

# Phenology of High-Arctic Arthropods: Effects of Climate on Spatial, Seasonal, and Inter-Annual Variation

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## SUMMARY

The short summers of the High Arctic pose a strong time constraint on the annual cycle of all organisms in this region. Although arctic arthropods can complete their development at very low temperatures, the predicted climatic changes may shift their phenology outside its normal range. Hence, arctic arthropods may become exposed to conditions to which they are not adapted. On the basis of long-term data from several plots of pitfall and window traps at Zackenberg in high-arctic Northeast Greenland, we document that the timing of emergence is closely related to date of snowmelt in nine taxa of common surface-active and flying arthropods. Average air temperature seemed to play a lesser role, although the duration from snowmelt to the date when 50% of the individuals in the season were caught (date50) was negatively related to the average daily air temperature during the same time interval in three of the nine taxa. Since short-term weather fluctuations appeared to have a small effect on capture numbers in pitfall and window traps, we suggest that timing of snowmelt is a good predictor of the phenology of most arthropods in high-arctic Greenland. The spatial synchrony of capture numbers between individual traps within plots was high. However, among pairs of plots, the spatial synchrony varied between taxa and habitats and declined with distance between plots for surface-dwelling taxa and with

difference in timing of snowmelt for the most abundant families of Diptera (Muscidae and Chironomidae). Detritus feeders (collembolans, mites and most larvae of Diptera) and predators (spiders of the families Linyphiidae and Lycosidae) were abundant throughout the summer season. In contrast, the abundance of more specialized groups, like butterflies (e.g., Nymphalidae) and parasitoid wasps (e.g., Ichneumonidae), was restricted to a narrow seasonal time window in the warmest part of the summer. Because of their narrow phenological range and their host specialization, these taxa may be most vulnerable to trophic mismatch. Furthermore, snowmelt is predicted to become more variable, and this may affect organisms in areas of late snowmelt most severely.

## I. INTRODUCTION

Studies of arctic arthropod ecology have focused primarily on the adaptations allowing species to cope with extreme climatic conditions, as well as on the mechanisms responsible for the observed low diversity of arthropods in the Arctic (e.g., [Downes, 1964](#); [Strathdee and Bale, 1998](#)). The current attention on climate change has motivated experimental work on the effects of rising temperatures on arthropod assemblages (e.g., [Dollery \*et al.\*, 2006](#)), but studies at the population and community levels are still sparse, especially concerning flying and surface-dwelling arthropods. The consequences of climate change for the life history and population dynamics of many arctic arthropod species are, therefore, still largely unknown ([Hodkinson \*et al.\*, 1998](#); [Bale \*et al.\*, 2002](#)). Clearly temperature is a central factor in the development and behaviour of poikilotherm organisms like arthropods, and both the timing of emergence and locomotory performance may be constrained by low temperatures ([Strathdee and Bale, 1998](#)). Hence, climate is likely to be an important driver of variation in the phenology as well as the abundance of arthropods in the Arctic ([Danks and Oliver, 1972](#)).

The environmental conditions of the High Arctic are extremely seasonal, and subzero temperatures prevail during most of the year. As a result, many arthropod species inhabiting this region have a long period of winter dormancy ([Downes, 1964](#); [Danks, 2004](#)), and multi-annual life cycles are common in, for example, spiders ([Pickavance, 2001](#); [Hammel, 2005](#)), Diptera ([Butler, 1982](#)) and Lepidoptera ([Morewood and Ring, 1998](#)). Characteristic taxa like Chironomidae and Culicidae have short adult stages serving mainly to complete reproduction and dispersal ([Danks and Oliver, 1972](#); [Corbet and Danks, 1973](#)). In insects, the emergence of adults normally coincides with the peak in food resources, availability of mates, or suitable egg-laying habitats ([MacLean, 1980](#)), but the actual timing of emergence may vary considerably

across taxa (Danks, 2004). Although some species are closely associated with specific host plants (e.g., Hodkinson and Bird, 1998) or host animals (e.g., Kutz *et al.*, 2005), studies of arctic pollinator networks have revealed that generalists are very common (Lundgren and Olesen, 2005). However, in the majority of arctic arthropod species, their detailed behavioural and ecological relationships to adjacent trophic levels remain relatively unknown.

In addition to the direct effect of climate on populations (Forchhammer and Post, 2004), climate change may also induce trophic mismatching (Stenseth and Mysterud, 2002). Trophic mismatch describes the situation where the temporal occurrence of dependent organisms on adjacent trophic levels is not matched, and the consumer–resource linkage is broken. For instance, following a warming climate the peak in insect abundance may already be declining before chicks of insectivorous birds have their peak demand for food (Visser *et al.*, 1998). Such asynchronous shifts in phenology across trophic levels may have even greater effect in the High Arctic because the short summers constrain the phenological flexibility for consumers to changes in timing of food abundance. Thus, to understand the ecological consequences of climatic changes in arctic ecosystems, there is a need to quantify the role of climate in the phenology of arthropods. This group of organisms is central for the functioning of several trophic levels in the Arctic, for example, as food for breeding waders (Meltøfte *et al.*, 2007).

Here, we address the question of how climate affects the terrestrial arthropod assemblage in a single ecosystem in Zackenbergdalen in high-arctic Northeast Greenland, based on data from the Zackenberg Basic monitoring programme (Meltøfte *et al.*, 2008, this volume). In particular, we focus on the effects of snow and temperature on the phenology of the most abundant taxa of arthropods and on their spatial variation in emergence patterns. First, we provide an overall description of the arthropod fauna and relative differences between sampling plots and years. Because of the multiannual life cycles and the moderate taxonomic resolution of the data we do not provide detailed analyses of inter-annual variation in capture numbers. Instead, we focus our analyses on the phenology of three Diptera families (Chironomidae, Muscidae and Sciaridae), one family of parasitoid wasps (Ichneumonidae), one family of Lepidoptera (Nymphalidae), two families of spiders (Lycosidae and Linyphiidae), collembolans and mites. The importance of temperature and plot-specific dates of snowmelt (defined as date of 50% snow-cover in the plot) for inter-annual variation in phenological events is analysed statistically. In addition, we estimate the spatial synchrony of capture numbers among traps within trapping plots and between pairs of plots. We end with a discussion of how differences in phenological sensitivity to climate across taxa can lead to trophic mismatch within the arthropod food web and its ecological repercussions.

## II. THE ARTHROPOD FAUNA AT ZACKENBERG

The entire arthropod fauna in any given locality can be described only by combining results of multiple trap types. Since the monitoring of arthropods at Zackenberg focuses on pitfall and window traps (Box 1), we restrict this description to flying and surface-dwelling species. During the years 1996–2005, a total of 567,644 arthropods were caught using window and pitfall traps (Table 1). Mites and collembolans constituted almost half of these (see Sørensen *et al.*, 2006, for details). Among the remaining specimens, 99.9% were either spiders or belonged to one of four orders of insects: Diptera, Hymenoptera, Hemiptera and Lepidoptera (Table 1). The majority of the mites were caught in plots 2, 5 and 7 (Table 1) where snowmelt occurs early. Collembolans were mainly caught in plots 3, 4 and 5, with much smaller numbers in plot 2 and 7 (Table 1). They are sensitive to changes in moisture (Lensing *et al.*, 2005), but may also respond to anoxia (Hodkinson and Bird, 2004), which is a common condition in areas of late snowmelt. A previous comparison of the density of mite and collembolans in plots 3, 4 and 5 based on soil samples from early August revealed a larger density of collembolans in plot 5, but no difference among the three plots for mites (Sørensen *et al.*, 2006).

In general, Diptera and especially Chironomidae dominate arctic insect communities (MacLean and Pitelka, 1971; Danks, 1981, 1992; Elberling and Olesen, 1999). Indeed, at Zackenberg we found that 34.8% of the total sample of insects and spiders were Chironomidae. The window traps (plot 1) and the pitfall traps in the fen (plot 2) caught the majority of the Chironomidae, suggesting an association to habitats with ponds and soil with high moisture content. The capture numbers of several other Diptera families, for example, Culicidae, Empididae, Phoridae and Scatophagidae, varied considerably between plots, and the plot where the majority of the individuals were caught differed between families. Culicidae (mosquitoes) is a well-known arthropod family in the Arctic, but the number of individuals in the traps at Zackenberg was moderate compared to other families of Diptera, probably related to the trap design. Indeed, a long-term study from arctic Canada used specially designed visual attraction traps, in contrast to the setup at Zackenberg, and demonstrated that differences in timing of emergence were related to pond depth and water temperature (Corbet and Danks, 1973). Muscidae were very common in most of the samples and they were found in all plots in roughly equal numbers. In contrast, the distribution of over-wintering sites of Mycetophilidae has previously been found to be very patchy (N.M. Schmidt and T.T. Høye, unpublished data). This is probably related to their specific habitat requirement for egg-laying and larval development (Böcher, 2001).

**Box 1****Arthropod Study Sites and Sampling Design**

Arthropods were captured continuously during summer in several different plots with varying average date of snowmelt (Box Table 1).

**Box Table 1** Description of the seven different trapping plots

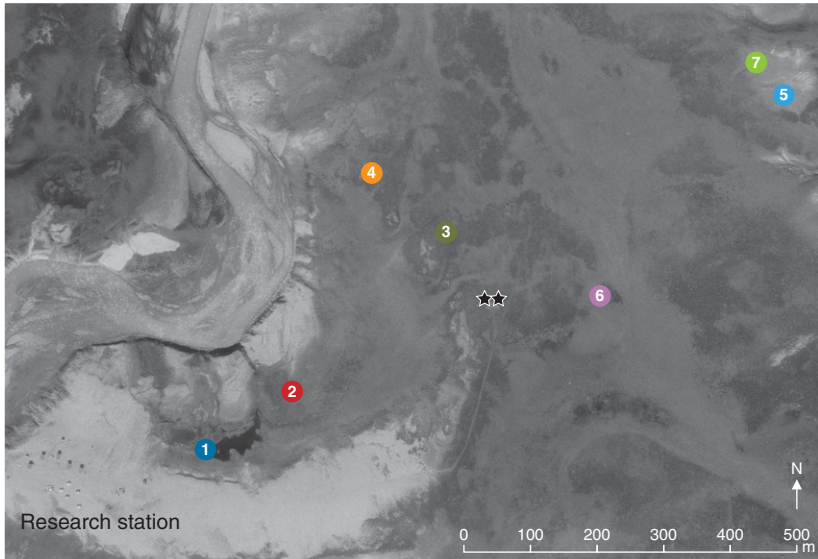
Plot no.	Trap type	Operating period	Description of habitat	Timing of snowmelt
1	Window	1996–2005	Small islet in shallow pond	Early
2	Pitfall	1996–2005	Wet fen dominated by mosses and grasses with <i>Salix arctica</i> on the tussocks	Early
3	Pitfall	1996–2005	Mesic heath dominated by lichens with <i>Cassiope tetragona</i> , <i>Dryas</i> sp. and <i>Salix arctica</i>	Late
4	Pitfall	1996–2005	Similar to plot 3, but less <i>Cassiope tetragona</i> and more <i>Dryas</i> sp. and grasses	Late
5	Pitfall	1996–2005	Arid heath dominated by lichens and <i>Dryas</i> sp.	Early
6	Pitfall	1996–1998	Snow-bed dominated by lichens and <i>Salix arctica</i>	Late
7	Pitfall	1999–2005	Similar to plot 5, but more exposed and with limited snow-cover during winter. Less <i>Salix arctica</i> and more <i>Dryas</i> sp. and grasses than plot 5	Early

The trap type and period of operation as well as a short description of the vegetation in the plots is given. The pitfall trap plots each have eight yellow plastic cups with a diameter of 10 cm, while the window trap plot consists of two window traps with windows measuring 20 × 20 cm and positioned perpendicular to each other (Jónsson *et al.*, 1986). All plots are located below 50 m elevation above sea level. Plots were grouped in either early or late snowmelt based on average date of snowmelt. Further information on inter-annual variation in date of snowmelt is given in Box Figure 2.

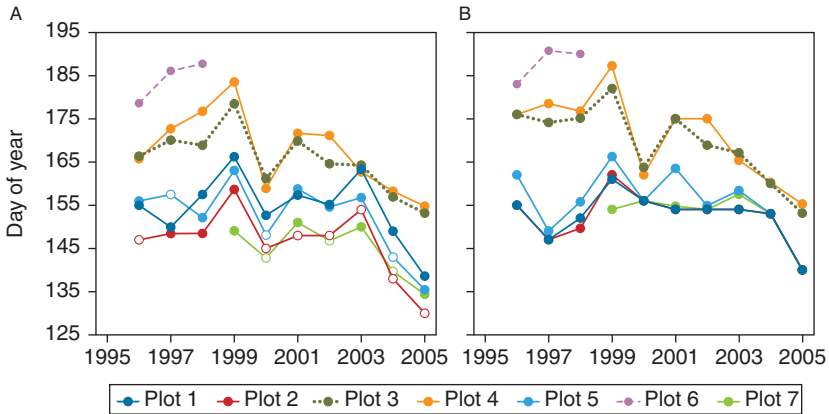
(continued)

**Box 1** (*continued*)

A climate station located within 600 m of the plots provided the weather data ([Box Figure 1](#)). Both pitfall and window traps were used ([Box Table 1](#)). The sampling in each of the plots started right after snowmelt. Thus, sampling started later in areas and years of late snowmelt than in areas and years of early snowmelt ([Box Figure 2](#)). All traps were emptied weekly. Mites and collembolans were only counted but most other arthropods were identified to the family level. Further details regarding sampling procedures are given in [Meltofte and Berg \(2006\)](#), and [Bay \(1998\)](#) provides a more detailed description of vegetation types.



**Box Figure 1** Orthophoto of the study area with the sampling plots (plot numbers indicated in dots), climate station (masts indicated by stars) and research station. Abrasion plateaus and snow are light while vegetated areas and ponds are in darker tones.



**Box Figure 2** (A) Inter-annual variation in the date of ice-melt on the surrounding pond (plot 1) or snowmelt (plots 2–7) and (B) the date of onset of the trapping period (day of the year May 11–July 14). In some years, snowmelt was prior to arrival at Zackenberg and snowmelt was back-estimated from Tiny Tag data loggers (Gemini Data Loggers Ltd., Chichester, UK), snow monitoring images (Hinkler *et al.*, 2002) or estimated from timing of snowmelt in other plots and the relative difference in timing of snowmelt between plots. These observations are indicated by open symbols.

The sampled specimens of Hemiptera were aphids Aphidoidea, scale insects Coccoidea, or the arctic-alpine seed bug *Nysius groenlandicus*. Numbers in all three groups were highly variable among years. Both aphids and scale insects were most numerous in the two plots of late snowmelt (plots 3 and 4), whereas *N. groenlandicus* was caught mainly in the driest plots (plots 5 and 7) during the warmest years. This is in accordance with previous findings for this species (Böcher and Nachman, 2001).

The most common family among Hymenoptera was the Ichneumonidae. Specimens were caught in all plots and all years, but primarily in the fen (plot 2) (Table 1). The second most common group of Hymenoptera was the superfamily Chalcidoidea, and like the arctic-alpine seed bug, this group was caught mainly in 2004 and 2005 (73.4% of the individuals), where the earliest snowmelt of all years was recorded (Box 1, Figure 2).

The majority of the adult Lepidoptera were either arctic fritillary *Clossiana chariclea* or polar fritillary *C. polaris* (Table 1), but arctic clouded yellow *Colias hecla* and species of the family Noctuidae were also found regularly. Although individuals were caught in all plots, only few were caught in the fen area (plots 1 and 2). Arctic clouded yellow was not caught at all in 2001, and since no specimens have been recorded prior to June 24 in other years, most individuals may have been killed by a snowstorm on June 15–16, 2001, as pupae.

**Table 1** Numbers of individuals of different taxa caught in seven different plots (see [Box 1](#) for characteristics of the plots)

Order or phylum	Family or species	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6	Plot 7	Sum
Acari		3748	42,731	10,230	12,514	47,564	2545	14,741	134,073
Aranea	Dictynidae	0	18	75	53	94	1	109	350
	Linyphiidae	77	13740	806	1088	1661	689	456	18517
	Lycosidae	17	2329	7363	5504	7506	653	4161	27533
	Thomisidae	0	8	157	220	526	8	390	1309
	Unidentified	0	0	1	2	2	0	0	5
Collembola		876	15,182	24,361	30,566	62,520	1954	12,460	147,919
Diptera	Agromyzidae	146	68	16	22	62	0	66	380
	Anthomyiidae	142	848	548	347	650	106	162	2803
	Calliphoridae	40	77	113	138	95	5	122	590
	Cecidomyiidae	47	7	8	16	21	1	17	117
	Ceratopogonidae	5954	136	54	117	44	–	84	6389
	Chironomidae	61,067	23,238	2572	4289	2688	1413	2036	97,303
	Culicidae	1603	68	97	94	42	9	50	1963
	Cyclorhapha larvae	0	82	5	9	71	0	107	274
	Empididae	137	6	10	73	11	5	17	259
	Muscidae	10,184	19,602	13,077	14,255	12,889	2973	9858	82,838
	Mycetophiliidae	123	646	66	66	268	353	216	1738
	Nematocera larvae	3	488	37	36	51	3	13	631
	Phoridae	7	9	69	45	704	98	3462	4394
	Scatophagidae	105	543	14	39	14	1	9	725
	Sciaridae	2008	881	2337	1308	1307	4230	1872	13,943
	Syrphidae	76	76	94	91	104	25	73	539
	Tachinidae	34	19	43	54	95	5	73	323
	Other <sup>a</sup>	14	20	4	27	30	8	37	140



Hemiptera	Aphidoidea	14	554	1210	651	93	4	644	3170
	Coccoidea	17	19	2513	1406	272	22	652	4901
Hymenoptera	<i>Nysius groenlandicus</i>	21	32	11	9	224	0	323	620
	Bombus sp.	30	8	27	34	32	1	13	145
	Braconidae	3	30	71	66	153	9	54	386
	Chalcidoidea	21	90	957	392	341	1	236	2038
	Ichneumonidae	421	1838	939	747	948	475	983	6351
	Scelionidae	0	1	180	88	34	0	116	419
Lepidoptera	Other <sup>b</sup>	2	11	6	13	20	3	65	120
	Nymphalidae	24	161	587	721	500	293	273	2559
	<i>Colias hecla</i> (Pieridae)	21	109	79	80	91	21	69	470
	Lepidoptera larvae	0	24	73	59	282	13	214	665
	Noctuidae	13	4	115	106	109	24	79	450
	Other <sup>c</sup>	9	9	4	14	16	0	6	58
Other <sup>d</sup>		33	172	5	14	11	0	3	238
Sum		87,037	123,920	69,187	75,617	142,393	15,954	54,388	567,644

Plots 6 and 7 were in operation only in the years 1996–1998 and 1999–2005, respectively. All other plots were operated in the years 1996–2005. Numbers in parentheses in footnotes indicate number of specimens recorded within taxa. Three pairs of Diptera families were not separated in all years (Anthomyiidae/Muscidae, Chironomidae/Ceratopogonidae and Mycetophilidae/Sciaridae). In these groups, the total number of individuals in each family was estimated from the proportion in each family in years when they were separated. See legend to [Figure 2](#) for details.

<sup>a</sup>Fanniidae (1), Heleomyzidae (25), Piophilidae (3), Tipulidae (60), Trichoceridae (18), Tipulidae larvae (21), Brachycera larvae (11).

<sup>b</sup>Ceraphronoidea (61), Cynipoidea (30), Megaspilidae (5), Tenthredinidae (1), Hymenoptera larvae (21), *Symphyta* sp. larvae (2).

<sup>c</sup>Lycaenidae (37), Geometridae (19), *Plebeius franklinii* (28), Tortricidae (2).

<sup>d</sup>Coleoptera (*Latridius minutus*) (2), Nematoda (9), Ostracoda (152), Siphonaptera (3), Tardigrada (6), Thysanoptera (62).

Zackenbergdalen hosts a total of eight species of spiders: one wolf spider, *Pardosa glacialis*; one Dictynidae, *Emblyna borealis*; five species of Linyphiidae, *Collinsia thulensis*, *Hilaira vexatrix*, *Erigone arctica*, *Erigone psychrophila* and *Mecynargus borealis*; and one Thomisidae, *Xysticus deichmanni* (Larsen and Scharff, 2003). Across years they have been sorted to family level, but in 1999, all spiders were sorted to species level, and a distinction between juveniles and adults was made (Larsen, 2001). The majority of the Linyphiidae were caught in the fen (plot 2) and, based on the data from 1999, most of these belonged to *E. psychrophila*. There was a tendency towards a bimodal distribution of Linyphiidae across the season in all plots, but not equally strong across years. This indicates that adult males die after mating early in the season and juveniles make up a larger proportion of the total capture in the latter part of the season. In corroboration, the bimodal peak was also observed in 1999, where juveniles and adults were separated and the second peak consisted almost entirely of juveniles. *P. glacialis* was mainly caught in plots 3, 4, 5 and 7, and the numbers caught in the fen (plot 2) varied widely between years. Since this plot is much wetter than the other plots and *P. glacialis* generally is less abundant, low soil moisture could be important for the distribution in this species. Indeed, in years of late snowmelt the capture rates of *P. glacialis* in plot 2 were smaller.

### III. ENVIRONMENTAL DRIVERS OF ARTHROPOD PHENOLOGY AT ZACKENBERG

Most studies of the phenology of arctic arthropod species have embraced only few years and have been limited to few families of Diptera: Chironomidae (Danks and Oliver, 1972; Danks, 1978; Hodkinson *et al.*, 1996) and Culicidae (Corbet and Danks, 1973), and one species of Hemiptera (Böcher, 1976). A key to this paucity of studies is probably that collecting data over entire seasons and across multiple years in remote areas with limited infrastructure is costly. In addition, there are methodological challenges associated with the tracking of phenological variation in arthropods (Box 2). Hence, little is known about the environmental drivers or abiotic conditions governing phenology of arctic arthropods (but see Høye *et al.*, 2007b).

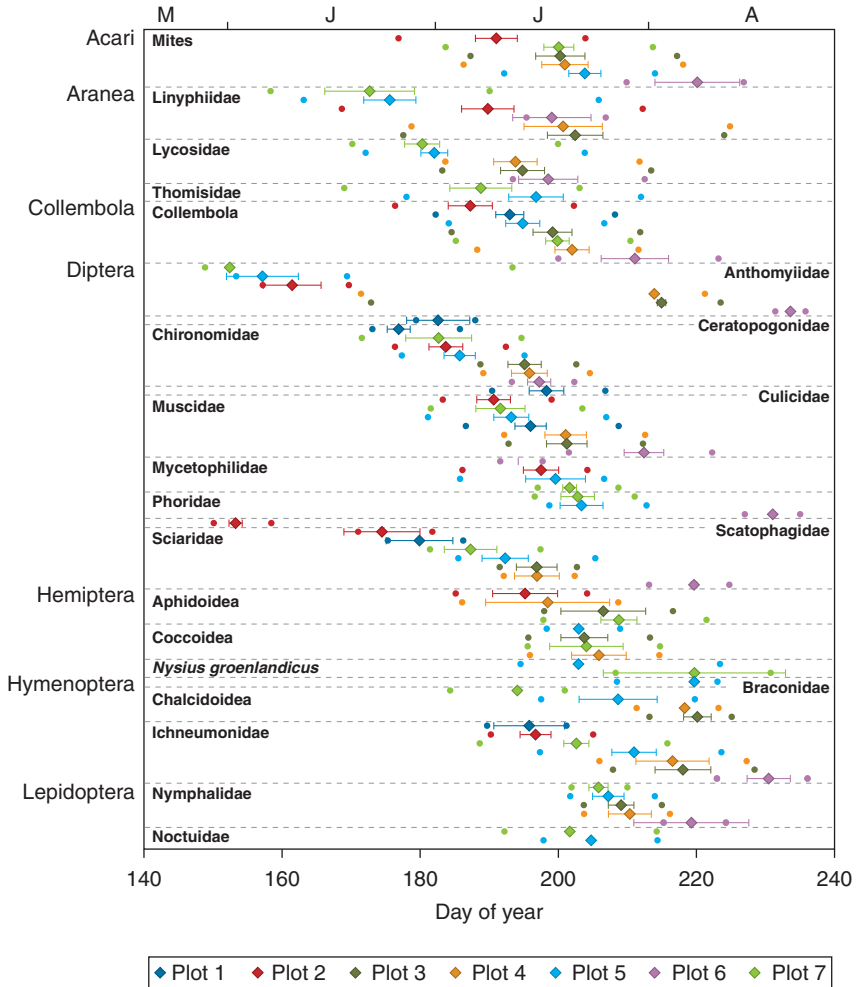
To characterise the seasonal development of capture numbers and, hence, the phenology of arthropods at Zackenberg, we quantified the date when 25, 50 and 75% of the annual catch was reached (henceforth termed date25, date50 and date75, respectively) for each plot, year and taxon following Corbet and Danks (1973). The timing of capture varied widely across arthropod taxa (Figure 1). For instance, the difference in timing of Anthomyiidae among plots was very pronounced and suggests that different species

**Box 2****Phenology Inferred from Pitfall and Window Trap Data**

It is well-known that capture numbers from passive traps like pitfall and window traps are a function of both population density and locomotory performance (Southwood and Henderson, 2000). Specifically, in the seasonal arctic environment, density is closely related to the phenological development, and locomotory performance is related to short-term weather fluctuations (Høye and Forchhammer, 2005; Høye and Forchhammer, submitted). The phenological development is typically a bell-shaped function of time through the summer, whereas weather may change on a daily basis. Therefore, we expect capture numbers to vary on both a seasonal and a daily time scale. We have previously used non-linear generalized additive models (GAM; Woods, 2006) to statistically separate the effects of density and short-term weather (Høye and Forchhammer, submitted). The advantage of the GAM modelling approach is that the explanatory power of weather parameters can be assessed statistically by simultaneously taking phenology of the organisms into account without *a priori* assumptions about the exact shape of the phenological development through the summer (Høye and Forchhammer, submitted).

On the basis of both daily and weekly sampling, we constructed four candidate models with each of four weather variables (temperature, solar radiation, wind and precipitation) and a non-linear spline function of capture date. We did this for each taxon in each trapping season in each plot. In this way we quantified the variance explained by a non-linear term estimating the seasonal development and a linear term estimating the effect of short-term weather fluctuations (Høye and Forchhammer, submitted). Lycosidae displayed the most pronounced response to short-term weather fluctuations based on these results. However, the most important weather variable (solar radiation) only explained on average 14.8% of the variation in capture numbers of Lycosidae after accounting for the seasonal development. For Linyphiidae, Muscidae and Chironomidae, the most important weather variable alone explained on average 7.1%, 6.5% and 5.9% of the variation in capture numbers, respectively. At the same time, the variance explained by the non-linear spline function ranged between 71% and 84%. The effect of weather fluctuations was slightly higher in the data set from daily sampling. This indicates that short-term fluctuations in weather do influence locomotory activity, and that this is reflected in variation in capture numbers from pitfall traps. However, the variation arising through changes in locomotory activity is much smaller than the seasonal variation. Therefore, it is expected to have a limited effect on estimates of the timing of the phenological development based on the pitfall and window trap data (Høye and Forchhammer, submitted).

predominate in plots 2, 5 and 7 compared to the plots 3, 4 and 6. In contrast, Nymphalidae, which is represented only by two species, exhibited very little variation in date50 across plots (Figure 1). It is also clear that Lepidoptera and Hymenoptera generally appear later than most families of Diptera (Figure 1),



**Figure 1** The phenology of all taxa represented by at least 50 individuals per season for each plot (day of year 140–240). Diamonds mark when 50% of the seasonal capture was reached (date50) and dots represent the average date at which 25 (date25) and 75% (date75) of the total capture within one season was reached. Error bars spanning 1 SE of date50 are given when estimates are based on averages across multiple years.

which probably relates to taxa-specific differences in the timing of resource availability and opportunities for reproduction. In some taxa, for example, mites, collembolans and spiders, the life stages are not entirely separated during the annual cycle and therefore individuals can be found throughout the summer season. This is evident in a longer time span between date25 and date75 in these groups (Figure 1).

We identified nine taxa, which were adequately represented in the samples, to allow for detailed statistical analysis of phenological patterns: Chironomidae, Muscidae, Sciaridae, Ichneumonidae, Nymphalidae, Linyphiidae, Lycosidae, collembolans and mites (Figure 2). Clearly, data at the species level would have been ideal, but from an ecosystems perspective information about the phenology and spatial variation of specific taxa is still valuable, especially from the rarely studied High Arctic fauna. We cannot rule out that the species composition within each taxon changes through the season or varies between trapping plots, but given the rarity of this kind of data from the region, our higher-taxon approach provides a necessary starting point. Also, there is a trade-off between taxonomic resolution and the number of individuals caught within each taxonomic unit. Even if the resources had been available, it is likely that sorting the entire data set to the species level would result in many species being represented only by few specimens. A statistical treatment of these species would therefore not have been possible. Hence, the benefit of high taxonomic resolution needs to be weighed against the statistical power of small data sets on each taxonomic unit.

For each of the nine taxa, we analysed the phenological variation in relation to the timing of snowmelt and temperature. We used linear models with date50 as the phenological response contrasted with plot-specific dates of snowmelt and average air temperature in the month preceding plot-specific snowmelt as predictors. We found that snowmelt was a better predictor of phenological variation than temperature in all taxa (results not shown). Consequently, we proceeded by analysing the effect of timing of snowmelt only and plot number on the date50. This set of linear models demonstrated a significant effect of snowmelt in all taxa except collembolans and Linyphiidae (Table 2). In addition there was a significant effect of plot in mites, collembolans, Chironomidae, Linyphiidae and Lycosidae, indicating that the duration from snowmelt to date50 displayed significant spatial variation in these taxa (Table 2).

Average air temperature at Zackenberg peaks by the end of July, and since the development rate of arthropods is likely to be temperature-dependent, the duration from snowmelt to date50 (i.e., the development period from over-wintering to adult stage) may be faster in late melting plots. To investigate this further, we calculated the number of days from plot-specific date of snowmelt to date50 for each plot and year for all nine taxa. Then we analysed the effect of average temperature and plot for the duration of this

development period. In most taxa, the duration of the development differed significantly between plots, and in Nymphalidae, Ichneumonidae and Muscidae warmer development periods were significantly shorter (Table 3).

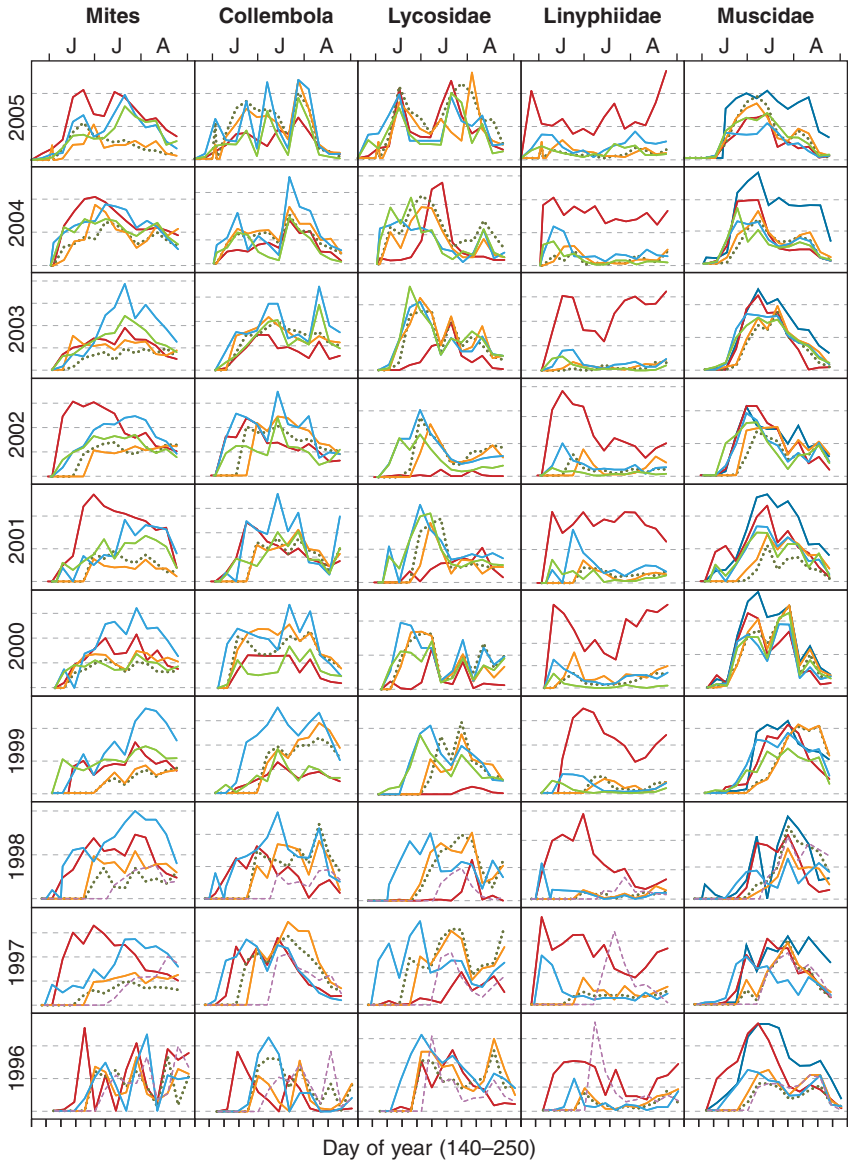
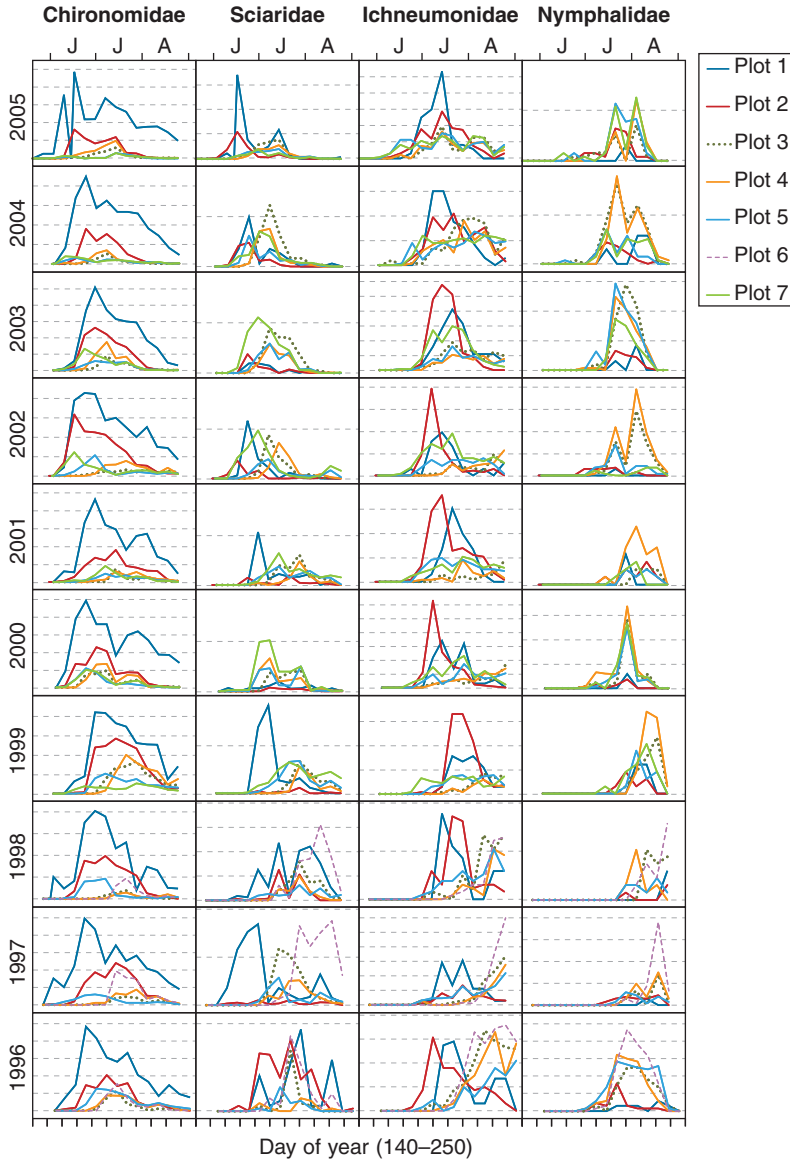


Figure 2 (continued)



**Figure 2** The  $\log_{10}$ -transformed number of individuals in nine taxa caught through the season (day of year 140–250) in the different trapping plots for the years 1996–2005. Day of year refers to the date when the traps were emptied and the value for any given day represents the catch for the preceding time interval (1 week). Horizontal gridlines are given in increments of 0.5 except in Linyphiidae where they indicate 0.25, and in Nymphalidae and Ichneumonidae where they indicate 0.1. Each sub-panel gives data for all plots in 1 year and each line within a sub-panel represents data from

Although this indicates that air temperature affects the development of arthropods, it is also possible that the relationship is due to individuals moving between plots. However, if organisms emerge mainly from the early melting plots and disperse to late melting plots, the duration between snowmelt and date50 would be shorter in late melting plots. There was an indication of the duration of development to be shorter in late melting plots in Lycosidae, but it was not a general pattern (Table 3). Hence, movement of individuals from early to late melting areas does not seem to be important.

#### IV. SPATIAL SYNCHRONY IN CAPTURE NUMBERS

Very mobile species of arthropods could easily move between the trapping plots included in this study. This suggests that capture numbers may be closely correlated between plots. Yet, the terrestrial ecosystem at Zackenberg consists of a mosaic of different vegetation types (Bay, 1998), and this could on the contrary reduce the spatial synchrony of captures even between individual traps within a plot. Also, variation in capture numbers is more related to the phenological development than to short-term weather fluctuations (Box 2), and the phenological development is closely coupled to timing of snowmelt, which is spatially variable. Hence, taxonomic differences in the degree of spatial synchrony of capture numbers within and among plots could indicate the responsible processes governing variation in capture numbers in each taxon.

To compare the degree of spatial correlation, we used permutation methods (Quinn and Keough, 2002) to draw sub-samples from the available

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one trapping plot. In the two spider families Linyphiidae and Lycosidae, juveniles and adults were not separated except for the year 1999, and the ratio of juveniles to adults is not constant across the season (T.T. Høye, unpublished data). Juveniles of Lycosidae cling to the abdomen of the mother during the first week after hatching (Böcher, 2001). Thus, trapping a female wolf spider with juveniles on its abdomen leads to the capture of 50 individuals or more. Likewise, bumblebees can host large numbers of mites on their body and the capture of a mite-infested bumblebee in a trap can result in the simultaneous capture of several hundred mites. After 1998, the capture numbers from individual traps were recorded individually and the spikes in the number of wolf spiders and mites in some traps were easily recognized. For wolf spiders and mites, we changed these spike numbers to the average of the other traps from the same capture period. Ceratopogonidae were not separated from Chironomidae in 1996, 1997, 1998 and 2000, Mycetophilidae were not separated from Sciaridae in 1996 and Anthomyiidae were not separated from Muscidae in 1996 and 2000. Across the years when these families were separated, Ceratopogonidae, Mycetophilidae and Anthomyiidae constituted 6.23, 8.88 and 3.24% of each pair, respectively. Hence, we used pooled numbers of each family pair in years when they were not separated.



**Table 2** Summary of final reduced multiple regression models of the date of 50% of annual capture (date50) for nine different arthropod taxa

TAXON	SNOW		PLOT							RES DF	$R^2$	P-VALUE
	COEF	SE	1	2	3	4	5	6	7			
Acari	0.734	0.1293	–	–10.29	–14.81	–16.01	–1.61	–10.87	0.00	38	0.65	<0.0001
Chironomidae	0.706	0.1173	–9.60	2.80	0.87	–0.03	–1.64	–10.23	0.00	48	0.70	<0.0001
Nymphalidae	0.458	0.1088	–	–	–	–	–	–	–	16	0.53	0.0007
Collembola	–	–	–	–12.62	–0.72	2.12	–5.04	11.21	0.00	44	0.39	0.0004
Ichneumonidae	0.819	0.1125	–	–	–	–	–	–	–	42	0.56	<0.0001
Linyphiidae	–	–	–	–4.93	10.58	8.32	–17.83	0.00	–	20	0.47	0.0102
Lycosidae	0.874	0.1133	–	–	–3.46	–6.44	–4.99	–16.15	0.00	34	0.79	<0.0001
Muscidae	0.564	0.0667	–	–	–	–	–	–	–	58	0.55	<0.0001
Sciaridae	0.729	0.0966	–	–	–	–	–	–	–	37	0.61	<0.0001

Observations from years and plots where less than 100 individuals were caught are omitted (less than 50 individuals for Nymphalidae and Ichneumonidae). Full models included date of snowmelt (SNOW), plot (PLOT), and their interaction. Insignificant terms were removed based on  $F$ -test of type 3 sums of squares ( $\alpha = 0.05$ ). Regression coefficients for date of snowmelt (COEF) with one standard error of mean (SE) and plot (indicated by plot number) if they remained in reduced models are provided. Residual degrees of freedom (RES DF),  $R^2$  and model  $p$ -values (P-VALUE) are given.

**Table 3** Summary of final reduced multiple regression models of the number of days between plot-specific date of snowmelt and date of 50% of annual capture (date50) for nine different taxa of arthropods

TAXON	TEMPERATURE		PLOT							RES DF	R <sup>2</sup>	P-VALUE
	COEF	SE	1	2	3	4	5	6	7			
Acari	–	–	–	–11.10	–20.32	–22.54	–3.54	–22.43	0.00	39	0.66	<0.0001
Chironomidae	–	–	–11.93	2.80	–4.55	–5.93	–3.96	–21.30	0.00	49	0.51	<0.0001
Nymphalidae	–4.38	0.916	–	–	–6.30	–7.69	–2.90	–13.70	0.00	12	0.90	<0.0001
Collembola	–	–	–	–14.54	–21.54	–21.14	–12.74	–28.48	0.00	44	0.39	0.0004
Ichneumonidae	–4.10	1.436	–8.85	–9.18	4.35	3.91	3.85	–0.48	0.00	36	0.35	0.0203
Linyphiidae	–	–	–	–	–	–	–	–	–	–	–	–
Lycosidae	–	–	–	–	–6.05	–9.31	–5.96	–21.11	0.00	35	0.52	<0.0001
Muscidae	–3.46	0.747	–	–	–	–	–	–	–	58	0.27	<0.0001
Sciaridae	–	–	–11.80	–0.64	–10.29	–13.59	–0.73	–9.18	0.00	32	0.41	0.0065

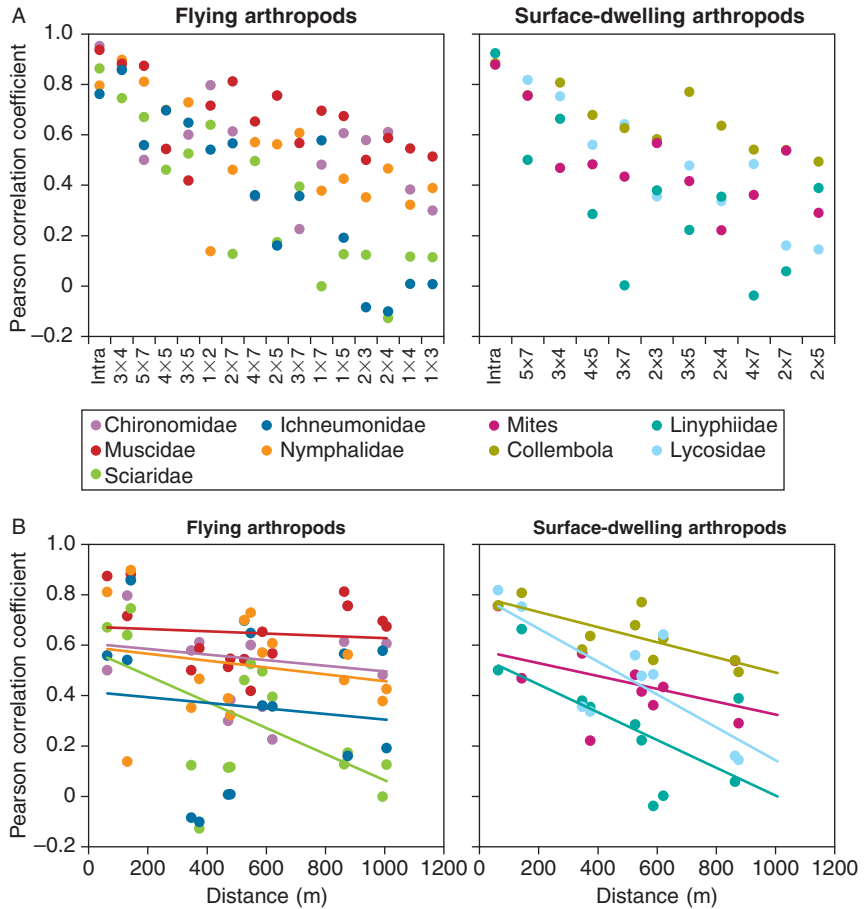
Observations from years and plots where less than 100 individuals were caught are omitted (less than 50 individuals for Nymphalidae and Ichneumonidae). Full models included average temperature in the interval between snowmelt and date50 (TEMPERATURE), plot (PLOT) and their interaction. Insignificant terms were removed based on *F*-test of type 3 sums of squares ( $\alpha = 0.05$ ). Regression coefficients for temperature (COEF) with one standard error of mean (SE) and plot (indicated by plot number) if they remained in reduced models are provided. Residual degrees of freedom (RES DF), *R*<sup>2</sup> and model *p*-values (P-VALUE) are given.

observations of spatial correlation within and among plots. In general, captures of all taxa were highly synchronous within plots (Figure 3A “Intra”) with butterflies Nymphalidae and parasitoid wasps Ichneumonidae exhibiting the lowest synchrony. The degree of spatial synchrony among plots varied considerably between taxa (Figure 3A). In addition, the inter-plot correlation differed markedly between pairs of plots. In particular, the correlation was high between the pairwise neighbouring plots 1 and 2, 3 and 4, and 5 and 7 for all taxa (Figure 3A). We did not find any relation to sample size of the data sets from which the sub-samples were drawn, and the result was not sensitive to the exclusion of the largest capture rates. However, we did find that for surface-dwelling arthropods, the spatial synchrony decreased with distance between plots (Figure 3B). For flying insects, synchrony was not related to distance between plots except for Sciaridae (Figure 3B). In this group, different species may be found in different habitats, and they may have different phenological patterns. In the other groups of flying insects, the distances between plots are probably short compared to their range, and differences in spatial synchrony may be more related to timing of snowmelt or the spatial distribution of resources than to dispersal. We found evidence of this for Chironomidae and Muscidae. Capture numbers in these groups were more closely correlated between plots differing by less than 10 days in average date of snowmelt than between plots differing by more than 10 days in average date of snowmelt.

Summarising, the high intra-plot synchrony strongly suggests that average capture rates for each plot adequately describes variation in capture rates of individual traps. Among plots, there was considerable variation in synchrony of capture numbers among pairs of plots. Captures of collembolans, Muscidae and Chironomidae showed the strongest correlation between plots, and the degree of spatial synchrony may to some extent be a function of geographical distance between plots in surface-dwelling arthropods and related to spatial variation in timing of snowmelt in flying arthropods. However, because of the limited taxonomic resolution, differences may to some extent be the result of different species composition among plots and trapping periods.

## V. DISCUSSION AND CONCLUSION

The arthropod data set used in this study is probably the most extensive from the entire Arctic, but limitations to the taxonomic resolution prevent a detailed phenological description of the arthropod species at Zackenberg. Nevertheless, compared to studies carried out in other high-arctic locations, such as Taimyr, Siberia (Tulp and Schekkerman, 2007), and Barrow, Alaska (MacLean and Pitelka, 1971; MacLean, 1980), the low capture rate of crane



**Figure 3** (A) Intra- and inter-plot spatial synchrony of five taxa of flying insects and four taxa of surface-dwelling arthropods. The eight traps in each plot were divided in two groups of four traps, and the weekly capture numbers averaged in each group produced one pair of observations. In this way, all possible pairs of averages of four and four pitfall traps ( $n = 35$ ) were calculated, and pairs where both values were zero were excluded. Each taxon is estimated separately and the values given under “Intra” are the average of 1000 permuted Pearson correlation coefficients. Each coefficient is estimated from a sub-sample of 1000 random observation from the full data set of all possible pairs across years and plots. A similar approach was used to quantify inter-plot spatial synchrony. First, capture rates per trap per day for each trapping period was calculated. Subsequently, a data set including all pairwise combinations between any two plots for any trapping period for any year for any taxon was constructed. All pairs including plot 6 were excluded, since this plot was in operation for 3 years only. All other pairs had at least 50 observations across years and trapping periods, and we calculated Pearson correlation coefficients from 100 random samples of 40 pairwise observations in each taxon. The x-axis gives the plot numbers for each pairwise correlation, for example, “3×4” between plot 3 and plot 4. (B) The relation between inter-plot synchrony and distance between pairs of plots is given separately for flying and surface-dwelling taxa. Regression lines are based on the least squares method.

flies (Tipulidae) at Zackenberg is striking. This family of insects is believed to form an important part of the diet of waders and other insectivorous birds breeding on the tundra in Alaska (Holmes, 1966) and Siberia (Tulp and Schekkerman, 2007). In contrast, the capture rate of Muscidae and spiders appears to be high at Zackenberg compared to Siberia and Alaska. Unfortunately, the sampling procedures differ between studies at these three sites. However, the low occurrence of Tipulidae at Zackenberg has been demonstrated by several different trapping techniques (Meltofte and Thing, 1997; Schmidt and Høye, 2006).

Our results demonstrate that the phenology, that is, the timing of occurrence of terrestrial arthropods at Zackenberg differed considerably among taxa and plots. For instance, the average date when 50% of the annual capture was reached (date50) varied by more than 2 months across taxa (Figure 1). This suggests that different taxa are clearly timed to different parts of the season. At the same time, date50 of the most abundant taxa was significantly related to date of snowmelt (Table 2). In fact, date of snowmelt was a better predictor of date50 than temperature, and only three of the nine taxa included in our analyses (Nymphalidae, Ichneumonidae and Muscidae) had significantly faster development (i.e., the duration from snowmelt to date50) in years where the temperature during this interval was higher (Table 3). We cannot rule out that the species composition within taxa differed between plots, and that this could be responsible for plot differences in duration of development. Alternatively, in some taxa, peak capture rates could reflect increased activity due to mate location behaviour (e.g., Lycosidae), which could be cued to a specific time during the season (i.e., a specific date). In mites and collembolans, the peak in capture numbers during the season was less pronounced than in other groups, but even so, date50 was clearly related to plot-specific timing of snowmelt, which demonstrates that local climatic conditions determine a large part of the inter-annual variation in the phenological development of high-arctic arthropods. Therefore, each taxon may have an optimal period of occurrence, but variation in timing of snowmelt may modify the exact timing of date50 in any given year. In addition, movement of individuals from over-wintering areas to summer habitats could affect estimates of phenology. For example, most Chironomidae over-winter as larvae in ponds, whereas adults can be found in many other habitats (Danks and Oliver, 1972; Danks, 1978). We found that the spatial synchrony of capture numbers is very high at the local scale (within each plot). At the landscape scale (between plots), synchrony varies between taxa. Spatial synchrony at this scale seems to be related to the distance between plots, but may also be influenced by differences in the date of snowmelt between plots. This is most clearly seen in the surface-dwelling species, probably because of their more limited mobility than their flying counterparts (Figure 3). Finally, weather-related locomotory activity as well as changes in population density

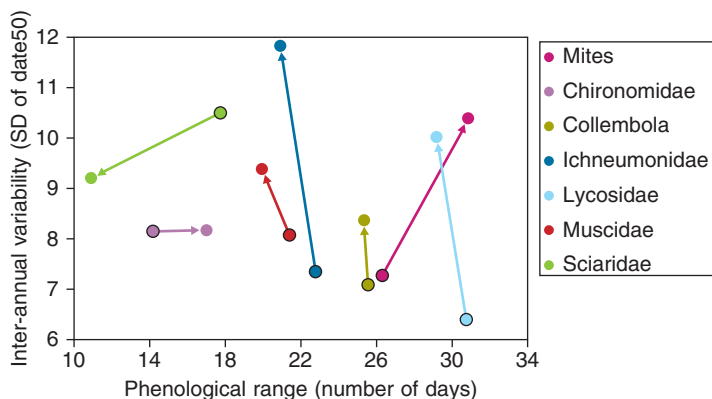
affects the number of individuals caught in a trap. A statistical separation of the variation in capture rates in one component related to density and another component related to activity demonstrated that although weather does influence activity, its importance is small relative to the phenological development. We conclude that the local phenology is clearly discernable in our data from pitfall and window traps. Specifically, the timing of snowmelt appears to be the most important predictor of phenology of arthropod taxa in high-arctic Greenland. This may be different from other parts of the Arctic, where a more maritime summer climate prevails, for example, on the northern coast of Siberia, where temperature appears to play a much larger role in invertebrate occurrence and activity (Schekkerman *et al.*, 2004).

Although few details are known about the foraging ecology of the arthropod taxa at Zackenberg presented in this study, they belong to several functionally distinct groups. The Diptera are mainly detritus feeders as larvae. As adults, the Chironomidae have limited energetic demands, since the main functions of their adult stage are reproduction and dispersal. Although adult Muscidae are generalists, they may have some importance as pollinators (Philipp *et al.*, 1990; Elberling and Olesen, 1999; Lundgren and Olesen, 2005), similarly to the Nymphalidae. While both collembolans and most mites feed on fungal hyphae, bacteria, or directly on dead organic matter, some mite species are predators or parasites (Böcher, 2001). To some extent spiders are cannibalistic, but judged from the prey selection of Linyphiidae and Lycosidae in general (Nyffeler, 1999), collembolans, mites and Diptera probably form considerable parts of their diet at Zackenberg. This means that there is at least some association between the different taxa in terms of inter-trophic interactions. Mites, collembolans and Diptera families are primary consumers and probably not very dependent on seasonally fluctuating resources. In contrast, Nymphalidae are dependent on timing of flowering, Ichneumonidae are dependent on butterfly larvae among which Nymphalidae species may be important, and spiders are predators on mites, collembolans and small species of Diptera (Böcher, 2001). The largest potential for trophic mismatch in the taxa treated in this study is therefore between pollinators and specific flower species and between parasitoids and lepidopteran larvae. There may, however, also be a risk of mismatch between wader chicks and insect prey (Meltofte *et al.*, 2007).

Over the decade of observations from Zackenberg, the phenology of plants, arthropods and birds has advanced considerably (Høye *et al.*, 2007b). This corresponds with an advancement of the timing of snowmelt in the sampling plots. However, the rates of changes vary greatly within and among groups of organisms. In particular, the trend is generally stronger in areas of late snowmelt than in areas of early snowmelt (Høye *et al.*, 2007b). Timing of snowmelt is predicted to become more variable between years, due to increased variability in winter precipitation and spring temperatures

(Stendel *et al.*, 2008, this volume). Because of snow accumulation this may be particularly pronounced in snow-beds, where snowmelt may occur later than now (Hinkler *et al.*, 2008, this volume). This could have significant effects for arthropods, since late-emerging species seem to be closely inter-trophically timed to the occurrence of their resources on lower trophic levels, for example, butterflies to flowering and parasitoid wasps to presence of host species for egg-laying. Recent studies from Zackenberg indicate that flower abundance in snow-beds will be reduced by later snowmelt (Høye *et al.*, 2007a) with potential negative consequences for pollinators. Overall, the phenology of abundant taxa within Diptera, Hymenoptera, Lepidoptera and spiders are all closely coupled to the timing of snowmelt (Table 2), which suggests that inter-annual variation in date50 of arthropods may increase particularly in areas of late snowmelt.

The consequences for trophic mismatch may be larger in the taxa occurring during a narrow period of the summer season (short phenological range) than in taxa occurring over a larger part of the season. At the same time, if there is no inter-annual variation in timing of occurrence in interacting species, the risk of trophic mismatching is likely to be small. The variation in timing of occurrence is larger in areas of late snowmelt than in areas of early snowmelt at Zackenberg. Furthermore, this difference between areas of



**Figure 4** The relation between the phenological range (the average number of days between the date when 25 [date25] and 75% [date75] of the annual capture of a taxon in a given plot is reached) and the inter-annual variation in the date when 50% of the annual capture (date50) is reached. For each taxon, the observations from early (plots 1, 2, 5 and 7) and late (plots 3, 4 and 6) melting plots are separated and the arrow between pairs of points highlights the direction and magnitude of change in the two parameters from early (dots with black circle) to late (dots with no black circle) melting plots. Linypiidae and Nymphalidae were excluded since they were not present in both early and late melting plots.

early and late snowmelt is most evident in taxa with long phenological range (Figure 4). This suggests that although these groups probably are less sensitive to trophic mismatch, because they occur over a large part of the season, they are also the most responsive groups to climatic conditions in late melting areas. A climatic shift towards more variable snowmelt in late melting areas make trophic mismatch most likely in these areas. Climatic changes may in the short term result in a change in the suitability of certain areas as habitat for arthropods, because early and late melting areas will be affected differently. On a longer time scale, altered composition of vegetation types may radically shift patterns of insect biodiversity. Indeed, climate-mediated changes in emergence patterns, abundance and diversity may have strong repercussions through the ecosystem.

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