabian. 2001. Spatial and temporal variability of the phenological seasons in Germany from 1951–1996. Global Change Biology 7:657–666.

Menzel, A., and P. Fabian. 1999. Growing season extended in Europe. Nature 397:659.

Miller-Rushing, A. J., and R. B. Primack. 2008. Global warming and flowering times in Thoreau's Concord: a community perspective. Ecology 89:332–341.

Molau, U., and P. Mølgaard, editors. 1996. ITEX Manual. Danish Polar Centre, Copenhagen, Denmark.

Post, E., P. S. Bøving, C. Pedersen, and M. A. MacArthur. 2003. Synchrony between caribou calving and plant phenology in depredated and non-depredated populations. Canadian Journal of Zoology 81:1709–1714.

Post, E., M. C. Forchhammer, N. C. Stenseth, and T. V. Callaghan. 2001. The timing of life history events in a changing climate. Proceedings of the Royal Society of London B 268:15–23.

Post, E., and N. C. Stenseth. 1999. Climatic variability, plant phenology, and northern ungulates. Ecology 80:1322–1339.

Price, M. V., and N. M. Waser. 1998. Effects of experimental warming on plant reproductive phenology in a subalpine meadow. Ecology 79:1261–1271.

Primack, R. B. 1987. Relationships among flowers, fruits, and seeds. Annual Review of Ecology and Systematics 18:409–430.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature 421:57–60.

Sibly, R. M. 1997. Life history evolution in heterogeneous environments: a review of theory. Pages 228–250 *in* J. Silvertown, M. Franco, and J. L. Harper, editors. Plant life histories: ecology, phylogeny, and evolution. Cambridge University Press, Cambridge, UK.

Silvertown, J., M. Franco, and J. L. Harper, editors. 1997. Plant life histories: ecology, phylogeny and evolution. Cambridge University Press, Cambridge, UK.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, UK.

Totland, Ø., and B. Schulte-Herbruggen. 2003. Breeding system, insect flower visitation, and floral traits of two alpine Cerastium species in Norway. Arctic, Antarctic, and Alpine Research 35:242–247.

Wahren, C. -H. A., M. D. Walker, and M. S. Bret-Harte. 2005. Vegetation responses in Alaskan tundra after 8 years of a summer warming and winter snow manipulation experiment. Global Change Biology 11:537–552.

Walther, G.-R., E. Post, P. Convey, A. Menzel., C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389–395.

Williams, G. C. 1966. Adaptation and natural selection. Princeton University Press, Princeton, New Jersey, USA.

Winkler, D. W., P. O. Dunn, and C. E. McCulloch. 2002. Predicting the effects of climate change on avian life-history traits. Proceedings of the National Academy of Sciences (USA) 99:13595–13599.