



UvA-DARE (Digital Academic Repository)

Phenology of high-arctic butterflies and their floral resources: species-specific responses to climate change

Høye, T.T.; Eskildsen, A.; Hansen, R.R.; Bowden, J.J.; Schmidt, N.M.; Kissling, W.D.

Published in:
Current Zoology

DOI:
[10.1093/czoolo/60.2.243](https://doi.org/10.1093/czoolo/60.2.243)

[Link to publication](#)

Citation for published version (APA):

Høye, T. T., Eskildsen, A., Hansen, R. R., Bowden, J. J., Schmidt, N. M., & Kissling, W. D. (2014). Phenology of high-arctic butterflies and their floral resources: species-specific responses to climate change. *Current Zoology*, 60(2), 243-251. DOI: 10.1093/czoolo/60.2.243

General rights

It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: <http://uba.uva.nl/en/contact>, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.

Phenology of high-arctic butterflies and their floral resources: Species-specific responses to climate change

Toke T. HØYE^{1,2,3*}, Anne ESKILDSEN^{2,4}, Rikke R. HANSEN³, Joseph J. BOWDEN³, Niels M. SCHMIDT^{3,5}, W. Daniel KISSLING⁶

¹Aarhus Institute of Advanced Studies, Høegh-Guldbergs Gade 6B, bldgs. 1630-1632, DK-8000 Aarhus C, Denmark

²Department of Bioscience, Kalø, Aarhus University, Grenåvej 14, DK-8410 Rønde, Denmark

³Arctic Research Centre, Aarhus University, C.F. Møllers Allé 8, bldg. 1110, DK-8000 Aarhus C, Denmark

⁴Department of Bioscience, Aarhus, Aarhus University, Ny Munkegade, bldg. 1540, DK-8000 Aarhus C, Denmark

⁵Department of Bioscience, Aarhus University, Frederiksborgvej 399, DK-4000 Roskilde, Denmark

⁶Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, P.O. Box 94248, 1090 GE Amsterdam, The Netherlands

Abstract Current global warming is particularly pronounced in the Arctic and arthropods are expected to respond rapidly to these changes. Long-term studies of individual arthropod species from the Arctic are, however, virtually absent. We examined butterfly specimens collected from yellow pitfall traps over 14 years (1996–2009) at Zackenberg in high-arctic, north-east Greenland. Specimens were previously sorted to the family level. We identified them to the species level and examined long-term species-specific phenological responses to recent summer warming. Two species were rare in the samples (Polaris fritillary *Boloria polaris* and Arctic blue *Plebejus glandon*) and statistical analyses of phenological responses were therefore restricted to the two most abundant species (Arctic fritillary, *B. chariclea* and Northern clouded yellow *Colias hecla*). Our analyses demonstrated a trend towards earlier flight seasons in *B. chariclea*, but not in *C. hecla*. The timing of onset, peak and end of the flight season in *B. chariclea* were closely related to snowmelt, July temperature and their interaction, whereas onset, peak and end of the flight season in *C. hecla* were only related to timing of snowmelt. The duration of the butterfly flight season was significantly positively related to the temporal overlap with floral resources in both butterfly species. We further demonstrate that yellow pitfall traps are a useful alternative to transect walks for butterfly recording in tundra habitats. More phenological studies of Arctic arthropods should be carried out at the species level and ideally be analysed in context with interacting species to assess how ongoing climate change will affect Arctic biodiversity in the near future [*Current Zoology* 60 (2): 243–251, 2014].

Keywords Arctic, Arthropod, Flight period, Greenland, Pitfall trap, Zackenberg

Phenology is a key indicator of species responses to climate change (Parmesan, 2006) and among terrestrial animals, ectotherms are particularly sensitive, probably because their developmental rates are closely related to variation in the abiotic environment (Høye et al., 2007; Thackeray et al., 2010). Butterflies in particular are frequently used as model organisms in phenological studies, because they respond rapidly to environmental change (Diamond et al., 2011; Illan et al., 2012; Roy and Sparks, 2000; Westwood and Blair, 2010). Additionally, their appeal to the general public has stimulated monitoring programs and has generated high-quality data, especially in temperate and boreal regions (Karlsson, In press; Roy and Sparks, 2000). Recent global warming, however, is particularly pronounced in the Arctic and empirical evidence suggests that Arctic

species across broad taxonomic scales are responding rapidly to these changes (Høye et al., 2007; Post et al., 2009). Unfortunately, long-term records of individual arthropod species from the Arctic are virtually absent and the phenological sensitivity to climate change in most arctic arthropod species remains to be estimated (Bale et al., 2002; Hodkinson et al., 1996; Hodkinson and Bird, 1998). The biological monitoring program at Zackenberg, north-east Greenland, represents an exception, where arthropods have been collected weekly during the growing season since 1996 and subsequently sorted to the family level (Schmidt et al., 2012).

Very little information exists about the drivers of phenological variation at the species level for Arctic arthropods, but family-level studies suggest that timing of snowmelt and temperature are important (Danks and

Received Dec. 17, 2013; accepted Mar. 20, 2014.

* Corresponding author. E-mail: tth@aias.au.dk.

© 2014 *Current Zoology*

Oliver, 1972; Høye and Forchhammer, 2008a, b; Strathdee and Bale, 1998). Snow cover acts as a constraint on arthropod growth and development in arctic and alpine environments (Forrest and Thomson, 2011; Iler et al., 2013a). Effectively, the timing of snowmelt opens and closes the activity season for many arthropods in the Arctic. For many species, this time period dictates the amount of resources they can accrue and utilize in the current season e.g. for reproduction, dispersal or to carry them over the winter into the following season. Temperature during the active season may modulate the effect of snowmelt on arthropod phenology by affecting their developmental rate (Hodkinson et al., 1996). In addition, many Arctic arthropod species, like spiders (Bowden and Buddle, 2012; Høye et al., 2009) and insects (Butler, 1982; Morewood and Ring, 1998), have multi-annual life cycles and their phenological responses to climate change may further depend on overwintering strategy or species-specific developmental cues.

Like their predicted shifts in distribution under climate change (Eskildsen et al., 2013; Leroux et al., 2013), phenological responses to climatic change in arthropods could be species-specific and have concealed consequences for trophic interactions. In arctic insects, the emergence of adults normally coincides with the peak in food resources, the availability of mates, or suitable egg-laying habitats (Danks, 2004; Høye and Forchhammer, 2008b; MacLean, 1980). Arctic pollinator communities are dominated by Diptera species that are generalized in their flower visitation patterns (Elberling and Olesen, 1999; Lundgren and Olesen, 2005). Among arctic flower visitors, however, butterflies visit only a subset of the available flowering plants (Olesen et al., 2008). Hence, butterflies form a relevant taxonomic group with which to examine species-specific phenological responses to climate change. Even if different butterfly species respond to changes in the same phenological cue, they can do so at different rates (Hegland et al., 2009). Hence, more subtle changes in the phenological response of a pollinator community may only be fully resolved with species-level information (Iler et al., 2013b).

Pollinator populations are often limited by the availability of floral resources (Potts et al., 2010). Such resource limitation can emerge if the flight season of a pollinator shifts relative to the flowering season of its plant resource causing a decrease in the temporal overlap of pollinators and flowers (Høye et al., 2013; Miller-Rushing et al., 2010). Moreover, in butterflies, the

availability of nectar resources can affect adult longevity and population dynamics (Boggs and Inouye, 2012; Cahenzli and Erhardt, 2012). Hence, if adult butterflies emerge in asynchrony with the flowering season or during a period of low flower availability, their flight season may become shorter with potential detrimental effects on population dynamics (Nilsson et al., 2008). We have recently demonstrated that the flowering season at our study site is shortening and this could affect resource availability and flight season duration in butterfly species (Høye et al., 2013).

Here, we examine species-specific phenological responses to recent warming in high-arctic butterflies and their temporal synchrony with floral resources. We use specimens collected as part of the Zackenberg Basic monitoring programme (Meltøfte and Rasch, 2008) that were previously identified to the family level. We identify these specimens to the species level and establish species-specific estimates of onset, peak and end of the flight season. For two species with sufficient data, we ask two specific questions: 1) Are onset, peak, and end of the flight seasons affected by recent rapid warming and changes in timing of snowmelt at Zackenberg? 2) To what extent is the duration of the flight season related to the timing of the flight season and the temporal overlap with the flowering season of relevant plant species.

1 Material and Methods

1.1 Study area and data

Data were collected at Zackenberg, north-east Greenland (74°28'N, 20°34'W) as part of the Zackenberg Basic monitoring programme. Although expanding, the growing season is currently limited to between early June and early September during which the average air temperature is around 4.5°C. Throughout the study period, temperature and snow depth were recorded hourly by an automated weather station (Hansen et al., 2008). Timing of snowmelt was estimated as the first date when less than 10 cm of snow was measured (Hinkler et al., 2008). The vegetation of the study area can be roughly divided into five major plant communities: fen, grassland, *Salix* snow-bed, *Cassiope* heath, and *Dryas* heath (Elberling et al., 2008).

Arthropods were monitored during 14 consecutive years (1996–2009) in one window trap plot and six pitfall trap plots in the vicinity (<2 km) of the weather station. Each pitfall trap plot (10 m × 20 m) consisted of eight pitfall traps during 1996–2006 and four pitfall traps thereafter. The pitfall traps were yellow plastic

cups 10 cm in diameter. The colour was chosen to attract flying insects while also catching surface-active arthropods. The window trap plot consisted of two traps each with two chambers. The two traps were placed perpendicular to each other. Arthropods caught in the traps were collected weekly during June, July and August. The window trap plot and the pitfall traps in arid heath (one plot), mesic heath (two plots) and in the fen (one plot) were in operation during the entire study period 1996–2009, while one snow-bed plot and one additional arid heath plot were only operated during the periods 1996–1998 and 1999–2009, respectively (see Schmidt et al., 2012 for details).

The entire butterfly community at Zackenberg consists of four species: Arctic fritillary, *Boloria chariclea* (Schneider), Polaris fritillary, *B. polaris* (Boisduval), Arctic blue, *Plebejus glandon* (de Prunner), and Northern clouded yellow, *Colias hecla* (Lefèbvre). Only one additional species, Small copper, *Lycaena phlaeas* (Linnaeus) has been observed in Greenland. All specimens caught in all years were previously identified to the family level (Nymphalidae, Lycaenidae and Pieridae) as part of Zackenberg Basic monitoring program. We identified the specimens to the species level and calculated species-specific estimates of onset, peak and end of the flight season.

The data set included a total of 3,868 specimens retrieved from the pitfall and window trap plots. As part of this study, we revisited a subset of 1,660 *Boloria* specimens, distributed evenly across all years. Because our subset represents more than half (51%) of all *Boloria* specimens in the collection, differences in phenology between *B. chariclea* and *B. polaris* in the subset would also likely reflect the total sample of specimens. A total of 35 specimens (out of 1,660) were identified as *B. polaris*, equalling just 2.1% of the *Boloria* specimens. For the purpose of making robust phenological esti-

mates, we assumed that all *Boloria* specimens not subject to species identification were *B. chariclea* since *B. polaris* made up such a small subset of the *Boloria* sp. specimens in the subset subject to species identification. The Lycaenid species *P. glandon* was even rarer ($n = 23$ specimens) than *B. polaris* in the samples across all years (Table 1). The low sample sizes prevented us from estimating inter-annual variation in the phenology of *B. polaris* and *P. glandon*. Adults of all four species of butterflies were only observed during July, August and early September (Table 1). Traps were occasionally flooded, destroyed by arctic foxes (*Vulpes lagopus*, Linnaeus), or trampled by muskoxen (*Ovibos moschatus*, Zimmermann), so the capture numbers in each plot were converted to individuals caught per trap per day for each trapping period, i.e. scaled by the number of active traps and the number of days each trap was active (see Høye and Forchhammer 2008b for further information).

The Zackenberg Basic monitoring program also included weekly observations of the number of buds, open and senescent flowers from the same locality and the same time periods within and across years on six flowering plant species (*Cassiope tetragona*, *Dryas octopetala*, *Papaver radicum*, *Salix arctica*, *Saxifraga oppositifolia* and *Silene acaulis*). These plant species are very common at the study site. The butterfly species *B. chariclea* has been observed on flowers of all six species and *C. hecla* has only been observed on *D. octopetala*, *S. arctica* and *S. acaulis* (Olesen et al., 2008). For *B. chariclea*, we used data on all six plant species and for *C. hecla* we used only data on the three plant species upon whose flowers the species has been observed. Each plant species was monitored in 3–6 plots (see Schmidt et al., 2012 for details). Both butterfly species have also been observed on flowers of other plant species, for which we have no data on flowering phenology. We used the data on flower phenology to

Table 1 Summary of phenological observations for four species of butterflies at Zackenberg, north-east Greenland (*Boloria chariclea*, *B. polaris*, *Colias hecla* and *Plebejus glandon*)

Species	First	Onset	Peak	End	Last	<i>n</i>
<i>B. chariclea</i>	168	200±2.0	212±2.3	224±1.7	245	3,235*
<i>B. polaris</i>	176	190	217	232	238	35*
<i>C. hecla</i>	176	194±2.4	205±2.6	218±2.3	238	575
<i>P. glandon</i>	196	196	204	211	224	23

All dates are given as days after 1st January. The first observation is the first date at which a butterfly of a particular species was found in a trap across all years (1996–2009) and the last observation is the last date across all years. Onset, peak and end indicate the mean day of year ± SE at which 10%, 50% and 90% of the annual sum of individuals were caught, respectively. Asterisks indicate that only 51% of the total collection of *Boloria* specimens was checked for *B. polaris* and the remaining specimens were assumed to be *B. chariclea*. The sample size, *n* gives the total number of specimens of a particular species identified from the traps.

characterize the temporal variability in floral resources available for each of the two butterfly species. An independent study of the pollination network at our site documented visits by *B. chariclea* to 15 plant species and to 5 plant species by *C. hecla* (Olesen et al., 2008).

1.2 Data analysis

Following Høye and Forchhammer (2008b), we defined onset, peak and end of the flight season of adult butterflies by dates at which 10%, 50% and 90% of the seasonal capture of a species was reached, respectively. The dates for onset, peak and end of the flight season were estimated by linear interpolation between weekly trapping periods. For instance, peak flight season was estimated by interpolation between the latest weekly trapping period in which less than 50% of the individuals were caught and the earliest weekly trapping period in which more than 50% of the individuals were caught. For each weekly trapping period, we pooled the number of individuals from all plots to base the phenological estimates on the largest number of individuals and because previous analyses of *Boloria* specimens demonstrated limited phenological variation among plots (Høye and Forchhammer, 2008b). Although low sample sizes prohibited us from estimating yearly phenology metrics for *B. polaris* and *P. glandon*, we calculated an average across years of onset, peak, and end of the flight season for future comparisons. All dates were expressed as day of year with 1st January equalling day 1. Flight season duration was estimated as the number of days between onset and end of the flight season. We quantified onset and end of the community-wide flowering season at a landscape scale based on the relevant plant species for each of the two butterfly species following the approach of Høye et al. (2013).

At the study site, snowmelt typically takes place during June, while the flight season of butterflies is typically in July and early August. We were interested in separating the effect of snowmelt from the effect of temperature after snowmelt on the timing of the butterfly flight season. Hence, we used mean daily July temperature as a predictor of timing of the butterfly flight season in addition to timing of snowmelt. We applied generalized linear models with a Gaussian error distribution (McCullagh and Nelder, 1998) with onset, peak, end, and duration of the flight season of *B. chariclea* and *C. hecla* as response variables. As predictors for models with onset, peak and end of the flight season, we used the mean daily temperature during July, the timing of snowmelt, and their interaction. Non-significant terms were removed successively using *F*-tests based on

type III sums of squares and starting with interaction terms and evaluating main effects only if interaction terms were non-significant. The correlation between timing of snowmelt and July temperature as well as between peak flight time of *B. chariclea* and *C. hecla* was estimated with Pearson correlation analysis. We calculated the temporal extent of overlap between the flowering season of relevant plant species (see above) and the butterfly flight season in days for *B. chariclea* and *C. hecla*, separately. We tested for trends in the duration of overlap during the study period and whether duration of the flight season was affected by onset of the flight season, the duration of the overlap with floral resources or their interaction. Finally, for analyses of temporal trends in peak flight time and overlap with flower seasons, year was used as a continuous predictor variable in simple linear regression models.

2 Results

The number of specimens was highest for *B. chariclea* ($n = 3,235$) and *C. hecla* ($n = 575$) and very low for *B. polaris* ($n = 35$) and *P. glandon* ($n = 23$). The earliest and the latest butterfly records were observations of *B. chariclea*, while the earliest observation of *P. glandon* was later than all other species and the latest observation of this species was also earlier than all other species. The average peak flight time was late July for *C. hecla* and *P. glandon*, and about ten days later in *B. chariclea* and *B. polaris* (Table 1). For *B. chariclea* and *C. hecla*, the timing of peak flight season varied markedly from year to year (Fig. 1), with a significant trend towards earlier peak flight season in *B. chariclea* (slope = -1.22 , $F_{1,12} = 6.14$, $P = 0.029$), but not in *C. hecla* (slope = -0.68 , $F_{1,12} = 1.12$, $P = 0.31$). In *B. chariclea*, onset, peak, and end of the flight period showed a statistically significant relationship with timing of snowmelt, mean daily July temperature, and their interaction (Table 2). In *C. hecla*, the onset, peak, and end of the flight season was, however, only significantly related to timing of snowmelt (Table 2). Timing of snowmelt and July temperatures were not significantly correlated (Pearson correlation: $r = -0.38$, $n = 13$, $P = 0.18$). The flight season of both butterfly species was generally later than the flowering season of the plant species that are visited by the butterflies and for which we had flower phenology data (Fig. 2). The duration of the flight season showed a statistically significant and positive relationship to the duration of overlap with floral resources in both *B. chariclea* (Fig. 3a) and *C. hecla* (Fig. 3b), but not with onset of the flight period or their interaction in any of the two

species (Table 3). The duration of overlap became smaller during the study period, but the relationship was not signi-

ficant for *B. chariclea* (slope = -0.080, $F_{1,12} = 0.13$, $P = 0.72$) or *C. hecla* (slope = -0.77, $F_{1,12} = 3.56$, $P = 0.084$).

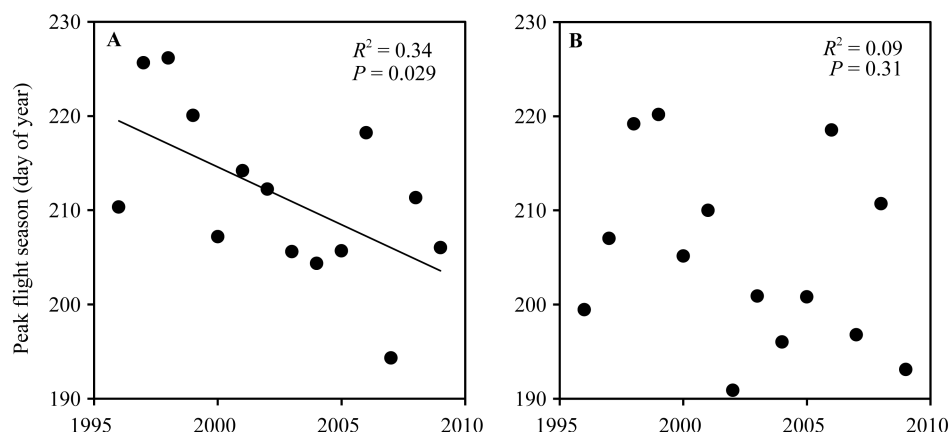


Fig. 1 Peak flight times of two butterfly species A) *Boloria chariclea* and B) *Colias hecla* during 1996–2009 at Zackenberg, north-east Greenland. Summary statistics (R^2 and P -values) based on simple linear regression analysis are given in each panel. Regression lines indicate that slopes are significantly different from zero.

Table 2 Results of generalized linear models of onset, peak and end of the flight season for two butterfly species (*Boloria chariclea* and *Colias hecla*) at Zackenberg, north-east Greenland, across 1996–2009 as a function of mean daily temperature during July and timing of snowmelt, as well as their interaction as continuous variables

Species	Event	Intercept	Snowmelt	Temp	Snowmelt:Temp	df	R^2	P
<i>B. chariclea</i>	Onset	-144.2±111.8	2.05±0.66	35.4±14.4	-0.21±0.09	10	0.73	0.0032
	Peak	-266.1±136.6	2.90±0.80	54.5±17.6	-0.33±0.10	10	0.73	0.0037
	End	-54.4±103.9	1.71±0.61	30.9±13.4	-0.19±0.08	10	0.69	0.0069
<i>C. hecla</i>	Onset	109.7±27.5	0.50±0.16	-	-	12	0.44	0.0096
	Peak	104.1±26.5	0.60±0.16	-	-	12	0.55	0.0025
	End	131.3±24.6	0.51±0.15	-	-	12	0.51	0.0043

Only models with significant parameters (at $\alpha = 0.05$) are shown. Parameters $\pm SE$ are presented along with residual degrees of freedom, coefficient of determination (R^2) and P -value.

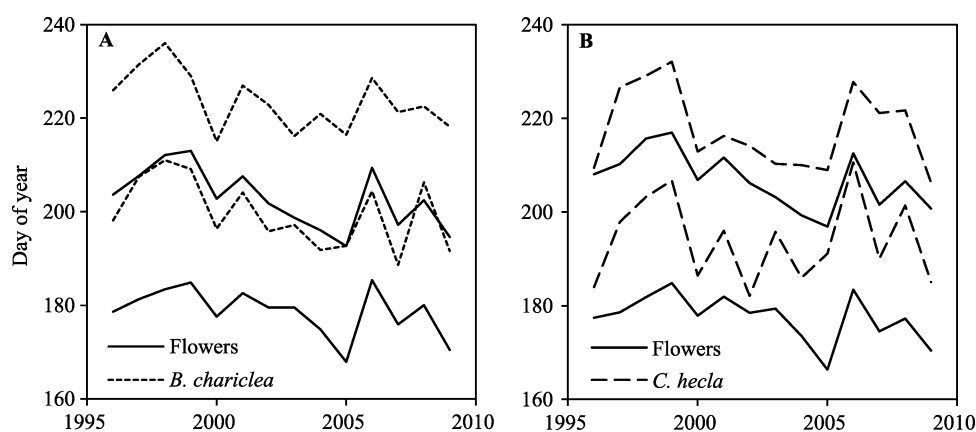


Fig. 2 The onset and end of the flight season of A) *Boloria chariclea* and community-wide flowering seasons for six flowering plant species (*Cassiope tetragona*, *Dryas octopetala*, *Papaver radiculatum*, *Salix arctica*, *Saxifraga oppositifolia* and *Silene acaulis*) which the butterfly species has been observed visiting and B) *Colias hecla* and community-wide flowering seasons for three flowering plant species (*Dryas octopetala*, *Salix arctica* and *Silene acaulis*) on which the butterfly species has been observed visiting

The lower line in each set is onset and the upper line is end of butterfly flight seasons (hatched lines) and flowering season (full lines).

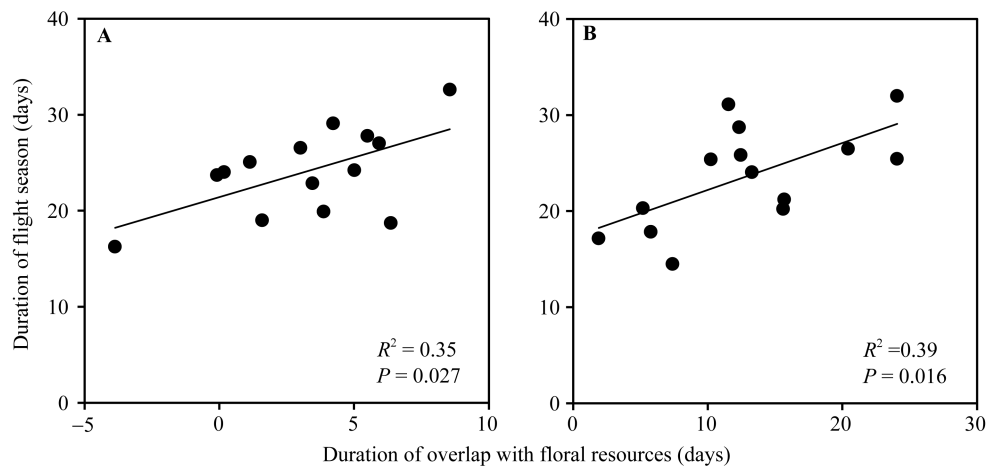


Fig. 3 Duration (end minus onset) in days of the flight season for A) *Boloria chariclea* and B) *Colias hecla* in relation to the overlap with the flowering season of six relevant plant species for *B. chariclea* and three relevant plant species for *C. hecla* (see text for details)

The overlap is negative in some years, because onset and end of seasons are defined by the date of 10% and 90% of butterflies and flowers observed during the season, respectively. Regression lines based on simple linear regression analysis along with R^2 and p -values are given in each panel.

Table 3 Results of generalized linear models of flight season duration for two butterfly species (*Boloria chariclea* and *Colias hecla*) at Zackenberg, north-east Greenland, from 1996–2009 as a function of the overlap with the flowering season of their respective plant species (upon which they have been observed), the onset of flight season, and their interaction as continuous variables

Species	Intercept	Overlap	Onset	Overlap:Onset	df	R^2	P
<i>B. chariclea</i>	21.41±1.46	0.83±0.33	-	-	12	0.35	0.027
<i>C. hecla</i>	17.32±2.52	0.49±0.17	-	-	12	0.39	0.016

Only models with significant parameters (at $\alpha = 0.05$) are shown. Parameters $\pm SE$ are presented along with residual degrees of freedom, coefficient of determination (R^2) and P -value.

3 Discussion

The literature on species-specific phenological responses to ambient climatic variability of Arctic arthropods is scant and to our knowledge this is the first study to span more than a decade of observations (Høye and Sikes, 2013; Leung and Reid, 2013). Given the species richness of arthropods in marine, freshwater and terrestrial environments in the Arctic, this illustrates an important knowledge gap that limits our ability to predict the consequences of rapid climate change for Arctic biodiversity (Meltofte 2013; Callaghan et al., 2004b; Post et al., 2009). We have previously demonstrated large family-level variation in estimates of timing of emergence over a broad range of terrestrial arthropods at Zackenberg (Høye et al., 2007; Høye and Forchhammer, 2008b). However, with family-level taxonomic resolution, it is not possible to separate the effects of changing species composition between years from the inter-annual variation in phenology of individual species (Callaghan et al., 2004a).

By identifying the individual species of a butterfly assemblage from the monitoring program at Zackenberg, we have made progress towards estimating species-specific phenological responses to recent climatic variation in the Arctic. The two abundant butterfly species indeed differ in their trend towards earlier flight time, their phenological responses to climatic variability, and in inter-annual variation in degree of temporal overlap with floral resources. This suggests that phenological responses measured at coarse taxonomic resolutions can mask important variability at the species level.

Our results indicate that timing of the flight season in high-arctic butterfly species is closely related to the timing of snowmelt. While the timing of the flight season in *C. hecla* is only related to timing of snowmelt, there is an additional effect of July temperature in *B. chariclea*, and this temperature effect interacts with timing of snowmelt. This suggests that the advancement of the flight season in *B. chariclea* with warmer temperatures is most pronounced with late snowmelt. The

lack of relationship to summer temperatures in timing of the flight season for *C. hecla* may be the reason why *C. hecla* is not showing a trend towards earlier flight time during the study period. The summer temperature has increased dramatically during the study period at our site (Høye et al., 2013). With future warming, the flight seasons of *B. chariclea* and *C. hecla* may shift relative to each other. Since peak flight date is generally ten days later in *B. chariclea* than in *C. hecla*, their flight times are likely to become more synchronized. A knowledge gap is whether future timing of snowmelt in the region will advance or be delayed, which is currently uncertain (Stendel et al., 2008).

The duration of butterfly flight seasons could be affected by the timing and duration of flowering seasons if the lifespan of each individual butterfly is constrained by access to floral resources. Adult longevity has been linked to nectar resources in some butterfly species (Cahenzli and Erhardt, 2012; Murphy et al., 1983). Our results demonstrate that the duration of the flight season varied by a factor of two over the study period in both butterfly species and was related to the duration of overlap with relevant floral resources. Other studies have found extending flight seasons, but these studies have used observations collected at much larger spatial extents (Roy and Sparks, 2000; Westwood and Blair, 2010). For instance, a recent study demonstrated extended flight seasons in northern butterfly communities in response to recent warming across Sweden (Karlsson In press). Flight seasons may also be extended when the flight seasons start earlier. This could happen by more pronounced protandry (i.e. males emerging earlier than females) in years of early snowmelt and warmer temperatures.

Our estimates of the onset and end of the flowering season of plant species known to be visited by the studied butterfly species is generally earlier than the flight season of the butterflies. Both species of butterflies are known to visit flowers of other plants as well and some of these are late flowering species (e.g. *Arnica angustifolia* and *Bistorta vivipara*). Hence, the apparent mistiming of the butterfly flight season with the flowering season presented here could be due to the subset of plant species for which we have data on flowering phenology. The butterfly flight season may also be timed primarily with particular phenological stages of the plant species used for oviposition, although this would not explain why flight season duration is related to the overlap with our subset of plant species. We consider it more likely that our measure of onset and end of the

flowering season is rather conservative. Indeed, in a pollination network study from our site, the same plant species were observed to flower later than the end of flowering in our permanent plots (J.-M. Olesen *unpublished data*).

Our results demonstrate that for high-arctic study sites it is possible to use pitfall trapping to census butterfly species. We used yellow pitfall traps as a method to trap both ground-active and flying insects in the same trap (Böcher and Meltofte, 1997). The large sample sizes for at least two species of butterflies using this technique suggests that this approach is useful for remote tundra localities as it does not require trained butterfly observers who are otherwise needed for conventional transect counts (Pollard and Yates, 1993). The separation of *B. chariclea* and *B. polaris* is difficult in the field and we provide new information on their relative abundance. We found less than 3% of the *Boloria* specimens to be *B. polaris*, suggesting that this species is much rarer at Zackenberg than *B. chariclea*. This could be linked to the distribution of their larval food plants or because of habitat segregation not picked up by our sampling design. We consider it unlikely that our subsampling procedure, where we identified 51% of the *Boloria* specimens, could have accidentally missed samples with a large proportion of *B. polaris* specimens. The low capture numbers for *B. polaris* and *P. glandon* could potentially be the result of these butterfly species not being attracted to the yellow colour of our pitfall traps, but independent data from a study of the pollination network at our study site support the idea that *B. polaris* and *P. glandon* are rare species in the area (J.-M. Olesen *unpublished data*).

The strong phenological response to climate variation that we document for high-arctic butterflies and the clear differences between the two most abundant species suggest that species-specific studies of populations of arctic arthropods should be a research priority. Future phenological studies of Arctic arthropods should ideally be analysed in context with interacting species to assess how ongoing climate change will affect Arctic biodiversity. Long-term records will be particularly helpful in attempts to identify the climatic constraints on the future persistence of high-arctic butterfly species (Post and Høye, 2013).

Acknowledgements We thank Zackenberg Basic for access to the ecosystem data. T.T.H. and A.E. acknowledge 15. Juni Fonden for funding and W.D.K. acknowledges a University of Amsterdam (UvA) starting grant. We appreciate comments on

a previous version of the manuscript by Oliver Schweiger and two anonymous reviewers.

References

- Bale JS, Masters GJ, Hodkinson ID, Awmack C, Bezemer TM et al., 2002. Herbivory in global climate change research: Direct effects of rising temperatures on insect herbivores. *Global Change Biol.* 8: 1–16.
- Böcher J, Meltofte H, 1997. Comparison of three different types of arthropod traps. In: Meltofte H, Thing H ed. *Zackenbergs Ecological Research Operations, 2nd Annual Report, 1996*. Copenhagen, Denmark: Danish Polar Center, Ministry of Research & Information Technology, 66–67.
- Boggs CL, Inouye DW, 2012. A single climate driver has direct and indirect effects on insect population dynamics. *Ecol. Lett.* 15: 502–508.
- Bowden JJ, Buddle CM, 2012. Life history of tundra-dwelling wolf spiders (Araneae: Lycosidae) from the Yukon Territory, Canada. *Can. J. Zool.* 90: 714–721.
- Butler MG, 1982. A 7-year life-cycle for 2 *Chironomus* species in arctic alaskan tundra ponds (Diptera, Chironomidae). *Can. J. Zool.* 60: 58–70.
- Cahenzli F, Erhardt A, 2012. Nectar sugars enhance fitness in male *Coenonympha pamphilus* butterflies by increasing longevity or realized reproduction. *Oikos* 121: 1417–1423.
- Callaghan TV, Bjorn LO, Chernov Y, Chapin T, Christensen TR et al., 2004a. Responses to projected changes in climate and UV-B at the species level. *Ambio* 33: 418–435.
- Callaghan TV, Bjorn LO, Chernov Y, Chapin T, Christensen TR et al., 2004b. Effects on the structure of arctic ecosystems in the short- and long-term perspectives. *Ambio* 33: 436–447.
- Danks HV, Oliver DR, 1972. Seasonal emergence of some high arctic Chironomidae (Diptera). *Can. Entomol.* 104: 661–686.
- Danks HV, 2004. Seasonal adaptations in arctic insects. *Integr. Comp. Biol.* 44: 85–94.
- Diamond SE, Frame AM, Martin RA, Buckley LB, 2011. Species' traits predict phenological responses to climate change in butterflies. *Ecology* 92: 1005–1012.
- Elberling B, Tamstorf MP, Michelsen A, Arndal MF, Sigsgaard C et al., 2008. Soil and plant community-characteristics and dynamics at Zackenberg. *Adv. Ecol. Res.* 40: 223–248.
- Elberling H, Olesen JM, 1999. The structure of a high latitude plant–flower visitor system: The dominance of flies. *Ecography* 22: 314–323.
- Eskildsen A, le Roux PC, Heikkinen RK, Høye TT, Kissling WD et al., 2013. Testing species distribution models across space and time: High latitude butterflies and recent warming. *Global Ecol. Biogeogr.* 22: 1293–1303.
- Forrest JRK, Thomson JD, 2011. An examination of synchrony between insect emergence and flowering in Rocky Mountain meadows. *Ecol. Monogr.* 81: 469–491.
- Hansen BU, Sigsgaard C, Rasmussen L, Cappelen J, Hinkler J et al., 2008. Present-day climate at Zackenberg. *Adv. Ecol. Res.* 40: 111–149.
- Hegland SJ, Nielsen A, Lázaro A, Bjerknes AL, Totland, 2009. How does climate warming affect plant-pollinator interactions? *Ecol. Lett.* 12: 184–195.
- Hinkler J, Hansen BU, Tamstorf MP, Sigsgaard C, Petersen D, 2008. Snow and snow-cover in central northeast Greenland. *Adv. Ecol. Res.* 40: 175–195.
- Hodkinson ID, Coulson SJ, Webb NR, Block W, Strathdee AT et al., 1996. Temperature and the biomass of flying midges (Diptera: Chironomidae) in the high Arctic. *Oikos* 75: 241–248.
- Hodkinson ID, Bird J, 1998. Host-specific insect herbivores as sensors of climate change in arctic and alpine environments. *Arct. Alp. Res.* 30: 78–83.
- Høye TT, Post E, Meltofte H, Schmidt NM, Forchhammer MC, 2007. Rapid advancement of spring in the High Arctic. *Curr. Biol.* 17: R449–R451.
- Høye TT, Forchhammer MC, 2008a. The influence of weather conditions on the activity of high-arctic arthropods inferred from long-term observations. *BMC Ecol.* 8: 8.
- Høye TT, Forchhammer MC, 2008b. Phenology of high-arctic arthropods: Effects of climate on spatial, seasonal and inter-annual variation. *Adv. Ecol. Res.* 40: 299–324.
- Høye TT, Hammel JU, Fuchs T, Toft S, 2009. Climate change and sexual size dimorphism in an arctic spider. *Biol. Lett.* 5: 542–544.
- Høye TT, Post E, Schmidt NM, Trøjelsgaard K, Forchhammer MC, 2013. Shorter flowering seasons and declining abundance of flower visitors in a warmer Arctic. *Nature Clim. Change* 3: 759–763.
- Høye TT, Sikes DS, 2013. Arctic entomology in the 21st century. *Can. Entomol.* 145: 125–130.
- Iler AM, Høye TT, Inouye DW, Schmidt NM, 2013a. Nonlinear flowering responses to climate: Are species approaching their limits of phenological change? *Phil. Trans. R. Soc. B* 368: 20120489.
- Iler AM, Inouye DW, Høye TT, Miller-Rushing AJ, Burkle LA et al., 2013b. Maintenance of temporal synchrony between syrphid flies and floral resources despite differential phenological responses to climate. *Glob. Change Biol.* 19: 2348–2359.
- Illan JG, Gutierrez D, Diez SB, Wilson RJ, 2012. Elevational trends in butterfly phenology: Implications for species responses to climate change. *Ecol. Entomol.* 37: 134–144.
- Karlsson B, In press. Extended season for northern butterflies. *Int. J. Biometeorol.*: doi:10.1007/s00484-00013-00649-00488.
- Leroux SJ, Larrivee M, Boucher-Lalonde V, Hurford A, Zuloaga J et al., 2013. Mechanistic models for the spatial spread of species under climate change. *Ecol. Appl.* 23: 815–828.
- Leung MC, Reid DG, 2013. New species records for butterflies (Lepidoptera) on Herschel Island, Yukon, Canada, with notes on natural history. *Can. Entomol.* 145: 227–234.
- Lundgren R, Olesen JM, 2005. The dense and highly connected world of Greenland's plants and their pollinators. *Arct. Antarct. Alp. Res.* 37: 514–520.
- MacLean SF, Jr., 1980. The detritus-based trophic system. In: (Brown J, Miller PC, Tieszen LL, Bunnell FL ed. *An Arctic Ecosystem: The Coastal Tundra at Barrow, Alaska*. Stroudsburg, PA: Dowden, Hutchinson & Ross, Inc., 411–457.
- McCullagh P, Nelder JA, 1998. *Generalized Linear Models*. 2nd edn. Boca Raton: Chapman & Hall/CRC.

- Meltofte H, 2013. Arctic Biodiversity Assessment: Status and Trends in Arctic Biodiversity. Akureyri: Conservation of Arctic Flora and Fauna.
- Meltofte H, Rasch M, 2008. The study area at Zackenberg. *Adv. Ecol. Res.* 40: 101–110.
- Miller-Rushing AJ, Høye TT, Inouye DW, Post E, 2010. The effects of phenological mismatches on demography. *Phil. Trans. R. Soc. B* 365: 3177–3186.
- Morewood WD, Ring RA, 1998. Revision of the life history of the High Arctic moth *Gynaephora groenlandica* (Wocke) (Lepidoptera: Lymantriidae). *Can. J. Zool.* 76: 1371–1381.
- Murphy DD, Launer AE, Ehrlich PR, 1983. The role of adult feeding in egg-production and population dynamics of the checkerspot butterfly *Euphydryas editha*. *Oecologia* 56: 257–263.
- Nilsson SG, Franzen M, Jonsson E. 2008. Long-term land-use changes and extinction of specialised butterflies. *Insect. Conserv. Diver.* 1: 197–207.
- Olesen JM, Bascompte J, Elberling H, Jordano P, 2008. Temporal dynamics in a pollination network. *Ecology* 89: 1573–1582.
- Parmesan C, 2006. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol., Evol. Syst.* 37: 637–669.
- Pollard E, Yates TJ, 1993. Monitoring butterflies for ecology and conservation: The British butterfly monitoring scheme. London: Chapman & Hall.
- Post E, Forchhammer MC, Bret-Harte MS, Callaghan TV, Christensen TR et al., 2009. Ecological dynamics across the Arctic associated with recent climate change. *Science* 325: 1355–1358.
- Post E, Høye TT, 2013. Advancing the long view of ecological change in tundra systems. *Phil. Trans. R. Soc. B* 368 20120477.
- Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O et al., 2010. Global pollinator declines: Trends, impacts and drivers. *Trends Ecol. Evol.* 25: 345–353.
- Roy DB, Sparks TH, 2000. Phenology of British butterflies and climate change. *Glob. Change Biol.* 6: 407–416.
- Schmidt NM, Hansen LH, Hansen J, Berg TB, Meltofte H, 2012. BioBasis: conceptual design and sampling procedures of the biological monitoring programme within Zackenberg basic. Aarhus: Aarhus University, Department of Bioscience.
- Stendel M, Christensen JH, Petersen D, 2008. Arctic climate and climate change with a focus on Greenland. *Adv. Ecol. Res.* 40: 13–43.
- Strathdee AT, Bale JS, 1998. Life on the edge: Insect ecology in arctic environments. *Annu. Rev. Entomol.* 43: 85–106.
- Thackeray SJ, Sparks TH, Frederiksen M, Burthe S, Bacon PJ et al., 2010. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Glob. Change Biol.* 16: 3304–3313.
- Westwood AR, Blair D, 2010. Effect of regional climate warming on the phenology of butterflies in boreal forests in Manitoba, Canada. *Environ. Entomol.* 39: 1122–1133.