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Effects of arthropod abundance on reproductive success in Svalbard snow bunting (*Plectrophenax nivalis*)

Master's thesis in Natural Resources Management

Supervisor: Brage Bremset Hansen

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Abstract

Arctic warming causes major environmental and biological changes, also affecting trophic interactions. Effects of climate change have already been observed in several Arctic-breeding migratory birds, with their reproductive success often depending on weather conditions and arthropods as a food source provided to nestlings. Here, I investigated the effects of variation in an arthropod abundance proxy on fitness-related parameters in the Svalbard snow bunting (*Plectrophenax nivalis*), and how such fluctuations may in turn be linked to annual variation in weather conditions. Eight years of data revealed large interannual variation in the amount and dynamics of arthropod abundance. Among the weather variables considered, I found only an apparent negative effect of wind on annual variation in cumulative arthropod abundance in the breeding season. Furthermore, arthropod abundance in the individual nestling period positively affected chick weight, with a tendency for a similar effect on fledging success. I also found strong indications of earlier onset of spring to have an additive positive effect on chick weight. My findings highlight the importance of variation in prey abundance, as well as annual timing of spring, for snow bunting reproductive success. This eight-year study found no evidence of weather conditions linked with climate warming to affect annual arthropod abundance in the breeding period. However, anticipated future warming in the high-Arctic may significantly alter population viability of migratory birds, both directly, and indirectly through trophic interactions.

Sammendrag

Arktisk oppvarming fører til store miljøforandringer og biologiske forandringer, samt påvirker trofiske interaksjoner. Effekter av klimaforandringer har allerede blitt observert hos flere arktiske hekkende trekkfugler, med deres reproduktive suksess som ofte er avhengig av værforhold og artropoder som matkilde for ungene. Her undersøkte jeg effekten av variasjon i en proxy for artropodeabundans på fitness-relaterte parametere i snøspurven (*Plectrophenax nivalis*) på Svalbard, samt undersøkte hvordan slike fluktuasjoner igjen kan bli koblet til årlig variasjon i værforhold. Åtte år med data avdekket store mellomårsvariasjoner i mengden og dynamikken av artropodeabundans. Blant de vurderte værvariablene fant jeg kun en tilsynelatende negativ effekt av vind på årlig variasjon i kumulativ artropodeabundans i hekkesesongen. Videre hadde artropodeabundans i den individuelle ungeperioden en positiv effekt på ungevekt, med tendenser til en lik effekt på utflyvingsuksess. Jeg fant også sterke indikasjoner på at tidligere vårstart hadde en positiv tilleggseffekt på ungevekt. Resultatene mine understreker viktigheten av variasjon i mattilgang, samt årlig timing av vårstart, for reproduktiv suksess hos snøspurven. Dette åtte år lange studiet fant ingen bevis på at værforhold knyttet til klimaendringer påvirker årlig artropodeabundans i hekkeperioden. Forventet fremtidig oppvarming i høy-Arktis kan derimot betydelig endre levedyktigheten til populasjoner av trekkfugler, både direkte, og indirekte gjennom trofiske interaksjoner.

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1. Introduction

The climate on Earth is changing, and the resulting environmental and biological consequences have been extensively studied by scientists worldwide (Walther et al., 2002; Parmesan, 2006; IPCC, 2014). The Arctic region is particularly affected, experiencing a temperature warming at a rate two to three times higher than the global average (Post et al., 2019). This Arctic amplification of climate change is causing major changes to the environment, mainly by reducing the extent and thickness of sea ice, decreasing glacier ice and terrestrial snow cover, melting permafrost, altering nutrient availability, and increasing vegetation productivity (Wassmann et al., 2011; Descamps et al., 2017). The ecological responses detected include e.g. phenological shifts like advanced plant flowering and invertebrate emergence (Høye et al., 2007; Ernakovich et al., 2014), and northward range expansion of species' distribution, which in turn can result in animal invasions affecting ecosystem dynamics (Kennedy et al., 2002; Post et al., 2009). Ultimately, the consequences of direct responses to warming can be reflected in disruption of trophic interactions, i.e. indirect effects, which have indeed been observed within some arctic food webs (Callaghan et al., 2004; Ims & Fuglei, 2005; Forchhammer et al., 2008; Post et al., 2019).

However, there is a general scarcity of studies on indirect warming-induced effects through trophic interactions in terrestrial Arctic ecosystems, mainly because of the complex properties of food web dynamics, and the difficulty of analysing them under climate change (Van der Putten et al., 2010; Kharouba et al., 2018). Food webs are complex consumer-resource systems, defined by several trophic levels and the relationship within and among them (Paine, 1980). Interacting species do not necessarily show the same response to climate warming (Schweiger et al., 2008), and there are typically not only consumption interactions to consider, but also the interplay with other interaction types like competition, symbiosis and parasitism (Ims & Fuglei, 2005). The fact that even observed direct effects of climate change are still small in several ecosystems (IPCC, 2014) further explains the overall difficulty of detecting concealed indirect effects operating through other species and trophic levels. However, trophic interactions are still likely key in successful predictions of warming-induced effects on both individual species and ecosystem dynamics (Araujo & Luoto, 2007; Van der Putten et al., 2010).

Arctic breeding migratory birds have generally short breeding seasons due to harsh weather, limited plant growth and seasonal food availability, which can become challenging in the face of climate warming (Both et al., 2010; Dunn & Winkler, 2010). Indirect effects of climate change have for instance resulted in trophic mismatches (Cushing, 1969; 1990) between breeding bird species and their food source, i.e. mismatched temporal occurrences of food abundance and food demands of developing young (Gaston et al., 2009; Visser et al., 2012). Such trophic decoupling can change the ability of breeding bird species to adapt to a new local climate (Visser, 2008; Van der Putten et al., 2010), for example by decreasing their reproductive success in a mismatch scenario (McKinnon et al., 2012; Saalfeld et al., 2019). However, in order to optimize conditions with regard to food abundance, many avian species have showed the ability to track abundance shifts of their prey, thereby timing their breeding for maximal reproductive success and fitness (Visser et al., 2012; Visser & Gienapp, 2019). This may on the other hand be restricted in future generations, due to limitations in phenotypic plasticity (Høye et al., 2007; Dunn & Winkler, 2010).

For many terrestrial bird species, arthropods (e.g. insects, spiders and mites) are the main food source provided to young nestlings during early development (Veistola et al., 1995). Arthropod abundance during the breeding season is tightly linked with reproductive success, where increased abundance and higher feeding rates result in higher offspring fitness (Martin, 1987; Perrins, 1991; Rauter et al., 2000; Burger et al., 2012; Pérez et al., 2016). Furthermore, reproductive success is influenced by the composition of arthropod prey species chosen for the nestlings by parents, where especially prey size matters (Schwagmeyer & Mock, 2008). The short-life cycle of arthropods and their ectothermic nature makes them especially affected by environmental changes (Cloudsley-Thompson, 1988; Bolduc et al., 2013). Their availability to insectivorous birds is largely controlled by both their activity and abundance; activity through short-term weather variables like temperature, precipitation and wind, and abundance through larger time scale (i.e. seasonal and annual) fluctuations in weather conditions like longer-term temperatures and timing of spring snow melt (Avery & Krebs, 1984; Perrins, 1991). In several study systems, arthropod abundance has advanced with warming springs (Høye & Forchhammer, 2008a; Tulp & Schekkerman; 2008; Shaftel et al., 2021), most likely mediating the advancement of breeding observed in several of their avian predators (Walther et al., 2002; Høye et al., 2007).

With a warming of 3-5°C the last 50 years, the Svalbard Archipelago has experienced the highest rate of temperature increase within the Arctic (Førland et al., 2011; NCCS, 2019), which has affected both marine and terrestrial ecosystems in the region (Descamps et al., 2017). The snow bunting (*Plectrophenax nivalis*) is a long-distance migrant nesting across the high-Arctic, and the only passerine regularly breeding on the high-Arctic islands of Svalbard (Espmark, 2016; BirdLife International, 2021). Their nestlings depend on arthropods as the main food source, where energetic demand increase with age prior to fledging (Hussell, 1972; Falconer et al., 2008). Thus, to some degree one may expect improved reproductive success if the nestling period (especially towards later stages) is temporally matched with arthropod abundance peaks (Cushing, 1969; Falconer et al., 2008; Dunn & Winkler, 2010). There exists however a trade-off, with potential costs of reproducing too early (e.g. giving susceptibility to cold weather events) or too late (e.g. having limited time for chick growth and development following fledging) in the season (Dunn & Winkler, 2010; Lameris et al., 2017).

In the high-Arctic, arthropod emergence is strongly affected by snow melt (Høye & Forchhammer, 2008a), but little is known about the annual fluctuations in arthropod abundance and community composition at Svalbard, and what climate factors drive the relationship. Furthermore, even though environmental drivers of reproductive success in the Svalbard snow bunting have been previously studied (Hoset et al., 2004; Hoset et al., 2009; Fossøy et al., 2014; Hoset et al., 2014; Lillehaug, 2019), the importance of arthropod abundance in the nestling period for reproductive success is not well known. Thus, further investigation into the trophic links between weather fluctuations, climate change, arthropods and snow buntings' reproductive success will provide new insights into current, as well as future, dynamics.

With Arctic amplification, climate change and related indirect effects across trophic interactions are expected to be more pronounced in the high Arctic. The Svalbard snow bunting therefore provides a good model system in which to explore climate-affected changes in trophic relationships. In the present study, my aim was therefore to examine the effects of variation in arthropod abundance on fitness-related parameters in snow buntings, and to investigate how such fluctuation may in turn be linked to annual variation in weather conditions. This was done by analysing and linking eight years of spatially coupled datasets on weather, arthropod abundance and snow bunting reproduction in Svalbard. First, I explored potential annual weather correlates of a proxy for annual cumulative arthropod abundance based on pitfall trap data. This link has remained largely unexplored (but see Høye & Forchhammer,

2008a&b; Shaftel et al., 2021), but I anticipated that especially warmer temperatures and earlier spring snow melt would increase arthropod abundance (Hodkinson et al., 1998; Tulp & Schekkerman; 2008). Second, I analysed how variation in arthropod abundance within and between breeding seasons affected key fitness-related traits in snow buntings, i.e. chick weight and fledging success. In particular, I expected to find increased arthropod abundance to have a positive effect on fitness-related parameters (Perrins, 1991; Burger et al., 2012; McKinnon et al., 2012).

2. Materials and methods

2.1 Study site and species

The study took place in the high Arctic archipelago of Svalbard, more specifically in the valley Adventdalen (78°13'N, 15°38'E; Appendix Figure A1), close to Longyearbyen. The study site was chosen due to its use in a long-term monitoring program of the local snow bunting population (Fossøy et al., 2014; Espmark, 2016), as well as for previous arthropod sampling (Skjøstad, 2008; Stolz, 2019; Hilmarsen, 2020). Adventdalen is characterized by its cold and harsh climate, with an average July temperature of 5.9°C and generally low levels of precipitation (190mm/yr in the standard normal period 1961-1990) (Johansen & Tømmervik, 2014). The arid landscape is dominated by snowbeds, ice wedges, dry slopes, barrens, and wet flats, consisting of typical arctic tundra vegetation like mosses, dwarf shrub and grasses (Elvebakk, 1994; Mora et al., 2015).

Despite a generally short growing season in Adventdalen (Le Moullec et al., 2019), the tundra vegetation is the home of a diverse invertebrate fauna. With over 1000 known terrestrial and freshwater arthropod species on Svalbard (Hodkinson, 2013), some of the key taxa found in Adventdalen include insects (Insecta), spiders (Araneae), springtails (Collembola) and mites (Acari). The insect fauna is mainly dominated by Diptera, such as Chironomidae and other fly species (Brachycera), but parasitic wasps (Hymenoptera) and aphids (Aphididae) are also encountered (Coulson et al., 2014). The timing of emergence probably differs between species, where community composition is expected to be highly dependent on local weather conditions and seasonal progression (Dahl et al., 2018; Shaftel et al., 2021). Unique for the high Arctic

arthropod community is the high ratio of 'primitive' forms like spiders and springtails, compared to more advanced groups of insects, which struggle more with adaptation to the harsh climate (Hodkinson, 2013).

The snow bunting has a circumpolar distribution, and it nests at high latitudes ranging from 50.1° to 83.6°N (Snell et al., 2018). They are the only regularly breeding songbird found at Svalbard, where the number of the local population is unknown, but probably around 1,000 – 10,000 breeding pairs (Norwegian Polar Institute, 2021a). Currently, its red list status on Svalbard (and Norway mainland) is of "Least Concern" (Artsdatabanken, 2020), but the North American population has shown a substantial decline over the last 40 years (BirdLife International, 2021), as well as an observed decline in the Fennoscandian population (Lehikoinen et al., 2019). The snow bunting normally arrives at the Svalbard breeding grounds in April, with average egg-laying starting before mid of June (Fossøy et al., 2014; Skøien, 2015). The breeding season continues until the mid of August, after which they migrate back to their wintering grounds; the Siberian steppe (Snell et al., 2018).

Snow buntings usually nest in natural structures like crevices, cavities and under boulders, but also easily make use of artificial structures such as buildings, concrete blocks, woodpiles and wooden nest-boxes (Hoset et al., 2014). Their modal clutch size is 6 eggs, with both an incubation period (from around fourth egg laid to hatching) and nestling period (from hatching to leaving nest) spanning over 13 days each (Fossøy et al., 2014). Even though most pairs raise only one clutch per breeding season, double-brooding can occur in situations of nest failure, early egg-laying and/or favourable climatic conditions (Espmark, 2016). Snow buntings are socially monogamous birds exhibiting bi-parental care, where both sexes contribute to provisioning of young, and the male helps feed the female while incubating (Hussell, 1972; Falconer et al., 2008). Nestling food diet consists solely of arthropods (Espmark, 2016), and Stolz (2019) found Svalbard snow buntings to provision their young opportunistically, but generally preferring larger-sized dipterian flies. Of natural predators, the arctic fox (*Vulpes lagopus*) has the largest effect on snow bunting survival, and depredates an average of 11.5% nests yearly (Espmark, 2016).

2.2 Data collection

2.2.1 Arthropod data

Arthropods have been collected in Adventdalen (Appendix Figure A1) in the years 2005 and 2014-2020, where abundance, biomass and diversity have been recorded using a specific sampling protocol at two specific sites. However, the length of each sampling season, as well as the sampling frequency, have varied somewhat (Table 1). Every year, arthropods were monitored in two different habitats, 300 meters apart. The first site was a *wet* marsh habitat dominated by bryophytes, grass species and *graminea*, while the second habitat was more *dry* moss tundra vegetated with *Salix polaris*, *Cassiope tetragona* and various sedges. Pitfall traps (2 m spacing) were set up with two parallel lines (3m apart) in each habitat. There were 5 traps in each line, making a total of 10 traps in each habitat. Pitfall traps are plastic cups (62 mm diameter) at ground level, here filled with water and Sun Light (Orkla, Oslo, Norway) to prevent arthropods from escaping, by reducing surface tension (Tulp & Schekkerman, 2008). The arthropods were collected from the traps by emptying the cups over a cotton cloth used as filter, before placing them on tubes containing 70% ethanol for preservation. These tubes were pooled by habitat for each sampling day. In some years, arthropods were collected every second day, and in some years every fourth day (Table 1).

I analysed the collected samples using a stereomicroscope with 6.3x – 40x zoom, where the number and taxonomic groups were recorded (using the taxonomy key by Søli (2018)) to analyse seasonal abundance and diversity. The arthropod identification method differed among years, as samples were identified down to family level in some years, and to order in other years. In order to analyse the same taxonomic groups across all years, I used the overall lowest grouping level possible. Diptera were divided into Brachycera and Nematocera, where Nematocera were further divided into Chironomidae and “other Nematocera”. Hymenoptera and Araneae were also identified and counted. Other groups like Collembola, Acari, Aphids and larvae (indetermined) were identified in several of the sampling years. However, as not all years included these groups, and because of their relative small presence in the snow bunting chick diet (because of small size and/or lifestyle; Hussell, 1972; Stolz, 2019), I did not include them in the arthropod analyses. The final five arthropod groups used in further investigations were thus Brachycera, Chironomidae, other Nematocera, Hymenoptera and Araneae.

To obtain measurements of arthropod biomass, I recorded the total dry weight (g) for each group in each sample. As an estimation of mean dry weight for an individual of each taxonomic group was done by Hilmarsen (2020), I used the same numbers in this analysis as a standardized biomass measure across all years. Estimation of mean individual weight was done separately for each group, by first choosing the sample of the season with the highest number of individuals (after abundance was recorded), and placing them in a petri dish. After dividing the dish into four equal parts, individuals from the first quarter were counted, dried and weighed. If the first quarter contained less than 30 individuals, the second quarter was also included, to obtain representative data. Then, the mean weight per individual was found by dividing the total weight in the quarter by the number of individuals in the quarter (Hilmarsen, 2020). In order to calculate the total biomass for each group in each sample across years, I multiplied the mean weight per individual by the number of individuals found in that sample. The biomass from each collection day was interpreted as a proxy for arthropod abundance, although true abundance is unknown (Shaftel et al., 2021).

In the present study, the total biomass from both wet and dry habitat samples from each collection day were added together to look at overall abundance, and further referred to as “one sampling event” (i.e. the total sum from 20 pitfall traps; 10 from each habitat). In order to produce comparable results, sampling frequency across years was made equal. In years where sampling took place every second day (Table 1), two subsequent arthropod samples were added together, to achieve a sampling frequency of every fourth day each year. Further on, whenever referring to sampling day, the date format was always; 1 = 1st of May. A total of 76 arthropod samples were collected during the years 2005 and 2014-2020 (only constituting the sampling frequency of every fourth day of each year), where 2018 was the year with the longest sampling period, and 2016/2020 with the shortest sampling periods (Table 1). For direct comparability, I only used the sampling period common across all years (day 49-65; 18th of June to 4th of July) in further statistical models, which constituted a total of 5 arthropod collection events each year.

2.2.2 Snow bunting data

The local population of snow buntings in Adventdalen has been monitored annually since 1998 (Fossøy et al., 2014), using the same protocol every year for data collection and recordings. However, the long-term dataset varies slightly between years when it comes to length of the

monitoring season (ranging from mid June to mid August), and number of nests found each year. In order to match years of arthropod sampling, I have only used the years 2005 and 2014-2020 in this study. The monitoring methodology includes the recording of several variables, where only a selection is used in subsequent analyses (see section 2.3).

Active snow bunting nests were located primarily along an abandoned cableway previously used for coal transport in Adventdalen (Appendix Figure A1). Here, wood posts were spaced out 50-100m apart, and made out a 7km long transect. Approximately 90 wooden nest boxes (especially made for snow bunting breeding) were placed on the wood posts, or on surrounding structures, where newly established nests were found by frequently checking every nest box during the study period. In addition, almost twice as many natural nests were located in the surroundings of the transect, mainly in cavities and rock boulders, but also in man-made structures like abandoned buildings and stacks of firewood. These were located by observing breeding behaviour of the male and female snow bunting, such as nest building activity, males feeding incubating females, or parents feeding newly hatched chicks (Hussell, 1972).

After a nest was located, it was regularly revisited to record several different data variables. When finding a nest during the incubation period, clutch initiation day (CID; the laying date of first egg in each nest) was estimated by back-dating. For this, it was assumed that females lay one egg per day until the clutch is completed, and that the incubation period lasts for 12 days, starting after laying of the fourth egg (Falconer et al., 2008). Furthermore, total clutch size (number of eggs laid), hatching date (when at least one egg was hatched), and number of hatched eggs was also recorded. If nests were located during the nestling period, hatching date was estimated by comparing the chick development (the oldest) to pictures of nestlings with known age. The nest was revisited at day eight after hatching, for weighing of each individual nestling. Due to logistics during field work, a few nests were weighed either before or after day eight. Weighing was done using two different spring scales (max. 50g or 100g, depending on the size of the nestling) and a cotton bag in which the chick was placed. During weighing, the nest was never left without at least one chick in it, as parents returning to an empty nest could result in abandonment (Personal communication C. Stolz). The number of fledglings was also recorded, defined as healthy nestlings heavier than 15g on day eight after hatching, as smaller chicks are unlikely to fledge (Fossøy et al., 2014). The nest was not revisited after day eight, because of premature fledging risk when disturbing the nest (Hoset et al., 2014). For all snow bunting breeding variables, date variables are further in the format; 1 = 1st of May.

Another variable noted was nest failure or unavailability. Throughout the season, several nests were observed depredated, or abandoned after possible predation risk. Nest material was torn out and eggs eaten by fox, or eggs could just go cold after the absence of the parents. Active nests could also be unavailable for recording, either of all or certain data, where e.g. only visual access to a nest gave parameters like CID and clutch size, but not nestling weight. Other nests were located too late in the nestling period (after day eight). These factors resulted in various parameters missing from several nest observations, where I had to exclude the nest in question from the dataset depending on the analysis (see section 2.3).

From the overall data sampled in the years 2005 and 2014-2020, a total of 743 nests were located, with a mean of 93 nests each year, ranging from 68 in 2017 to 110 in 2020. After excluding nests due to nest failure or unavailability, the sample size was 407 identified nests, with a mean of 51 nests each year, ranging from 19 in 2017 to 68 in 2020. Out of these, 157 nests were laid in nest boxes, and the remaining 250 were identified as natural nests (including rock boulders etc., and nests in/on artificial structures).

2.2.3 Environmental data

To examine the effect of local weather on arthropod abundance, I used environmental data from a weather station situated at Longyearbyen Airport (78°15'N, 15°30'E) in subsequent analyses. The station is operated by the Norwegian Meteorological Institute, and is located approximately 4km away from the study site. Weather data during the study years was extracted from their website; <https://seklima.met.no/observations/>, which included mean daily temperature (°C), total daily precipitation (mm), and mean daily measured wind (m/s). I used the mean of all three weather variables during the arthropod sampling period (18th of June to 4th of July) in the analyses of annual variation in cumulative arthropod abundance (see section 3.1). This was to examine the effect of short-term weather fluctuations, which have shown to influence arthropod abundance (Bolduc et al., 2013; Shaftel et al., 2021).

I further used the weather data to create annual snow melt variables, where both onset of spring and winter snow fall have shown to influence spring snowmelt (Wipf & Rixen, 2010; Cooper et al., 2011). Spring temperatures were used to calculate an annual day for timing of winter end

(Julian day), which is a variable defined as the first day in a 10-day moving window, when the average temperature reaches above 0°C (LeMoullec et al., 2019). Furthermore, a variable of total winter snowfall (mm) (from November to April) was calculated by summarizing precipitation falling on days with temperatures < 1°C (Hansen et al., 2013).

2.3 Statistical analyses

All data analyses was done using R version 4.0.2 (R Core Team, 2020), with the lme4 and MuMIn libraries (Bates et al., 2015; Bartoń, 2020).

To explore how the arthropod community composition and abundance differed both within and between years, I plotted the abundance per sampling day for each arthropod group each year (using the “geom_smooth” function from the ggplot2 package (Wickham, 2016)). Additionally, the overlapping sampling period across years, day 49-65 (18th of June to 4th of July), was plotted to allow for interannual comparisons of the same time span. To avoid biased estimates, this common sampling period was used for arthropod measurements in all statistical models. As both Brachycera and Araneae represent main components of the total recorded arthropod abundance (see section 3.1), and are also proven to be essential components of the nestling diet in insectivorous birds (Hågvar et al., 2009; Stolz, 2019), I focused on these groups separately in further analyses, in addition to all arthropods in total.

To investigate whether an overall relationship was present between annual variation in cumulative arthropod abundance (n = 8) and annual environmental conditions, I fitted linear models (LMs) using the “lm” function (Bates et al., 2015). I also fitted two additional models, with cumulative Brachycera and Araneae abundance (i.e. the most dominating arthropod groups) as response variables (n = 8), to investigate potential differences between the groups in their relationship to environmental drivers. Cumulative arthropod abundance is here defined as the sum of arthropod biomass (g) from samples collected within the overlapping sampling period (18th of June to 4th of July). The explanatory environmental variables initially included in all three models were mean daily temperature, precipitation and wind (from 18th of June to 4th of July), total snowfall in the preceding winter, and timing of winter end each year. Furthermore, precipitation and timing of winter end were not included as covariates in the same

model, as these variables showed correlation coefficients above the defined threshold (Appendix Table A1).

The best-fit model in the above analysis was chosen based on The Akaike's Information Criterion adjusted for sample size (AICc)(Akaike, 1974). I compared the *a priori* defined models fitted with Maximum likelihood (ML), where the candidate model set was constructed based on biologically relevant hypotheses (Mazerolle, M. J., 2021). Furthermore, I also ranked models (based on AICc) by using all possible allowed combinations of covariates (using the MumIn package (Barto'n, 2020)), to make sure no potential effects would be mistakenly excluded from the candidate model set. The highest-ranked model ($\Delta\text{AICc} = 0$) was regarded as the most parsimonious given the candidate model set, and lower-ranked models with $\Delta\text{AICc} < 2$ were regarded as additional supported models (Burnham and Anderson, 2002). The five highest-ranked models are presented in tables (see section 3), which in all cases also include all models with $\Delta\text{AICc} < 2$. Furthermore, AICc weights (w_i) are presented, to display the level of support for a model being the most parsimonious given the candidate models and the data (Anderson, 2008). Parameter estimates are presented with standard error (SE, in tables), as well as 95% confidence intervals (CI, in text) found through the "confint" function using likelihood profiles (Bates et al., 2015).

I tested for collinearity in the continuous explanatory variables by using Pearson's correlation coefficient (Appendix Table A1), to avoid multicollinearity. I set the correlation coefficient threshold between variables at ± 0.50 , although both higher and lower limits have previously been recommended (Dormann et al., 2012; Kalnins, 2018). Diagnostic plots were made (mainly using the DHARMA package (Hartig, 2020)) for each top ranked model, to visually and quantitatively inspect if model assumptions were met, and to check for outliers. Model assumptions tested for in this and subsequent analyses include normality of residuals and random effects, homoscedasticity (assume that variance of the residuals is equal across groups) and linearity between residuals and fitted values.

Variation in snow bunting chick weight was investigated by fitting linear mixed models (LMMs) using the "lmer" function (Bates et al., 2015), with individual chick weight (usually measured at day eight) as response variable ($n = 1166$). This response variable was used in three different sets of candidate models, with different arthropod measures; the first set with arthropod abundance in the nestling period as an explanatory variable, and the two other

candidate sets using Brachycera or Araneae abundance as explanatory variables. Thus, it was possible to investigate potential differences between the groups in their importance for chick weight. I calculated the explanatory variable “(arthropod/Brachycera/Araneae) abundance in the nestling period” by summarizing the biomass (g) from the two closest arthropod samples preceding weighing day of the individual chick. The nestling period as used here, was from hatching day to weighing day. Therefore, the biomass measure represented a proxy for arthropod abundance during the eight day long nestling period, since arthropod sampling frequency was every fourth day. Only nests with weighing days coinciding with the common arthropod sampling period (day 49-65) were included in the analyses, which means 279 out of 407 nests (69%) identified during the eight study years.

In addition to the abundance measure, I also included the following explanatory variables in all three global models; number of hatched eggs in the nest (controlling for e.g. intra-clutch competition), chick age at weighing day (controlling for unequal timing of weighing, ranging from day 6-10), including a second-order term (allowing for a decelerating growth curve), and nest type (divided into natural nests and nest boxes). I also included the interaction term between arthropod abundance and nest type, as there was a possibility of arthropod abundance affecting chick weight differently depending on the nest being natural or in a nest box. Additionally, I included year and nest identity (nestID) as random effects in all models, to account for non-independence within years and nestlings within nests (Harrison et al., 2018). Because of few years with data, and the main goal of assessing arthropod effects, weather variables were not included as predictors in this analysis (but see Hoset et al., 2004; Fossøy et al., 2014; Skøien, 2015).

The nests included in these analyses were only the ones available at weighing day (here defined as available nests), thus, all predated/abandoned/unavailable nests at that point were excluded from the analyses. Therefore, when I investigated variation in chick weight, all nests included at least one chick surviving until weighing day. The AICc model selection procedure previously described was used to find the best-fit model, where presented models were refitted with restricted maximum likelihood (REML) after model selection, as they were LMMs (Searle & Corbeil, 1976). Both the marginal and conditional R^2 were reported for the mixed models, which specifies variance explained by the fixed effects, and variance explained by both fixed and random effects, respectively (Nakagawa & Schielzeth, 2013). I tested for collinearity in the

continuous explanatory variables by using Pearson's correlation coefficient (Appendix Table A2).

To investigate how arthropods affected snow bunting chick fledging success, generalized linear mixed models (GLMMs) were fitted using the “glmer” function (Bates et al., 2015), with a binomial error distribution and logit link function (Harrison et al., 2018). I modelled the response variable, further referred to as fledging success, as the number of fledged chicks over the number of not fledged chicks in each nest ($n = 279$). As above for chick weight, this only applied for nests where at least one chick had survived until weighing day. Again, three different sets of candidate models were used, distinguished by three different explanatory variables; arthropod/Brachycera/Araneae abundance in the nestling period. The additional explanatory variables included in each global model were number of hatched eggs and nest type (and its interaction with arthropod abundance) as fixed effects, and year as a random effect. As above for chick weight, weather variables were not included as predictors in this analysis. The same AICc model selection procedure as described above was used to find the best-fit model, and collinearity of variables tested for (Appendix Table A2).

3. Results

3.1 Variation in weather and arthropod abundance

During the eight study years, the mean number of arthropod sampling events per year was 9.5, varying between 6 in 2016/2020, to 15 in 2018 (Figure 1). When analysing the complete sampling period, 2014 was the year with the highest recorded biomass per sample, with a mean of $0.71\text{g} \pm 0.17$ (SE), while 2016 had the lowest recorded mean of $0.12\text{g} \pm 0.02$ (Figure 1). Generally, arthropod abundance increased as the season progressed, before at some point stabilizing and/or starting to decrease (Figure 1). The timing of these changes vary among years and groups. Brachycera and Araneae were the two most dominating arthropod groups in terms of abundance throughout the study years, where Araneae appeared to emerge early in the season, while Brachycera dominated more towards later in the season (Figure 1). Chironomidae and other Nematocera were measured in small quantities throughout the whole season, while

Hymenoptera mostly emerged in later stages. The common sampling period among years was shown to be placed relatively early in the season of arthropod abundance (Figure 1).

Cumulative arthropod abundance in the common sampling period (18th of June to 4th of July) varied across the eight study years (2005 and 2014-2020; Figure 1 and 2), with an overall mean of $1.08\text{g} \pm 0.25$ ($n = 8$), ranging from 0.50g in 2019 to 2.69g in 2014. Cumulative Brachycera and Araneae abundance also showed interannual variation (Figure 2), with a mean of $0.53\text{g} \pm 0.17$ and $0.46\text{g} \pm 0.12$, respectively. Weather variables recorded in the study period (18th of June to 4th of July) showed considerable interannual fluctuations, with mean daily temperature ranging from 5.4°C to 7.4°C, mean total daily precipitation from 0.02mm to 0.95mm, and mean daily measured wind from 3.3m/s to 5.8m/s (Figure 2). Across the eight study years, total snowfall in the preceding winter ranged from 28mm in 2020 to 86mm in 2019, and timing of winter end varied from 3rd of May in 2018 to 30th of May in 2017 (Figure 2).

The highest-ranked model for variation in cumulative arthropod abundance only included the negative effect of wind ($\beta = -0.59$, CI[-1.076, -0.054], Table 2, Figure 3), and explained 52% of the variation in the data ($R^2_{\text{multiple}} = 0.52$). The only other candidate model with $\Delta\text{AIC}_c < 2$ was the intercept model, which was almost as parsimonious (Table 2). The highest-ranked model for variation in cumulative Brachycera abundance gave similar results (Appendix Table A3a), with wind as the only explanatory variable ($\beta = -0.38$, CI[-0.730, -0.024]). For variation in cumulative Araneae abundance, the only model with $\Delta\text{AIC}_c < 2$ included intercept only (Appendix Table A3b).

3.2 Arthropod abundance affecting chick weight

Mean chick weight varied across the study years of 2005 and 2014-2020 (Figure 2), ranging from $23.4\text{g} \pm 0.3$ ($n = 85$) in 2017, to $27.1\text{g} \pm 0.3$ ($n = 105$) in 2014. The related mean arthropod abundance measured in each nestling period showed an even larger interannual variation (Figure 2), ranging from $0.18\text{g} \pm 0.01$ ($n = 86$) in 2015, to $1.24\text{g} \pm 0.02$ ($n = 105$) in 2014. Mean Brachycera abundance in the nestling period was at its lowest in 2016 and peaked in 2014, while mean Araneae abundance ranged from lowest in 2019 to highest in 2005 (Figure 2).

The highest-ranked model for annual variation in chick weight in relation to overall arthropod abundance, included arthropod abundance in the nestling period, number of hatched eggs, and chick age at weighing day (Table 3). Arthropod abundance had a positive effect on chick weight ($\beta = 1.89$, CI[0.289, 3.395], Figure 4a), number of hatched eggs a negative effect ($\beta = -0.50$, CI[-0.830, -0.189], Figure 4b), and chick age a positive effect ($\beta = 1.83$, CI[1.078, 2.585], Figure 4c). 42% of the variance in chick weight was explained by both fixed and random effects, with solely fixed effects being responsible for 8% ($R^2_{\text{marginal}} = 0.08$, $R^2_{\text{conditional}} = 0.42$). Model 2 and 3 also had $\Delta\text{AIC}_c < 2$ (Table 3), including nest type as an additional fixed factor, and the second-order term of chick age as an additional fixed factor, respectively.

The highest-ranked model for annual variation in chick weight in relation to Brachycera abundance gave almost identical results (Appendix Table A4a), including Brachycera abundance in the nestling period ($\beta = 1.80$, CI[-0.003, 3.540]), number of hatched eggs ($\beta = -0.50$, CI[-0.820, -0.178]), and chick age ($\beta = 1.84$, CI[1.086, 2.598]). However, the 95% CI for the effect of Brachycera abundance slightly overlapped zero. The best-fit model for variation in chick weight in relation to Araneae abundance only included a negative effect of number of hatched eggs, and a positive effect of chick age (Appendix Table A4b).

Visual inspection of the co-fluctuations of the data time-series (Figure 2) indicated nestling weight variation to be highly synchronous with fluctuations in timing of winter end from year to year. I therefore performed a post hoc test, adding timing of winter end to the best ranked model, to analyse whether there was an additive effect of the weather variable. By adding this covariate, model selection now revealed the newly fitted model as the top ranked model ($\text{AIC}_c = 6030.1$ (ΔAIC_c from the previous top ranked model = 4.3), $w_i = 0.75$), where earlier winter end had a high positive effect on chick weight ($\beta = -0.06$, CI[-0.101, -0.016]). Other parameter estimates did not change substantially (arthropod abundance $\beta = 2.29$, number of hatched eggs $\beta = -0.44$, chick age $\beta = 1.76$).

3.3 Arthropod abundance affecting fledging success

Throughout the study years, the mean probability of chicks fledging per hatched egg ranged from $75\% \pm 0.03$ ($n = 54$) in 2005, to $91\% \pm 0.02$ ($n = 44$) in 2020 (Figure 2). As expected, the

correlation between mean annual fledging success and mean annual chick weight (section 3.2) was high (Pearson's correlation coefficient = 0.64).

The highest-ranked model for annual variation in fledging success in relation to overall arthropod abundance, included arthropod abundance in the nestling period, number of hatched eggs, and nest type (Table 4). Overall, fixed effects explained 26% of the variance in fledging success ($R^2_{\text{marginal}} = 0.26$, $R^2_{\text{conditional}} = 0.36$). The number of hatched eggs had a high negative effect on fledging success ($\beta = -0.45$, CI[-0.634, -0.274], Figure 5b), while the positive effect of arthropod abundance ($\beta = 0.66$, CI[-0.204, 1.483], Figure 5a) and the negative effect of nest type natural ($\beta_{\text{natural}} = -0.24$, CI[-0.530, 0.047], Figure 5c), were both rather uncertain. There was thus almost equal support for several models without arthropod abundance and nest type (i.e. $\Delta\text{AICc} < 2$) (Table 4).

The highest-ranked model for annual variation in fledging success in relation to Brachycera abundance gave almost identical results (Appendix Table A5a), including Brachycera abundance in the nestling period ($\beta = 0.75$, CI[-0.237, 1.636]), number of hatched eggs ($\beta = -0.45$, CI[-0.634, -0.274]), and nest type ($\beta_{\text{natural}} = -0.24$, CI[-0.530, 0.045]). Again, the 95% CIs overlapped zero for Brachycera abundance and nest type, indicating uncertainty in the estimates of the variables. The best-fit model for variation in fledging success in relation to Araneae abundance only included the two variables number of hatched eggs and nest type (Appendix Table A5b).

A similar post hoc test as above for chick weight was performed, in order to investigate the influence of timing of winter end as an additive effect. Model selection indicated a possible negative effect of timing of winter end on fledging success, but this effect was highly uncertain as the newly fitted model was ranked as the sixth best ($\text{AICc} = 638.9$, $\Delta\text{AICc} = 1.6$, $w_i = 0.10$), and with the 95% CI substantially overlapping zero ($\beta = -0.01$, CI[-0.039, 0.021]). Other parameter estimates did not change substantially (arthropod abundance $\beta = 0.70$, number of hatched eggs $\beta = -0.44$, nest-type $\beta = -0.25$).

3. Discussion

Our understanding of how warming-induced long-term changes in the high-Arctic environment affect trophic interactions has remained poor. Here, by monitoring and coupling breeding characteristics of snow buntings, and the abundance of their nestlings' food source, I have demonstrated important potential pathways through which climate change may impact the viability of migratory passerines. Eight years of data revealed large interannual variation in the amount and dynamics of arthropod abundance, showing Brachycera and Araneae to be the clearly most dominating groups (Figure 1). Results indicated a negative effect of wind on annual variation in cumulative arthropod abundance in the breeding season (Figure 3), but no evident effects of weather variables linked with climate warming. Arthropod abundance in the nestling period was however shown to positively affect chick weight (Figure 4), with a tendency for a similar effect on fledging success (Figure 5). Variation in Brachycera, a dominant group in terms of biomass, seemed to largely drive this relationship. Furthermore, post-hoc tests strongly indicated that earlier winter end (i.e. earlier onset of spring) had an additive positive effect on chick weight, while the effect on fledging success was less certain. These findings suggest that impacts of future warming on Arctic migratory passerines may operate through both direct and indirect effects.

Drivers of snow buntings' food availability and fitness-related parameters

Wind was the only weather variable having a substantial effect on cumulative arthropod abundance from 18th of June to 4th of July, showing a rather large effect size, although uncertain (as the intercept model was almost equally supported). When ranging from the lowest to the highest annual mean wind observed, the cumulative arthropod abundance (mean across years = 1.08g) was predicted to decrease with almost 1.50g (Figure 3). High wind speed has previously been shown to have a negative effect on arthropod availability (Tulp and Schekkerman, 2008; Bolduc et al., 2013; Shaftel et al., 20121). As catches from pitfall traps are not a measure of the true abundance of the arthropods, but rather the interaction between their activity and abundance (i.e. availability) (Southwood & Henderson, 2000; Woodcock, 2005), their catchability must be considered. Short-term weather fluctuations like daily wind can have a greater effect on daily arthropod activity than abundance (Tulp and Schekkerman, 2008), where arthropods could be less active in strong winds due to the risk of being blown away.

However, Høye & Forchhammer (2008b) investigated the effectiveness of pitfall traps in catching the representative number of arthropods, and found changes in activity due to short-term weather variables to have a limited effect on the abundance estimate.

The apparent lack of influence from weather variables such as temperature and timing of winter end is surprising, as these affect arctic arthropod abundance in several study systems (Hoset et al., 2004; Høye & Forchhammer, 2008a; Tulp and Schekkerman, 2008; Shaftel et al., 2021). A limited sample size of eight years could have inhibited detection of any potential effects of local weather conditions in the models, which also explains the uncertain effect of wind on arthropod abundance. The limited within-season arthropod sampling period of the present study (18th of June to 4th of July) could also potentially influence the predictive power of weather variables, i.e. a longer sampling period may have resulted in stronger or clearer weather effects. Another explanation could be that the Svalbard arthropod community is less sensitive to yearly weather fluctuations compared to lower-latitude study systems, and rather time their emergence based on other external cues such as photoperiod resulting from the diurnal cycle (Strathdee & Bale, 1998).

As predicted, high arthropod abundance in the nestling period of snow bunting chicks was associated with increased chick weight, although the effect size was not substantial. By extending from the minimum to the maximum amount of collected arthropods, the predicted observed chick weight increased with over 2.0g (Figure 4), with mean chick weight being 25g. The positive relationship between arthropod abundance and fledging success was more uncertain (95% CI overlapping zero). When keeping all other model covariates constant at their means, the estimated probability of fledging (mean = 0.82) increased from around 0.80 to 0.90 when ranging from the lowest to the highest amount of collected arthropods (Figure 5). These results correspond with the tight link observed between reproductive success in birds feeding their young with arthropods, and the abundance of this resource during breeding season (Perrins, 1991; Burger et al., 2012; McKinnon et al., 2012).

Not surprisingly, given the strong dominance of Brachycera in the arthropod samples, the results were almost similar when replacing arthropod abundance with Brachycera abundance. This may also indicate Brachycera to be the primary food source influencing chick growth and survival, which is in accordance with previous findings of insectivorous birds preferring larger sized prey items for their nestlings (McCarty & Winkler, 1999; Schwagmeyer & Mock, 2008).

As Brachycera is characterized as an insect group with large-sized individuals relative to the other groups identified at Svalbard, their apparent importance could be explained by the relationship between optimizing parental feeding effort vs. nestling growth. Higher biomass is caught per item when selecting Brachycera, which were also shown to be highly abundant throughout the study period (except in the earliest days of the season). Furthermore, a study on Svalbard snow bunting selectivity in nestling provisioning (Stolz, 2019), found a positive selection towards many dipteran families, which mostly constitutes the Brachycera group.

On the other side, even though Araneae also comprise a large portion of the collected arthropods in several years, the group did not seem to have a substantial effect on the fitness-related parameters. This may indicate a scenario where Araneae are not preferred by parents as a nestling food source at Svalbard, despite their high abundance around the breeding area, which is in accordance with findings by Stolz (2019). However, Araneae are reported to be an important food source for snow bunting nestlings in Greenland (Asbirk & Franzmann, 1978). Another explanation for their apparent lack of influence on reproductive success, could be a general overrepresentation of the group in the pitfall traps, through higher catchability (Uetz & Unzicker, 1976; Norment, 1987). Araneae availability to the snow bunting could in reality be relatively lower compared to e.g. Brachycera, thereby explaining their restricted influence on chick weight and fledging success.

Clearly, 2014 was an outlier in terms of both higher arthropod abundance in the overall sampling period and arthropod abundance in each nestling period (Figure 2), potentially with a strong effect on the results of the model selection as well as model output. Other environmental variables were therefore believed to have an effect on reproductive success. Visual inspection of annual co-fluctuations indicated that year-to-year fluctuations in timing of winter end may influence fluctuations in fitness-related parameters (Figure 2), which was why post-hoc tests were performed. The year 2014 was an exception to these apparent co-fluctuations, which could be explained by exceptionally low wind that year (Figure 2). Low wind could result in reduced exposure of the chicks (Bakken, 1990; Skjøstad, 2008) and higher catchability of arthropods for the parents (Cherry & Barton, 2017), both potentially improving reproductive success. The result of increased chick weight with earlier winter end may seem to contradict previous studies on the Svalbard snow bunting (Hoset et al., 2009; Fossøy et al., 2014), which revealed higher spring temperatures to result in earlier egg laying, and earlier egg laying to result in reduced reproductive success (counter to many avian species; Verhulst & Nilsson, 2008). However, the

opposing findings can be linked to the restricted period of time in which monitored nests are analysed (18th of June to 4th of July), which can be viewed as relatively mid-late in the breeding season of the snow bunting, as average egg laying start before mid of June (Fossøy et al., 2014). Thus, these post-hoc findings allowing for an additive weather effect in the modelling, suggest early onset of spring to increase reproductive success measured mid-late in the breeding season, which does not necessarily oppose the previous findings.

Additional factors believed to be of importance for chick weights and fledging rates were also included in the model analyses. Brood size (i.e. number of hatched eggs) had a substantial negative effect on chick weight, as was predicted according to life-history theory in general (Stearns, 1992), and findings in the snow bunting and other avian species (DeKogel, 1997; Rytönen & Orell, 2001; Espmark et al., 2016). The effect size was relatively large, showing an estimated decrease in chick weight of around 2.5g when going from sharing a nest with two vs. seven hatched siblings (Figure 4). The effect was also large for fledging success, indicating an estimated drop in fledging probability from around 0.96 to 0.73, when all other covariates were kept constant at their means (Figure 5). A nest-type variable was also included in the highest-ranked fledging success model, with natural nests believed to be more exposed to predation and extreme weather compared to nests laid in nest-boxes (Espmark, 2016), thus possibly resulting in lower reproductive success for the snow bunting. The covariate showed both high uncertainty and a low effect size, with a drop in fledging probability from around 0.86 in nest boxes to 0.83 in natural nests (keeping all other covariates constant at their means)(Figure 5). Thus, results indicate variability in nest-type to be of less importance for snow bunting reproductive success.

Other additional factors not included here could also explain reproductive success, but this was largely restricted by few years of data (arthropod sampling). These factors include weather variables like temperature, precipitation and wind, together with regional climate indexes, as some of these factors have been suggested to influence snow bunting reproductive success at Svalbard (Hoset et al., 2004; Fossøy et al., 2014; Skøien, 2015). Unfortunately, the limited overlap in sampling period between years (arthropods) also largely restricted the possibility of analysing measurements of phenology, such as timing of snow bunting breeding versus arthropod emergence/peak, i.e. the effects of a trophic match/mismatch on reproductive success.

Implications and Future Directions

In the present study, I have highlighted the importance of arthropod abundance for reproductive success in the Svalbard snow bunting, primarily by enhancing chick growth. As high nestling weight has been proven essential for juvenile survival and breeding in other species (Magrath, 1991; Linden et al., 1992; Both et al., 1999), it is likely that this effect on chick weight will, in turn, influence recruitment into the breeding population of the Svalbard snow bunting. Furthermore, 69% of all available nests identified had a nestling period within 18th of June to 4th of July (common arthropod sampling period), which seems relatively early in the arthropod emergence season (Figure 1; Bolduc et al., 2013; Dahl et al., 2018). This may lend support to the notion by Fossøy et al. (2014) of a possible trophic mismatch for the Svalbard snow bunting, i.e. timing of breeding could be too early in relation to peak arthropod abundance. However, this is a likely trade-off, where later onset of breeding could result in restricted time for further chick growth and development following fledging and before migrating to the wintering grounds (Dunn & Winkler, 2010; Lameris et al., 2017). Continued future warming may still lead to a disruption of the trophic interactions, where key arthropods' phenology may change at a different rate than onset of breeding (Visser et al., 1998; Both et al., 2009; Dunn & Winkler, 2010; Clausen & Clausen, 2013; Lehikoinen et al., 2019). The observed negative long-term trend in nestling weight across a 15-year study period of the local snow bunting population (Fossøy et al., 2014), may be a result of such mismatch, although this still needs to be tested. Similar consequences have also been presented in other study systems (Visser et al. 1998, Both and Visser 2001; Saalfeld et al., 2019).

In order to acquire more information on how climate change will impact the snow bunting-arthropod dynamics in the future, further investigations into the timing of breeding events versus peak arthropod abundance are needed. Longer-term studies expanding over the whole arthropod emergence cycle each summer, and over more years, will enable us to analyse the fitness consequences of timing of breeding relative to the timing of seasonal resource abundance. We can thus test the trophic match-mismatch hypotheses (on e.g. chick weight and fledging success) (McKinnon et al., 2012), which can eventually help to predict future population viability in the Svalbard snow bunting. Furthermore, experimental studies investigating how varying levels of arthropod abundance will directly affect offspring fitness in the snow bunting, can also increase our knowledge around the population's reliance on arthropods. Manipulation of arthropod availability to the provisioning parents (see e.g. Arcese

& Smith (1988) for song sparrows (*Melospiza melodia*) can give indications of the amount of food abundance which is needed for sufficient chick growth and survival, e.g. by finding a certain arthropod abundance threshold needed for mean chick weight to be reached. Thus, even though the present study has improved our understanding of the associations between weather, arthropod abundance and snow bunting reproduction at Svalbard, further investigations are clearly needed to get a more holistic view of the ecosystem, and how climate warming may alter its trophic interactions.

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Tables

Table 1. Metadata of arthropod sampling in Adventdalen, Svalbard, in years 2005 and 2014-2020. Sampling period = range from first to last arthropod collection event, where 1 = 1st of May, Sampling frequency = frequency of the arthropod collection events.

Year	Sampling period	Sampling frequency
2005	43-79	Every 2 nd day
2014	45-81	Every 2 nd day
2015	43-79	Every 2 nd day
2016	43-67	Every 2 nd day
2017	43-75	Every 4 th day
2018	39-97	Every 4 th day
2019	41-89	Every 4 th day
2020	49-69	Every 4 th day

Table 2. Linear models from AIC_c model selection, explaining variation in cumulative arthropod biomass (g) among years (response variable). Additional explanatory variables only included in lower ranked models are not represented in the table (see section 2.3 for details). The table shows parameter estimates (β) with standard errors (\pm SE), as well as the number of parameters (K), AIC_c values with the respective Δ AIC_c value, and AIC_c weights (w_i) for each model. Explanatory variables included are mean recorded daily wind (m/s) and temperature (°C) from 18th of June to 4th of July, and total snowfall (mm) in the preceding winter. Variables in the highest-ranked model with a 95% CI not overlapping zero (see text, section 3), is marked in bold.

Model	Explanatory variables				Model selection criteria		
	Intercept	Wind	Temperature	Snowfall	K	AIC _c (Δ)	w_i
1	4.04 \pm 1.17	-0.59 \pm 0.23	-	-	3	21.9 (0.0)	0.37
2	1.08 \pm 0.25	-	-	-	2	22.2 (0.3)	0.32
3	5.34 \pm 0.97	-0.63 \pm 0.17	-	-0.02 \pm 0.01	4	24.4 (2.5)	0.11
4	3.62 \pm 1.92	-	-0.42 \pm 0.31	-	3	25.7 (3.8)	0.06
5	2.07 \pm 0.81	-	-	-0.02 \pm 0.01	3	25.9 (4.0)	0.05

Table 3. Linear mixed effects models from AIC_c model selection, explaining variation in snow bunting chick weight (g) (response variable), in relation to overall arthropod abundance (g). All models include year and nestID as random effects, and additional explanatory variables only included in lower ranked models are not represented in the table (see section 2.3 for details). The table shows parameter estimates (β) with standard errors (\pm SE), as well as the number of parameters (K), AIC_c values with the respective Δ AIC_c value, and AIC_c weights (w_i) for each model. All models have been refitted with REML before presenting parameter estimates. Explanatory variables included are arthropod biomass in the respective nest's nestling period (g), number of hatched eggs, natural nest type (in contrast to nests laid in nest boxes [intercept]), chick age at weighing day (only allowed in models with the first-order term), and the second-order term of chick age at weighing day. Variables in the highest-ranked model with a 95% CI not overlapping zero (see text, section 3), is marked in bold.

Model	Explanatory variables						Model selection criteria		
	Intercept	Arthropod biomass	No. hatched	Nest type (natural)	Age	Age ²	K	AIC _c (Δ)	w_i
1	12.79 \pm 3.24	1.89 \pm 0.79	-0.50 \pm 0.16	-	1.83 \pm 0.39	-	7	6034.4 (0.0)	0.34
2	13.32 \pm 3.27	1.85 \pm 0.82	-0.53 \pm 0.17	-0.41 \pm 0.32	1.82 \pm 0.39	-	8	6035.0 (0.6)	0.25
3	23.31 \pm 17.20	1.82 \pm 0.81	-0.50 \pm 0.16	-	-0.85 \pm 4.32	0.17 \pm 0.27	8	6036.1 (1.7)	0.14
4	24.88 \pm 17.20	1.77 \pm 0.85	-0.53 \pm 0.17	-0.42 \pm 0.32	-1.12 \pm 4.31	0.19 \pm 0.27	9	6036.7 (2.3)	0.11
5	13.77 \pm 3.25	-	-0.52 \pm 0.16	-	1.81 \pm 0.39	-	6	6037.3 (2.9)	0.08

Table 4. Binomial generalized linear mixed effects models from AIC_c model selection, explaining variation in snow bunting chick fledging success (response variable), in relation to overall arthropod abundance (g). All models include year as random effect, and additional explanatory variables only included in lower ranked models are not represented in the table (see section 2.3 for details). The table shows parameter estimates (β) with standard errors (\pm SE), as well as the number of parameters (K), AIC_c values with the respective Δ AIC_c value, and AIC_c weights (w_i) for each model. Explanatory variables included are arthropod biomass in the respective nest's nestling period (g), number of hatched eggs, natural nest type (in contrast to nests laid in nest boxes [intercept]), and the interaction between natural nest type and arthropod biomass (NTN : T). Variables in the highest-ranked model with a 95% CI not overlapping zero (see text, section 3), is marked in bold.

Model	Explanatory variables					Model selection criteria		
	Intercept	Arthropod biomass	No. hatched	Nest type (natural)	NTN : T	K	AIC _c (Δ)	w_i
1	4.05 \pm 0.59	0.66 \pm 0.41	-0.45 \pm 0.09	-0.24 \pm 0.15	-	5	637.3 (0.0)	0.26
2	4.28 \pm 0.58	-	-0.45 \pm 0.09	-0.23 \pm 0.15	-	4	637.6 (0.3)	0.22
3	3.79 \pm 0.57	0.61 \pm 0.40	-0.43 \pm 0.09	-	-	4	637.9 (0.6)	0.19
4	4.02 \pm 0.56	-	-0.43 \pm 0.09	-	-	3	637.9 (0.7)	0.19
5	4.19 \pm 0.61	0.27 \pm 0.55	-0.46 \pm 0.09	-0.42 \pm 0.24	0.59 \pm 0.60	6	638.4 (1.2)	0.15

Figures

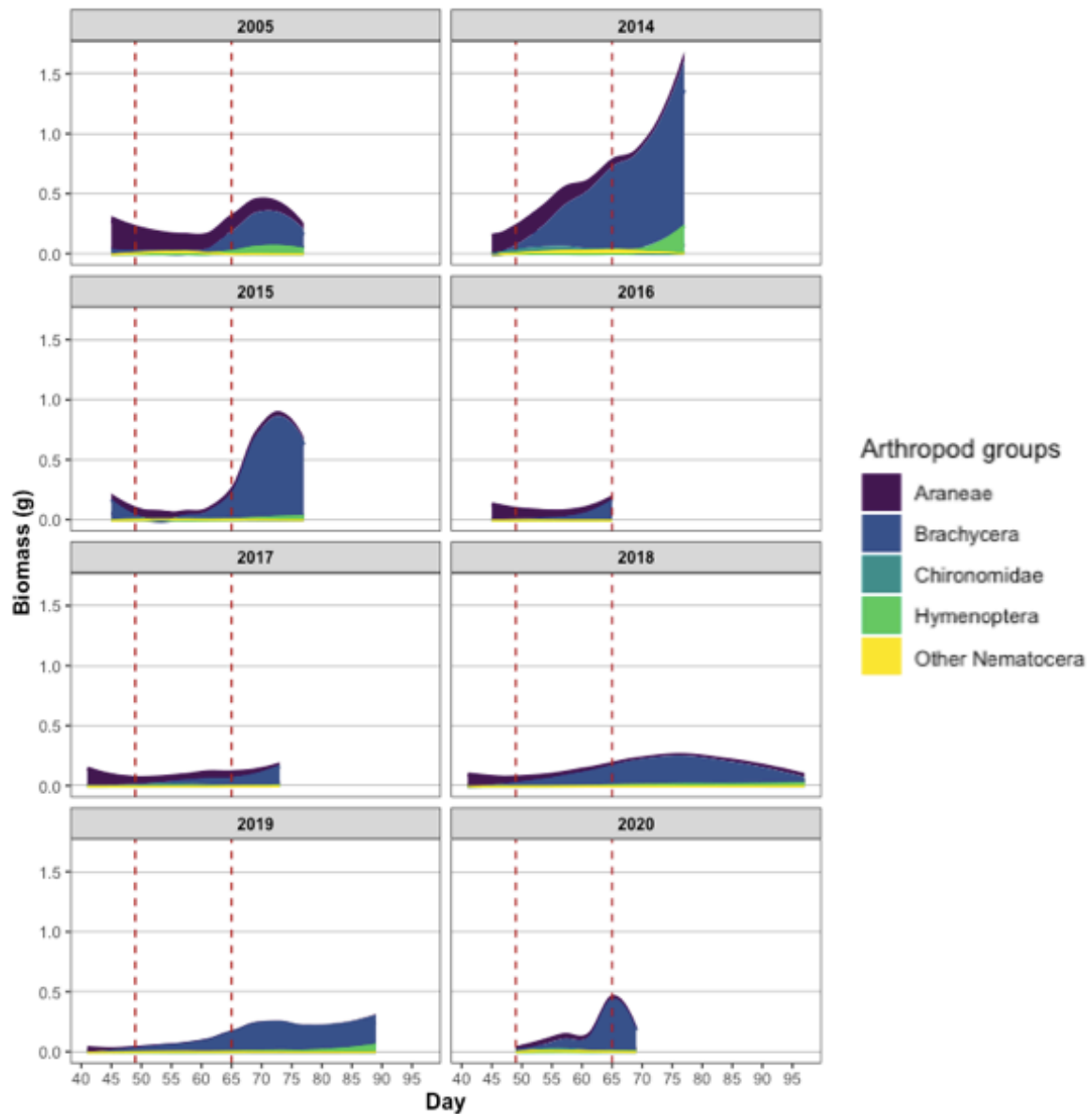


Figure 1. Seasonal and annual variation in arthropod biomass from 2005, 2014-2020, sampled in Adventdalen, Svalbard. Measured by 20 pitfall traps per sampling day in both wet and dry habitats, for the arthropod groups Araneae, Brachycera, Chironomidae, Hymenoptera, and other Nematocera. Day 1 = 1st of May. Red dotted lines delineate the period that is covered by all years (day 49-65).

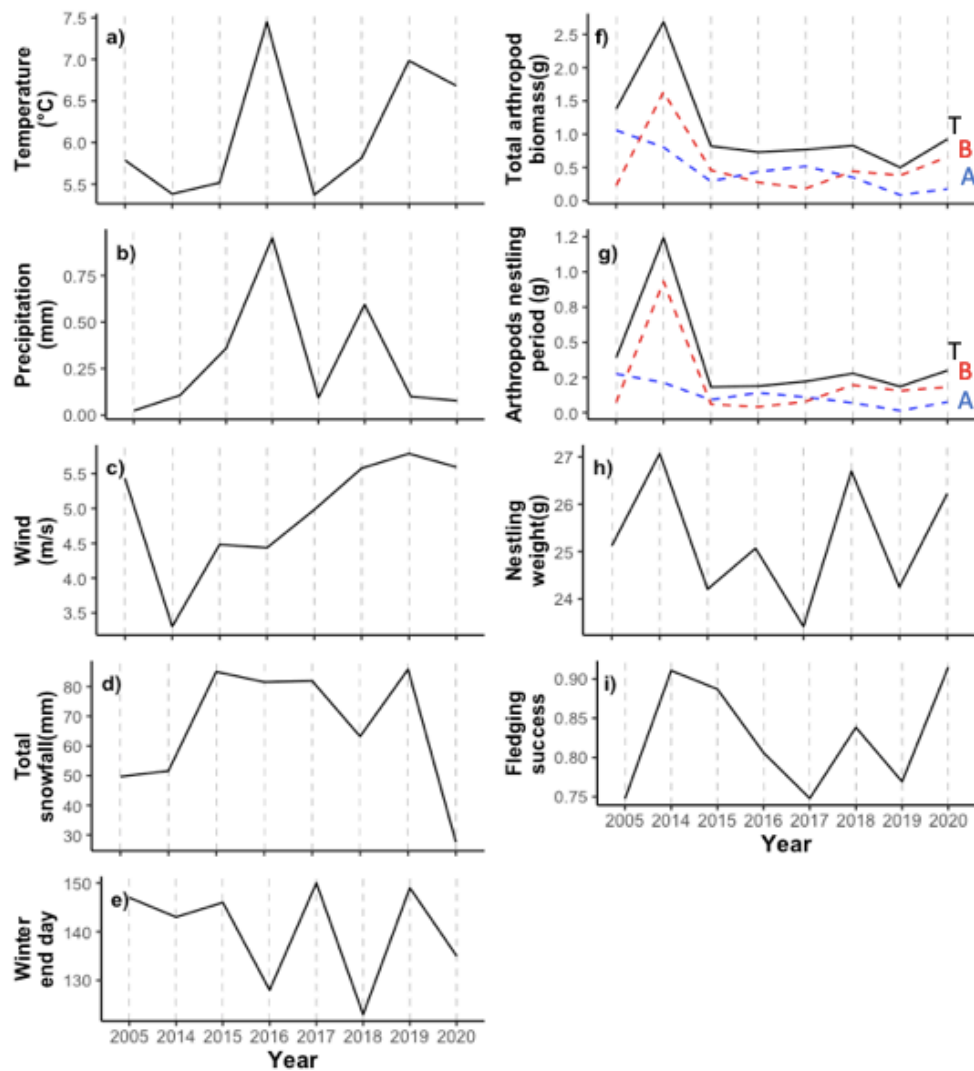


Figure 2. Annual mean values in years 2005, 2014-2020 of **a)** daily temperature from 18th of June to 4th of July, **b)** total daily precipitation from 18th of June to 4th of July, **c)** daily measured wind from 18th of June to 4th of July, **d)** total snowfall in preceding winter from November to April, **e)** timing of winter end (Julian days), **f)** total cumulative arthropod biomass in the common sampling period (18th of June to 4th of July), where T = arthropods in total, B = Brachycera, A = Araneae, **g)** arthropod biomass in the nestling period (8 days before weighing) of snow bunting chicks, where T = arthropods in total, B = Brachycera, A = Araneae, **h)** individual nestling weight, and **i)** probability of fledging.

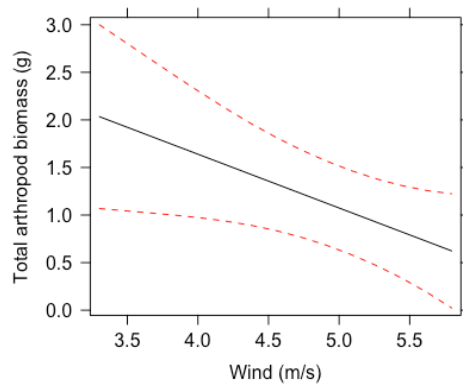


Figure 3. Effect plot of estimate from Model 1, Table 2, showing the effect of mean daily wind on annual total cumulative arthropod biomass. The variable is measured from 18th of June to 4th of July. Red dotted lines represent lower and upper 95% confidence intervals.

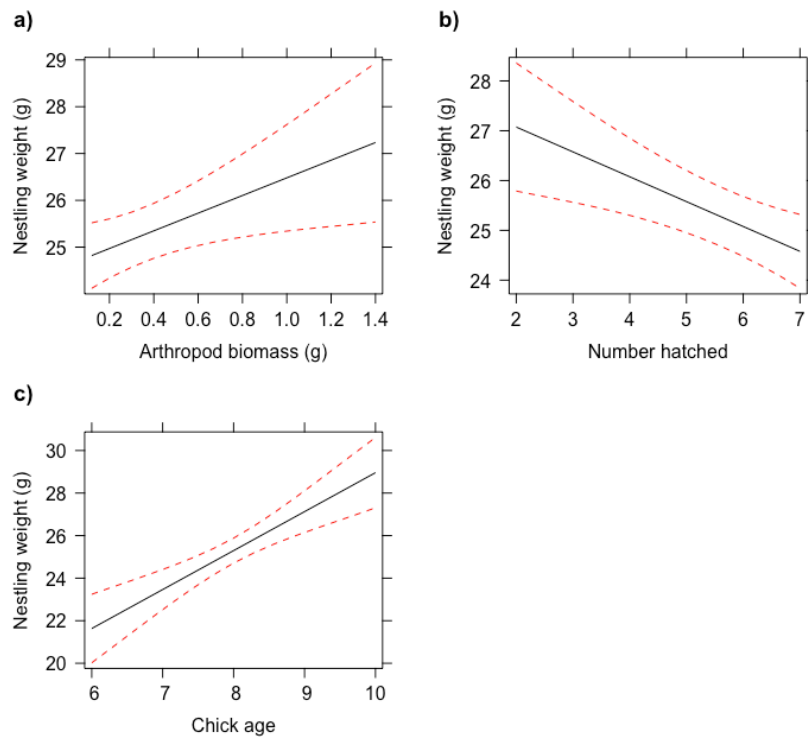


Figure 4. Effect plots of estimates from Model 1, Table 3, showing effects on mean nestling weight of a) arthropod biomass in the nestling period, b) number of hatched eggs, and c) chick age at weighing day. Red dotted lines represent lower and upper 95% confidence intervals.

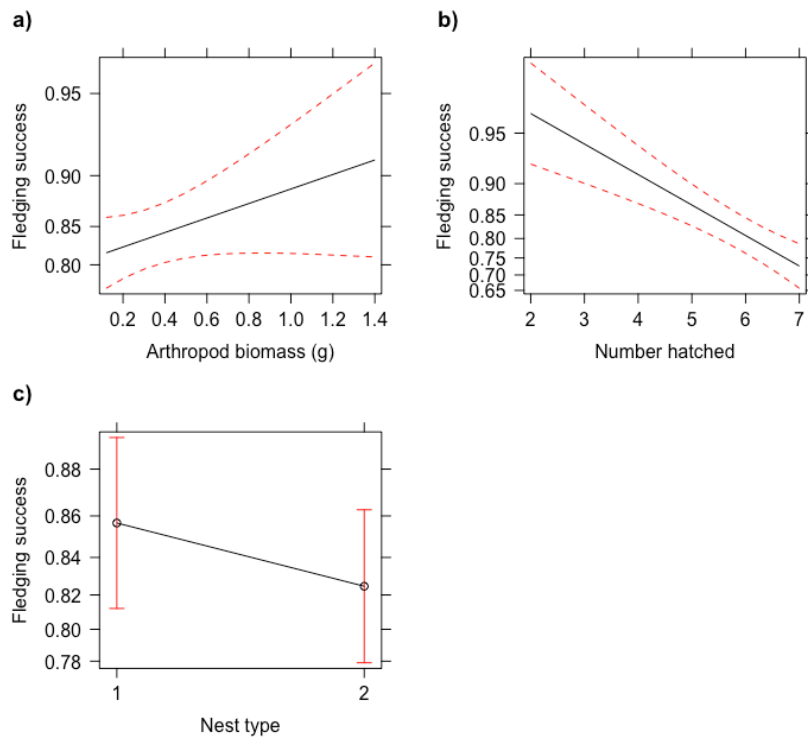


Figure 5. Effect plots of estimates from Model 1, Table 4, showing effects on chick fledging success of a) arthropod biomass in the nestling period, b) number of hatched eggs, and c) nest type (1 = nest box, 2 = natural). Red dotted lines/bars represent lower and upper 95% confidence intervals.

Appendix

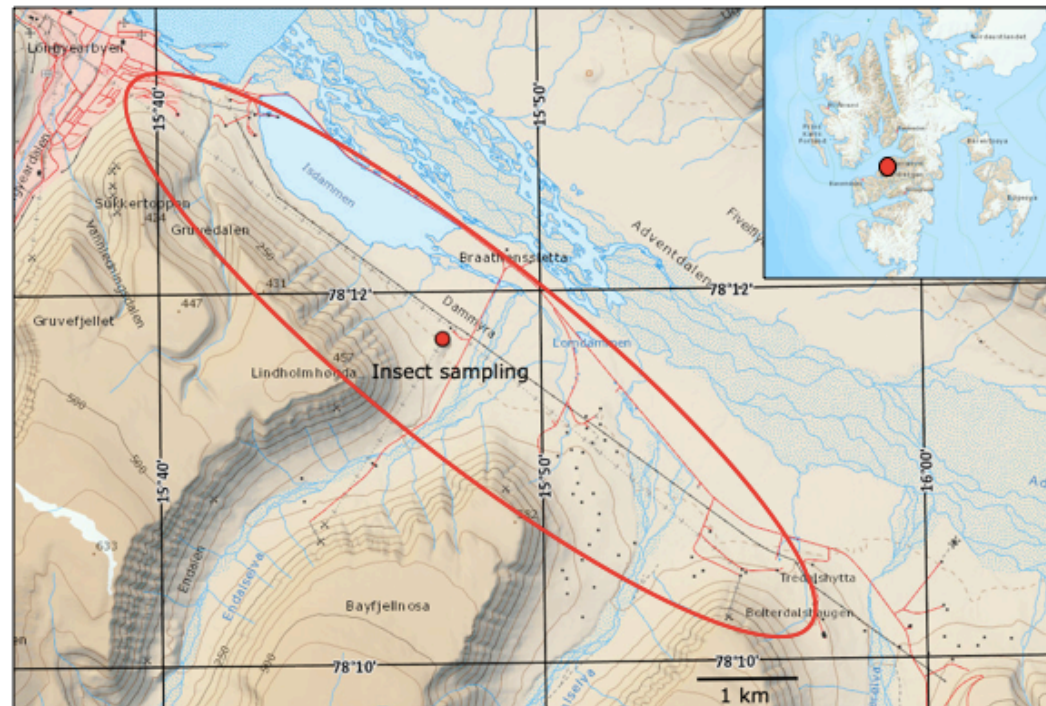


Figure A1. Geographical location of the study site in the valley Adventdalen, Svalbard ($78^{\circ}13'N$, $15^{\circ}38'E$). The red ellipse represents the approximate study area of snow bunting nest monitoring, while the insect sampling area is located by the red pin. The map is using a base map from the Norwegian Polar Institute (2021b).

Table A1. Pearson’s correlation coefficients between continuous explanatory variables in the modelling of interannual variation in cumulative arthropod biomass (g). All explanatory variables are measured in years 2005, 2014-2020. Temperature = mean daily temperature (°C) from 18th of June to 4th of July, Precipitation = total daily precipitation (mm) from 18th of June to 4th of July, Wind = mean daily measured wind (m/s) from 18th of June to 4th of July, Snowfall = total snowfall (mm) in preceding winter, and Winter end = timing of winter end (see section 2.2.3 for details).

	Temperature	Precipitation	Wind	Snowfall	Winter end
Temperature	-				
Precipitation	0.45	-			
Wind	0.32	-0.16	-		
Snowfall	0.08	0.39	-0.08	-	
Winter end	-0.37	-0.75	-0.07	0.23	-

Table A2. Pearson’s correlation coefficients between continuous explanatory variables in the modelling of variation in snow bunting chick weight (g) and fledging success. All explanatory variables are measured in years 2005, 2014-2020. No. hatched = Number of hatched eggs, Age = chick age at weighing day, Arthropod biomass = arthropod biomass (g) in the nestling period, Brachycera biomass = Brachycera biomass (g) in the nestling period, Araneae biomass = Araneae biomass (g) in the nestling period.

	No. hatched	Age	Arthropod biomass	Brachycera biomass	Araneae biomass
No. hatched	-				
Age	0	-			
Arthropod biomass	-0.01	-0.04	-		
Brachycera biomass	-0.04	-0.06	0.94	-	
Araneae biomass	0.05	0.04	0.38	0.05	-

Table A3. Linear models from AIC_c model selection, explaining variation among years in a) cumulative Brachycera biomass (g) (response variable), and b) cumulative Araneae biomass (g) (response variable). Additional explanatory variables only included in lower ranked models are not represented in the table (see section 2.3 for details). The table shows parameter estimates (β) with standard errors (\pm SE), as well as the number of parameters (K), AIC_c values with the respective Δ AIC_c value, and AIC_c weights (w_i) for each model. Explanatory variables included are mean recorded daily wind (m/s), temperature (°C) and precipitation (mm) (in A3b.) from 18th of June to 4th of July, and total snowfall (mm) in the preceding winter. Variables in the highest-ranked model with a 95% CI not overlapping zero (see text, section 3), is marked in bold.

a)

Model	Intercept	Explanatory variable			Model selection criteria		
		Wind	Temperature	Snowfall	K	AIC _c (Δ)	w_i
1	2.41 \pm 0.73	-0.38 \pm 0.14	-	-	3	15.5 (0.0)	0.46
2	0.53 \pm 0.17	-	-	-	2	16.0 (0.5)	0.36
3	1.14 \pm 0.56	-	-	-0.01 \pm 0.01	3	20.1 (4.5)	0.05
4	3.13 \pm 0.70	-0.39 \pm 0.12	-	-0.01 \pm 0.01	4	20.2 (4.7)	0.04
5	1.48 \pm 1.47	-	-0.15 \pm 0.24	-	3	21.0 (5.5)	0.03

b)

Model	Explanatory variable					Model selection criteria		
	Intercept	Wind	Temperature	Precipitation	Snowfall	K	AIC _c (Δ)	w _i
1	0.46 ± 0.12	-	-	-	-	2	10.1 (0.0)	0.68
2	1.13 ± 0.69	-0.13 ± 0.14	-	-	-	3	14.5 (4.4)	0.08
3	1.34 ± 0.99	-	-0.14 ± 0.16	-	-	3	14.7 (4.6)	0.07
4	0.56 ± 0.16	-	-	-0.56 ± 0.65	-	3	14.7 (4.7)	0.07
5	0.74 ± 0.41	-	-	-	-0.004 ± 0.01	3	15.0 (5.0)	0.06

Table A4. Linear mixed effects models from AIC_c model selection, explaining variation in snow bunting chick weight (g) (response variable), in relation to Brachycera and Araneae abundance (g). All models include year and nestID as random effects, and additional explanatory variables only included in lower ranked models are not represented in the table (see section 2.3 for details). The table shows parameter estimates (β) with standard errors (\pm SE), as well as the number of parameters (K), AIC_c values with the respective Δ AIC_c value, and AIC_c weights (w_i) for each model. All models have been refitted with REML before presenting parameter estimates. Explanatory variables included are a) Brachycera biomass in the respective nest's nestling period (g), b) Araneae biomass in the respective nest's nestling period (g), number of hatched eggs, natural nest type (in contrast to nests laid in nest boxes [intercept]), chick age at weighing day, and the second-order term of chick age at weighing day (only allowed in models with the first-order term). Variables in the highest-ranked model with a 95% CI not overlapping zero (see text, section 3), is marked in bold.

a)

Model	Explanatory variables						Model selection criteria		
	Intercept	Brachycera biomass	No. hatched	Nest type (natural)	Age	Age ²	K	AIC _c (Δ)	w_i
1	13.00 \pm 3.25	1.80 \pm 0.86	-0.50 \pm 0.16	-	1.84 \pm 0.39	-	7	6035.5 (0.0)	0.31
2	13.57 \pm 3.27	1.72 \pm 0.89	-0.52 \pm 0.17	-0.42 \pm 0.32	1.82 \pm 0.39	-	8	6036.1 (0.6)	0.23
3	24.16 \pm 17.23	1.71 \pm 0.88	-0.49 \pm 0.16	-	-1.00 \pm 4.33	0.18 \pm 0.27	8	6037.2 (1.7)	0.13
4	13.77 \pm 3.25	-	-0.52 \pm 0.16	-	1.81 \pm 0.39	-	6	6037.3 (1.8)	0.13
5	25.79 \pm 17.22	1.61 \pm 0.91	-0.53 \pm 0.17	-0.43 \pm 0.32	-1.28 \pm 4.31	0.20 \pm 0.27	9	6037.7 (2.2)	0.10

b)

Model	Explanatory variables						Model selection criteria		
	Intercept	Araneae biomass	No. hatched	Nest type (natural)	Age	Age ²	K	AIC _c (Δ)	w _i
1	13.77 ± 3.25	-	-0.52 ± 0.16	-	1.81 ± 0.39	-	6	6037.3 (0.0)	0.35
2	30.02 ± 17.15	-	-0.55 ± 0.16	-0.46 ± 0.32	-2.15 ± 4.31	0.25 ± 0.27	8	6038.6 (1.3)	0.18
3	13.63 ± 3.27	1.87 ± 4.07	-0.52 ± 0.16	-	1.80 ± 0.39	-	7	6039.0 (1.7)	0.15
4	14.24 ± 3.29	1.65 ± 4.17	-0.56 ± 0.17	-0.452 ± 0.32	1.78 ± 0.39	-	8	6039.2 (1.9)	0.13
5	28.53 ± 17.21	1.82 ± 4.10	-0.53 ± 0.16	-	-2.00 ± 4.33	0.24 ± 0.27	8	6040.3 (3.0)	0.08

Table A5. Binomial generalized linear mixed effects models from AIC_c model selection, explaining variation in snow bunting chick fledgling success (response variable), in relation to Brachycera and Araneae abundance (g). All models include year as random effect, and additional explanatory variables only included in lower ranked models are not represented in the table (see section 2.3 for details). The table shows parameter estimates (β) with standard errors (\pm SE), as well as the number of parameters (K), AIC_c values with the respective Δ AIC_c value, and AIC_c weights (w_i) for each model. Explanatory variables included are a) Brachycera biomass in the respective nest's nestling period (g), b) Araneae biomass in the respective nest's nestling period (g), number of hatched eggs, natural nest type (in contrast to nests laid in nest boxes [intercept]), and the interaction between a) natural nest type and total Brachycera biomass (NTN : B), and b) natural nest type and Araneae biomass (NTN : A). Variables in the highest-ranked model with a 95% CI not overlapping zero (see text, section 3), is marked in bold.

a)

Model	Explanatory variables					Model selection criteria		
	Intercept	Brachycera biomass	No. hatched	Nest type (natural)	NTN : B	K	AIC _c (Δ)	w_i
1	4.14 \pm 0.58	0.75 \pm 0.46	-0.45 \pm 0.09	-0.24 \pm 0.15	-	5	637.3 (0.0)	0.26
2	4.28 \pm 0.58	-	-0.45 \pm 0.09	-0.23 \pm 0.15	-	4	637.6 (0.3)	0.23
3	4.02 \pm 0.56	-	-0.43 \pm 0.09	-	-	3	637.9 (0.6)	0.19
4	3.87 \pm 0.55	0.69 \pm 0.45	-0.43 \pm 0.09	-	-	4	638.0 (0.6)	0.19
5	4.20 \pm 0.59	0.42 \pm 0.62	-0.45 \pm 0.09	-0.31 \pm 0.18	0.52 \pm 0.70	6	638.9 (1.6)	0.12

b)

Model	Explanatory variables					Model selection criteria		
	Intercept	Araneae biomass	No. hatched	Nest type (natural)	NTN : A	K	AIC _c (Δ)	w _i
1	4.28 ± 0.58	-	-0.45 ± 0.09	-0.23 ± 0.15	-	4	637.6 (0.0)	0.37
2	4.02 ± 0.56	-	-0.43 ± 0.09	-	-	3	637.9 (0.4)	0.31
3	4.25 ± 0.61	0.29 ± 1.67	-0.45 ± 0.09	-0.23 ± 0.15	-	5	639.6 (2.1)	0.13
4	3.99 ± 0.59	0.27 ± 1.66	-0.43 ± 0.09	-	-	4	640.0 (2.4)	0.11
5	4.40 ± 0.63	-0.72 ± 1.91	-0.45 ± 0.09	-0.46 ± 0.63	1.68 ± 1.47	6	640.4 (2.9)	0.09

