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# Body mass growth in nestlings of Svalbard snow buntings (*Plectrophenax nivalis*) in response to seasonal variation in arthropod biomass

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## Abstract

Breeding birds are facing a myriad of trade-offs during their life cycle to maximize survival and reproduction leading to high fitness during their life time. For migrating birds one of these trade-offs include when to forage and regain strength after a long migration distance to the breeding ground, and when to stop foraging and start breeding. The snow bunting (*Plectrophenax nivalis*) population breeding on Svalbard depend on arthropods as food for their nestlings, and their reproductive success is therefore assumed to be sensitive to fluctuations in arthropod abundance during the short summer season. Here, I investigated how snow bunting nestling body mass and growth depended on daily fluctuations in an arthropod abundance proxy. This was done by repeatedly collecting arthropods in pitfall traps and measuring nestling body weight four, six, and eight days after hatching in Adventdalen, Svalbard. There were fluctuations in both arthropod abundance and nestling weight and growth throughout the season. The arthropod biomass abundance was found to have a positive effect on the growth between day four and six, as well as being strongly correlated with the ambient temperatures. An effect of arthropod abundance on growth was only found in artificial nest boxes, and not natural nests. I found no strong evidence that the arthropod abundance affected the growth from day six to eight or any correlation with the weight. The nestlings weighed during the period with low arthropod abundance were mostly young (four to six days old) and lived in artificial nest boxes (due to the quick inhabitation of nest boxes compared to natural nests). A critical biomass value for the nestlings would justify the lack of correlation found between arthropod abundance and other growth factors, with sufficient access to food supply with high arthropod abundance. The present study shows that the study population is mainly affected by arthropod fluctuations at the beginning of the season and more generally, gives insight to how the food resource is affecting the breeding phenology of a passerine migrant during one season.

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## Sammendrag

Hekkende fugler står overfor et utall avveininger i løpet av deres livssyklus for å maksimere overlevelse og reproduksjon som fører til høy levedyktighet. For trekkfugler inkluderer en av disse avveiningene å lete etter mat og regenerere styrke etter en lang migrasjonssavstand til hekkeplassen, og når du skal slutte å lete etter mat og starte reproduksjon. Snøspurv (*Plectrophenax nivalis*) på Svalbard er avhengig av leddyrliv som fôr for ungene sine, og deres reproduksjonssuksess antas derfor å være følsom for svingninger i forekomsten av leddyrliv i løpet av den korte sommersesongen. Her undersøkte jeg hvordan snøspurvungenes kroppsmasse og vekst var avhengig av daglige svingninger i leddyrlivstanden. Dette ble gjort ved å gjentatte ganger samle leddyrliv i feller og måle ungenes kroppsvikt fire, seks og åtte dager etter klekking i Adventdalen, Svalbard. Det var svingninger i både leddyrlivforekomst og snøspurvungenes vekt og vekst gjennom sesongen. Leddyrlivforekomsten ble funnet til å ha en positiv effekt på veksten mellom dag fire og seks, i tillegg til at den var sterkt korrelert med omgivelsestemperaturene. Leddyrlivforekomsten påvirket kun veksten i kunstige reirbokser, og ikke i naturlige reir. Jeg fant ingen sterke bevis for at leddyrlivforekomsten påvirket veksten fra dag seks til åtte eller noen korrelasjon med vekt. Snøspurvungene som ble veid i perioden med lav leddyrlivforekomst var stort sett små (fire til seks dager gamle) og bodde i kunstige reirbokser (på grunn av den raske innflyttingen i reirbokser sammenlignet med naturlige reir). En kritisk biomasseverdi for snøspurvungene ville forklart den manglende korrelasjonen mellom leddyrlivforekomst og andre vekstfaktorer, med en stor nok tilgang på mat ved høy leddyrlivforekomst. Denne studien viser at studiepopulasjonen hovedsakelig er påvirket av svingninger i leddyrlivforekomsten i begynnelsen av sesongen og mer generelt gir innblikk i hvordan matressursen påvirker hekkefenologien til en migrerende spurvefugl i løpet av en sesong.

# Introduction

The life of breeding birds contains many challenges, such as finding food, avoid being predated, finding a mate and reproduce (Ricklefs, 1968). This can be summarized as surviving and successfully raising offspring to independence. To achieve this they are, according to life history theory, facing a myriad of trade-offs that are crucial for succeeding (Williams, 1966). This includes decisions on when they should prioritize reproduction versus survival and when they should prioritize current broods over possible future broods (Williams, 1966). All of these decisions affect their offspring, and can impact their rate of body growth, fledgling success and survival (Ricklefs, 1968). Several studies of passerines have established that the weight of the nestlings is an important early life history trait because of the positive correlation between weight and first-year survival (Perrins, 1965; Ringsby et al., 1998). Ringsby et al. (1998) discovered that, by studying different reproductive traits and conditional traits of nestlings in a house sparrow (*Passer domesticus*) population, the larger fledglings survived more often than the smaller ones.

Life-history theory is research on the broader concepts of biology, connecting research on behaviour, ecology, population biology and evolution together with the organisms and populations in their environments (Ricklefs, 2000). According to life history-theory, phenology is affected by an interaction of ecological impact on survival and reproduction, and trade-offs among life history traits (Stearns, 2000). Phenology refers to the seasonal timing of life cycle events (Lieth, 1974), such as when to mate, molt and migrate. Several studies found that food availability affects the timing of breeding, and thereby the breeding success (Naef-Daenzer and Keller, 1999; Perrins, 1970; Verboven and Visser, 1998; Visser and Verboven, 1999). The study of Naef-Daenzer and Keller (1999) investigated the relationship between prey density and foraging performance in great tit (*Parus major*) and blue tit (*Cyanistes caeruleus*). It was found that foraging success by the parents was highly affected by the peak of food abundance, causing the nestlings to have a peak in the growth correlating to the peak of food abundance. Consequently, selection will act to appropriately match the time of breeding to the emergence of arthropods for the insectivorous avian species (Marciniak et al., 2007; Young, 1994). In order to raise successful offspring it is important that the peak food availability is matched with the need for food, and it has been shown that avian breeding season coincide with the peak of food abundance (Moreau, 1950; Lack, 1950). This correlation between food peak and peak of demand can change if the birds breeding do not coincide with the emergence of arthropods. Research show that if the food supply is reduced, the nestlings will be negatively affected by having lower weight than the ones having a more abundant food supply (Siikamäki, 1998).

The change in food peak and demand peak correlation can be caused by climate change causing a shift towards earlier spring and summer (Walther et al., 2002). The climate is now changing, and due to the higher concentrations of CO<sub>2</sub> and other greenhouse gases, the atmosphere is getting warmer (An, 2018). The warmer temperatures will have an effect on different aspects of the animal world, including the phenology of organisms (Walther et al., 2002). If the shift in timing of breeding is not able to keep up with the changing time of resource abundance, this “mismatch” has a potential effect on the reproductive success



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(Visser and Gienapp, 2019). A lot of research has been done on this "match/mismatch"-theory, showing an increasing mismatch between the timing of reproduction and timing of food emergence, in response to global warming, see for example the meta-analysis conducted by Root et al. (2003).

Most avian species have a sigmoid body growth curve (Figure A1 in appendix). A sigmoid growth curve means that the individuals have a modest growth at the beginning of their growth period, followed by a steeper growth midway, before it flattens out at the end of the growth period (Ricklefs, 1968). The shape of the growth curve is usually stable, but the growth rate can differ from individual to individual with the impact of different variables. Sibling competition within broods can alter the growth rate significantly, with a higher growth for the larger nestlings (Lack, 1956; Hussell, 1972; Ricklefs, 1965). Sibling competition causes a lower growth rate in larger broods relative to smaller broods (Smiseth et al., 2007). Other factors that could impact the growth curve is resource availability, with a lower abundance causing lower growth (Siikamäki, 1998), timing of breeding (Naef-Daenzer and Keller, 1999) and temperature, with an increase in temperature causing a "mismatch" between phenological traits leading to a lower growth (Visser and Gienapp, 2019).

In highly seasonal environments, such as the High Arctic, the timing of successful breeding for avian species is fragile due to the short spring and summer, causing the breeding period to be short and intense. The offspring of migratory birds have to not only survive the nestling period, but also be able to survive the migration shortly after successful fledging from the nest (Lack, 1950; Forsman and Mönkkönen, 2003). Examination of survival rates of nestlings and fledglings of some species show that there is a strong tendency for the young that are hatched early in the season to have the greatest chance of survival and reproduction (Perrins, 1970). Most avian land-bound species found on Svalbard are migratory birds that arrive at Svalbard during spring and leave in the fall (Løvenskiöld, 1954). This means that they have to arrive at their breeding place, recover from the migration, find a mate and raise successful offspring in a short time period due to the short summer-time in the High Arctic. Compared with resident species, migratory birds are assumed to be more sensitive to the spring phenology changes, because environmental cues in overwintering or spring staging areas might differ from the breeding area, due to different responses to climate change (Both, 2010)

The snow bunting (*Plectrophenax nivalis*) is a long-range migratory bird breeding in the Arctic, and is therefore among the species expected to be most affected by the predicted shifts in spring phenology. This is because of the rapid effect of climate change the arctic is showing, and migratory birds being more vulnerable to change in climate than resident birds. Migratory birds are more vulnerable because their signals at their wintering ground will not necessarily match those at their breeding grounds (Visser and Gienapp, 2019). Snow buntings are therefore expected to potentially be highly affected by the climate change although it is not clear how they will respond to these changes (Fossøy et al., 2015). The most important food source for several Arctic breeding birds is tundra arthropods. The Svalbard snow buntings only feed their nestlings with different arthropod taxa, apparently depending on abundance (Stolz, 2019). The snow bunting population on Svalbard is therefore interesting to investigate when exploring the relationship between phenology of arthropods and birds. More generally it is interesting to investigate the im-

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pacts of climate change on patterns of match-mismatch in High Arctic tundra ecosystems using snow buntings as a study species. It is therefore interesting to investigate how dependent the nestlings, and their growth rates, are on the insect abundance in the area. It has been discovered that the reproductive success and nestling survival is strongly related to weather variables for the Svalbard snow bunting (Fossøy et al., 2015; Lillehaug, 2019). The arthropod abundance on Svalbard has been strongly correlated with the peak of active nests, and it has been determined what their diet consists of using metabarcoding (Skjøstad, 2008; Stolz, 2019). So far it has not been examined how the arthropod biomass fluctuations are affecting the growth fluctuation of nestlings during breeding season.

**Hypothesis and predictions.** The aim of the present study is to investigate how short-term fluctuations in the arthropod abundance is affecting the variation in body mass and growth of snow bunting nestlings on Svalbard, during the summer season of 2019. I expect that increased food supply will have a positive effect on the growth.

# Materials and methods

## 2.1 Study site and species

The fieldwork was conducted in Adventdalen on Svalbard (78° 13'N, 15° 38'E). The specific area for the data collection was in Adventdalen (Figure A2 in Appendix), and the data was collected between 10.06.2019 - 28.07.2019. Svalbard consist of mainly Arctic tundra and belongs to the High Arctic with harsh and cold climate. The snow bunting is a High Arctic songbird, and is the only passerine which breeds regularly in Svalbard (?). They have been studied since 1995 (Espmark, 2016). Time of egg-laying varies among years, but most of the breeding individuals start egg-laying around the middle of June (Fossøy et al., 2015). There is usually a 13-day incubation period, followed by a 13-day nestling period with a mean of six eggs in each nest (Espmark, 2016). Their natural breeding site on Svalbard is in screes, beneath stones and in other small cavities, hereafter referred to as "natural nests". They also breed in a variety of man-made structures like stacks of firewood, cavities at cabins and nest boxes on wooden pylons (Bangjord et al., 1999), hereafter referred to as "nest boxes". The snow buntings have biparental care, where both the male and female feed their offspring and the diet of the chicks consists entirely of arthropods (Hoset et al., 2004).

## 2.2 Measurements of nestling

The nestlings were weighed when they were four, six and eight days old (day 0 being the hatching day). To obtain an approximate hatching date, it was assumed that the incubation period was 12 days after the fourth egg was laid ?. The risk of early fledging is high after day eight if humans disturb the nests, so after day eight the nests were left alone. When the nestlings were four days old, they were marked with a colored plastic ring around one foot, to keep track of each individuals growth. The ring was removed at day eight. The nestlings were weighed using a fabric bag with a known weight, in which the chicks were placed inside. The weight was recorded using two different Pesola spring balances, one capable of measuring up to 50 grams and the other up to 150 grams. The smallest balance was used on nestlings at day four and six, while the largest was used on nestlings at day eight due to the nestlings and fabric bag weighing more than 50 grams at day eight. The weighing was conducted as shielded as possible to protect the nestlings from environmental conditions. The nestlings in each nest were weighed in two turns, never leaving the nest without any nestlings in it, to reduce the time spent outside the nest and to minimise loss of body heat. This also reduced the risk of parents returning to feed the nestlings and finding an empty nest. Returning to an empty nest could lead to the parents assuming all of their offspring have died, and therefore abandon their nest. To calculate the growth rate from day four to six and six to eight, the average weight in these intervals was divided by the number of hours that had passed between the two weightings,

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as shown in equation 2.1. This provided a growth rate for the nestlings in grams per hour.

$$\text{Growth rate (g/h)} = \frac{\text{Weight (g)}}{\text{Hour (h)}}. \quad (2.1)$$

28 nests were included in the study, 157 number of chicks, at average 6 chicks in each nests, ranging from 5 to 7 chicks per nests. One nest was excluded from the 28 nests in the present study (Figure A3 in appendix). In this nest, weight of chicks were measured at day 3 instead of day four. This nest was excluded because it was the sole nest early in the season. This nest also had only one surviving offspring after day 3, and would therefore not be representative of expected growth.

## 2.3 Arthropod sampling and identification

Arthropods were sampled using pitfall traps to investigate the abundance in the study area every fourth day. The traps were made of two white plastic cups (68 mm diameter) stacked on top of each other. They were buried below the ground with the brim of the cup in line with the ground. The traps were filled with water and a few drops of detergent (Sun light, Lilleborg AS, Oslo, Norway), which prevented the arthropods from escaping by breaking up the surface tension between the water molecules at the top of the cup. Ten pitfall traps were placed in two rows in two different habitats, one dry and one wet habitat in Adventdalen (Figure A4 in appendix). The dry habitat consisted mostly of *Cassiope tetragona* heaths, while the wet habitat included *Sphagnum* ssp. mosses and graminoids vegetation. The two habitats were located approximately 300 meters apart. The traps were emptied in the afternoon of every fourth day, by sieving the captured arthropods over a fine cloth. The arthropods were stored in 70% alcohol after capture. This procedure has been carried out in previous studies at the exact same location (Skjøstad, 2008; Stolz, 2019).

The arthropods were sorted into groups according to which order they belonged to, that is Collembola, Aranea, Acari, Diptera and Hymenoptera. Diptera was further divided into Brachycera and Nematocera. The family Chironomidae was also identified within Nematocera, whereas the rest of Nematocera were labelled "other Nematocera". The Brachycera were sorted into groups according to their size, one consisting of large Brachycera above 5cm and the other of small Brachycera below or equal to 5cm. Larvae were found in the samples, although they were not identified and only classified as larvae. A stereo microscope with 6.3x to 40x zoom was used to identify the different orders, using the key of Søli (2018). The length of the insects were measured from head to the end of the body by placing the individual on a measured paper. The arthropods within each group from each sampling day were weighed to obtain mean biomass from each group. For each group, the sample with the highest number of individuals was chosen and placed in a petri dish. The petri dish was divided into four sections, and if there were more than thirty individuals in the first quarter, they were removed, counted, dried and weighed. This weight was divided by the number of individuals to obtain the average weight per individual. If there were less than thirty individuals in the first quarter, the second quarter was also included to ensure a sufficient sample size to get a representative average of the group. The mean biomass

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for each group per date was calculated by multiplying the individual weight with the total number of individuals captured in each group from each date (Equation 2.2).

$$\text{Biomass } (g) = \text{Weight per individual } (g) \times \text{Number of individuals} \quad (2.2)$$

Arthropods were sampled every fourth day. The number of sampled insects belonging to each group were fitted using a generalized additive model (function `gam` in the `mgcv`-package (Wood, 2017)) with Poisson distributed errors and a log link function. The degree of the smoothing spline was automatically estimated as part of the fitting procedure. Using day number as the linear predictor variable allowed for smoothed predicted values for the number of insects for all 4-day periods (thus also for days in-between the sampling days). Some of the analyses however required estimates of e.g. daily number of insects to calculate daily values of biomass. Such daily values of number of insects were obtained by implementing a numerical optimization procedure in TMB (Kristensen et al., 2016). Daily numbers of insects, say  $N_t$ , were calculated as  $N_t = N_{t-1} + \sigma z_t$ , where the unknown variables  $z_t$  followed a standard normal distribution  $z_t \sim N(0, 1)$ . Other parameters estimated as part of the estimation procedure were  $\sigma$  and  $N_1$ . Finally, writing  $Y_T$  for a smoothed estimate for a given 4-day period, it was required that  $\sum_{t=T-3}^T N_t \approx Y_T$  by adding a penalty term on deviations, in practise resulting in  $\sum_{t=T-3}^T N_t = Y_T$ . Values for  $N_t$  obtained by this procedure were subsequently used to calculate daily values of biomass by multiplying the estimated daily numbers of insects by the estimated weight per individual. Finally, these daily estimates of biomass were used to calculate biomass for time periods of different length such as per day, 2 days, 4 days and 8 days.

As the weather conditions were assumed to affect both the nestling weight and the arthropod abundance, the correlation between weather conditions and arthropod biomass was investigated (Table A1 in Appendix). Weather data was obtained from Longyear Airport meteorological station, via the Norwegian Meteorological Institute ([www.eKlima.met.no](http://www.eKlima.met.no)). Daily mean precipitation, temperature and wind were used because these factors were assumed to have the most impact on arthropod abundance. Because the daily mean temperature and arthropod biomass were correlated, and because it may be difficult to distinguish between the direct and indirect effect of weather parameters on nestling growth, the weather data was not included in the further analysis. Additionally, the  $AIC_c$  tables (Table A2 A3, A4 and A5 in Appendix) show that including the weather variables in the models does not affect the results.

## 2.4 Statistical analyses

Data analysis was performed in R version 3.6.1 (R Core Team, 2020). Linear mixed effect models were used to investigate the effect of arthropod biomass on the weight of the nestlings at day four, on the growth rate between day four to six and between six to eight, and on the weight at day eight. The models were fitted using the function “`lmer`” from the package ‘`nlme`’ (Bates et al., 2015). The type of nest, clutch size, and the centered nestling weight at the start of the growth rate period in interest were also included in the models. These predictors were chosen based on previous literature indicating that these factors could influence the nestling growth. Nest number was included as a random factor

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to account for the non-independence between nestlings within nests. The significance level was set at a p-value  $< 0.05$ , and a p-value below 0.1 was considered a trend in the present study.

The weights at day four and six were centered by taking the average weight of the brood and subtract the weight of every individual in the nest. Thereby measuring the within brood variation by comparing the individual weight between siblings. With nest as a random effect in the models it was ensured that the within brood variance and between nest variance was considered, and therefore avoiding pseudoreplication as well as controlling for unknown differences within broods (Van de Pol and Wright, 2009).

For the main models, weather was not taken into consideration, because it is an explanatory factor that was not the main focus for the research question. Figure A5 shows the variation in temperature, precipitation and wind over the same period in the summer season that the arthropods were collected. When comparing these data with the arthropod abundance in the same time period there is a co fluctuation in the changes of temperature and arthropod biomass (FigureA5). Which is confirmed by a correlation matrix (table A1), where there is a high correlation between temperature and arthropod biomass. This means that they are highly affected by each other and can not be separated in any models. When performing a model selection ( $AIC_c$ ) with the weather variables the model with the lowest Akaike Information Criterion (AIC) is considered to be the best fitted model, when performing a model selection (Akaike, 1974). Correcting for small sample size in the present study a low ( $AIC_c$ ) score was considered the best fitted model. When  $\Delta AIC_c$  was below 2, there was good enough support from the data to consider this a fitted model. Where several models had  $\Delta AIC_c < 2$ , the models were not separable.

# Results

In the present study we observed a total of 28 nests, of which 15 were placed in nest boxes and 13 in natural nests (table 1). Due to predation in two nest boxes and two unsuccessful natural nests, due to unknown reasons, 24 nests were still active at day eight. Of the 157 nestlings hatched, 34 died between day four and eight, which resulted in 113 nestlings surviving to day eight (table 2). The mean weight of snow bunting nestlings over the season did not vary drastically, but all weight means were lower at the end of the season (Figure 1a)). The weight means in the start of the season were 12.25 grams (SD = 5.40), 20.59 grams (SD = 6.31) and 26.0 grams (SD = 5.36) for day four, six and eight, respectively. At the end of the season these means had dropped slightly to 11.08 grams (SD = 2.76), 20.0 grams (SD = 2.61) and 23.3 grams (SD = 2.11). There was also a slight decrease in growth rate during the season, as shown in Figure 1b. The first three nests in the season had a mean growth rate of 0.17 g/h (SD = 0.05) and 0.09 g/h (SD = 0.04) for the four to six and six to eight intervals, respectively. At the end of the season the mean growth rate for the same intervals were 0.15 g/h (SD = 0.02) and 0.07 g/h (SD = 0.02) for the last nest. The growth rate was also found to be higher from day four to six than day six to eight. Both the growth and growth rate fluctuated slightly during the season as shown in Figure 1 a) and b) respectively. Most of the nests hatched before the main peak in arthropod abundance (Figure 1 c) and d)). Weight (Figure 2) and growth rate (Figure 3) of nestlings growing up in nest boxes and natural nests did not differ much, although the weights were in general higher in nest boxes than in natural nests for day four and six (Figure 2). The growth rate between day six and eight was lower in nest box nestlings than the ones in natural nests.

The number of arthropods collected from the pitfall traps fluctuated throughout the season. The total number of individuals collected per sampling interval varied from 74 individuals at the beginning of the season (10.06.2019) to 763 at the end of the season (28.07.2019) (Figure 4). Aranea was the dominant group at the beginning (n=74 individuals), while large Brachycera (n=385), Hymenoptera (n=198) and other Nematocera (n=140) were dominant at the end of the season. The number of arthropod showed two peaks during the season, the first with 429 individuals (23.06.2019) and the second with 646 individuals (09.07.2019) (Figure 4). When investigating the biomass of the arthropods, we found that the dominant arthropods early in the season were larger compared to later in the season, making the total biomass trapped smaller during the first peak than the second peak. Large Brachycera were the biggest arthropods overall, and were responsible for almost all the biomass caught in the traps and they were dominant in number of individuals with the highest number being 378 individuals caught in one day.

When looking at the linear mixed-effect models there was no effect of neither arthropod biomass over four days ( $P = 0.40$ ) nor the clutch size at day four ( $P = 0.64$ ) on the nestling weight at day four. There was however a trend for nest type ( $P = 0.092$ ), with a tendency toward a higher body weight in nest boxes compared to natural nests. All estimates, standard errors, degrees of freedom, t-values and p-values from all models are presented in table 3.

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There was a significant positive effect of centered weight at day four ( $P = 0.0025$ ) on the nestling growth rate from day four to six, with an increased growth rate with increasing weight at day four (Figure 6 a)). Clutch size at day six had a significant negative effect ( $P = 0.031$ ) on growth rate from day four to six, with a decrease in growth rate with an increase in clutch size (Figure 6b)). The nestling growth rate from day four to six was significantly lower in the nest boxes compared to the natural nests ( $P = 0.030$ ). There was no effect of arthropod biomass over two days ( $P = 0.27$ ). There was however a significant interaction effect between arthropod biomass and nest box ( $P = 0.018$ ) on the nestling growth rate from day four to six, with an increase in growth rate with increasing arthropod biomass for nestlings in nest boxes (Figure 6 c)). All estimates, standard errors, degrees of freedom, t-values and p-values from all models are presented in table 3.

There was no effect of neither arthropod biomass over two days ( $P = 0.33$ ), the nest type ( $P = 0.13$ ) nor the centered weight at day six ( $P = 0.86$ ) on the nestling growth rate from day six to eight. There was however a trend for clutch size at day eight ( $P = 0.071$ ), with a tendency toward an increased growth rate with decreasing clutch size. All estimates, standard errors, degrees of freedom, t-values and p-values from all models are presented in table 3.

There was no effect of neither arthropod biomass over eight days ( $P = 0.57$ ), the nest type ( $P = 0.77$ ) nor the clutch size at day eight ( $P = 0.48$ ) on the nestling weight at day eight. All estimates, standard errors, degrees of freedom, t-values and p-values from all models are presented in table 3.



# Discussion

The present study has demonstrated how variation in snow bunting nestling growth in High Arctic Svalbard is only partly linked to temporal fluctuations in arthropod abundance during summer. By collecting arthropods in pitfall traps and measuring nestling body weight four, six and eight days after hatching, I found that large variation and short-term fluctuations characterized both the arthropod abundance, which was strongly correlated with ambient temperatures (tableA1), and nestling weight and growth rate on a daily basis throughout the season (Figure 1). Estimated daily total arthropod biomass had a positive effect on nestling growth between day four and six (Figure 1, Table 3), yet only in artificial nest boxes. In contrast, I found no strong evidence of an effect of arthropods on other growth (day six to eight) or weight (day 4 and 8) parameters (Table 3).

Total arthropod biomass only had a statistically significant (positive) effect on growth rate from day four to six on nestlings in nest boxes. This partly supports the prediction that arthropod biomass will influence the nestling weight development positively. In particular, the early season growth rates fluctuated largely in correspondence with the arthropod biomass fluctuations in the same time period, indicating that during this period their growth is to some degree affected by food availability, as shown in previous studies (Naef-Daenzer and Keller (1999); Hoset et al. (2004)). Naef-Daenzer and Keller (1999) had a peak energy flow that correlated with the peak food abundance, and with lower energy flow both before and after, making the arthropod peak correlating with the growth peak throughout the season. While in the present study, the similarities between the arthropod abundance and the growth rate from day four to six stopped after the value of arthropod biomass surpassed the first peak of the arthropod biomass, with no strong growth response to the second, dominant peak in arthropods. This could indicate that the nestlings have a critical arthropod biomass value around 0.2 grams, where there is no effect of arthropod abundance above the value due to sufficient food resources. Previous studies found that growth of nestlings are negatively affected by low food abundance (Siikamäki, 1998), indicating that the critical period for nestling growth is when the food abundance is low. This could also explain why the growth rate was seemingly not that affected during and after the second and major peak, with less fluctuating nestling growth rates during this time of the season.

Figure 1 c) shows that the hatching date of most of the nests are before the highest peak of arthropod biomass (Figure 1 d)), which indicates that the snow buntings are not breeding until the emergence of arthropods in the area. They are therefore showing a phenological timing of breeding that is affected by the food availability, as Naef-Daenzer and Keller (1999) also discovered for great and blue tit. The apparently high correlation between the timing of arthropod abundance and the peak of active nests in previous years (Skjøstad, 2008) was not clear for summer 2019. With the growth rate being higher from day four to six than day six to eight indicates that the sigmoid growth curve is steepest from day four to six and that the curve flattens at day six to eight (A1). Even if the growth curve is flattened the need for a high food supply remains. The higher body mass of the older nestlings (day eight) requires a higher food-intake than their younger counterparts

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(day six), as well as the fact that the older nestlings use their energy on producing other phenological traits than growth, such as a thick feather coat.

The nestlings were not affected equally between the two nest types. The high number of nests found in boxes at the start of the season (Figure 3) is expected because they have been shown to be preferred by the snow bunting pairs, and are therefore inhabited first (Espmark, 2016). This preference could come from a myriad of things, such as large amounts of snow in the locations of the natural nests, making the boxes more equipped for nesting early in the season. While the natural nests are used later in the season when the snow has melted in the areas with suitable natural cavities available. The location of the nest boxes are on the tundra in the lower areas of Adventdalen, where the snow melts earlier than further up in the mountains, but with fewer suitable nest options other than the nest boxes. The nest boxes are the main drivers for the fluctuations for the overall growth rate at the beginning of the season (Figure 1 b)). This could be the reason why the arthropod biomass abundance is only significantly affecting the growth from day four to six of the nest box nestlings. Since the growth rate from day four to six in nest boxes was the earliest weight data (Figure 3) they appeared to be in the critical period with low arthropod abundance. There was a tendency towards a positive effect of nest boxes on the weight at day four, indicating that the nestlings weighed more at day four in the nest boxes than the natural nests. The nest boxes are shown to be better for the nestling success, because they are found to be better shelters for weather and predation, likely causing a higher growth for the nestlings (Espmark, 2016). In the present study there was no clear indication that the nest boxes facilitated a higher growth than the natural nests, apart from that the growth from day four to six correlated with arthropod abundance. This can, however, also be related to the temporal differences in use of boxes versus natural nests, making a direct comparison difficult.

There was no statistically significant effect of arthropod biomass on the other growth and body mass parameters. In addition to it possibly being because of the timing of nest boxes in comparison to the other parameters affecting growth, some other explanations were considered. Certain arthropod groups could be more important for the growth of the snow bunting nestling, despite lower biomass than the large Brachycera group. This was explored, as shown in table A6, A7, A8 and A9, where the groups individually did not explain any more than the total arthropod biomass in table 3. However, for the nestling growth between day four to six, there is a significant positive effect of the small Brachycera, Chironomidae and other Nematocera. It could be that large Brachycera are too large for the youngest nestlings to eat and digest, and therefore the most abundant group is not affecting the growth in the same way as the other groups mentioned above. The nestlings are at their smallest from day four to six, and the groups mentioned above are much smaller than the large dominant Brachycera group. They are also the groups that are most dominant, aside from large Brachycera, especially before 01.07.2019, where 16 out of the 28 nests are located. There is also a tendency that Aranea affects the growth rate from day six to eight, and this is peculiar because the Aranea group is only prominent at the beginning of the season, and were hardly trapped after 01.07.2019 4. In general, interpretations of taxa-specific analyses should be made with care, due to problems associated with multiple testing and "type 1 error". Another possible explanation was weather variables being the main factor affecting growth, because that has been shown in previous work on weather

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variables affecting Svalbard snow bunting survival (Fossøy et al., 2015; Lillehaug, 2019). A model selection analysis was performed, showing no indication that the wind, precipitation or temperature explained more than the arthropod biomass (Table A2, A3, A4 and A5 in appendix).

Clutch size negatively influenced growth rate from day four and six, and with a similar tendency in growth rate from day six to eight, indicating that a larger brood size is causing higher competition between siblings, and less food per offspring, which coincides with results found in previous studies (Smiseth et al., 2007). This can also explain why the centered weight at day four is positively correlated with the growth rate from day four to six. The larger siblings out-compete the others, resulting in a higher growth rate. This result matches what is found in snow bunting and other species in previous studies (Lack, 1956; Hussell, 1972; Ricklefs, 1965).

The use of pitfall traps has its limitations regarding how well they represent the arthropods in an area. Pitfall traps only capture arthropods that move on the ground, and are also biased toward the more mobile species, as mobile species cover more ground per day and would therefore be more likely to be caught. Making the traps biased towards more active species (Yi et al., 2012). This causes the pitfall traps to only capture a subset of the species in the area. For this particular research project however, the pitfall traps are arguably representative of a snow bunting's diet. Due to high wind and cold climate of the arctic, most arthropods move on the ground (Coulson et al., 2003). The snow bunting is also a ground-feeding bird, and the arthropods found in the feces of the snow buntings are found in the pitfall traps used (Stolz, 2019), indicating that using pitfall traps are sufficient for investigating the relationship between food abundance and nestling growth parameters.

The arthropod pitfall traps were collected every fourth day, as it had been done previous years (Stolz, 2019), but for the present study it would have been optimal to collect the traps every day so that it would make it easier to compare the day to day data with the specific events from day to day over the different data sets. However solving this by smoothing the data using the GLAM-function in R is a good option, because it takes into consideration that the findings in a trap at a certain day is the result of the combined arthropod number in the trap over the previous three days as well as the capture day.

Further studies should investigate how the arthropod biomass affects the nestling weight and growth rate over several years, to get a better view of how these seasonal fluctuations are changing over several years as well. To also take into consideration weather variables over a multitude of years would be interesting to investigate.

**Concluding remarks.** In conclusion the total arthropod abundance is affecting the nestling growth of snow bunting nestlings, but not during the entire growth of the nestling period. The significant positive effect of the arthropod on nestlings was only clear for the growth rate between day 4 and 6, and only in nestlings in artificial nest boxes. The majority of the nests in the present study hatched before the major peak in arthropod abundance, and the Svalbard snow bunting population therefore seems to be in synchrony with their food supply.

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# Tables

**Table 1:** An overview of the snow bunting data set on nest level

<b>Nest level</b>	<b>Number of nests</b>
Total	28
Nest boxes	15
Natural nests	13
Predated	2
Unsuccessful	2
Nests still active at day 8	24

**Table 2:** An overview of the snow bunting data set on individual level

<b>Individual level</b>	<b>Number of individuals</b>
Number of eggs	164
Alive day 4	157
Alive day 6	128
Alive day 8	113

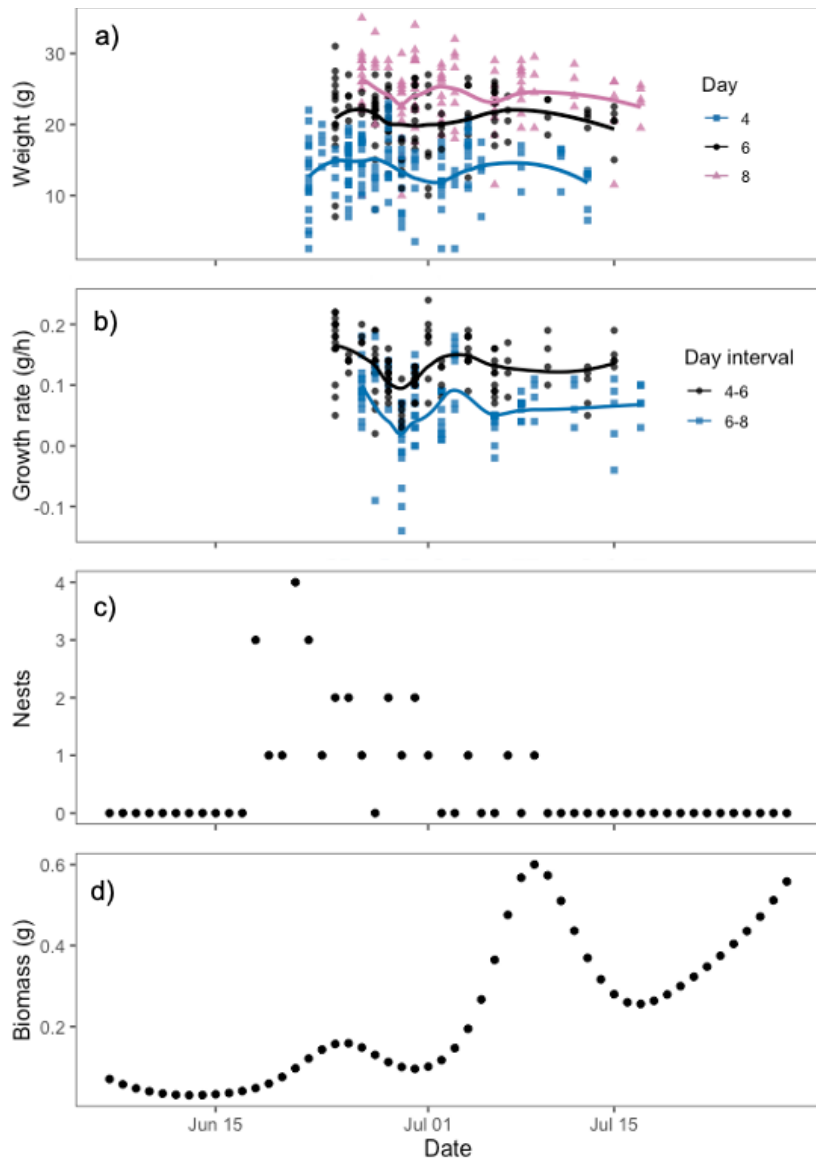
**Table 3:** Parameter estimates from linear mixed-effects models with weight at day 4, day 8, growth rate from day 4-6 and from day 6-8 as response variables. Total biomass, nest type, initial weight and clutch size were the explanatory variables. SE = standard error, df = degrees of freedom

<b>Responses and predictor variables</b>	<b>Estimate</b>	<b>SE</b>	<b>df</b>	<b>t-value</b>	<b>p-value</b>
<b><i>Weight at day 4</i></b>					
(Intercept)	13.96	4.70	25.07	2.97	0.0065
Total biomass over 4 days	4.45	5.21	26.29	0.86	0.40
Nest type (nest box)	1.95	1.11	23.29	1.76	0.092
Clutch size at day 4	-0.36	0.75	24.16	-0.47	0.64
<b><i>Growth rate from day 4 to day 6</i></b>					
(Intercept)	0.24	0.045	22.77	5.25	<0.001
Total biomass over 2 days	-0.12	0.102	21.49	-1.14	0.27
Nest type (nest box)	-0.067	0.029	20.71	-2.32	0.030
Centered weight day 4	0.0030	0.00098	102.90	3.10	0.0025
Clutch size at day 6	-0.017	0.0076	22.74	-2.30	0.031
Total biomass:Nest type (nest box)	0.92	0.36	20.86	2.57	0.018
<b><i>Growth rate from day 6 to day 8</i></b>					
(Intercept)	0.20	0.060	20.37	3.40	0.0028
Total biomass over 2 days	-0.11	0.11	19.09	-1.00	0.33
Nest type (nest box)	-0.033	0.021	19.34	-1.57	0.13
Centered weight at day 6	-0.00021	0.0011	89.02	-0.18	0.86
Clutch size at day 8	-0.021	0.011	20.22	-1.90	0.071
<b><i>Weight at day 8</i></b>					
(Intercept)	28.36	4.57	22.05	6.21	<0.001
Total biomass over 8 days	-1.86	3.18	20.59	-0.59	0.57
Nest type (nest box)	-0.47	1.55	19.52	-0.30	0.77
Clutch size at day 8	-0.55	0.76	21.58	-0.72	0.48

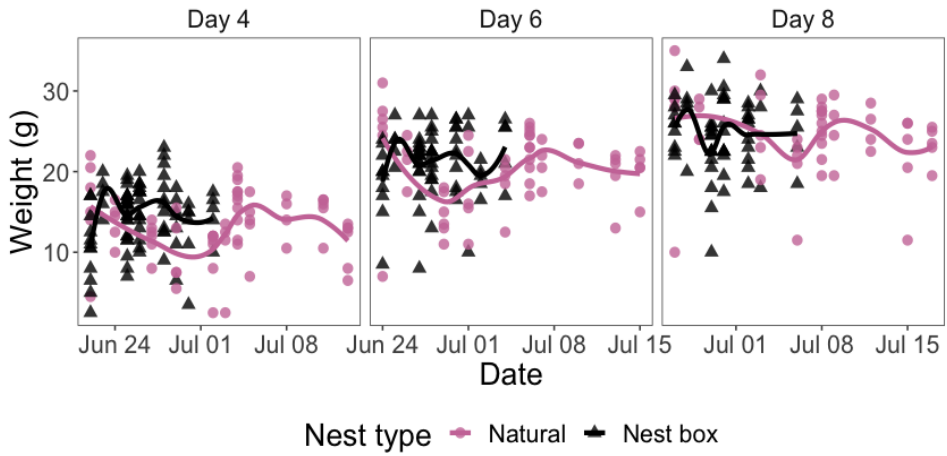


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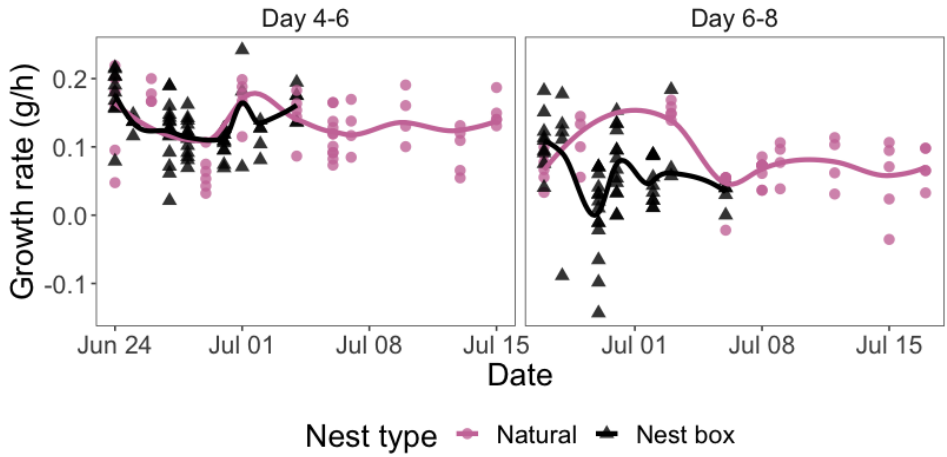
# Figures



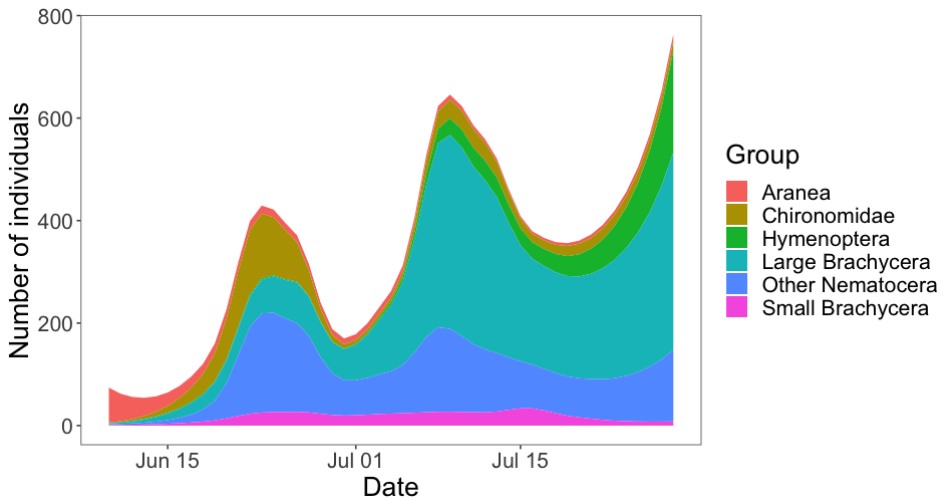
**Figure 1:** Changes in a) nestling weight in grams, b) nestling growth rate in grams per hour, c) hatching date and d) arthropod biomass in grams over the summer period of 2019.



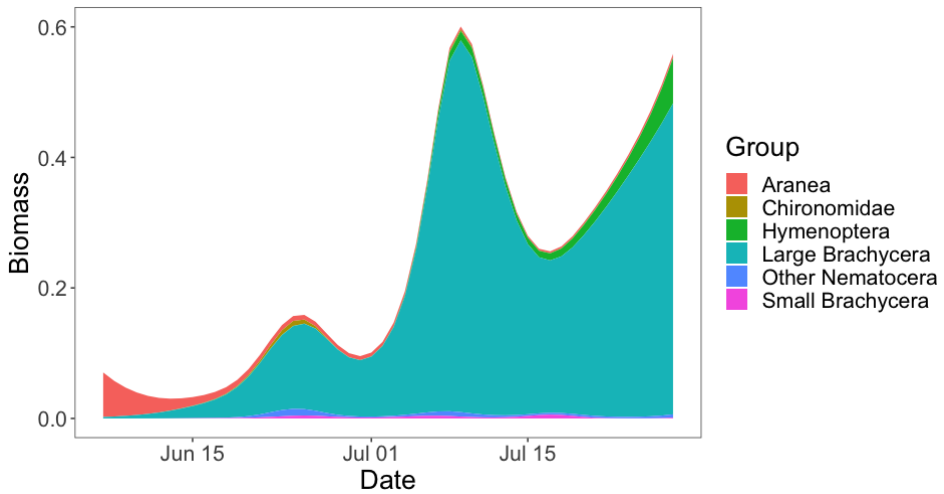
**Figure 2:** The weight of every nestling at day 4, 6 and 8 divided by the two different nest types. The pink points are natural nests and the black triangle's are nest boxes.



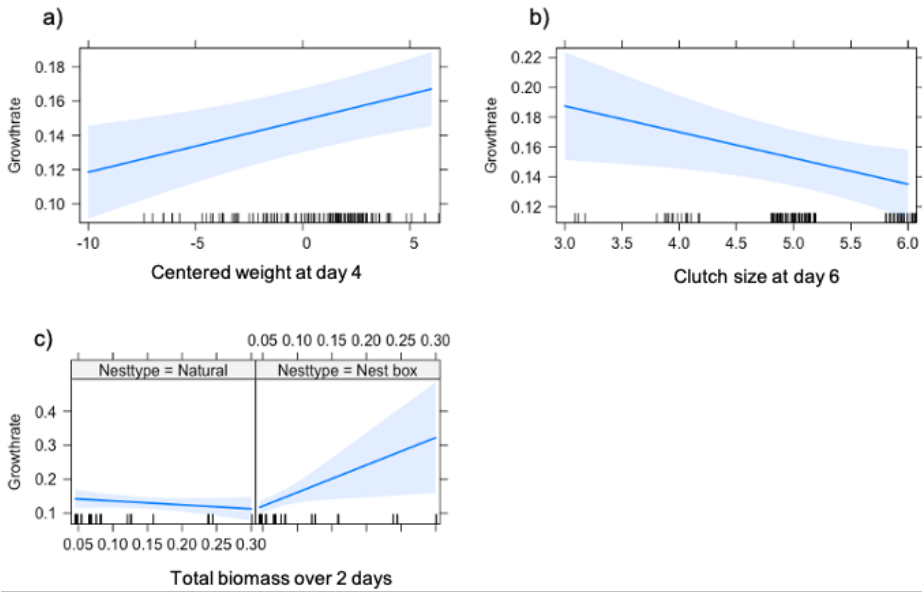
**Figure 3:** The growth rate of every nestling from day 4 to day 6 and from day 6 to day 8, divided by the two different nest types. The pink points are natural nests and the black triangle's are nest boxes.



**Figure 4:** The number of arthropods in every group over the summer season of 2019 on Svalbard



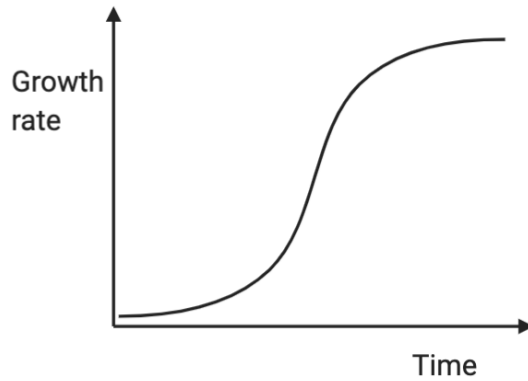
**Figure 5:** The biomass in gram of arthropods in every group over the summer season of 2019 on Svalbard



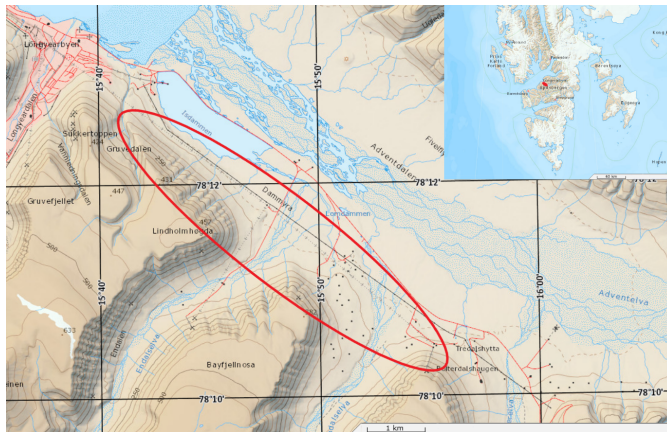
**Figure 6:** Effect plots of factors and covariates affecting growth rate from day 4 to day 6 (g/h) of weight at day 4, clutch size at day 6 and arthropod biomass in both natural nest and nest box, on Svalbard the summer of 2019.

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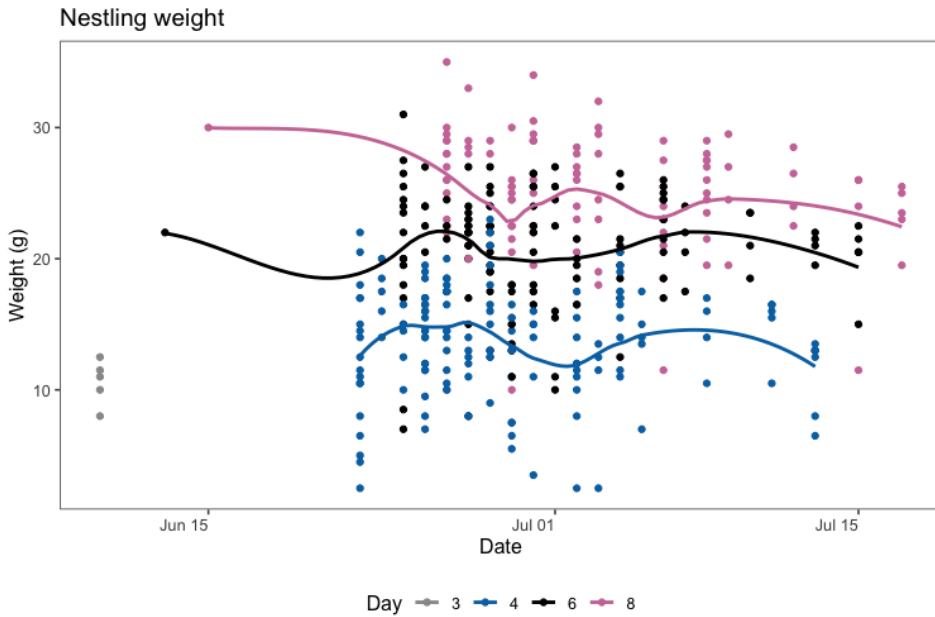
# Appendix



**Figure A1:** A sigmoid growth rate curve.



**Figure A2:** Location of the study site in Adventdalen, Svalbard ( $78^{\circ} 13'N$ ,  $15^{\circ} 38'E$ ) marked with a red oval, with coordinated marked on the grid. The small map shows the location of Adventdalen (red filled circle) in Svalbard. The map was constructed by expanding on a map from the Norwegian Polar Institute.



**Figure A3:** The nestling weight data with the excluded nest included.



**Figure A4:** Pitfall trap setup in the wet habitat on Svalbard, where the red circles marks the traps (© Christian Stolz 2018).

**Table A1:** A correlation matrix for Arthropod biomass, temperature (average °C per day), precipitation(average millimeter per day), wind(average meter per second per day) and date

	Biomass	Temperature	Precipitation	Wind	Date
Biomass		0.748	0.213	-0.202	0.807
Temperature			0.269	-0.072	0.511
Precipitation				-0.153	0.193
Wind					-0.024

**Table A2:** All models with  $\Delta AIC_c < 2$  from model selection with Weight at day 4 as response variable. Table shows parameter estimates ( $\beta$ ) for intercept and explanatory variables.  $AIC_c$ ,  $\Delta AIC_c$  and  $AIC_c$  weight ( $w_i$ ) are shown for all candidate models. Clutch4 = Clutch size at day 4, wind = mean wind (m/s) per day, nest = natural nest and nest boxes, precipitation = mean precipitation (mm) per day, temperature = mean temperature ( $^{\circ}C$ ) per day, Biomass = total arthropod biomass.  $W_i$  = model weight.

Model rank	Explanatory variables											Model selection criteria			
	Intercept	Date	Clutch4	Wind	Nest	Precipitation	Temperature	Biomass	Wind:Nest	Precipitation:Nest	Temperature:Nest	Biomass:Nest	AICc	$\Delta AIC_c$	Wi
553	5.136				+		1.024			+			847.4	0.00	0.092
557	8.768			-0.517	+		0.961			+			847.8	0.40	0.076
1	13.850												849.3	1.90	0.036

**Table A3:** All models with  $\Delta AIC_c < 2$  from model selection with growth from day 4 to 6 as response variable. Table shows parameter estimates ( $\beta$ ) for intercept and explanatory variables.  $AIC_c$ ,  $\Delta AIC_c$  and  $AIC_c$  weight ( $w_i$ ) are shown for all candidate models. CW4 = centered weight at day 4, clutch6 = Clutch size at day 6, wind = mean wind (m/s) per day, nest = natural nest and nest boxes, precipitation = mean precipitation (mm) per day, temperature = mean temperature ( $^{\circ}C$ ) per day, Biomass = total arthropod biomass.  $W_i$  = model weight.

Model rank	Explanatory variables											Model selection criteria				
	Intercept	CW4	Date	Clutch6	Wind	Nest	Precipitation	Temperature	Biomass	Wind:Nest	Precipitation:Nest	Temperature:Nest	Biomass:Nest	AICc	$\Delta AIC_c$	Wi
98	0.0634	0.00302					-0.0678	0.01199						-468.2	0.00	0.260
102	0.119	0.00299		-0.00952			-0.06288	0.0107						-468.2	0.02	0.258
100	10.120	0.00303	-0.0011				-0.06339	0.0124						-467.5	0.72	0.182
114	0.00529	0.00300				+	-0.06652	0.01271						-466.7	1.53	0.121

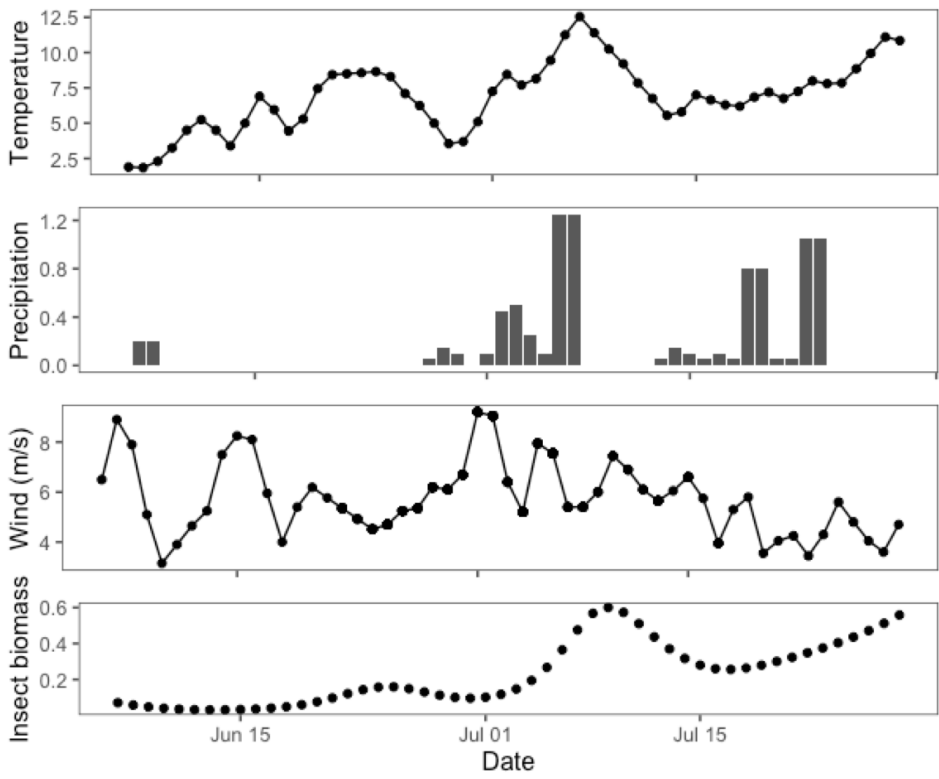
**Table A4:** All models with  $\Delta AIC_c < 2$  from model selection with growth from day 6 to 8 as response variable. Table shows parameter estimates ( $\beta$ ) for intercept and explanatory variables.  $AIC_c$ ,  $\Delta AIC_c$  and  $AIC_c$  weight ( $w_i$ ) are shown for all candidate models. CW6 = centered weight at day 6, clutch8 = Clutch size at day 8, wind = mean wind (m/s) per day, nest = natural nest and nest boxes, precipitation = mean precipitation (mm) per day, temperature = mean temperature ( $^{\circ}C$ ) per day, Biomass = total arthropod biomass.  $W_i$  = model weight.

Model rank	Explanatory variables											Model selection criteria				
	Intercept	CW6	Date	Clutch8	Wind	Nest	Precipitation	Temperature	Biomass	Wind:Nest	Precipitation:Nest	Temperature:Nest	Biomass:Nest	AICc	$\Delta AIC_c$	Wi
5	0.1669			-0.02041										-348.7	0.00	0.055
23	47.1300		-0.002595	-0.02312		+								-348.3	0.46	0.044
21	0.1837			-0.02149		+								-348.1	0.64	0.040
1	0.06777													-347.6	1.13	0.031
13	0.20720			-0.01938	-0.007187									-347.5	1.22	0.030
37	0.16940			-0.02017			-0.01694							-347.0	1.72	0.023
149	0.020250			-0.02125		+			-0.10790					-346.9	1.84	0.022

**Table A5:** All models with  $\Delta AIC_c < 2$  from model selection with Weight at day 8 as response variable. Table shows parameter estimates ( $\beta$ ) for intercept and explanatory variables.  $AIC_c$ ,  $\Delta AIC_c$  and  $AIC_c$  weight ( $w_i$ ) are shown for all candidate models. CW4 = centered weight at day 4, clutch8 = Clutch size at day 8, wind = mean wind (m/s) per day, nest = natural nest and nest boxes, precipitation = mean precipitation (mm) per day, temperature = mean temperature ( $^{\circ}C$ ) per day, Biomass = total arthropod biomass.  $W_i$  = model weight.

Model rank	Explanatory variables													Model selection criteria		
	Intercept	CW4	Date	Clutch8	Wind	Nest	Precipitation	Temperature	Biomass	Wind:Nest	Precipitation:Nest	Temperature:Nest	Biomass:Nest	$AIC_c$	$\Delta AIC_c$	$W_i$
2	24.10	1.083												599.2	0.00	0.101
34	24.45	1.082					-1.566							560.3	1.10	0.058
4	1691.00	1.082	-0.09219											560.3	1.17	0.056
10	26.04	1.083			-0.3068									561.0	1.80	0.041





**Figure A5:** Changes in weather and arthropod biomass over the summer period of 2019.

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**Table A6:** Linear mixed-effect model controlling for nests as a random factor.

<b>Responses and predictor variables</b>	<b>Estimate</b>	<b>SE</b>	<b>df</b>	<b>t-value</b>	<b>p-value</b>
<i>Weight at day 4</i>					
(Intercept)	14.13	4.65	24.97	3.04	0.0055
<i>Large Brachycera over 4 days</i>	4.40	5.37	26.20	0.82	0.42
Nest box	1.97	1.13	23.31	1.75	0.094
Clutch size at day 4	-0.37	0.75	24.09	-0.49	0.63
(Intercept)	12.99	4.39	25.07	2.96	0.0066
<i>Small Brachycera over 4 days</i>	698.73	480.79	23.31	1.45	0.16
Nest box	1.10	1.06	23.07	1.04	0.31
Clutch size at day 4	-0.32	0.71	24.24	-0.45	0.65
(Intercept)	15.62	4.24	24.67	3.69	0.0011
<i>Hymenoptera over 4 days</i>	59.86	158.80	25.31	0.38	0.71
Nest box	1.78	1.15	23.17	1.55	0.14
Clutch size at day 4	-0.51	0.74	23.89	-0.70	0.49
(Intercept)	15.96	3.99	24.97	4.00	<0.001
<i>Chironomidae over 4 days</i>	71.10	205.47	23.29	0.35	0.73
Nest box	1.44	1.13	23.02	1.27	0.22
Clutch size at day 4	-0.55	0.72	24.02	-0.77	0.45
(Intercept)	15.00	4.17	25.21	3.60	0.0014
<i>Other Nematocera over 4 days</i>	137.93	170.09	23.57	0.81	0.43
Nest box	1.24	1.12	23.18	1.11	0.28
Clutch size at day 4	-0.47	0.72	24.24	-0.64	0.53
(Intercept)	16.74	4.50	24.74	3.72	0.0010
<i>Aranea over 4 days</i>	-104.23	450.60	23.09	-0.23	0.82
Nest box	1.73	1.19	22.89	1.46	0.16
Clutch size at day 4	-0.57	0.72	23.73	-0.79	0.44

**Table A7:** Linear mixed-effect model controlling for nests as a random factor.

<b>Responses and predictor variables</b>	<b>Estimate</b>	<b>SE</b>	<b>df</b>	<b>t-value</b>	<b>p-value</b>
<i>Growth rate from day 4 - 6</i>					
(Intercept)	0.24	0.046	22.59	5.18	<0.001
<i>Large Brachycera over 2 days</i>	-0.13	0.11	21.35	-1.16	0.26
Nest box	-0.060	0.029	20.59	-2.09	0.049
centering weight at day 4	0.0030	0.00098	102.70	3.11	0.0024
Clutch size at day 6	-0.018	0.0078	22.54	-2.28	0.032
Large Brachycera:Nest box	0.91	0.40	20.74	2.27	0.034
(Intercept)	0.19	0.038	23.92	4.96	<0.001
<i>Small Brachycera over 2 days</i>	21.18	7.35	21.08	2.88	0.0089
Nest box	0.011	0.011	21.21	0.99	0.33
centering weight at day 4	0.0029	0.00098	102.50	2.99	0.0035
Clutch size at day 6	-0.018	0.0070	22.91	-2.56	0.018
(Intercept)	0.24	0.047	23.34	5.12	<0.001
<i>Hymenoptera over 2 days</i>	-4.08	3.63	22.03	-1.13	0.27
Nest box	-0.010	0.016	21.21	-0.63	0.54
centering weight at day 4	0.0031	0.00098	102.20	3.11	0.0024
Clutch size at day 6	-0.019	0.0083	23.10	-2.31	0.030
(Intercept)	0.21	0.038	23.38	5.68	<0.001
<i>Chironomidae over 2 days</i>	12.62	5.17	20.51	2.44	0.024
Nest box	0.0022	0.011	21.14	0.20	0.85
centering weight at day 4	0.003	0.001	102.40	3.05	0.0030
Clutch size at day 6	-0.018	0.0073	22.80	-2.48	0.021
(Intercept)	0.20	0.038	23.44	5.21	<0.001
<i>Other Nematocera over 2 days</i>	8.89	3.51	20.67	2.53	0.020
Nest box	0.0062	0.011	21.09	0.56	0.58
centering weight at day 4	0.0030	0.00098	102.40	3.04	0.0030
Clutch size at day 6	-0.018	0.0072	22.80	-2.42	0.024
(Intercept)	0.18	0.045	22.77	3.93	<0.001
<i>Aranea over 2 days</i>	21.67	12.09	21.46	1.79	0.087
Nest box	-0.012	0.014	21.19	-0.86	0.40
centering weight at day 4	0.0030	0.00098	102.40	3.10	0.0025
Clutch size at day 6	-0.020	0.0079	23.13	-2.52	0.019

**Table A8:** Linear mixed-effect model controlling for nests as a random factor.

<b>Responses and predictor variables</b>	<b>Estimate</b>	<b>SE</b>	<b>df</b>	<b>t-value</b>	<b>p-value</b>
<i>Growth rate from day 6 - 8</i>					
(Intercept)	0.20	0.059	20.37	3.41	0.0027
<i>Large Brachycera over 2 days</i>	-0.11	0.11	19.09	-1.009	0.33
Nest box	-0.033	0.021	19.34	-1.57	0.13
centeringweight at day 6	0.00021	0.0011	89.02	-0.18	0.86
Clutch size at day 8	-0.021	0.011	20.22	-1.91	0.071
(Intercept)	0.18	0.061	20.49	3.02	0.0067
<i>Small Brachycera over 2 days</i>	1.18	14.43	19.65	0.082	0.94
Nest box	-0.020	0.019	19.86	-1.03	0.32
centering weight at day 6	0.00020	0.0011	88.88	-0.17	0.87
Clutch size at day 8	-0.022	0.012	20.092	-1.88	0.075
(Intercept)	0.21	0.058	20.55	3.62	0.0017
<i>Hymenoptera over 2 days</i>	-5.32	3.69	19.12	-1.44	0.17
Nest box	-0.042	0.022	19.27	-1.89	0.074
centering weight at day 6	0.00021	0.0011	89.13	-0.19	0.85
Clutch size at day 8	-0.022	0.011	20.29	-1.99	0.061
(Intercept)	0.19	0.058	20.42	3.24	0.0041
<i>Chironomidae over 2 days</i>	-11.54	21.14	18.85	-0.55	0.59
Nest box	-0.026	0.020	19.40	-1.30	0.21
centering weight at day 6	0.00020	0.0011	88.95	-0.17	0.87
Clutch size at day 8	-0.021	0.012	20.16	-1.80	0.087
(Intercept)	0.19	0.059	20.38	3.13	0.0052
<i>Other Nematocera over 2 days</i>	-1.08	9.08	19.12	-0.12	0.91
Nest box	-0.022	0.020	19.56	-1.10	0.29
centering weight at day 6	0.00020	0.0011	88.90	-0.17	0.86
Clutch size at day 8	-0.021	0.011	20.11	-1.84	0.080
(Intercept)	0.13	0.063	20.10	2.05	0.054
<i>Aranea over 2 days</i>	30.63	17.69	19.28	1.73	0.099
Nest box	-0.044	0.021	19.15	-2.08	0.051
centering weight at day 6	0.00022	0.0011	89.19	-0.19	0.85
Clutch size at day 8	-0.024	0.011	20.38	-2.22	0.038

**Table A9:** Linear mixed-effect model controlling for nests as a random factor.

<b>Responses and predictor variables</b>	<b>Estimate</b>	<b>SE</b>	<b>df</b>	<b>t-value</b>	<b>p-value</b>
<i>Weight at day 8</i>					
(Intercept)	28.39	4.51	22.03	6.29	<0.001
<i>Large Brachycera over 8 days</i>	-2.01	3.23	20.54	-0.62	0.54
Nest box	-0.50	1.55	19.50	-0.33	0.75
Clutch size at day 8	-0.56	0.76	21.57	-0.73	0.47
(Intercept)	26.42	5.04	22.54	5.24	<0.001
<i>Small Brachycera over 8 days</i>	84.96	587.65	20.02	0.15	0.89
Nest box	0.20	1.17	20.03	0.17	0.87
Clutch size at day 8	-0.49	0.76	21.31	-0.64	0.53
(Intercept)	28.43	4.14	22.39	6.87	<0.001
<i>Hymenoptera over 8 days</i>	-82.71	91.45	20.33	-0.90	0.38
Nest box	-0.80	1.53	19.49	-0.52	0.61
Clutch size at day 8	-0.58	0.75	21.63	-0.77	0.45
(Intercept)	26.35	3.79	22.49	6.95	<0.001
<i>Chironomidae over 8 days</i>	191.40	185.97	19.92	1.03	0.32
Nest box	-0.12	1.14	19.94	-0.10	0.92
Clutch size at day 8	-0.49	0.74	21.60	-0.66	0.51
(Intercept)	25.38	4.02	22.42	6.31	<0.001
<i>Other Nematocera over 8 days</i>	160.52	155.03	20.20	1.04	0.31
Nest box	0.068	1.11	19.99	0.061	0.95
Clutch size at day 8	-0.48	0.74	21.62	-0.65	0.52
(Intercept)	23.58	4.24	21.05	5.56	<0.001
<i>Aranea over 8 days</i>	383.11	253.54	19.29	1.51	0.15
Nest box	-0.97	1.31	19.13	-0.75	0.47
Clutch size at day 8	-0.60	0.72	21.59	-0.83	0.42