Faculty of Biosciences, Fisheries, and Economics

Department of Arctic and Marine Biology

To keep or not to keep track of time in eternal sunshine?

Diel activity patterns of Svalbard arthropods during polar day

Maria Huntsaar

Master's thesis in Biology BIO-3950, February 2024

To keep or not to keep track of time in eternal sunshine?

Diel activity patterns of Svalbard arthropods during polar day

Maria Huntsaar

Master of Science in Biology - Northern Populations and Ecosystems,

February 2024

Supervisors:

Prof. Stephen J. Coulson, University Centre in Svalbard, Department of Arctic Biology

Prof. Nigel Yoccoz, The Arctic University of Norway, Department of Arctic and Marine Biology

Prof. Toke T. Høye, Aarhus University, Department of Ecoscience

AARHUS UNIVERSITY

NORGES ARKTISKE UNIVERSITET · UIT ·

UNIS
The University Centre in Svalbard

Table of contents

Acknowledgements

Foreword

This thesis aimed to investigate whether arthropod-visitors of *Silene acaulis* cushions showed evidence of diel activity patterns in Svalbard's polar day, something that to my knowledge has not been extensively studied at this latitude.

This project was based on already collected, but not yet analysed, time-lapse imagery linked to Bjørndalen Integrated Gradients project (BIG). The data was collected during summer 2020 by UNIS employees. Toke T. Høye then retrieved and formatted the images, which were then provided to me along with the help on how to deal with the annotation data. I annotated the images and analysed the data with the help of Nigel Yoccoz. I also worked as a field assistant for UNIS (University Centre in Svalbard) on the project in summer 2021, so even though I did not contribute with collecting the analysed data, I am familiar with the project and its setup in Bjørndalen.

Abstract

Organisms on Earth are exposed to cyclic changes in environmental variables due to Earth's rotation around it's axis. As a response, many organisms adapt their behaviour in a rhythmic manner, which is often cued by 24h light-dark cycles. However, in the Arctic, traditional 24h light-dark cycle cues do not exist for long periods at the time. Arthropods play an important role in the high latitude ecosystems, yet little is known about their diurnal cycles and the impact of these cycles in the climate change context. Presence or absence of diurnal activity patterns in arthropod-visitors on *Silene acaulis* cushions was investigated in Svalbard with the use of time lapse imagery. This study showed some indication of diurnal activity in Diptera and nocturnal activity patterns in Acari. Compared to similar studies from lower latitudes within the Arctic, arthropod activity did not show such a robust diurnal pattern nor strong influence by weather variables as has been described during the polar day. However, abundances showed very high variability within days, between days and between cameras. Due to lack of reference studies from the high Arctic, it is not possible to determine if observed high variance in abundance is a distinctive characteristic of this system or specific to the observed year.

Introduction

The Arctic presents a set of unusual environmental characteristics that organisms that inhabit those areas need to adapt to. One of such condition is the special light regime - long periods of constant darkness get replaced with constant light with a fast change between the two extremes. Most organisms on Earth are exposed to rhythmic changes in environmental conditions and synchronising their behaviour and life-stages with these cycles is usually beneficial. The strongest environmental cue to initiating these cycles has been thought to be 24h light-dark cycle. Yet, in the Arctic, this cycle is missing for long periods at the time, rendering the most universal synchronisation cue ineffective for the majority of the year. How the lack of light-darkness cycle effects activity patterns in mammals and birds has been investigated to some degree (e.g. Reierth & Stokkan, 1998; Loe et al., 2007; van Oort et al., 2007; Ashley et al., 2012; Ware et al., 2020), but the findings have been conflicting. Yet, the Arctic invertebrate community has traditionally been seen to be simple (e.g. Hodkinson & Coulson, 2004) and remains relatively poorly understood, in particular with respect to activity patterns.

Activity patterns

Due to Earth's rotation around its axis and orbiting around the Sun, most organisms on Earth are exposed to regular and predictable cycles in environmental conditions. Duration of those cycles varies - rhythms can be circatidal (last roughly 12 hours), circadian (roughly 24 hours), circalunar (around 28 days), circannual (one year) etc. As a response to exposure to rhythmic variations in environmental conditions, many animals have evolved to synchronise activity patterns and physiological processes according to these cyclic patterns.

Diel activity patterns refers to how organisms distribute their activity throughout 24h. Activity can be distributed within in different ways, e.g. some species or individuals are active for long periods at the time, while others exhibit only brief peaks of activity (Refinetti, 2008). Animals can be mostly active during daytime (diurnal), at night (nocturnal), during twilight (crepuscular), their activity may be irregular (arrhythmic) or occur at any point throughout the day (cathemeral). Daily rhythms can be cued by external factors (exogenous) and disappear in constant external conditions, or they may have a more internal basis (endogenous) and continue even when the external cues are lacking (Aschoff, 1960).

The most influential (and universal) timing cue has been suggested to be the daily light-dark cycle caused by Earth's rotation around its axis (Aschoff, 1960). Yet, light cycles differ to a large extent within the world. Near the equator, annual variation in light conditions is small with roughly 12h light and 12h dark period throughout the year. In polar regions, on the other hand, day length varies to a large degree with months of constant light or darkness and fast transition periods between the two extremes.

Many organisms from a wide variety of taxa around the world use day or photoperiod length as an anticipatory cue for seasonal preparations to maximise their fitness (Bradshaw & Holzapfel, 2007). Usage of these cues allows reindeer to fatten and grow a thicker coat prior to onset of winter or helps northern deer species time their oestrus and breeding in way that lactation occurs at the time when food is most abundant (Clutton-Brock et al., 1982; Suttie & Webster, 1995). Similar to seasonal rhythms, behaviour can be adjusted to specific times throughout the day. An organism's temporal niche, organisation of behaviours to certain portions of the 24h cycle, is assumed to have ecological significance (Kronfeld-Schor & Dayan, 2003; Hut et al., 2012) and can have fitness benefits, as organisms can alter their activity and life functions, e.g. predator avoidance, foraging or reproduction, to more suitable times of the day (Fenn and Macdonald, 1995; Daan and Aschoff, 2001; Bradshaw and Holzapfel, 2007). For example, a population of generally nocturnal Norway rats (*Rattus norvegicus*) has shown diurnal activity patterns in presence of nocturnal predators (Fenn & Macdonald, 1995). Most populations in the habitat were nocturnal, yet one of populations was exposed to frequent night-time predation by red foxes. As a result, rats from that population were active in the mornings and evenings, instead of the night. When individuals from the diurnal population were relocated to predator-free environment, they reverted back to their nocturnal behaviour patterns in foraging behaviour. In this case, switching to diurnal activity pattern likely aids with predator avoidance (Fenn & Macdonald, 1995). Honey-bees can anticipate the peak of nectar production in flowers and adjust their foraging activity accordingly (Aschoff, 1986). In certain arid areas, bees actively avoid foraging during the period when nectar has the highest sugar content prioritising higher water content over energetic benefits from nectar (Willmer, 1986; Olesen, 1988). Limiting ones activity to certain periods of the day can therefore be beneficial to the organism. It is believed that diel activity patterns are strongly cued by changes in light conditions. Yet, organisms inhabiting polar areas experience conditions where light changes minimally throughout the 24h cycle for long periods at the time. Therefore, loss of circadian rhythmicity is suggested to be a trait that theoretically allows to maximise the foraging period in highly seasonal polar regions (van Oort et al., 2007).

Yet, the question of presence or absence of diurnal activity patterns in resident polar organisms during periods of constant daylight (or constant darkness) seems to be more complex than originally thought to be as studies have produced conflicting results on this topic. Lack of circadian rhythms during periods of continuous light or darkness has been suggested to be a characteristic of Arctic/ polar resident vertebrates (van Oort et al., 2007). Based on that theory, circadian clock is expected to run freely in the absence of light cues resulting in free-running or arrhythmic activity patterns.

Earlier studies on Svalbard reindeer seem to support that suggestion as the authors found no evidence of circadian rhythmicity in reindeer's activity during the polar day. Quite the opposite, their activity was described as arrhythmic (shorter than 24h) throughout the whole duration of the constant light period (van Oort et al., 2005; van Oort et al., 2007; Loe et al., 2007). Similarly, laboratory studies on ptarmigans from Svalbard show no 24h rhythmicity in their activity in constant light or dark conditions (Reierth & Stokkan, 1998; Appenroth et al., 2020; Appenroth et al., 2021a, Appenroth et al., 2021b). Yet, the more recent studies on Svalbard reindeer shows that even though some physiological traits lose daily rhythms, others keep circadian rhythmicity throughout most of the year (Arnold et al., 2018). Arnold et al. (2018) observed a loss of circadian rhythmicity only during the peak foraging period, while rhythmicity was retained for the rest of the polar day.

Similar to findings in Arnold et al., (2018) on Svalbard reindeer, studies on other Arctic species found in Svalbard have suggested that activity patterns might not solely be linked to presence of light, but also food availability. Polar bears tend to keep circadian rhythmicity through most of the year. Yet, this daily activity pattern seems to be overrun for a part of the polar day as arrhythmic behaviour was observed during main hunting and feeding period with high variance in behaviour between individuals (Ware et al., 2020). Arctic charr seems to follow a similar pattern - utilise the resources when they are abundant and become arrhythmic for parts of the light (dark season) (Hawley et al., 2017).

Studies on invertebrates regarding daily activity patterns in polar regions are scarce as most of them focus on seasonal variation, rather than within-day variation in abundance. Insects in Finnish Lapland (67°- 69°N) do not seem to utilise the whole 24h period, even when the light conditions would be suitable for their activity. Instead, robust diel-scale pattern in foraging activity was observed both in Diptera and Hymenoptera (Stelzer & Chittka, 2010; Zoller et al., 2020). For both

of these insect groups, activity was highest during noon (mid-day), lower in the mornings and evenings with little activity during night-time.

As arthropods are ectotherms, their activity is heavily influenced by the environmental conditions. Arctic arthropod activity varies within the season as different taxa emerge at different times, depending on their phenology, which is linked to different variables such as time of snowmelt or flowering in pollinator's case (Høye et al., 2008a; Gillespie et al., 2016; Tiusanen et al., 2016). On a smaller scale, arthropod activity is tightly influenced by the local weather conditions, being mostly influenced by temperature, solar radiation and wind speed (Høye & Forchhammer, 2008b; Tulp & Schekkerman, 2008; Zoller et al., 2020).

All in all, assumption that light/dark cycles are the main cues for synchronising rhythms in behaviour might not be true in the polar context due to extended periods of continuous light or darkness. Ashley et al. (2012) suggest that some organisms living in the polar areas might instead use alternative cues such as sun's azimuth, variations in ultraviolet light, food availability or even social interactions in order to keep circadian rhythms going. It is also possible that circadian rhythms may run, but be temporary masked by other, non-circadian, factors such as food (Ashley et al., 2012; Hawley et al., 2017; Ware et al., 2020). Yet, studies on this topic in the Arctic are scarce and often limited to lower latitudes.

Terrestrial arthropods of Svalbard

Arctic arthropod community and food-webs have been seen as simple and lacking in complexities, especially compared to ecosystems at lower latitudes. Yet, this traditional view is being challenged as new research emerges (e.g. Høye & Culler, 2018).

Invertebrate biodiversity in polar areas is generally poorly known and documented, but Svalbard is relatively well-researched compared to other Arctic regions. Most of the knowledge on the invertebrate fauna in Svalbard is based on findings from the warmer and milder western part of the archipelago, data from east and north is more scarce (Coulson et al., unpublished). New species are frequently being described (Pilskog, 2011; Chaubet et al., 2013; Gwiazdowicz et al., 2012a, 2012b; Miko & Monson, 2013; Kolodochka & Gwiazdowicz, 2014; Seniczak et al., 2014; Kiedrowicz et al., 2016; Skoracki & Zawierucha, 2016), indicating that the system is not as species-poor as once thought.

Over 1000 species of terrestrial and freshwater invertebrates have been described in Svalbard (Coulson et al., 2014; Coulson et al., unpublished). The most species rich invertebrate groups are insects and rotifers, followed by mites. Around 230 insect and 190 mite species have been described after 1989 (Coulson et al., unpublished) but with increasing number of studies and usage of molecular tools, these numbers are expected to increase.

Arctic arthropod community plays a central role in many ecosystem processes, e.g. decomposition, nutrient cycling, pollination, herbivory, predation, parasitism and provides an important link in the food-web as prey (Aronsson et al., 2021). Almost 90% of the global flowering species are animal-pollinated (Ollerton, Winfree &Tarrant, 2011). In the relatively species-poor and dry Arctic environment, wind-and self-pollination increase in their importance compared to lower latitudes (Rech et al., 2016).Yet, large amount of plants still rely heavily on insect pollination for maximising their seed set (Kevan, 1972; Urbanowicz et al., 2018) and consequently influencing their growth and reproduction (Galen & Stanton, 1991; Cooper et al., 2011; Semenchuk et al., 2013). Svalbard lacks bumblebees and honeybees, that are generally considered to be highly effective pollinators. Instead, the pollinator guild is dominated by non-specialist pollinators from order Diptera (Gillespie et al., 2016), with around 140 Diptera species being described (Coulson et al., unpublished). The most numerous group being Chironomidae with 71 species (Stur & Ekrem, 2020), followed by Sciaridae with 18 species (Menzel et al., 2020). Flying insects are also an important food source for birds that migrate to the Arctic for breeding. For example, Diptera makes up the majority of the diet of snow bunting chicks (Stolz et al., 2023). Arctic arthropods are an essential part of the Arctic ecosystem, but they are sensitive towards environmental changes (Johnson & Jones, 2016).

Climate change

The Arctic is currently experiencing at least two times faster climatic change than the global average, a phenomenon know as Arctic amplification (Kattsov et al., 2005; IPCC, 2013; AMAP, 2017). Svalbard is amongst the fastest changing areas in the Arctic. Between 1988-2017, the average yearly temperatures have already risen by 1.5°C and within the last 50 years, the yearly mean temperature has risen by 4°C with a 7°C increase in average air temperature during winters (Hanssen-Bauer et al., 2019). This warming trend has been linked to drastic decreases in sea ice coverage north of Svalbard and in the Barents Sea (Kohnemann et al., 2017; Isaksen et al., 2022).

Yet, temperature is just one of the variables that can be experienced by the individuals in their daily lives. Climate change is expected to alter weather and precipitation patterns in the Arctic, increasing the occurrence of extreme weather events (Walsh et al., 2011). Rainfall is modelled to increase and snowfall to decrease throughout most of the year (McCrystall et al., 2021). Within the last 50 years, Svalbard's yearly precipitation has already increased by 65%, while the snow-cover season is 20 days shorter now (Hanssen-Bauer et al., 2019). As the timing of snowmelt has direct effects on plant and insect phenology, this change is expected to alter species phenology (Mortensen et al., 2016). Arctic growing season is already short, condensed and highly seasonal, therefore, this system is prone to development of phenological mismatches between trophic levels (Høye & Forchhammer, 2008b). Mismatch-induced decrease in seed set has already been observed in some plants (Kudo & Cooper, 2019). Increased occurrence of extreme weather events could influence arthropod daily activity due to increases in wind speeds or precipitation levels, but possible interactions between diel rhythmicity and weather are not understood yet.

In addition, the rate, which Arctic region is changing, might be too fast for the organisms to naturally adapt to (Wassmann et al., 2011). Most Arctic species have longer generation times than the lower latitude counterparts, e.g. a mite species found in Svalbard, *Ameronothrus lineatus,* has a life-span of 5-8 years (Søvik, 2003a; Søvik, 2003b). The combination of faster changes than the global average and relatively long generation times, can make organisms living in the Arctic especially vulnerable towards climatic changes.

The aim of this study is to investigate whether arthropod-visitors of *Silene acaulis* cushions show signs of diurnal activity patterns during the polar day, and whether potential patterns in activity are linked to abiotic factors.

Hypothesis:

1) Activity of *Silene acaulis* visitors is constant (and shows no diurnal patterns) throughout the polar day when diurnal light cues are not present

2) In addition to the time of the day, *S.acaulis* visitors are also influenced by abiotic variables - e.g. temperature, wind and precipitation.

Materials & methods

Study site

Imaging took place at a high-Arctic study site in Bjørndalen, Svalbard, around 6 km from the town of Longyearbyen (Fig. 1). Svalbard is an archipelago located between 74°- 81°N and 10°- 35°E. As Svalbard is located far north, it experiences extended periods of midnight sun. In Longyearbyen, the closest settlement to Bjørndalen study site, sun does not set below the horizon between 18th April and 23rd August.
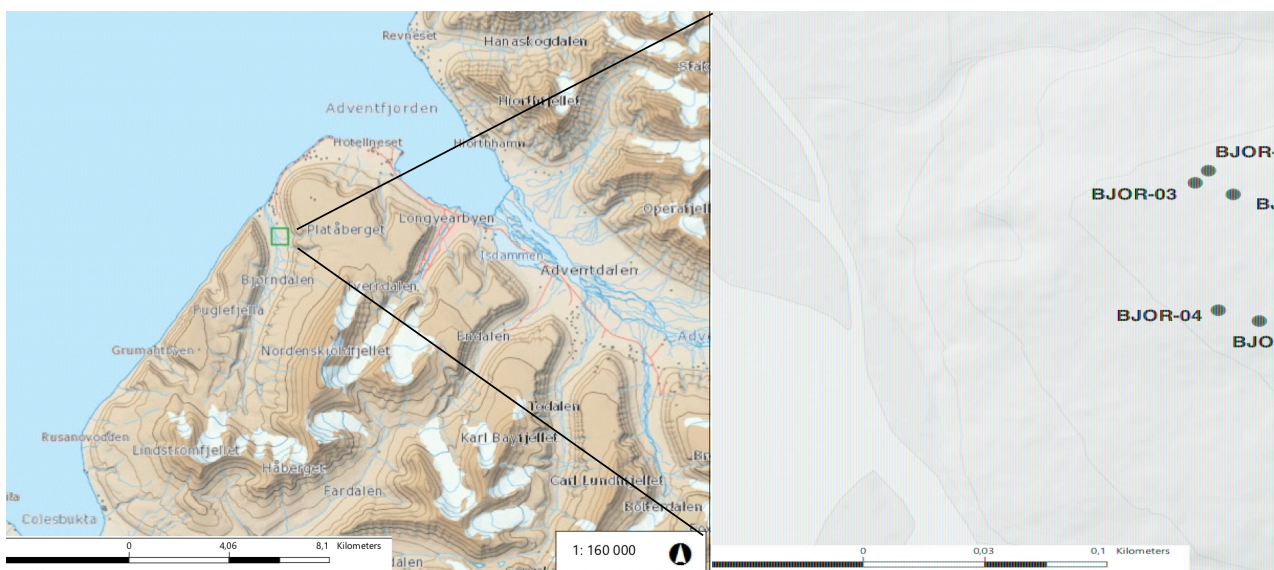

Figure 1. Map showing the location of Bjørndalen and the study sites within the valley. The map was acquired from TopoSvalbard.

Traditionally, Bjørndalen has been classified to belong to the middle Arctic tundra sub-zone (bioclimatic sub-zone C), which is the mildest sub-zone found within the archipelago. Middle Arctic tundra sub-zone characterises areas, where the mean July temperatures are between 4-6°C and growing season lasts for 2.5 to 3 months (Elvebakk, 1997). Vegetation within the middle Arctic tundra zone is dominated by dwarf-shrubs such as *Dryas octopetala* and *Cassiope tetragona* or herbs like *Bistorta vivipara* (Elvebakk, 2005). After 2000, the study area has climatically been closer to climatic sub-zone D (Southern Arctic tundra zone) than sub-zone C (Jepsen et al., 2019). The west coast is in generally warmer and less dry than the eastern side of Svalbard due to the influence of warm West Spitsbergen current. During summer (June, July and August) 2020, average temperature near Longyearbyen was 7.2°C, total precipitation over the three summer months was

~51mm (the Norwegian Meteorological Institute). July 25th was also the hottest day recorded in Svalbard, with the air temperature reaching around 22°C at Svalbard airport.

Camera setup

This thesis is part of BIG (Bjørndalen Integrated Gradients) project, which has been running since summer 2019 (BIG, 2019). Therefore, the methods for data collection follow already established guidelines to ensure data compatibility for longterm studies.

Ten waterproof TimelapseCam Pro cameras were placed in aluminium boxes to protect them from the elements (mainly rain). A camera was mounted on a metal frame over each plot, ca 60cm above the ground pointing downwards towards a *Silene acaulis* cushion (Fig. 2a). The imaged plots include mostly *S. acaulis* cushions with as little of surrounding vegetation as possible (Fig 3). Memory cards and batteries were exchanged every week. Due to the solar angle the cameras and frame only briefly shaded the cushions and never during the measurement periods. More detailed description of the methods can be found in Ween (2022).
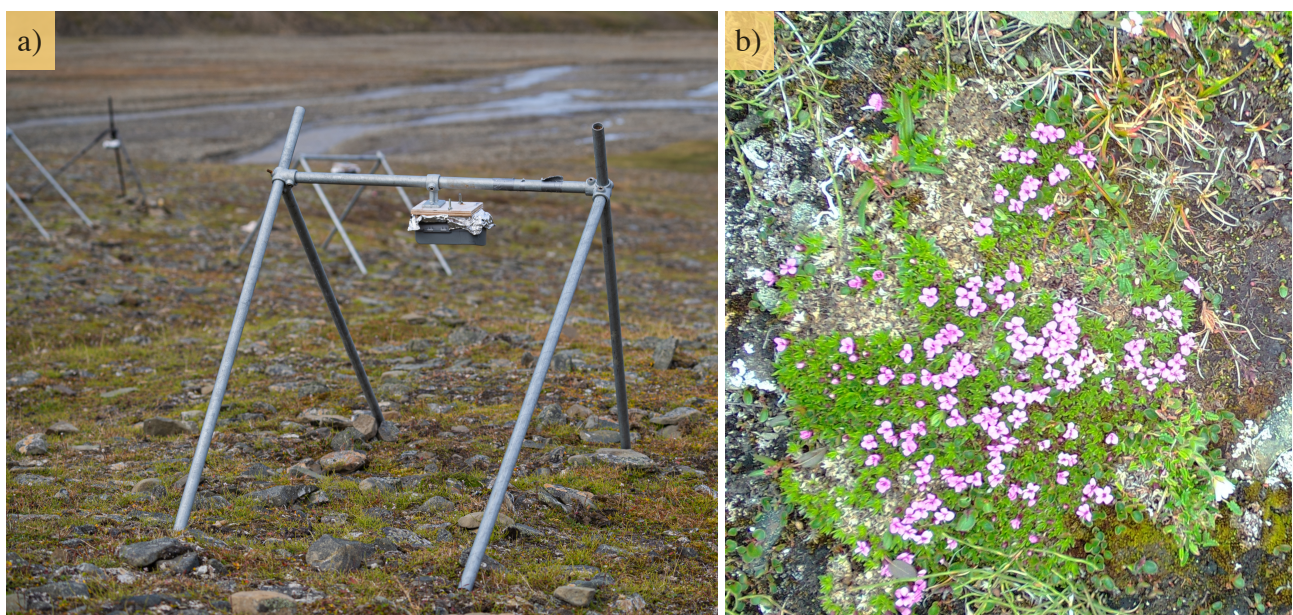

Figure 2. a) An example of the camera setup (photo by Simen S. Hjelle) b) An example of gathered images of *Silene acaulis* cushions.

Image Annotations

Time-lapse cameras took photos of each *S. acaulis* cushion each minute throughout the whole growing season of 2020 - from snowmelt and emergence of first vegetation to the first snowfalls. A subset of images was annotated - the subset consisted of images taken around the peak flowering period in order to maximise the potential of spotting possible visitors. In this case, the photos were

taken between 26th June (DOY 178) and 26th July (DOY 208) depending on the flower conditions of each observed cushion (Table 1). Images from six out of ten cameras were annotated due to the large amount of images and time-consuming nature of manual annotation process. In order to ensure an even coverage of data throughout the whole 24h period, images taken during the first 10 minutes of each hour were annotated (11 images per hour). 30 933 images were annotated in total (Table 1).

Table 1. Overview of the annotations from six cameras set up over *Silene acaulis* cushions in Bjørndalen study sites. Images were taken in the summer 2020. Images taken the first 10 minutes of each hour of the day during the peak flowering season were annotated.

Camera ID	DOY (start)	DOY (end)	No of days	Photos annotated
BJOR-01	188	208	21	5540
BJOR-03	184	199	16	4220
BJOR-04	186	199	14	3669
BJOR-05	182	209	28	7375
BJOR-09	178	203	26	6858
BJOR-11	191	203	13	3271
			Total	30933

Images were annotated manually using VGG (Visual Geometry Group) Image Annotator Tool 2.0.12. Two different monitors - BenQ SW2700PT (2560x1440 resolution, 27-inch monitor) and HP LP2475w (1920x1080 resolution, 24-inch monitor) were used for the annotation process. Even though the resolutions and size of the monitors were different, the resolution of the annotated images was the greatest limitation to visitor identification and annotations made on different monitors were comparable and should not have a significant influence on the observation rates.
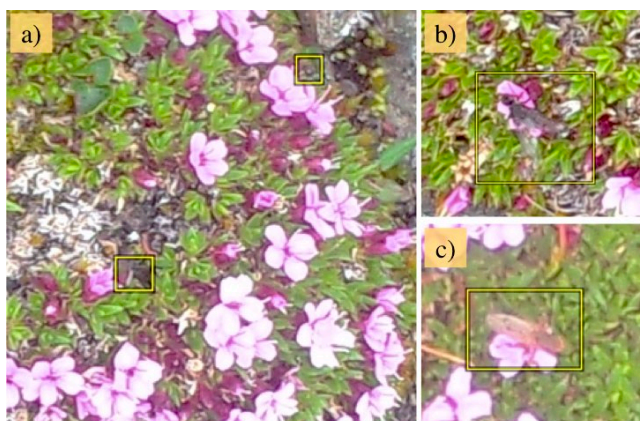

Figure 3. a) An example of the annotation process b) Annotated Diptera (>9mm) c) Annotated Diptera (>9mm)

Three characteristics were marked on each image - taxonomy of the insect, location of the insect and the weather conditions (cloudy, sunny or rainy) (Fig. 3). The individuals were assigned to one of the seven broader taxonomic groups (Acari, Diptera etc. (Table 2), for further details see Appendix 1)) as classification on a smaller taxonomic level was not possible due to image quality and limited visibility of the characteristics of the individuals.

Table 2. Overview of the characteristics used in the annotation process for assigning an observation into the taxonomic groups with more than n=15 observations.

Taxonomic group	Identification characteristics
Acari	Round body, generally orange, almost star-shaped, legs visible
Diptera (further divided into size-classes)	Two transparent wings, solid body
Diptera >9mm	Length of the insect the same as the diameter flower or longer, often Muscid flies or similar
Diptera 5-9mm	Length of the insect between half the flower diameter to almost the whole flower diameter, often seem to be smaller flies
Diptera <5mm	Length of the insect shorter than half of the diameter of the flowers, often smaller Chironomids
Lepidoptera	Caterpillar or non-clear wings
Unidentified inv.	Insect-like features or movement based on previous/later images, generally too small to identify

In order to ensure data compatibility with other studies linked to this project, Diptera was further divided into size-classes, based on an assumption that an average open *Silene acaulis* flower is 10mm wide (as in Klausen (2022)).

Weather data

An on-site weather station was not functioning in summer 2020, therefore weather data from the study site was not available. Instead, data from the closest weather station, Svalbard Airport (~4.7km away, Fig. 4), was used to acquire hourly data on mean air temperatures (2m above ground), mean wind speed, cloud cover and precipitation (Norwegian Centre for Climate Services, 2024). Additional data on soil temperatures (5cm below ground) was acquired from a nearby study site in Bjørndalen (~1km away, Fig. 4). Soil temperatures from two probes used for the measurements were averaged to be further used in the analysis.
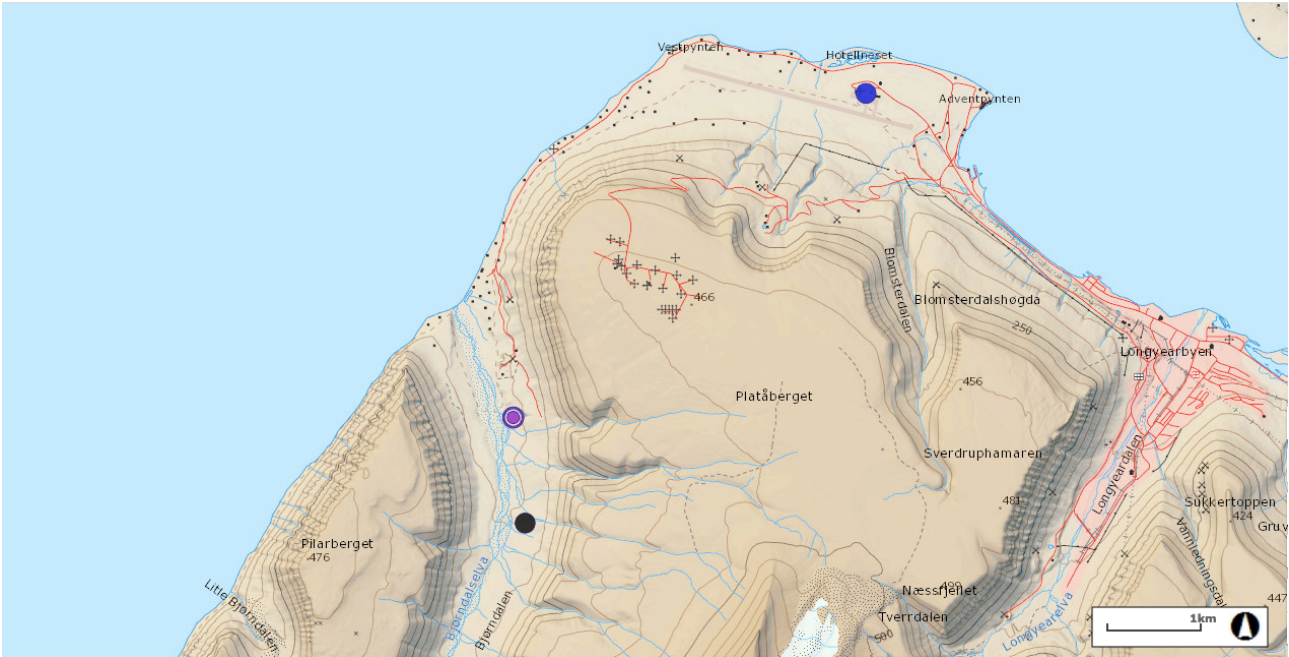
Figure 4. Map showing the location of Bjørndalen study site, where time-lapse cameras monitored *Silene acaulis* cushions (purple), location of the soil temperature measurement site (black) and Svalbard airport weather station (blue), from where hourly average air temperatures, wind speeds, cloud cover and precipitation data was collected from. The map was acquired from TopoSvalbard.

Statistical analysis

In total, close to 31 000 images were annotated. Statistical analysis focused on the most numerous groups (Acari, Diptera and unidentified individuals). Lepidoptera was excluded from the analysis since repeated counts of presumably the same individuals were the major contributors to the dataset. Caterpillars that entered the view of the camera would remain there up to a few days. As they moved around relatively little, distinguishing between periods of activity and inactivity was mostly not possible, resulting in exclusion from the analysis. Some larger Diptera individuals were observed on darker surfaces outside the cushions, presumably basking. The proportion of such individuals within the dataset was low, they moved around more frequently than Lepidoptera individuals and as large Diptera are relatively common in the habitat, it was not possible to determine if the same individuals were spotted repeatedly. Due to these constraints, they were included from the analysis, unlike Lepidoptera individuals.

Statistical analyses were conducted using R (version 4.2.3) (R Core Team, 2023). In order to investigate the relation between abundance of *Silene* visitors and time of the day and different weather variables, generalised additive models (GAM) were fitted to the data using the mgcv R package (Wood, 2017). Due to the circular nature of time of the day (0 is the same as 24h), package "circular" was used to manipulate the hours.

First, GAMs were fitted to each arthropod group (Diptera <5mm, Diptera 5-9mm, Diptera >9mmm, Acari and unidentified individuals). The models included hour, air temperature, soil temperature, wind speed, cloud cover and precipitation with DOY and camera ID as predictor variables to describe the main patterns in arthropod abundance in relation to different weather variables. To account for between and within-day variation in the weather variables, daily averages and within-day differences from the daily averages were incorporated in models predicting counts. Due to complex and non-linear relationships between arthropod abundance and hour or the weather variables, predictor variables were fitted using a spline-based smoother. In addition, when the hour was used as a predictor, I used circular cubic splines to have continuous predictions (i.e. same value for 0h and 24h). Due to over-dispersion of the count data, all models were run using a negative binomial distribution (Warton, 2022).

After fitting the initial models, a new model was fitted separately for each of the groups using only the variables that had showed significance in the initial models. Significance and the relation between abundance and predictor variables was assessed based test statistics, p-values and 95% confidence intervals provided in the gam() function of the mgcv library.
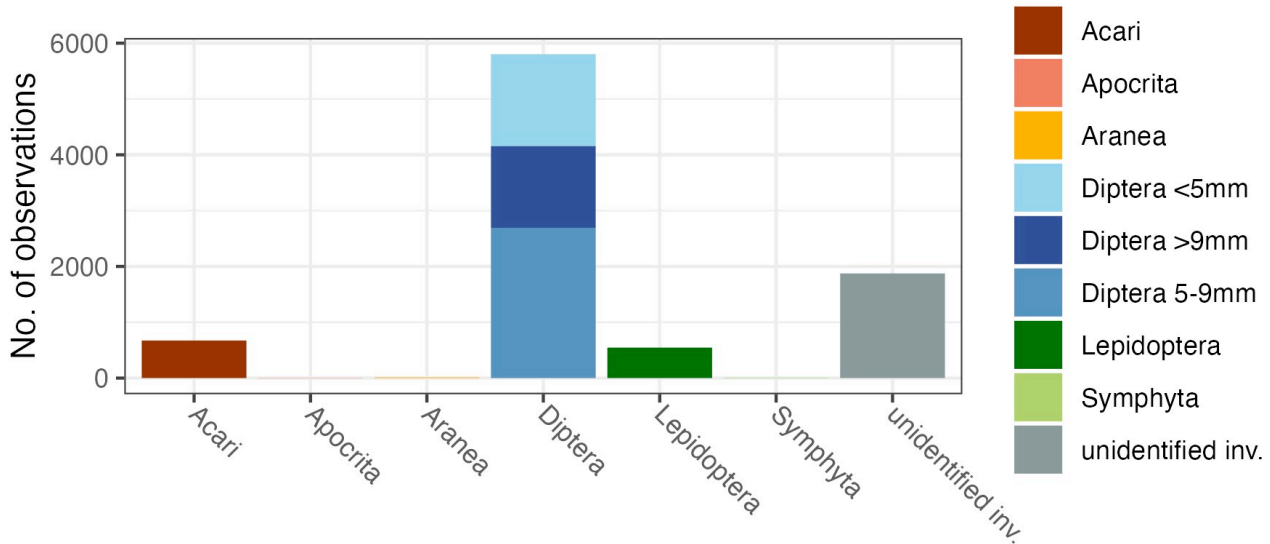
Results

Community composition

Figure 5. a) Total numbers of individuals counted by taxa based on time-lapse images taken in Bjørndalen in summer 2020.

Around 9000 individuals (n=8923) were counted in total, with the most numerous taxa being Diptera (n=5802), followed by unidentified individuals (n=1875) and Acari (n=673) (Fig.5). About half of the observed Diptera individuals were medium-sized individuals (Diptera 5-9mm). The biggest Diptera (Diptera >9mm) and the smallest size-class (Diptera <5mm) were counted fewer times, with respectively 1463 and 1648 observations. Juvenile Lepidoptera were observed 546 times, Apocrita, Aranea and Symphyta were all found only on a few occasions (n<15) (Fig. 5).
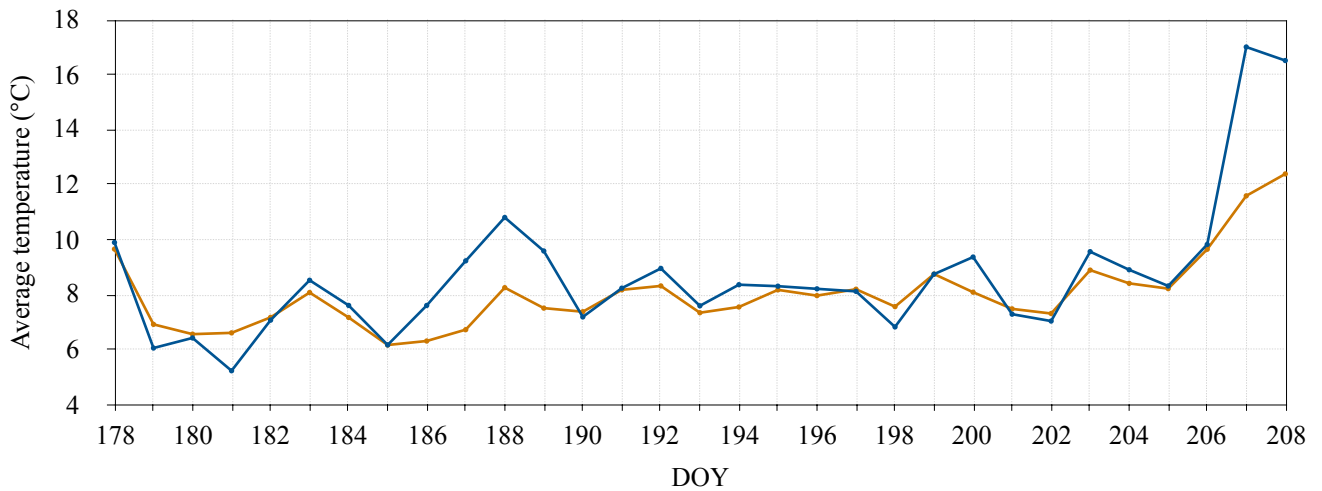
Weather variables

Figure 6. Mean daily air (blue) and soil (orange) temperatures during the study period between 26th June and 26th July, 2020 (DOY 178-208). Air temperatures are taken from Svalbard airport weather station (data acquired from Norwegian Centre for Climate Services (2024), soil temperatures from Bjørndalen, about 1km south of the study site.

Daily mean air and soil temperatures show a similar trend of a slight drop in temperatures in the beginning of the study period, relatively stable fluctuations in the middle of the observation period and a larger peak in temperatures at the end of the observation period (Fig. 6). Compared to daily air temperatures, change in soil temperatures has often a smaller amplitude. Daily average temperatures fluctuated relatively little between the days and soil temperature followed the same general trends as air temperature, just with a smaller amplitude. Fluctuations in air and soil temperatures within the day were more prominent and did not always fluctuate in the same manner, e.g. soil temperatures would occasionally fluctuate with a larger amplitude than air temperatures (Appendix 2). Interestingly, the study period also included the day with the highest recorded air temperature in Svalbard, when in the afternoon of 25th July (DOY 207) air temperature at Svalbard airport rose to 21.7°C.
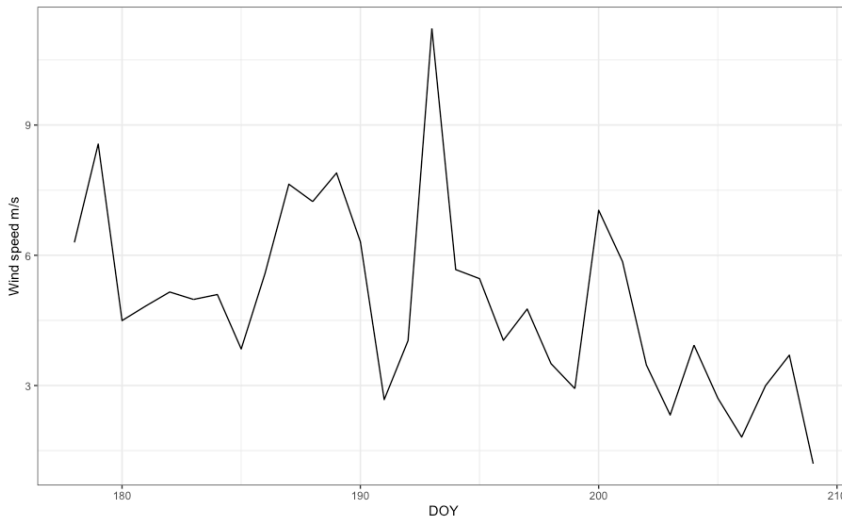
Figure 7.. Average daily wind speed (m/s) during the study period in Svalbard airport weather station. Data acquired from Norwegian Centre for Climate Services (2024).

Average wind speeds varied considerably between (and within) the days. Highest average daily wind speeds occurred in the middle of the study period and the lowest wind-speeds occurring towards the end (Fig 7.).
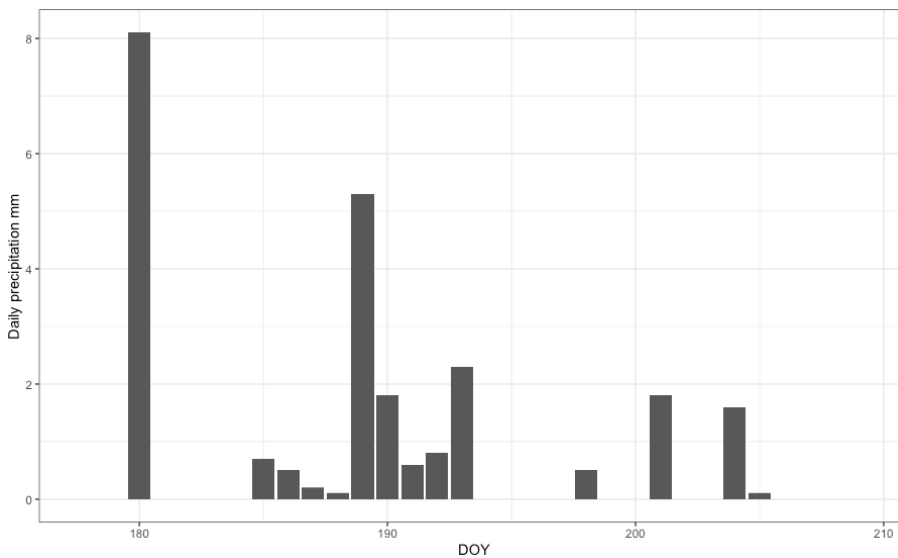
Figure 8. Sum of daily precipitation (mm) from Svalbard airport weather station. Data acquired from Norwegian Centre for Climate Services (2024).

Precipitation was low throughout the whole study period with a few days with higher levels of precipitation. Around the middle of the study period, a week with consecutively rainy days occurred, while the rest of the time, rainy days would be preceded and followed by days with no precipitation (Fig. 8).

16

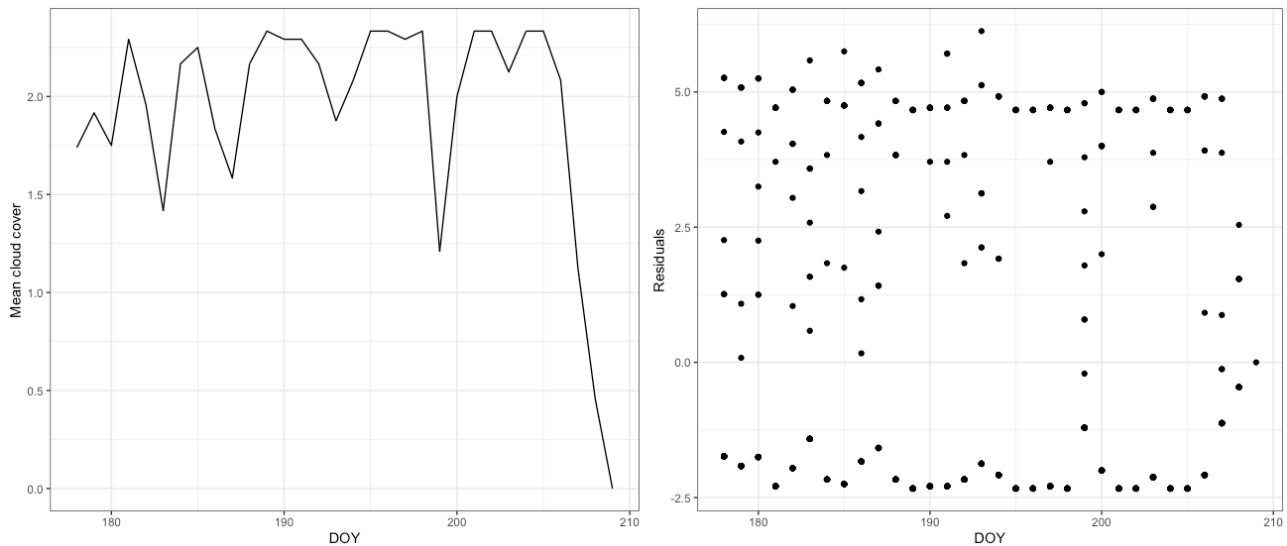Figure 9.Mean daily cloud cover on a scale 0-8 (scale is based on how many eights of the sky is covered with clouds, 0=no clouds, 8=completely overcast). Variation in hourly cloud cover in Svalbard airport weather station. Data acquired from Norwegian Centre for Climate Services (2024).

During most of the days, some level of cloud cover was observed. The only continuously clear days occurred at the end of the study period. Yet, due to the dynamic nature of cloud movement, days had large variation in the hourly cloud cover recordings with some hours being clear and some having overcast conditions (Fig. 9).

Patterns in arthropod abundance in relation to abiotic variables

Arthropods from all of the groups were observed throughout the whole 24h cycle (Fig. 10). Total counts of the medium-sized Diptera (Diptera 5-9mm) and largest Diptera (Diptera >9mm) were lower between midnight and around 5 in the morning than later in the day. Sum of hourly Acari observations was lower around midnight and higher during the night (between 21 and 2 in the morning). Counts of the smallest Diptera and unidentified individuals were relatively evenly spread across the whole 24h cycle (Fig. 11).
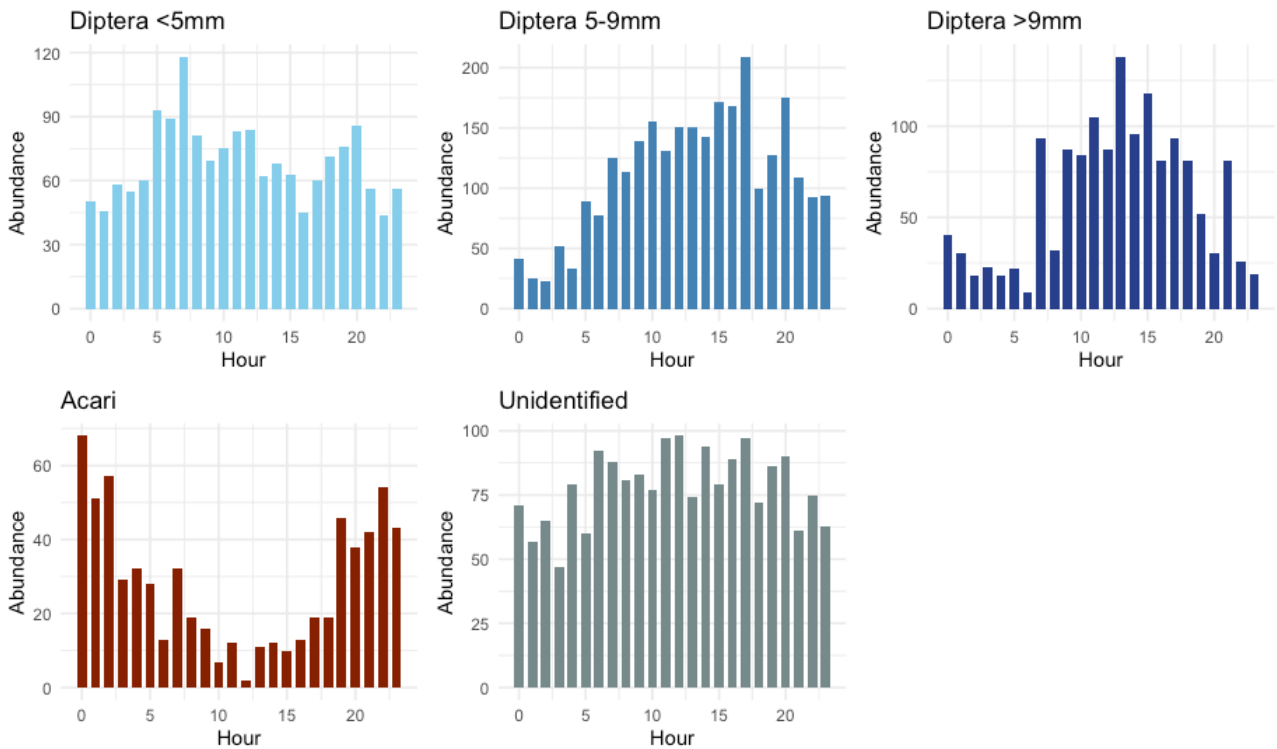
Figure 10. Sum of individuals counted per hour throughout the whole observation period.

Individuals could be spotted at any time during the 24h cycle and most of the time in relatively low numbers (Fig. 11). However, the variation in the numbers of observations was large, especially for medium-sized Diptera.
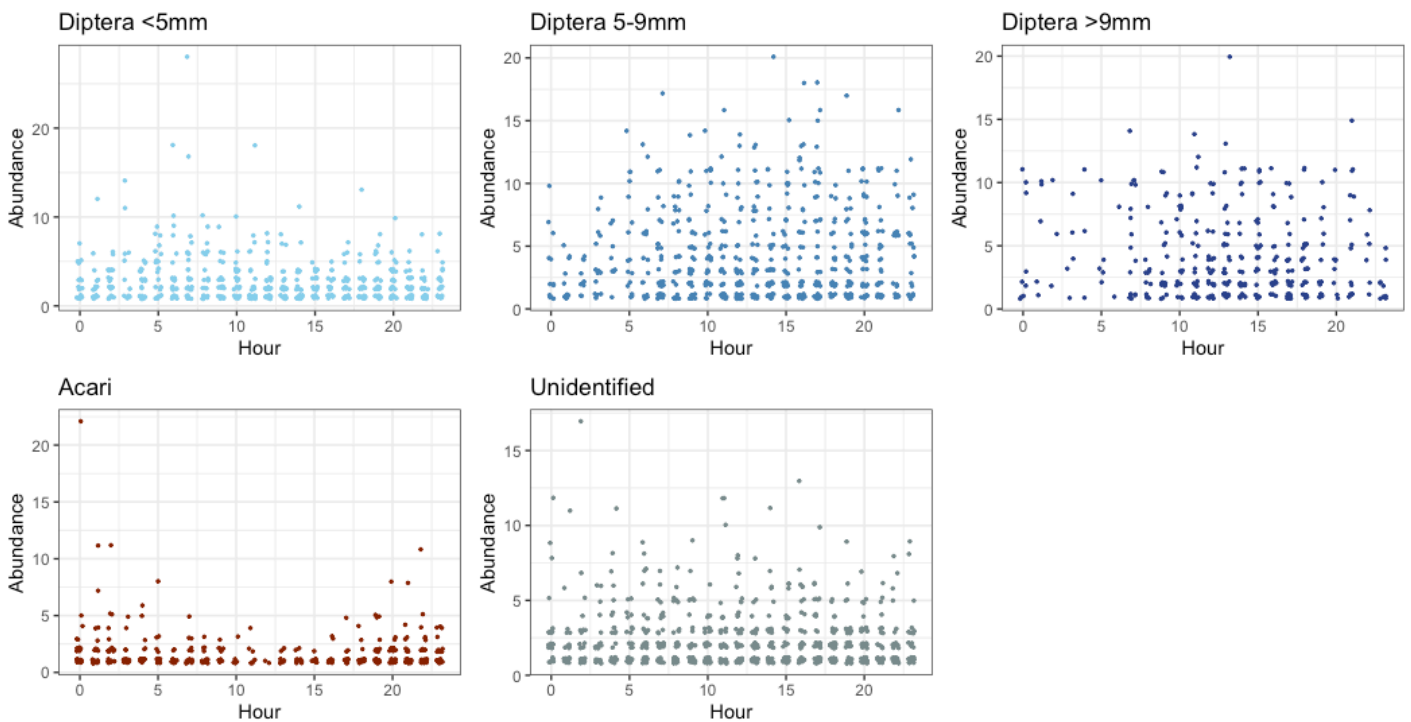
Figure 11. Hourly number of arthropod observations between 26th June and 26th July, 2020. Data points were jittered to showcase multiple observations with the same value.

Hour

Figure 12. Relationships between the abundances of the most common groups of arthropods and spline based smoothed variable for hour (time of the day). Hourly abundances from different cameras were kept as separate data points.

The data on hourly abundances had exceptionally high variance, especially for 5-9mm and >9mm Diptera size-classes, and no pronounced activity pattern could be observed in those size classes (Fig. 12). Removal of Camera ID minimised the variance in the data and revealed some indications of diurnal activity patterns in medium and large Diptera size classes (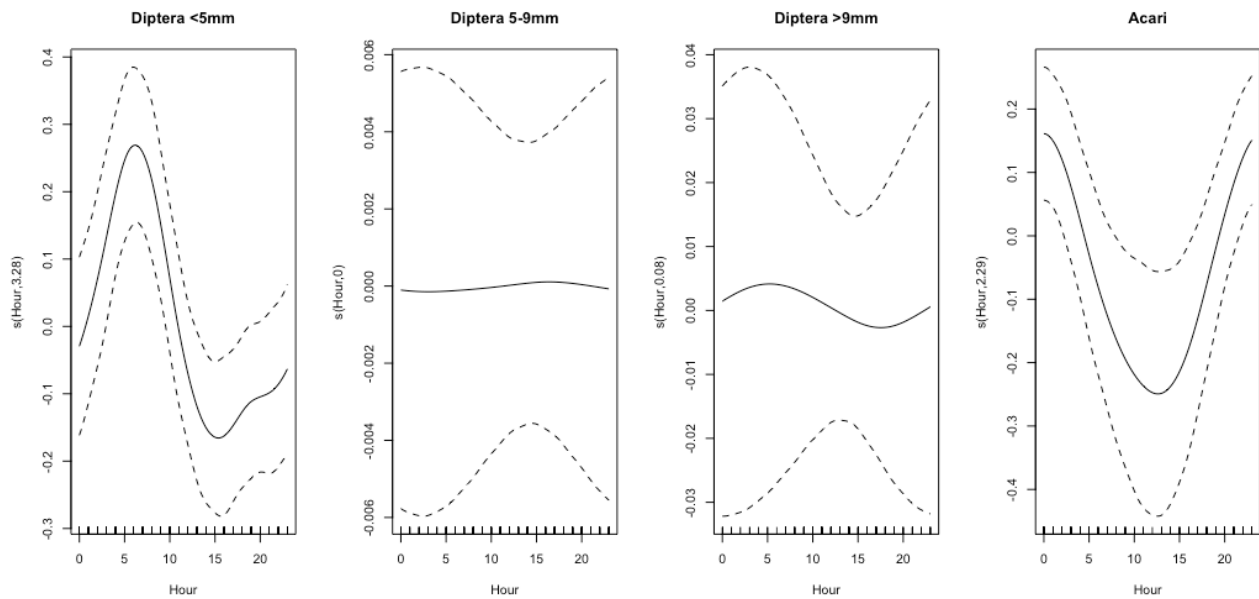Fig. 13). Smallest size Diptera (Diptera <5mm) was observed more often in the morning, with peak observation time between 6 and 7 in the morning after which the observations dropped. Lowest amount of observations occurred around midnight (Fig. 13). The other Diptera size-classes were more numerous later in the day. Medium-sized Diptera showed two peaks in their abundances, first between 8 and 9 in the morning and a second one in the afternoon, at around 5 in the evening. The largest Diptera showed some indication of a peak in abundance around mid-day, but the variance in their numbers was very high and the pattern was weak. Acari showed evidence of nocturnal activity with higher rates of observations occurring at "night-time" (around midnight) and lowest numbers of individuals were counted around mid-day (Fig. 12).
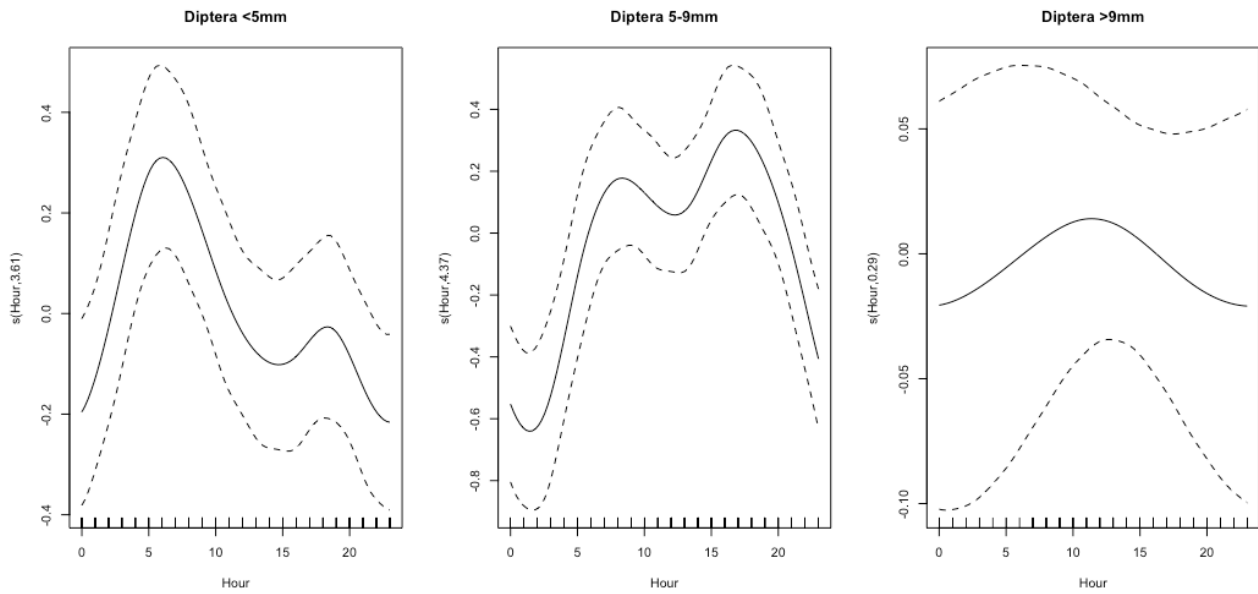
Figure 13. Relationships between the abundances of Diptera size classes and spline based smoothed variable for hour (time of the day). Hourly abundances from different cameras were summed together to provide a singular datapoint for each hour of each day.

Day of the year

Figure 14. Relationships between the abundances of the most common groups of arthropods and spline based smoothed variable for DOY (day of year).

For all of the groups, the number of observations varied between the days. Yet all of the groups had large variation in the abundances, indicated by wide confidence intervals (Fig. 14). The smallest Diptera showed relatively similar daily observation rates until the middle of the observation period, after which the daily observation numbers started to drop slightly.

Medium-sized Diptera seemingly had a peak in count numbers in the middle of the observation period, with lower numbers before and after. The biggest Diptera numbers increased until around

DOY 201, after which they levelled out with a slight possible drop in the numbers. Acari observations increased towards the middle of the observation period with roughly levelling out afterwards.

Air and soil temperature
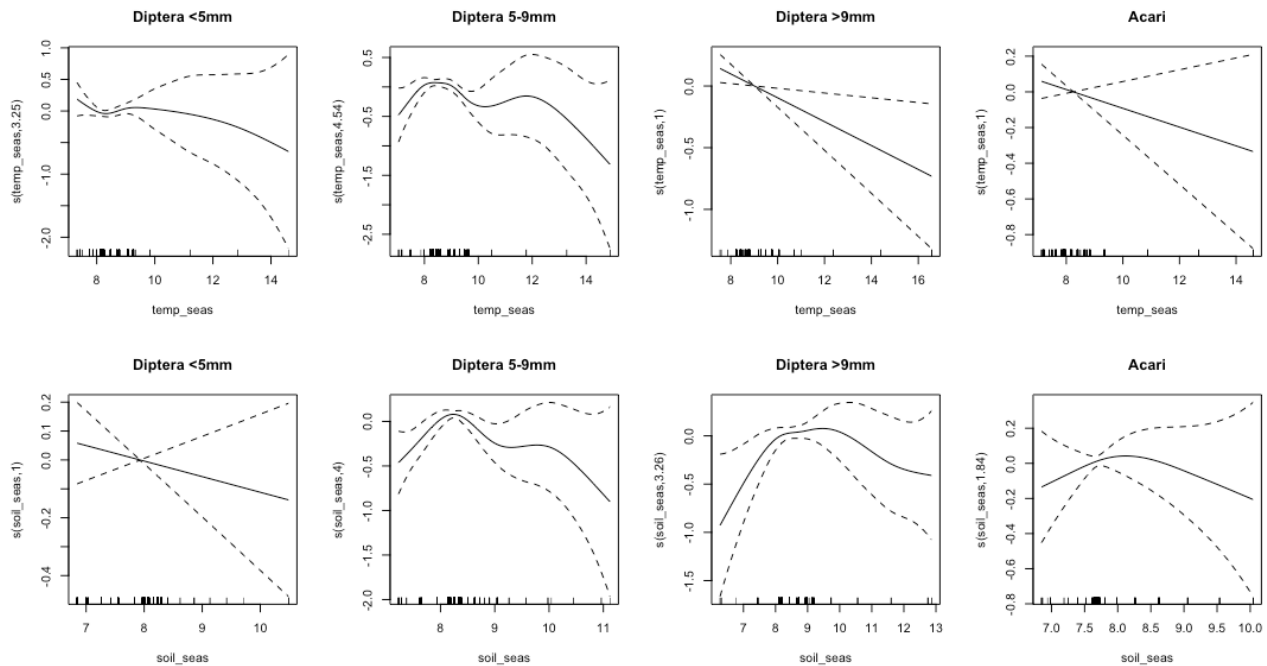
Figure 15. Relationships between the abundances of the most common groups of arthropods and spline based smoothed variable for average daily temperatures (temp_seas) and average daily soil temperatures (soil_seas).

The effect air and soil temperature had on abundances was similar (Fig. 15). The numbers of the biggest Diptera and Acari observations dropped with increasing air temperatures. Abundance of medium-sized Diptera also dropped with increasing temperatures, but more prominently only after daily average air temperatures rose above 12°C. The observation numbers of smallest Diptera remained relatively stable regardless of the air temperature.

The smallest Diptera numbers were negatively effected by increasing soil temperatures (Fig. 15). Abundance of medium-sized Diptera, biggest Diptera and Acari increased at first with increasing soil temperatures, but experienced slight drops in abundances when mean daily soil temperatures exceeded 8.5°C, 10°C and 8.5°C respectively.
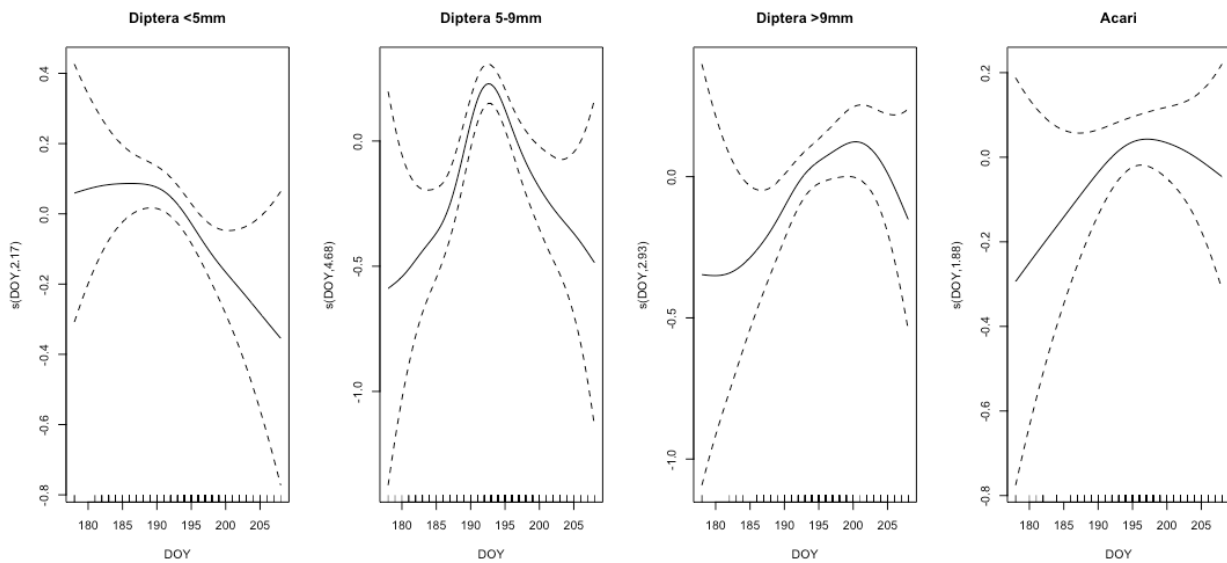
Wind speed
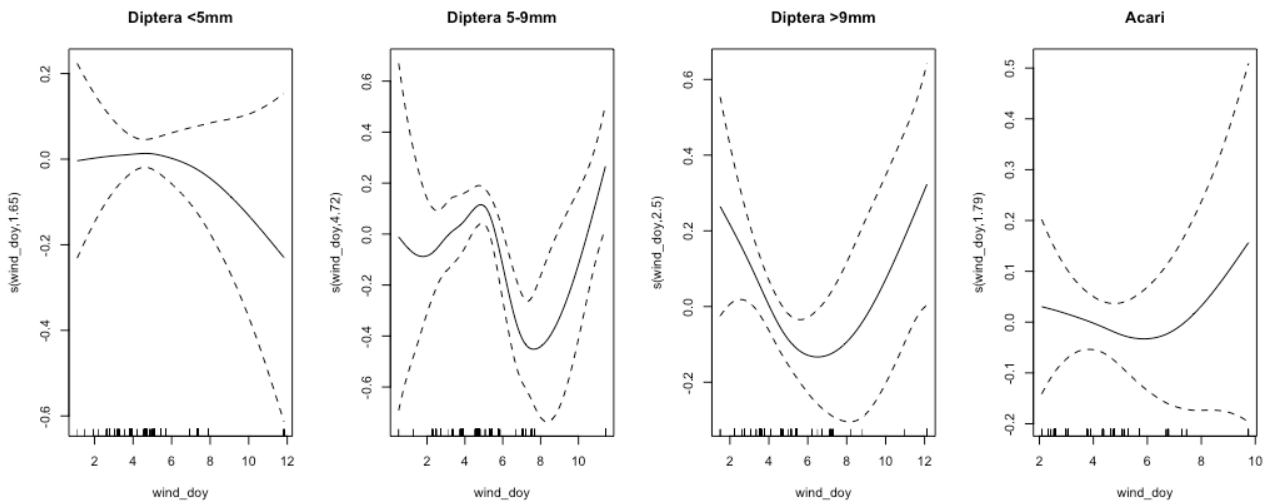
Figure 16. Relationships between the abundances of the most common groups of arthropods and spline based smoothed variable for average daily wind speed (wind_doy).

The smallest Diptera had relatively stable numbers regardless of the wind speed, but similar to effects of previous variables, there was high variation in the data (Fig. 16). The other Diptera size classes (Diptera 5-9mm and Diptera >9mm) showed increased observation rates when daily average wind speeds were close to 8 m/s and 6 m/s, respectively. Interestingly, the numbers of medium-sized Diptera also first increased slightly until around 5 m/s and then dropped before increasing again when average hourly wind speeds were exceeding 8 m/s.

Diptera <5mm

The variable that explained variation in abundance of the smallest Diptera the best was hour (time of the day) (Table 3).   It was also the only variable out of the observed variables that had a significant effect in explaining the data. Yet, this model only explains a small portion of the variation (6.95% of the deviance) in the data.

Table 3. Approximate significance of the smooth terms from the generalised additive model run with the variables that best explain the variation in the smallest size-class of Diptera (<5mm) abundance data. This model was run with hourly abundances as an response variable, Camera ID as a fixed effect and hour as a smooth term, using negative binomial distribution.

Abundance ~s(hour, bs= "cc") + CameraID				
	edf	Ref.df	Chi.sq	p-value
s(Hour)	3.219	8	22.02	2.03e-05
R-sq (adj)		0.037		
Deviance explained		6.95%		

Diptera 5-9mm

For medium-sized Diptera, the variables that had best described the variation in abundance were DOY (day of the year) and daily average wind speeds (wind_doy) (Table 4). However, they explained only a small part of the variation in the data (12.6% of the deviance) with most of the variation remaining unexplained.

Table 4. Approximate significance of the smooth terms from the generalised additive model run with the variables that best explain the variation in the medium size-class of Diptera (5-9mm) abundance data. This model was run with hourly abundances as an response variable, Camera ID as a fixed effect, DOY (day of the year) and daily average wind speed (wind_doy) as a smooth terms, using negative binomial distribution.

Abundance ~ s(DOY) + s(wind_doy) + CameraID				
	edf	Ref.df	Chi.sq	p-value
s(DOY)	3.55	4.446	31.28	7.86e-06
s(wind_doy)	4.132	4.930	12.85	0.0203
R-sq (adj)		0.0876		
Deviance explained		12.6%		

Diptera >9mm

Abundance of the largest Diptera (>9mm) was best described by hourly air temperatures and daily average wind speeds (Table 5). Similar to the other groups, the variance in data was large and the model can only explain a small proportion of this variation (13.6% of deviance explained by air temperature and wind speeds).

Table 5. Approximate significance of the smooth terms from the generalised additive model run with the variables that best explain the variation in the largest size-class of Diptera (>9mm) abundance data. This model was run with hourly abundances as an response variable, Camera ID as a fixed effect, hourly air temperature (air temperature) and daily average wind speed (wind_doy) as a smooth terms, using negative

Abundance ~ s(air temperature) + s(wind_doy) + CameraID

	edf	Ref.df	Chi.sq	p-value
s(air temperature)	1.658	2.037	10.956	0.00431
s(wind_doy)	2.443	2.967	8.342	0.04381
R-sq (adj)		0.0919		
Deviance explained		13.6%		

Acari

The variable with the most explanatory strength to describe the variance in Acari abundance was time of the day (hour) (Table 6). The variance was also explained by within-day variance in wind speed (wind residuals). Similar to the previous groups, variance in Acari abundance data is high and the model only explains a small part of this variance. This model, that included only the variables that had a significant effect in explaining the variance in abundance, only described 8.95% of the deviance.

Table 6. Approximate significance of the smooth terms from the generalised additive model run with the variables that best explain the variation in Acari abundance data. This model was run with hourly abundances as an response variable, Camera ID as a fixed effect, hour and wind residuals (wind_res) as smooth terms, using negative binomial distribution.

Abundance ~ s(Hour, bs = "cc") + s(wind_res) + CameraID

	edf	Ref.df	Chi.sq	p-value
s(Hour)	2.291	8.000	11.505	0.00154
s(wind_res)	1.001	1.001	4.661	0.03092
R-sq (adj)		0.0267		
Deviance explained		8.95%		

Unidentified individuals

The effects different variables have on the abundance of unidentified individuals share similarities with Diptera. Unidentified individuals were most numerous around mid-day and least numerous close to midnight (Fig. 17). Similar to medium-sized Diptera (Fig. 13), they showed two peaks in their abundance, first around DOY 190 and second, around DOY 203. Similar to other groups, numbers of unidentified individuals decreased with rising soil temperatures (Fig.15). Their abundance increased with rising air temperatures until hourly average exceeded 11°C, after which there are some indications of slight decrease in observation numbers (Fig. 17). Average hourly wind speed that was lower than 4 m/s or exceeding 6 m/s had a negative effect on the observed numbers of unidentified individuals. However, their numbers were higher when wind speeds were between 4 and 7 m/s.
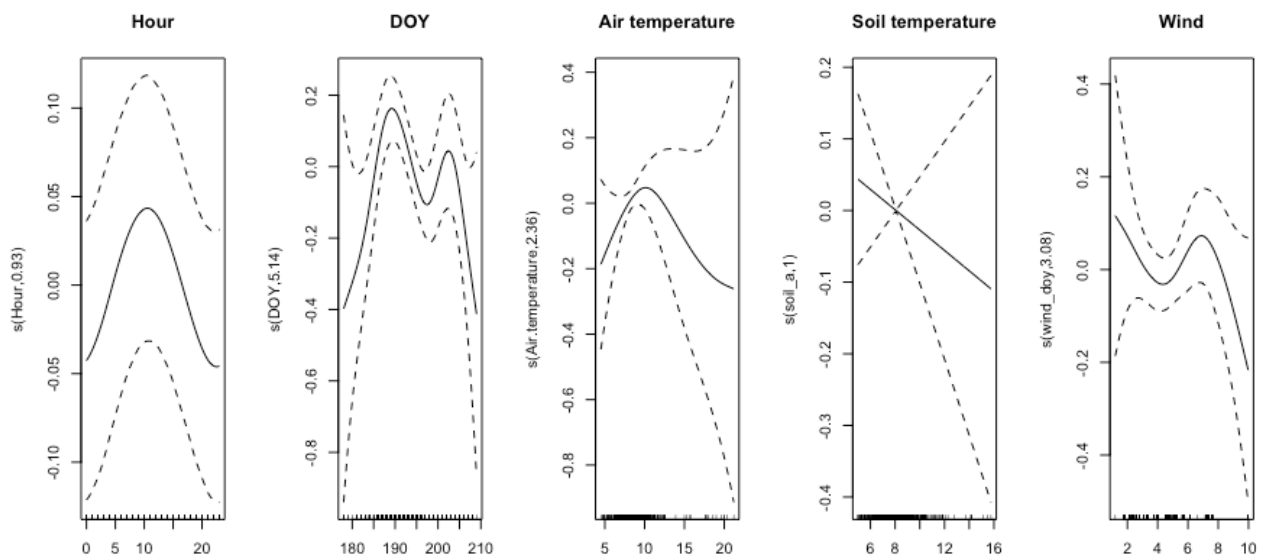
Figure 17. Relationship between abundance of unidentified individuals and spline based smoothed variables for hour, DOY (day of year), average hourly air and soil temperatures and average hourly wind speed.

Variance in the abundance of unidentified individuals was best described by DOY and by a smaller degree by hourly average wind speed (Table 7). However, the variance in abundance is high and these variables only explain a small part of this variance (explain 13.2 % of the deviance).

Table 7. Approximate significance of the smooth terms from the generalised additive model run with the variables that best explain the variation in the unidentified individuals abundance data. This model was run with hourly abundances as an response variable, Camera ID as a fixed effect, DOY (day of the year) and hourly mean wind speeds as smooth terms, using negative binomial distribution.

Abundance ~ s(DOY) + s(wind_doy) + CameraID

	edf	Ref.df	Chi.sq	p-value
s(DOY)	5.838	6.964	30.681	5.86e-05
s(Mean.wind.speed)	1.694	2.140	7.678	0.0242
R-sq (adj)		0.0793		
Deviance explained		13.2%		

Discussion

Previous studies in the Arctic have shown that arthropod activity varies within the season and different species emerge at different times (Høye & Forchammer, 2008a). Yet, very little research has been conducted on daily or even hourly scale and research on daily activity patterns in constant daylight has taken place only at lower latitudes (Stelzer & Chittka, 2010; Zoller et al., 2020). Due to their small size, activity patterns of Arctic arthropods have been difficult to monitor, but time-lapse imagery makes monitoring of these smaller organisms more feasible.

The main aim of this study was to investigate whether arthropods in Svalbard show evidence of diurnal activity patterns and the hypothesis of these patterns not being evident was rejected. Contrary, evidence of diel activity patterns was found - all Diptera size classes showed varying levels of diurnality and Acari activity was nocturnal (Fig. 13). Yet the evidence was weak and was statistically significant only for the smallest Diptera size-class and Acari (Fig. 12; Table 3-7). It is difficult to determine whether or not this pattern is typical for high latitude arthropods as very little research has been conducted on Arctic arthropods in general and no extensive studies have focussed on this topic.

The only study from Svalbard found no evidence of diurnality (Djurberg, 2021). However, studies from lower latitudes, above the Arctic circle, have shown robust diurnal activity patterns in pollinators, where flower-visitor abundance peaked in the middle of the day, even though individuals could be spotted throughout the whole observation period (Stelzer & Chittka, 2010; Zoller et al., 2020). Studies on reindeer have shown that populations living in Svalbard experienced a higher degree of arrhythmicity in their behaviour than populations living at lower latitudes, even though populations in both locations experienced polar day (van Oort et al., 2007). When findings from this study are compared to Zoller et al. (2020), a similar trend between populations is evident. Most studied organisms in Svalbard show evidence of loss of circadian rhythms for smaller or larger degree during the polar day (or night), e.g. polar bears, arctic char, ptarmigans, reindeer (Hawley et al., 2017; Arnold et al., 2018; Appenroth et al., 2020; Ware et al., 2020). Yet, most of them stick to diurnal activity patterns for the majority of the year and polar day or night. Therefore arrhythmic behaviour patterns in arthropods are not unexpected in context of the other Svalbard residents, but neither is the weak evidence of diurnality.

Interestingly, contrary to the expectations, Acari showed statistically significant nocturnal pattern in abundance (Fig. 12; Table 6). This pattern is difficult to explain, but it could be a residual adaptation from lower latitudes. It is believed that acarofauna of Svalbard is relatively young and most likely consists of species that re-colonised the archipelago from lower latitudes (e.g. Beringia and mid-Siberia) within the last 10 000 - 15 000 years, after the last glacial maximum (Ávila−Jiménez & Coulson, 2011; Ingólfsson & Landvik, 2013; Coulson et al., 2014).

The second aim of this study was to investigate the links between arthropod abundance and abiotic variables. It has been established that insect activity is linked to local weather with temperature being the most important predictor for flying insects (Herrera, 1990; Totland, 1994; Hodkinson et al., 1996; Danks, 2004; Høye & Forchhammer, 2008b; Zoller et al., 2020). Considering that arthropods are ectotherms and that their activity levels depend on external factors, their activity would be expected to be positively affected by warmer temperatures.

Yet, temperature significantly explained abundance of only the largest Diptera with no significance being shown for the other size-classes. Also, surprisingly, abundance of the largest Diptera (and the other groups, even though the relation was not significant) was negative associated with temperature (Fig. 15; Table 5). The negative association between temperature and abundance could be linked to unusually high temperatures experienced towards the end of the observation period (Fig. 6). On 25th July, between 17 and 18 in the afternoon, temperature of 21.7°C was measured at the Svalbard Airport weather station, which is the warmest temperature ever recorded in Svalbard (NCCS, 2024). In comparison, the average air temperature between June and August of that year, was 7.2°C (NCCS, 2024). In Finnish Lapland, Zoller et al. (2020) observed a dip in pollinator visitation rates in the middle of the warmer-than-average days and suggest that the trend might be linked to thermal optimal of the specific species. As data on thermal optimals for different Arctic species is currently lacking, this hypothesis is difficult to assess. Previous studies on chironomids (the most likely group of the smallest Diptera) indicate that they avoid high temperature and wind speed conditions due to desiccation risk (Hodkinson et al., 1996). Generally, when the air temperatures are around +10°C, which is usual in the Arctic summer, chironomid activity increases with higher temperatures. In temperate regions, where temperatures are higher, the need for maintaining water balance becomes more important and activity can decrease in favour of water conservation (Willmer, 1982; Willmer, 1983). Similar trade-offs might also occur in the Arctic, when arthropods experience unusually high temperatures.

Furthermore, Arctic habitats are extremely heterogeneous and local environmental conditions vary on a small scale. Air temperature measured two meters above the ground, does not necessarily show what temperatures organisms in the environment are exposed to. Many Arctic plants grow in cushion growth form, which allows arctic and alpine plants to create their own microclimate. In ambient temperature of +4°C , temperatures within cushions can rise up to +27°C . Therefore, temperatures inside *Silene acaulis* cushions, or in other microhabitats, can be considerably differ from the ambient temperatures (Körner, 2003; Convey et al., 2015).

This study did reveal some patterns in daily activity of arthropods, but only a very small proportion of the variance in abundance was explained by the abiotic variables (Table 3-7). This is linked to very high variability in abundances within and between the days and cameras. Some of the variance could be minimised through avoiding distinguishing between cameras and adding annotations from all cameras together, e.g. daily activity patterns were then more apparent (Fig. 13). Yet, this manipulation would result in a loss of precision as different days were covered to a different degree and overrepresented compared to others (Table 1). Arctic habitats are highly heterogeneous and observed cushions vary in the amount of flowers they produce and in the timing of phenological events. Removing the variance of the cameras would not entail the complexity of the observed situation and would leave perhaps an overly simplified view of the system. It is also possible that some other variables could be more influential in explaining the daily variance in the abundance data, e.g. flower area. Since the used weather data originated from Svalbard airport, roughly 5km away from the study site in a more exposed area, it is also possible that conditions in Bjørndalen differed from the conditions measured at the weather station. Furthermore, comparison with other years would help to determine if high variance in the daily patterns is usual. High inter-annual variance in insect abundance on a seasonal scale is commonly described in the Arctic (e.g. Aronsson et al., 2021) and Zoller et al. (2020) showed that daily activity patterns varied between years. Comparison of the results from this study to data from a different year could help to determine if observed activity patterns were representative of the overall activity patterns, yet due to the lack of comparative studies, this is currently not possible.

However, considering that the statistical models were adapted to cope with the high variance in the dataset (e.g. usage of negative binomial distribution) and the Arctic is an inherently stochastic environment with high inter-annual variance in different variables, it is plausible that the observed variance is simply a characteristic of the system that helps species to adapt to this environment.

The Arctic is experiencing fast and dramatic climatic change, which is expected to have implications on organisms that are highly specialised to this specific environment. As organisms react to fast environmental change at different rates and Arctic growing season is already short and condensed, the system is vulnerable towards trophic mismatches (Høye et al., 2007; Høye et al., 2013; Iler et al., 2013; Gillespie et al., 2016; Schmidt et al., 2016). Indications of decreased overlap between flowering plants and pollinators have already been observed (Høye et al., 2013; Schmidt et al., 2016; Tiusanen et al., 2016). Seasonal effects on timings of phenological events of different organisms have been looked into, but the issue has rarely been investigated on smaller than seasonal scale.

Whether diel activity patterns could play an additive role in leading to development of mismatches between trophic levels is a difficult question to answer due to to lack of research on activity rhythms of different trophic levels, their interactions and the plasticity of these rhythms. Yet, since climate change is so prominent and fast in the Arctic, it is a topic worth looking into. Flying insects play an important role in the ecosystem as pollinators for flowering plants and as prey for bird species, yet pollinator numbers are declining across the Arctic. In Zackenberg, eastern Greenland, muscid fly abundance has decreased roughly by 80% during the last two decades (Loboda et al., 2017).

Most of the studies on mismatches focus on seasonal asynchrony between the emergence of flowers and their respective visitors. *Silene acaulis* flowers are open throughout the whole 24h cycle, but the flower rewards are not available to the same degree throughout the daily cycle. Nectar production, its sugar content and pollen amounts in flowers can vary over the course of the day (Herrera, 1990; Witt et al., 1999). The pollen export and consequently, seed production, of flowering plants is higher when their own diel patterns and the peak activity of their most efficient pollinators are synchronised (Stebbins, 1970; Herrera, 1990).

In addition to pollination, flying insects are prey for various bird species. For example, adult chironomids are an important food item for chicks of snow buntings and waders (e.g. dunlin, red phalarope or turnstone) (Hodkinson et al., 1996). Many migratory birds, e.g. snow buntings, retain their circadian rhythms when flying further north (Krüll, 1976; Ashley et al., 2012). Therefore, availability of insects for food is dependent both on their overall abundance in the environment but also on the synchronisation between the activity patterns of the birds and insects.

All in all, potential mismatches are more likely to occur due to seasonal changes rather than small-scale changes in daily activity patterns. Yet, the synchronisation period between trophic levels is already short and shortening further due to climate change. Furthermore, climate change is expected to increase the likelihood of extreme weather events (Walsh et al., 2011). It could be hypothesised that if extreme weather events, such as unusually high temperatures, do alter activity patterns of arthropods, daily mismatches between pollinators and flowering plants or flying arthropods and nesting birds could occur. This could minimise the already short season of overlap even further.

Conclusions

This is the first study of this kind looking into daily activity patterns in arthropods at such high latitudes and some indications of rhythmic behaviour was discovered. However, the data had a large degree of variance and the models fitted using abiotic variables could only explain a small proportion of this variance. It is plausible that the daily activity patterns of High Arctic arthropods in polar day is highly variable, which could be an adaptation to cope with the highly variable and stochastic environment. Yet, further research is needed to determine if this is indeed the case.

References

Abarca, M., & Spahn, R. (2021). Direct and indirect effects of altered temperature regimes and phenological mismatches on insect populations. *Current Opinion in Insect Science, 47*, 67–74. doi:10.1016/j.cois.2021.04.008

Appenroth, D., Melum, V. J., West, A. C., Dardente, H., Hazlerigg, D. G., & Wagner, G. C. (2020). Photoperiodic induction without light-mediated circadian entrainment in a high arctic resident bird. *Journal of Experimental Biology, 223*(16). doi:10.1242/jeb.220699

Appenroth, D., Nord, A., Hazlerigg, D. G., & Wagner, G. C. (2021a). Body temperature and activity rhythms under different photoperiods in high Arctic Svalbard Ptarmigan (Lagopus Muta Hyperborea). *Frontiers in Physiology, 12*. doi:10.3389/fphys.2021.633866

Appenroth, D., Wagner, G. C., Hazlerigg, D. G., & West, A. C. (2021b). Evidence for circadian-based photoperiodic timekeeping in Svalbard Ptarmigan, the northernmost resident bird. *Current Biology, 31*(12). doi:10.1016/j.cub.2021.04.009

Arctic Monitoring and Assessment Programme (AMAP) (2017). *Snow, Water, Ice and Permafrost in the Arctic (SWIPA).* Arctic Monitoring and Assessment Programme (AMAP), Oslo, Norway

Arnold, W., Ruf, T., Loe, L. E., Irvine, R. J., Ropstad, E., Veiberg, V., & Albon, S. D. (2018). Circadian rhythmicity persists through the Polar Night and midnight sun in Svalbard Reindeer. *Scientific Reports, 8*(1). doi:10.1038/s41598-018-32778-4

Aronsson, M., Heiðmarsson, S., Jóhannesdóttir, H., Barry, T., Braa, J., Burns, C.T., Coulson, S.J., Cuyler, C., Falk, K., Helgason, H., Lárusson, K.F., Lawler, J.P., Kulmala, P., MacNearney, D., Oberndorfer, E., Ravolainen, V., Schmidt, N.M., Soloviev, M., Coon, C., & Christensen, T. (2021). State of the Arctic Terrestrial Biodiversity. Report. *Conservation of Arctic Flora and Fauna International Secretariat,* ISBN 978-9935-431-94-3, Akureyri, Iceland

Aschoff, J. (1960). Exogenous and endogenous components in circadian rhythms. *Cold Spring Harbor Symposia on Quantitative Biology, 25*, 11–28. doi:10.1101/sqb.1960.025.01.004

Aschoff, J. (1986). Anticipation of a daily meal: A process of "learning" due to entrainment. *Italian Journal of Zoology, 20*(2), 195–219. doi:10.1080/00269786.1986.10736499

Ashley, N. T., Schwabl, I., Goymann, W., & Buck, C. L. (2012). Keeping time under The midnight sun: Behavioral and plasma melatonin profiles of Free−living Lapland Longspurs (Calcarius lapponicus) during the Arctic Summer. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology, 319*(1), 10–22. doi:10.1002/jez.1768

Ávila-Jiménez, M. L., & Coulson, S. J. (2011). A Holarctic biogeographical analysis of the collembola (arthropoda, hexapoda) unravels recent post-glacial colonization patterns. *Insects, 2*(3), 273–296. doi:10.3390/insects2030273

Bjørndalen Integrated Gradients - a High-Arctic Field Laboratory (BIG). (2019). Retrieved from https://www.unis.no/project/big/ [Accessed 23.01.2024]

Bradshaw, W. E., & Holzapfel, C. M. (2007). Evolution of animal photoperiodism. *Annual Review of Ecology, Evolution, and Systematics, 38*(1), 1–25. doi:10.1146/annurev.ecolsys.37.091305.110115

Chaubet, B., Derocles, S. A. P., Hullé, M., Le Ralec, A., Outreman, Y., Simon, J.-C., & Tomanović, Ž. (2013). Two new species of aphid parasitoids (hymenoptera, braconidae, aphidiinae) from the High Arctic (Spitsbergen, Svalbard). *Zoologischer Anzeiger - A Journal of Comparative Zoology, 252*(1), 34–40. doi:10.1016/j.jcz.2012.03.001

Clutton-Brock, T. H., Guinness, F. E., & Albon, S. D. (1982). *Red deer: Behaviour and ecology of two sexes.* Edinburgh: Edinburgh University Press.

Convey, P., Abbandonato, H., Bergan, F., Beumer, L. T., Biersma, E. M., Bråthen, V. S., … Coulson, S. J. (2015). Survival of rapidly fluctuating natural low winter temperatures by High Arctic soil invertebrates. *Journal of Thermal Biology, 54*, 111–117. doi:10.1016/j.jtherbio.2014.07.009

Cooper, E. J., Dullinger, S., & Semenchuk, P. (2011). Late snowmelt delays plant development and results in lower reproductive success in the High Arctic. *Plant Science*, *180*(1), 157–167. doi:10.1016/j.plantsci.2010.09.005

Coulson, S.J., Bartlett, J., Boström, S., Brittain, J., Christoffersen, K. S., Convey, P., De Smet, W., Dózsa-Farkas, K., Ekrem, T., Fjellberg, A., Füreder, L., Gillespie, M. A.K., Gustafsson, D., Gwiazdowicz, D.J., Kaczmarek, Ł., Kolicka, M., Laniecki, R., Moerman, T. M., Seniczak, S., Seniczak, A., Simon, J.-C., Stur, E., Søli, G., Wieczorek, K., Zawierucha, K., Zmudczynska-Skarbek, K., (unpublished). On the terrestrial and freshwater invertebrate diversity of the High Arctic archipelago of Svalbard: a revised species inventory and synopsis of the community

Coulson, S. J., Convey, P., Aakra, K., Aarvik, L., Ávila-Jiménez, M. L., Babenko, A., Biersma, E., Boström, S., Brittain, J., Carlsson, A.M., Christoffersen, K.S., De Smet, W.H., Ekrem, T., Fjellberg, A., Füreder, L., Gustafsson, D., Gwiazdowicz, D.J., Hansen, L.O., Holmstrup M., Kaczmarek, L., Kolicka, M., Kuklin, V., Lakka, H-K., Lebedeva, N., Makarova, O., Maraldo, K., Melekhina, E., Ødegaard, F., Pilskog, H.E., Simon, J.C., Sohlenius, B., Solhøy, T., Søli, G., Stur, E., Tanaevitch, A., Taskaeva, A., Velle, G. Zawierucha, K., & Zmudczyńska-Skarbek, K. (2014). The terrestrial and freshwater invertebrate biodiversity of the archipelagoes of the Barents Sea; Svalbard, Franz Josef Land and Novaya Zemlya. *Soil Biology and Biochemistry*, *68*, 440–470. doi:10.1016/j.soilbio.2013.10.006

Daan, S., & Aschoff, J. (2001). The entrainment of circadian systems. In R. Y. Moore, F. W. Turek, & J. S. Takahashi (Eds.), *Circadian clocks* (pp. 7–43). Boston: Springer.

Danks, H. V. (2004). Seasonal adaptations in Arctic insects. *Integrative and Comparative Biology*, *44*(2), 85–94. doi:10.1093/icb/44.2.85

Djurberg, E. L. (2021). *Eternal sunshine on the flower - spotted ground. Investigating diel rhythms during midnight sun on high - Arctic pollinators* (Bachelor's Thesis). Umeå University: Umeå.

Elvebakk, A. (1997). Tundra diversity and ecological characteristics of Svalbard. In F. E. Wielgolaski (Ed.), *Ecosystems of the world 3: polar and alpine tundra* (pp. 347–359). Amsterdam: Elsevier.

Elvebakk, A. (2005). A vegetation map of Svalbard on the scale 1:3.5 mill. *Phytocoenologia*, *35*(4), 951–967. doi:10.1127/0340-269x/2005/0035-0951

Fenn, M. G., & Macdonald, D. W. (1995). Use of middens by Red Foxes: Risk reverses rhythms of Rats. *Journal of Mammalogy*, *76*(1), 130–136. doi:10.2307/1382321

Galen, C., & Stanton, M. L. (1991). Consequences of emergence phenology for reproductive success in *Ranunculus adoneus* (Ranunculaceae). *American Journal of Botany*, *78*(7), 978–988. doi:10.1002/j.1537-2197.1991.tb14502.x

Gillespie, M. A., Baggesen, N., & Cooper, E. J. (2016). High arctic flowering phenology and plant–pollinator interactions in response to delayed snow melt and simulated warming. *Environmental Research Letters*, *11*, 115006. doi:10.1088/1748-9326/11/11/115006

Gwiazdowicz, D., Coulson, S., Grytnes, J.-A., & Pilskog, H. (2012a). The bird ectoparasite *Dermanyssus Hirundinis* (Acari, mesostigmata) in the high arctic; a new parasitic mite to Spitsbergen, Svalbard. *Acta Parasitologica*, *57*(4), 378-384. doi:10.2478/s11686-012-0050-5

Gwiazdowicz, D., Solhøy, T., Coulson, S., Lebedeva, N., & Melekhina, E. (2012b). First record of *Vulgarogamasus immanis* (Acari, mesostigmata) in Svalbard. *Polish Polar Research*, *33*(1), 35–39. doi:10.2478/v10183-012-0001-8

Hanssen-Bauer, I., Førland, E.J., Hisdal, H., Mayer, S., Sandø, A.B., & Sorteberg, A. (Ed.) (2019). Climate in Svalbard 2100 - a knowledge base for climate adaptation. Norway, Norwegian Centre of Climate Services (NCCS) for Norwegian Environment Agency (Miljødirektoratet), 208pp. (NCCS report 1/2019). doi: 10.25607/OBP-888

Hawley, K. L., Rosten, C. M., Haugen, T. O., Christensen, G., & Lucas, M. C. (2017). Freezer on, lights off! Environmental effects on activity rhythms of fish in the Arctic. *Biology Letters*, *13*(12), 20170575. doi:10.1098/rsbl.2017.0575

Herrera, C. M. (1990). Daily patterns of pollinator activity, differential pollinating effectiveness, and floral resource availability, in a summer-flowering Mediterranean shrub. *Oikos*, *58*(3), 277. doi:10.2307/3545218

Hodkinson, I. D., & Coulson, S. J. (2004). Are high arctic terrestrial food chains really that simple? – The Bear Island Food Web Revisited. *Oikos*, *106*(2), 427–431. doi:10.1111/j.0030-1299.2004.13091.x

Hut, R. A., Kronfeld-Schor, N., van der Vinne, V., & De la Iglesia, H. (2012). In search of a temporal niche. *Progress in Brain Research*, *199*, 281–304. doi:10.1016/b978-0-444-59427-3.00017-4

Hodkinson, I. D., Coulson, S. J., Webb, N. R., Block, W., Strathdee, A. T., Bale, J. S., & Worland, M. R. (1996). Temperature and the biomass of flying midges (Diptera: Chironomidae) in the High Arctic. *Oikos*, *75*(2), 241-248. doi:10.2307/3546247

Høye, T. T., & Culler, L. E. (2018). Tundra arthropods provide key insights into ecological responses to environmental change. *Polar Biology*, *41*(8), 1523–1529. doi:10.1007/s00300-018-2370-x

Høye, T. T., & Forchhammer, M. C. (2008a). Phenology of High‒Arctic Arthropods: Effects of Climate on Spatial, Seasonal, and Inter‒Annual Variation. *Advances in Ecological Research*, 40, 299-324. doi:10.1016/s0065-2504(07)00013-x

Høye, T. T., & Forchhammer, M. C. (2008b). The influence of weather conditions on the activity of high-arctic arthropods inferred from long-term observations. *BMC Ecology*, *8*(1), 8. doi:10.1186/1472-6785-8-8

Høye, T. T., Post, E., Meltofte, H., Schmidt, N. M., & Forchhammer, M. C. (2007). Rapid advancement of spring in the High Arctic. *Current Biology*, *17*(12), R449-R451. doi:10.1016/j.cub.2007.04.047

Høye, T. T., Post, E., Schmidt, N. M., Trøjelsgaard, K., & Forchhammer, M. C. (2013). Shorter flowering seasons and declining abundance of flower visitors in a warmer Arctic. *Nature Climate Change*, *3*(8), 759–763. doi:10.1038/nclimate1909

Iler, A. M., Høye, T. T., Inouye, D. W., & Schmidt, N. M. (2013). Nonlinear flowering responses to climate: Are species approaching their limits of phenological change? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1624), 20120489. doi:10.1098/rstb.2012.0489

Ingólfsson, Ó., & Landvik, J. Y. (2013). The svalbard–Barents Sea ice-sheet – historical, current and future perspectives. *Quaternary Science Reviews*, *64*, 33–60. doi:10.1016/j.quascirev.2012.11.034

Intergovernmental Panel on Climate Change (IPCC). (2013). *Climate Change 2013: The Physical Science Basis*. Working Group II Contribution to the IPCC 5th Assessment Report.

Isaksen, K., Nordli, Ø., Ivanov, B., Køltzow, M. A., Aaboe, S., Gjelten, H. M., … Karandasheva, T. (2022). Exceptional warming over the Barents area. *Scientific Reports*, *12*. doi:10.1038/s41598-022-13568-5

Jepsen, J.U., Arneberg, P., Ims, R.A., Siwertsson, A. & Yoccoz, N.G. (2019) *Test av fagsystemet for økologisk tilstand. Erfaringer fra pilotprosjekter for arktisk tundra og arktisk del av Barentshavet*. NINA, Rapport 1674, Norsk institutt for naturforskning.

Johnson, S. N., & Jones, T. H. (2016). Introduction to global climate change and terrestrial invertebrates. *Global Climate Change and Terrestrial Invertebrates*, 1–8. doi:10.1002/9781119070894.ch1

Kattsov, V. M., Källén, E., Cattle, H., Christensen, J., Drange, H., Hanssen-Bauer, I., Jóhannesen, T., Karol, I., Räisänen, J., Svensson, G., & Vavulin, S. (2005). Future climate change: modeling and scenarios for the Arctic. Arctic Climate Impact Assessment, Cambridge University Press, Cambridge, 99-150.

Kevan, P. G. (1972). Insect pollination of high Arctic Flowers. *The Journal of Ecology*, *60*(3), 831-847. doi:10.2307/2258569

Kiedrowicz, A., Rector, B. G., Zawierucha, K., Szydło, W., & Skoracka, A. (2016). Phytophagous Mites (Acari: Eriophyoidea) recorded from Svalbard, including the description of a new species. *Polar Biology*, *39*(8), 1359–1368. doi:10.1007/s00300-015-1858-x

Klausen, L. (2022). *Spatio-temporal Diptera visitation to Silene acaulis flowers studied with time-lapse cameras in Svalbard and Greenland* (Master's Thesis). The Arctic University of Norway, Tromsø.

Kohnemann, S. H., Heinemann, G., Bromwich, D. H., & Gutjahr, O. (2017). Extreme warming in the Kara Sea and Barents Sea during the winter period 2000–16. *Journal of Climate*, *30*(22), 8913–8927. doi:10.1175/jcli-d-16-0693.1

Kolodochka, L. A., & Gwiazdowicz, D. J. (2014). A new species of predaceous mite of the genus *Neoseiulus Hughes* (Acari, Phytoseiidae), with redescriptions of *N. magnanalis* (Thor) and N. ellesmerei (Chant & Hansell), from Svalbard, High Arctic. *Zootaxa*, *3793*, 441–452. doi:10.11646/zootaxa.3793.4.3

Kronfeld-Schor, N., & Dayan, T. (2003). Partitioning of time as an ecological resource. *Annual Review of Ecology, Evolution, and Systematics*, *34*(1), 153–181. doi:10.1146/annurev.ecolsys.34.011802.132435

Krüll, F. (1976). Zeitgebers for animals in the continuous daylight of High Arctic Summer. *Oecologia*, *24*(2), 149–157. doi:10.1007/bf00572756

Kudo, G., & Cooper, E. J. (2019). When spring ephemerals fail to meet pollinators: Mechanism of phenological mismatch and its impact on plant reproduction. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1904), 20190573. doi:10.1098/rspb.2019.0573

Körner, C. (2003). *Alpine plant life: Functional Plant Ecology of high mountain ecosystems* (2nd ed.). Berlin: Springer.

Loboda, S., Savage, J., Buddle, C. M., Schmidt, N. M., & Høye, T. T. (2017). Declining diversity and abundance of High Arctic fly assemblages over two decades of rapid climate warming. *Ecography*, *41*(2), 265–277. doi:10.1111/ecog.02747

Loe, L. E., Bonenfant, C., Mysterud, A., Severinsen, T., Øritsland, N. A., Langvatn, R., Stien, A., Irvine, R., & Stenseth, N. Chr. (2007). Activity pattern of Arctic reindeer in a predator-free environment: No need to keep a daily rhythm. *Oecologia*, *152*(4), 617–624. doi:10.1007/s00442-007-0681-7

McCrystall, M. R., Stroeve, J., Serreze, M., Forbes, B. C., & Screen, J. A. (2021). New climate models reveal faster and larger increases in Arctic precipitation than previously projected. *Nature Communications*, *12,* 6765. doi:10.1038/s41467-021-27031-y

Menzel, F., Gammelmo, Ø., Olsen, K. M., & Köhler, A. (2020). The Black Fungus Gnats (Diptera, Sciaridae) of Norway – part I: Species records published until December 2019, with an updated checklist. *ZooKeys*, *957*, 17–104. doi:10.3897/zookeys.957.46528

Miko, L., & Monson, F. D. (2013). Two interesting damaeid mites (Acari, Oribatida, Damaeidae Berlese, 1896) from the British isles and Svalbard (Spitsbergen, Norway), with a description of Kunstidamaeus Arcticus n.sp. *Acarologia*, *53*(1), 89–100. doi:10.1051/acarologia/20132077

Mortensen, L. O., Schmidt, N. M., Høye, T. T., Damgaard, C., & Forchhammer, M. C. (2016). Analysis of trophic interactions reveals highly plastic response to climate change in a tri-trophic high-arctic ecosystem. *Polar Biology*, *39*(8), 1467–1478. doi:10.1007/s00300-015-1872-z

Norwegian Centre for Climate Services (NCCS). (2024). *Observations and weather statistics*. Retrieved from https://seklima.met.no/observations/ [Accessed 24.01.2024]

Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, *120*(3), 321–326. doi:10.1111/j.1600-0706.2010.18644.x

Olesen, J. M. (1988). Floral biology of the Canarian *Echium wildpretii*: bird—flower or a water resource to desert bees? *Acta Botanica Neerlandica*, *37*(4), 509–513. doi:10.1111/j.1438-8677.1988.tb02157.x

Pilskog, H.E. (2011). *The Invertebrate Fauna of Svalbard Bird Nests: Ecology and as Facilitating Colonisation of an Arctic Archipelago*. (Master's thesis). The University of Bergen, Bergen.

R Core Team (2023). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from https://www.R-project.org/.

Rech, A. R., Dalsgaard, B., Sandel, B., Sonne, J., Svenning, J.-C., Holmes, N., & Ollerton, J. (2016). The macroecology of animal versus wind pollination: Ecological factors are more important than historical climate stability. *Plant Ecology & Diversity*, *9*(3), 253–262. doi:10.1080/17550874.2016.1207722

Refinetti, R. (2008). The diversity of temporal niches in mammals. *Biological Rhythm Research*, *39*(3), 173–192. doi:10.1080/09291010701682690

Reierth, E., & Stokkan, K.-A. (1998). Activity rhythm in high Arctic Svalbard Ptarmigan (*lagopus mutus hyperboreus*). *Canadian Journal of Zoology*, *76*(11), 2031–2039. doi:10.1139/z98-173

Semenchuk, P. R., Elberling, B., & Cooper, E. J. (2013). Snow cover and extreme winter warming events control flower abundance of some, but not all species in high Arctic Svalbard. *Ecology and Evolution*, *3*(8), 2586–2599. doi:10.1002/ece3.648

Seniczak, S., Seniczak, A., Gwiazdowicz, D. J., & Coulson, S. J. (2014). Community structure of Oribatid and Gamasid mites (Acari) in moss-grass tundra in Svalbard (Spitsbergen, Norway). *Arctic, Antarctic, and Alpine Research*, *46*(3), 591–599. doi:10.1657/1938-4246-46.3.591

Schmidt, N. M., Mosbacher, J. B., Nielsen, P. S., Rasmussen, C., Høye, T. T., & Roslin, T. (2016). An ecological function in crisis? the temporal overlap between plant flowering and pollinator function shrinks as the Arctic warms. *Ecography*, *39*(12), 1250–1252. doi:10.1111/ecog.02261

Skoracki, M., & Zawierucha, K. (2016). Chenophila Nanseni sp. n. (Acari: Syringophilidae) parasitising the barnacle goose in Svalbard. *Polish Polar Research*, *37*(1), 121–130. doi:10.1515/popore-2016-0002

Stebbins, G. L. (1970). Adaptive radiation of reproductive characteristics in angiosperms, I: Pollination mechanisms. *Annual Review of Ecology and Systematics*, *1*(1), 307–326. doi:10.1146/annurev.es.01.110170.001515

Stelzer, R. J., & Chittka, L. (2010). Bumblebee foraging rhythms under the midnight sun measured with radiofrequency identification. *BMC Biology*, *8, 93*. doi:10.1186/1741-7007-8-93

Stolz, C., Varpe, Ø., Ims, R. A., Sandercock, B. K., Stokke, B. G., & Fossøy, F. (2023). Predator–prey interactions in the Arctic: dna metabarcoding reveals that nestling diet of snow buntings reflects arthropod seasonality. *Environmental DNA*, *5*(6), 1234–1251. doi:10.1002/edn3.439

Stur, E., & Ekrem, T. (2020). The Chironomidae (Diptera) of Svalbard and Jan Mayen. *Insects*, *11*(3), 183. doi:10.3390/insects11030183

Suttie, J. M., & Webster,, J. R. (1995). Extreme seasonal growth in Arctic deer: Comparisons and Control Mechanisms. *American Zoologist*, *35*(3), 215–221. doi:10.1093/icb/35.3.215

Søvik, G., & Leinaas, H. P. (2003a). Adult survival and reproduction in an arctic mite, A*meronothrus lineatus* (acari, Oribatida): Effects of temperature and winter cold. *Canadian Journal of Zoology*, *81*(9), 1579–1588. doi:10.1139/z03-113

Søvik, G., & Leinaas, H. P. (2003b). Long life cycle and high adult survival in an Arctic population of the mite *Ameronothrus lineatus* (Acari, Oribatida) from Svalbard. *Polar Biology*, *26*(8), 500–508. doi:10.1007/s00300-003-0510-3

Tiusanen, M., Hebert, P. D., Schmidt, N. M., & Roslin, T. (2016). One fly to rule them all—muscid flies are the key pollinators in the Arctic. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1839), 20161271. doi:10.1098/rspb.2016.1271

Totland, Ø. (1994). Influence of climate, time of day and season, and flower density on insect flower visitation in Alpine Norway. *Arctic and Alpine Research*, *26*(1), 66-71. doi:10.2307/1551879

Tulp, I., & Schekkerman, H. (2008). Has prey availability for arctic birds advanced with climate change? Hindcasting the abundance of tundra arthropods using weather and seasonal variations. *ARCTIC*, *61*, 48-60. doi:10.14430/arctic6

Urbanowicz, C., Virginia, R. A., & Irwin, R. E. (2018). Pollen limitation and reproduction of three plant species across a temperature gradient in western Greenland. *Arctic, Antarctic, and Alpine Research*, *50*(1). doi:10.1080/15230430.2017.1414485

van Oort, B. E., Tyler, N. J., Gerkema, M. P., Folkow, L., Blix, A. S., & Stokkan, K.-A. (2005). Circadian organization in Reindeer. *Nature*, *438*(7071), 1095–1096. doi:10.1038/4381095a

van Oort, B. E., Tyler, N. J., Gerkema, M. P., Folkow, L., & Stokkan, K.-A. (2007). Where clocks are redundant: Weak circadian mechanisms in reindeer living under polar photic conditions. *Naturwissenschaften*, *94*(3), 183–194. doi:10.1007/s00114-006-0174-2

Walsh, J. E., Overland, J. E., Groisman, P. Y., & Rudolf, B. (2011). Ongoing climate change in the Arctic. *AMBIO*, *40*(Suppl1), 6–16. doi:10.1007/s13280-011-0211-z

Ware, J. V., Rode, K. D., Robbins, C. T., Leise, T., Weil, C. R., & Jansen, H. T. (2020). The clock keeps ticking: Circadian rhythms of free-ranging polar bears. *Journal of Biological Rhythms*, *35*(2), 180–194. doi:10.1177/0748730419900877

Warton, D. I. (2022). *Eco-stats: Data Analysis in Ecology: From T-tests to multivariate abundances*. Cham, Switzerland: Springer International Publishing.

Wassmann, P., Duarte, C. M., Agusti, S. & Sejir, M. (2011). Footprints of climate change in the Arctic marine ecosystem. *Global Change Biology,* 17 (2), 1235 – 1249. doi:10.1111/j.1365-2486.2010.02311.x

Ween, R. (2022). *Timing is everything: Within-plant flowering phenology impacts fruit production in the Arctic-Alpine cushion plant Silene acaulis (L.) Jacq. (*Master's Thesis). The Arctic University of Norway, Tromsø.

Willmer, P. G. (1986). Foraging patterns and water balance: Problems of optimization for a xerophilic bee, *Chalicodoma Sicula. The Journal of Animal Ecology*, *55*(3), 941-962. doi:10.2307/4426

Willmer, P. G. (1982). Hygrothermal determinants of insect activity patterns: The Diptera of water−lily leaves. *Ecological Entomology*, *7*(2), 221–231. doi:10.1111/j.1365-2311.1982.tb00661.x

Willmer, P. G. (1983). Thermal constraints on activity patterns in nectar−feeding insects. *Ecological Entomology*, *8*(4), 455–469. doi:10.1111/j.1365-2311.1983.tb00524.x

Witt, T., Jürgens, A., Geyer, R., & Gottsberger, G. (1999). Nectar dynamics and sugar composition in flowers of Silene and Saponaria species (Caryophyllaceae). *Plant Biology*, *1*(3), 334–345. doi:10.1111/j.1438-8677.1999.tb00261.x

Wood, S. (2017). *Generalized Additive Models: An Introduction with R* (2nd ed.). Chapman and Hall/CRC Press.

Zoller, L., Bennett, J. M., & Knight, T. M. (2020). Diel-scale temporal dynamics in the abundance and composition of pollinators in the Arctic Summer. *Scientific Reports*, *10*(1), 21187. doi:10.1038/s41598-020-78165-w

Appendix 1

Characteristics used for assigning annotations to a specific taxonomic group and location or for describing the weather on the image.

Arthropod	Can see appendages and/or body (on one or multiple consecutive images). If cannot distinguish appendages, identify smaller insects based on the movement between consecutive images (e.g. if it is not an insect and debris flowing in wind, all the particles would move in the same direction).	
Regional attribute	Division of the attribute	Identification characteristics
Taxonomy		
	Acari	Round body, generally orange, almost star-shaped, legs visible
	Apocrita	Narrow body, clear wings, relatively long antennaes
	Aranea	Body divided into two parts/round body, legs prominent
	Coleoptera	No visible wings
	Diptera (further divided into size-classes)	Two transparent wings
	Diptera >9mm	Length of the insect the same as the diameter flower or longer, often Muscid flies or similar
	Diptera 5-9mm	Length of the insect between half the flower diameter to almost the whole flower diameter, often seem to be Chironomids or smaller flies
	Diptera <5mm	Length of the insect shorter than half of the diameter of the flowers, often smaller Chironomids
	Lepidoptera	Caterpillar or non-clear wings
	Symphyta	Visible antennae, clear wings
	unidentified inv.	Insect-like features or movement based on previous/later images, generally too small to identify
Location		
	Outside cushion	Whole body of the insect is outside the cushion
	On cushion not flower	Whole body of the insect within the cushion limits
	On flower	Body/head of the insect on the flower *flower - open flower, where petals clearly visible, not a closed bud nor a flower in later withering stage where all the petals have turned brown)
Weather		
	Sun	Prominent shadows
	Rain	See raindrops on the surrounding ground/rocks/camera itself
	Cloudy	Weak to no shadows

Appendix 2

Hourly air and soil temperature fluctuations within the day throughout the study period. Blue line indicates air temperatures, while orange line illustrates the fluctuations in soil temperatures.