Master's thesis

NTNU
Norwegian University of Science and Technology
Faculty of Natural Sciences
Department of Biology

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The influence of arthropods availability on fledgling morphology and reproductive success in wild house sparrows

Master's thesis in Natural Resources Management
Supervisor: Thor Harald Ringsby
Co-supervisor: Thomas Kvalnes, Peter Sjolte Ranke, Michael Le Pepke
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Abstract

Population declines of farmland birds and arthropods have been reported worldwide. The reduced arthropod availability has been suggested to be a driver behind insectivorous bird declines through predator-prey interactions by having less prey items available for these birds. It is therefore important to gain knowledge about how variation in the arthropod community impacts life history traits and morphological traits at higher trophic levels. This study investigated how reproductive success and fledgling morphology was influenced by temporal and spatial variation in arthropod communities in farm and non-farm habitats in eight island populations of house sparrows (*Passer domesticus*) in northern Norway. The results showed that both arthropod abundance and biomass increased throughout the season, where arthropod biomass was higher on islands with farms. Abundance and biomass of arthropods were positively associated with fledgling morphology but there was no evidence for an influence on the number of fledglings produced. Thus, the seasonal variation in the arthropod community may have a substantial positive influence on the fledglings, where an increase in arthropod biomass and abundance during the nestling period was associated with increased fledgling mass and size. In light of environmental change and land use change, the effect time of season had on both arthropod and house sparrow populations in addition to the impact the arthropod community had on the development of fledglings through trophic interactions need to be considered in future research on insectivorous bird species and biodiversity declines. Especially knowledge about what groups of arthropods different species of insectivorous species prefers in their diet, could prove to be important in future management of biodiversity.

Sammendrag

Over hele verden rapporteres det om nedgang i antall innsekter samt fugler i kulturlandskapet. Redusert tilgjengelighet av leddyr har vært foreslått som en mulig årsak til nedgangen av insektspisende fugler gjennom interaksjoner mellom byttedyr og dets predator ved å endre tilgangen av byttedyr for slike fugler. Det er derfor viktig å få kunnskap om hvordan variasjonen i leddyrsamfunnet påvirker livshistorietrekk og morfologiske trekk hos arter av høyere trofisk nivå. Denne studien undersøkte hvordan reproduktiv suksess og morfologien hos reirunger ble påvirket av variasjoner i tid og rom i leddyrsamfunnet hos åtte subpopulasjoner av gråspurv (*Passer domesticus*) med tilhold i gårdshabitater og ikke gårds-habitater. Resultatene viste at både antall og biomasse av leddyr økte gjennom sesongen, hvor biomasse av leddyr i gjennomsnitt var høyere på øyer med gårdsdrift. Antallet og biomassen av leddyrene hadde en positiv innvirkning på morfologien hos reirungene, men det var ingen bevis for at det påvirket antallet reirunger som var produsert. Denne studien viste at den sesongmessige variasjonen i leddyrsamfunnet har en betydelig positiv innvirkning på reirungene ved å påvirke kroppsmasse og størrelse hos reirungene. I lys av endringer i arealbruk og klima, bør den sesongmessige effekten på leddyr- og gråspurvpopulasjonene bli tatt i betrakting i fremtidig forskning på insektspisende fugler og nedgangen av biodiversitet. I tillegg bør fremtidig forskning se nærmere på påvirkningen leddyrsamfunnet har på utviklingen hos reirungene via deres trofiske interaksjoner, spesielt i sammenheng med å kartlegge hvilke leddyr ulike arter av insektetende fugler preferer noe som kan forbedre fremtidig forvalting av biodiversitet.

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Introduction

Loss of biodiversity through habitat destruction, overharvesting and climate change is a severe threat to ecosystems worldwide and is directly linked to anthropogenic effects on the environment (IPBES, 2019; CBD, 2022). Climate change has been shown to affect the phenology of populations, the spatial distribution of species, and the composition of communities (Parmesan & Yohe, 2003; Menzel et al., 2006; Schwartz et al., 2006)**.** In recent years several studies have reported a decline in the number of insects (Hallmann et al., 2017; Dirzo et al., 2014; Van Klink et al., 2020; Wagner et al., 2021; Møller, 2020), where multiple drivers have been suggested for these declines, such as land use change, habitat loss, degradation, climate change and pollution (Jacobsen et al., 2022; Wagner et al., 2021; Cardoso et al., 2020; Sánchez-Bayo & Wyckhuys, 2019). The loss of insects has the potential to influence important functions and services in the ecosystem as well as the structure of insect communities and may influence other organisms that are dependent on insects through trophic interactions (Cardoso et al., 2020).

It has been suggested that a decline in insect availability is an important driver behind the observed decline of insectivorous farmland birds (Frampton et al., 2000), and an increasing number of empirical studies demonstrate a positive relationship between arthropod availability and life history traits such as survival and reproductive success in insectivorous birds (Burger et al., 2012; Møller, 2013; Samplonius et al., 2016; Nell et al., 2023; Grames et al., 2023; Orłowski et al., 2017; Searcy et al., 2004; Saalfeld et al., 2019; Seress et al., 2018). Predator-prey interactions are suggested to be a driver shaping the spatial and temporal variation in insect communities (Zverev et al., 2020). For instance, Nell et al. (2023) demonstrated how the arthropod community could influence the insectivorous coastal cactus wren (*Campylorhynchus brunneicapillus*) in California, USA. They demonstrated a lack of consistency between the arthropods with highest biomass in the environment and the arthropods present in the birds' diet, and that reproductive success only was positively related to the abundance of some arthropod taxa (Nell et al., 2023). A reduced food availability seems to explain both an observed increase in mortality and a reduced body mass in another passerine, great tits (*Parus major*) (Seress et al., 2018). Møller (2013) showed that a declined insect availability resulted in a reduced breeding success, lower adult body mass, and reduced adult annual survival in the barn swallow (*Hirundo rustica*).

Arthropod availability has been linked to early-life development in insectivorous birds. A recent metanalysis showed that food availability had a positive effect on fledgling body condition and reproductive success across many passerine species (Grames et al., 2023). Accordingly, both Orłowski et al. (2017) and García-Navas & Sanz (2011) discovered a positive effect of the proportion of caterpillars on nestling condition in two different insectivorous birds. Similarly, during a caterpillar peak pied flycatchers (*Ficedula hypoleuca*) nestlings had a higher weight, longer tarsus length and a longer wing length (Samplonius et al., 2016). García-Navas & Sanz (2011) showed that by having a varied diet that incorporated other nutritional sources than just caterpillars was beneficial to Mediterranean blue tit (*Cyanistes caeruleus*) nestlings. This corresponds with other studies that have detected positive effects of a varied diet by influencing the growth rate, body size and breeding success (Searcy et al., 2004; Saalfeld et al., 2019; Møller 2013; but see Imlay et al., 2017). Warmer springs has been shown to result in earlier insect emergence, which also may influence the fitness of birds that feed their nestlings on insects (Burgess et al., 2018; Both et al., 2010). Warmer springs has been shown to cause a temporal asynchrony between the peak nestling demand from insectivorous bird species (e.g., pied flycatchers, blue tits (*Cyanistes caeruleus*), and great tits) and the peak in caterpillar biomass (Burgess et al., 2018). However, the responses to warmer springs will vary among species, where multiple brooded species is suggested to be less susceptible to such early spring asynchronies as the reproductive output of multiple brooded species depends on the availability of food throughout the breeding season (Visser & Both, 2005; Dunn et al., 2011).

Parental investment can be linked to offspring body mass and survival, as parents invest more resources to reduce fledgling mortality (Brode et al., 2021; Ringsby et al., 2009). For instance, Ringsby et al. (2009) suggested that increased parental care measured as feeding frequencies in house sparrows (*Passer domesticus*) had a positive influence on fledgling survival and the number of fledglings. Limitation in resources creates a conflict in energy allocation between prioritizing the fitness of the current offsprings or prioritizing the fitness of the parents through future reproductive success (Godfray, 1995; Trivers, 1974; Van Noordwijk & De Jong, 1986). Hence, the parents need a strategy of either prioritizing some offsprings of better quality or by investing equally in all offsprings (Godfray, 1995). It has been suggested that parental provisioning rates increased with an increasing brood size, and that larger offspring tend to receive higher investment from the parents (Cleasby et al., 2013; Mock et al., 2009). Parental investment is likely to be affected by environmental effects by influencing the brood size. Accordingly, it has previously been shown that parental investment influenced the brood size, where brood size has been reported to be affected by environmental factors like precipitation and food availability (Brode et al., 2021; Cox et al., 2019; Schöll & Hille, 2020; Winkler et al., 2013; Donald et al., 2001).

Habitat heterogeneity might impact insectivorous bird populations, as temporal and spatial variation in the abundance of arthropod has been linked to the temporal and spatial variation in the morphology of insectivorous species, hence differences in the habitat could impact the availability of arthropods (Evans et al., 1997; Blondel et al., 1991; Ringsby et al., 2002). For instance, added organic matter from grazing livestock has been shown to increase the net primary productivity, and that productivity and habitat heterogeneity influence bird populations and the arthropod community (Ryals & Silver, 2013; Cabrera et al., 2009; Prather & Kaspari, 2019; Dillon & Conway, 2021; Morris, 1981; Morris, 2000; Humbert et al., 2009). Accordingly, Musitelli et al. (2016) found that the distribution of barn swallows in breeding habitats was positively influenced by the presence of cow sheds and livestock likely due to an increase in arthropod prey abundance. This was further supported by the findings of Hollander et al. (2015), where the arthropod abundance was higher in farmland areas compared to forest clear-cuts in Belgium. Furthermore, Grüebler et al. (2010) showed that differences in habitat quality affected barn swallow nestling success depending on whether there was livestock and manure present or not, where manure close to nesting sites increased nestling survival.

Deficient invertebrate availability has been reported to affect body mass, reproductive success, and nestling survival in different species of insectivorous birds (Grames et al., 2023; Møller, 2013; Saafeld et al., 2019; Seress er al., 2018). Seress et al. (2012) observed a higher fledgling success and body mass in house sparrows and linked these observations to larger prey items in rural areas in Hungary. Another study on house sparrows in England observed that the availability of aphids was positively correlated with nestling survival (Peach et al., 2008). This provides support for the hypothesis that a deficient diet could potentially result in a poor nestling growth and reduced survival in the house sparrow.

In a metapopulation of house sparrows in an archipelago in northern Norway the interaction between the morphology, breeding success and the arthropod community has been closely monitored during the breeding season since 2017 in eight island populations. This offers a unique opportunity to study how the house sparrow populations are influenced by the spatiotemporal variation in the arthropod community. First, the abundance and biomass of arthropods through time (i.e., season and years) and between habitat types (i.e., farm island population or non-farm island population) will be investigated. Second, the knowledge about the arthropod community will be related to the fledgling diet composition through metabarcoding of faecal samples. Third, the study will investigate how habitat type (i.e., farm or non-farm habitats) and the variance in the arthropod community (i.e., arthropod abundance and biomass) influenced the number of fledglings in the metapopulation. Finally, the relationship between the variance in fledgling morphology (i.e., fledgling weight and tarsus length) and the variance of arthropod abundance and arthropod biomass will be investigated.

Methodology

Study system

The house sparrow is a bird species with a wide geographic range (Anderson, 2006). The house sparrow is listed as least concern by the International Union for Conservation of Nature (IUCN) however the European Bird Census Council (EBCC) have recorded a declining population trend in the period 1980-2013 (International Union for Conservation of Nature, 2022; European Bird Census Council, 2019). In 2021 the house sparrow was categorized as near threatened by the Norwegian Biodiversity Information Centre in Norway due to an observed decline between 15-30% across 12 years (Stokke et al., 2021). The house sparrow is a multi-brooded species, and typically lay between one to three clutches in Norway with an average of five eggs (Ringsby et al., 1998).

This study was conducted in an archipelago at Helgeland in northern Norway (66°33’N, 12°50’E) where insular populations of house sparrows have been closely monitored since 1993 by using capture mark recapture methodology and records of breeding activity during the breeding season from April to August (Araya-Ajoy et al., 2021; Ringsby et al., 2002). The data were collected in the period 2017-2019 at eight islands: Hestmannøy (with subpopulations in the north and south: Storselsøy and Hestmona), Gjærøy (with subpopulations in the north and south), Indre Kvarøy, Træna, Sleneset, Lovund, Nesøy and Selvær (Figure 1). Islands were categorized into farm islands that had cattle farms and where house sparrow populations lived in close association with barns and cowsheds, and non-farm islands where house sparrow populations were found living in gardens in nest boxes in the inhabited island villages. There were four non-farm islands (i.e., Lovund, Selvær, Træna, and Sleneset), and four farm islands (i.e., Hestmannøy, Gjerøy, Indre Kvarøy, and Nesøy) (Table 1, Figure 1). Note that Indre Kvarøy stopped the farm activity in 2017 and thereby might resemble a non-farm island by nesting in nest boxes despite having inactive cowsheds.

Data collection

Measurement of reproductive success and morphological traits

During the breeding season every active nest were monitored weekly, where the number of eggs and nestlings were recorded and where morphological traits were measured. At the age of 8-13 days, fledglings were marked with a unique combination of colour plastic leg-rings and numbered metal ring provided by the Norwegian Bird Ringing Centre. The number of fledglings were recorded as a measure of parental reproductive success, and fledgling body mass was measured to the nearest 0.1 g using a Pesola 50 g balance spring weight. As a measure of body size tarsometatarsus length (i.e., tarsus length) was measured by trained field workers using calipers to 0.1 mm precision, see Pepke et al. (2022). The morphological traits were age-standardized to 11 days after hatching, in order to account for the variation in the measurements due to variation in age (see Kvalnes et al., 2018). While the fledglings were handled the nests were blocked using a cotton bird bag to minimize distress for the parents, and all measures of morphology and number of fledglings for each brood were taken on the same day to avoid unnecessary disturbance (Ringsby et al., 1998).

Collection of arthropod data

From 2017-2019 malaise traps were employed to passively collect data of primarily flying arthropod abundance and biomass from eight islands. There was a minimum of one trap for each island, except for Hestmannøy and Gjerøy that has two subpopulations and hence two malaise traps, resulting in ten malaise traps in total (Table 1, Figure 1). All malaise traps sites were established in 2017 except Nesøy and Gjerøy north, which was established in 2019. The traps were located in close proximation to the house sparrow populations to collect the arthropods present close to nest sites. Malaise traps is a method of capturing mainly flying insects, but occasionally other insects and taxa are trapped as well. In this study spiders were not removed from the results thereby this study uses the terminology arthropods. This study used sea, land and air malaise traps (SLAM, standard type II) (MegaView Science Co, Taiwan) that worked by having four mesh fabric panels where the arthropods could enter on all four sides with a white sloping roof which were guiding the arthropods along the slope before being funnelled to a container with 96% ethanol where the arthropods were collected (Costa & Borges, 2021; Skvarla et al., 2021). The setup for the malaise trap used in this study is shown in Figure 2.

After every week the container was emptied and replaced with a new one. The starting date of each new container in addition to the collection date of each container was recorded. All the collected arthropod specimen were identified to predefined taxonomic groups, mainly to the taxonomic level of family, by Jon Kristian Skei. The weekly arthropod biomass was measured by weighing representative individuals (ranging between 1-1983 per sample) within each taxon that was present in one weekly sample (n=52) to an accuracy of 0.00001 grams (wet weight) before starting a drying process for 48 hours at 70 ºC. The sample was then weighed a second time, before it was dried for another 24 hours at the same temperature and weighed a final time. The calculation for weekly arthropod biomass for each taxon used the mean dry weight from the second and third measurements, multiplied with the weekly arthropod abundance for each taxon, and then lastly summarized to get the biomass for each container (see details in Julseth, 2019).

DNA-metabarcoding

In 2017 faecal matter from 85 house sparrow nestlings at the islands of Træna and Hestmannøy were collected in 99% ethanol and stored at -20 °C before being sent to the laboratory (Julseth, 2019). The faecal matter was collected from several nestlings from several nests each month through the breeding season at Træna and Hestmannøy. DNA-metabarcoding was used for investigating which taxa of arthropods that were found in nestling sparrows' diet, by investigating the diversity among DNA sequences in the mitochondrial gene cytochrome c oxidase subunit 1 (CO1) to identify species (Hebert et al., 2003).

The metabarcoding procedure is presented in detail in Stolz (2019) and summarized here. DNA was extracted by collecting 500 mg of the faecal samples to dry off the ethanol followed by applying FastDNA Spin Kit for Soil protocol (MP Biomedicals, 2016). This study used ZBJ-ArtF1c and ZBJ-ArtR2c as arthropod primers (Zeale et al., 2011). When executing the polymerase chain reaction 25 µL volume was used when adhering to the 16S Metagenomic Sequencing Library Preparation protocol (Illumina, 2013). At NTNU Genomics Core Facility an Illumina NextSeq 500 System was used on single-end 1x300 bp sequences after normalizing the templates with the SequalPrep Normalization Plate Kit (Invitrogen, 2008). The Barcode of Life Database (BOLD) was accessed through mBRAVE (Ratnasingham & Hebert, 2007). Sequences were then assembled into Operational Taxonomic Units (OTUs) by the mBRAVE software, where these OTUs were then matched to the OTUs of BOLD. For further details about the laboratory work and the metabarcoding data see Stolz (2019).

Statistical analyses

The statistical analyses were conducted in the software R (v4.2.1; R Core Team, 2022), where generalized mixed effect models (GLMMs) were constructed using the glmmTMB package (v1.1.5; Brooks et al., 2017). GLMMs allows both fixed and random effects and may fit a range of different distributions. In total there were five response variables where arthropod biomass, fledgling body mass, and fledgling size were modelled using a gaussian distribution, while arthropod abundance and number of fledglings were modelled using a negative binomial and a poisson distribution, respectively. Additionally, the morphological data had a structure where broods were nested within islands. The R-package performance (v0.10.0; Lüdecke et al., 2021) was used on global models to check for overdispersal to avoid over-confidence due to having more variance in the data than what is assumed by the poisson or negative binomial distributions (Hector, 2021, p. 176). Likelihood ratio tests (LRT) were used to test the significance of the parameters of interest in the different global models that were addressed (see supplementary materials), by comparing two models fitted by maximum likelihood that only differ in one parameter (Hector, 2021). For the LRT test, twice the difference in log-likelihood between two models is chi-square (χ^2) distributed with df1-df2 degrees of freedom. Figures were made using the ggplot2 package (v3.4.1; Wickham, 2016).

The global models constructed to explain the observed variation in arthropod abundance and biomass included six predictor variables: habitat type (farm or non-farm), year, week, a quadratic effect of week (week^2), in addition to two different interactions between week, habitat type and year, where week was mean centred. The squared effect of week (i.e., week^2) was included to test the hypothesis of how the seasonal variations (i.e., variation due to week) affected the variation in arthropods (i.e., nonlinear, or linear). The interaction between week and habitat type, and week and year were included to test the hypotheses of how the seasonal effect on the variation of arthropods differed among years and between habitat types.

The next section of analyses aimed to explain how the variance in the number of fledglings per brood and the variance in morphological traits in fledglings (i.e., body mass and tarsus length) could be explained by the variance in arthropods through the season and between habitat types. Abundance and biomass of arthropods were both separated into two categories based on arthropod abundance and mass, respectively, during early (0-5 days after hatching) and later (6-10 days after hatching) nestling stages, to account for a potential difference in arthropod dependency due to offspring age (Anderson, 2006). Arthropod abundance was separated into the abundance during early nestling stages (“abundance 5”), and the abundance during later nestling stages (“abundance 10”). The same separation was done for the arthropod biomass from malaise traps, where “biomass 5” was the biomass available during early nestling stages, and “biomass 10” was the biomass available during later nesting stages. In order to avoid the problem of multicollinearity among the predictors, abundance 5, abundance 10, biomass 5, biomass 10 (all Pearson correlation coefficients > 0.65), four models were composed for each response variable to investigate the effect of the arthropod community on fledgling morphology and reproductive success as separate hypotheses, see Table S3-S5 in supplementary materials. All four arthropod measures were mean centred where the arthropod abundances were additionally divided by 1000 to ease model convergence before fitting the models. Separate analyses were run where the response variables included the number of fledglings, body mass, and size, where all global models included the following explanatory variables; year, habitat type, arthropod measurement (i.e., abundance 5, abundance 10, biomass 5, biomass 10), and the interaction between an arthropod measurement and habitat type. The final models were obtained on evaluation of the variables according to likelihood ratio tests.

Muff et al. (2022) suggested using the terminology of evidence for describing the degree of uncertainty in statistical analyses instead of significance. The argument is to evaluate the degree of uncertainly by a gradient instead of solely focusing on a significance threshold. This gives a more in depth understanding of the uncertainties instead of simply reporting if the results were significant or not. Muff et al. (2022) suggested the classifications of no evidence ($p > 0.1$), weak evidence ($0.05 < p > 0.1$), moderate evidence ($0.01 < p > 0.05$), strong evidence ($0.001 < p > 0.01$), and very strong evidence ($0.0001 < p > 0.001$). This study has implemented the gradient and terminology suggested by Muff et al. (2022).

Results

The average arthropod abundance per week in each trap was 628 ± 28 individuals (*n* = 515, SD = 625, range = [1, 4450]), and a corresponding average biomass of 0.44 ± 0.03 g (*n* = 515, SD = 0.61, range = [0.00, 5.54]). House sparrow nests had an average of 3.01 ± 0.07 fledglings (median = 3, *n* = 530, SD = 1.71, range = [0, 7]), with an average body mass of 26.39 ± 0.11 g (*n* = 1595, SD = 4.43, range = [7.5, 37.3]) and an average tarsus length of 19.07 ± 0.03 mm (*n* = 1595, SD = 1.35, range = [12.48, 22.16]).

Seasonal changes in arthropod abundance and biomass

The abundance of arthropods increased throughout the season, peaked around week 27-34 (July-August) and displayed a slight decrease late in the season, ($\chi^2 = 62.660$, $p < 0.001$, Table 2, Figure 3A). There was strong evidence for a difference between years in the seasonal change in abundance ($\chi^2 = 96.249$, $p < 0.001$, Table 2, Figure 3A,), but no evidence for a difference in arthropod abundance between habitat types ($\chi^2 = 0.834$, $p = 0.361$). Additionally, there was no evidence that the seasonal change in arthropod abundance was dependent on the habitat type ($\beta_{\textit{Habitat type x Week}} = -0.0107 \pm 0.0115$, CI$_{\text{Habitat type x Week}}$ = [-0.0326, 0.0123], $\chi^2 = 0.786$, $p = 0.375$).

The total arthropod biomass increased throughout the season ($\chi^2 = 166.004$, $p < 0.001$, Table 3, Figure 3B), with no evidence for a nonlinear change over the season ($\beta_{\textit{Week\^{}2}} = 0.0004 \pm 0.0007$, CI$_{\text{Week\^{}2}}$ = [-0.0009, 0.0018], $\chi^2 = 0.380$, $p = 0.538$). However, the seasonal change in arthropod biomass depended on both year and habitat type (Year x Week: $\chi^2 = 6.888$, $p = 0.032$, Habitat type x Week: $\chi^2 = 14.196$, $p < 0.001$).

Which arthropods seem to make out most of the diet?

The metabarcoding data from Træna and Hestmannøy pooled across the season showed that the taxa of Tipuloidea, Scathophagidae, and Chironomidae were the most frequent in the diet of the house sparrow nestlings (Table 4). While the taxa that was highly present in the malaise traps at Træna and Hestmannøy included Lepidoptera (46931), Hymenoptera (10052), and from Diptera in particular the (super-)families of Tipuloidea (14348), and Chironomidae (9693). Especially Tipuloidea seemed to be highly present in both diet and in arthropod abundance. Thus, the results show that a large part of the content in the malaise traps can also be found in the fledgling diet, and that the trap content may therefore be suitable to estimate arthropod availability from the perspective of house sparrows.

Did arthropods influence reproductive success and morphology of house sparrow fledglings?

The number of fledglings

There were no evidence for an effect of arthropod abundance in the early or late nestling period on the number of fledglings in the nest aged 8-13 days (Early abundance: $\chi^2 = 0.045$, $p = 0.832$, Table 5A, Figure 4A, early interaction: $\beta_{Abundance/1000 \times Habitat\ type} = 0.0034 \pm 0.1261$, CI $_{\text{Abundance*Habitat type}}$ = [-0.2438, 0.2505], $\chi^2 = 0.001$, $p = 0.979$, Late abundance: $\chi^2 = 0.087$, $p = 0.768$, Table 5B, Figure 4B, Late interaction: $\beta_{Abundance/1000 \times Habitat\ type} = -0.0494 \pm 0.1429$, CI $_{\text{Abundance*Habitat type}}$ = [-0.3295, 0.2308], $\chi^2= 0.119$, $p = 0.172$). Additionally, non-farm islands had a higher number of fledglings compared to farm islands (Early: $\chi^2 = 16.624$, $p < 0.001$, Late: $\chi^2 = 16.546$, $p < 0.001$). There was weak evidence for a difference in the number of fledglings among years when looking at arthropod abundance during early nestling period ($\chi^2 = 7.659$, $p = 0.022$), and no evidence for å difference among years when looking at arthropod abundance during late nestling period ($\chi^2 = 7.825$, $p = 0.730$) (Table 5, Figure 4).

There was no evidence for an effect of arthropod biomass on the number of fledglings (Early biomass: $\chi^2 = 0.022$, $p = 0.882$, Table 6A, Figure 4C, Early interaction: $\beta_{Biomass \times Habitat\ type} = -0.0209 \pm 0.1681$, $CI_{Biomass \times Habitat\ type}$ = [-0.3503, 0.3085], $\chi^2 = 0.016$, $p = 0.901$, Late biomass: $\chi^2 = 0.020$, $p = 0.887$, Late interaction: $\beta_{Biomass \times Habitat\ type} = -0.0203 \pm 0.1664$, $CI_{Biomass \times Habitat\ type}$ = [-0.3464, 0.3058], $\chi^2 = 0.015$, $p = 0.903$) (Table 6B, Figure 4D). However, there was strong evidence for more fledglings being produced on non-farm islands (Early: $\chi^2 = 16.576$, $p < 0.001$, Late: $\chi^2 = 16.616$, $p < 0.001$), and weak evidence for a difference in the number of fledglings among years (Early: $\chi^2 = 7.828$, $p = 0.020$, Late: $\chi^2 = 7.826$, $p = 0.020$) (Table 6, Figure 4).

Fledgling body mass

There was weak evidence for an effect of arthropod abundance on fledgling body mass in the early and later nestling period which was independent of habitat type (Early abundance: $\chi^2 = 5.699$, $p = 0.017$, Table 7A, Figure 5A, early interaction: $\beta_{Abundance/1000 \times Habitat\ type} = -0.7378 \pm 0.8566$, CI $_{\text{Abundance/1000 x Habitat type}}$ = [-2.4167, 0.9411], $\chi^2 = 0.740$, $p = 0.390$, Late abundance:

$\chi^2 = 4.115$, $p = 0.043$, Table 7B, Figure 5B, Late interaction: $\beta_{\mathit{Abundance/1000\ x\ Habitat\ type}} = -0.607 \pm 0.970$, CI $_{\text{Abundance/1000 x Habitat type}}$ = [-2.5084, 1.2941], $\chi^2 = 0.391$, $p = 0.532$). Additionally, the fledgling body mass varied among years (Early: $\chi^2 = 27.505$, $p < 0.001$, Late: $\chi^2 = 29.619$, $p < 0.001$), while no evidence for a difference in fledgling body mass between habitat types were detected (Early: $\chi^2 = 0.675$, $p = 0.411$, Late: $\chi^2 = 0.600$, $p = 0.438$) (Table 7, Figure 5).

The evidence for an effect of arthropod biomass on the fledgling body mass was strong during the late nestling period but absent in the early nestling period (Early biomass: $\chi^2 = 2.229$, $p = 0.135$ (Table 8A, Figure 5C, Late biomass: $\chi^2 = 6.736$, $p = 0.009$, Table 8B, Figure 5D). Additionally, there was a trend for a difference between habitat types in the effect of arthropod biomass on fledgling body mass (Early interaction: $\beta_{\mathit{Biomass\ x\ Habitat\ type}} = 2.0788 \pm 1.1003$, CI $_{\text{Biomass x Habitat type}}$ = [-0.0778, 4.2354], $\chi^2 = 3.553$, $p = 0.059$, Late interaction: Late biomass: $\chi^2 = 6.736$, $p = 0.009$, Late interaction: $\beta_{\mathit{Biomass\ x\ Habitat\ type}} = 2.1072 \pm 1.1345$, CI $_{\text{Biomass x Habitat type}}$ = [-0.1164, 4.3308], $\chi^2 = 3.437$, $p = 0.064$), and strong evidence for a difference in fledgling body mass between years (Early: $\chi^2 = 26.797$, $p < 0.001$, Late: $\chi^2 = 26.270$, $p < 0.001$) (Table 8, Figure 5).

Fledgling body size

Arthropod abundance was positively associated with fledgling body size in the early and late nestling period independent of habitat type (Early abundance: $\chi^2 = 9.979$, $p = 0.002$, Table 9A, Figure 6A, early interaction: $\beta_{\mathit{Abundance/1000\ x\ Habitat\ type}} = -0.0626 \pm 0.2678$, CI $_{\text{Abundance x Habitat type}}$ = [-0.5875, 0.4623], $\chi^2 = 0.055$, $p = 0.815$, Late abundance: $\chi^2 = 7.796$, $p = 0.005$, Table 9B, Figure 6B, Late interaction: $\beta_{\mathit{Abundance/1000\ x\ Habitat\ type}} = -0.2091 \pm 0.3023$, CI $_{\text{Abundance x Habitat type}}$ = [-0.8016, 0.3833], $\chi^2 = 0.477$, $p = 0.490$). Fledgling body size also differed among years (Early: $\chi^2 = 34.873$, $p < 0.001$, Late: $\chi^2 = 37.853$, $p < 0.001$), however there were no evidence for a difference in tarsus length between habitat types (Early: $\chi^2 = 2.776$, $p = 0.096$, $\chi^2 = 2.565$, $p = 0.109$).

There was also moderate evidence for a difference in the effect of arthropod biomass on fledgling tarsus length between habitat types (Early biomass x Habitat type: $\chi^2 = 9.908$, $p = 0.002$, Late biomass x Habitat type: $\chi^2 = 7.323$, $p = 0.007$, Table 10, Figure 6C-D). Additionally, there was strong evidence for a difference in tarsus length among years (Early: $\chi^2 = 31.463$, $p < 0.001$, Later: $\chi^2 = 31.871$, $p < 0.001$, Table 10).

Discussion

The present study indicated that there was temporal variance both among years and within the seasons in the biomass and abundance of the arthropod community (Table 2-3). Simultaneously the results suggested that fledgling size and fledgling mass were affected by the arthropod abundance and arthropod biomass, where the number of fledglings and fledgling size also differed between habitat types (i.e., farm and non-farm) (Table 5, 6, 10). Accordingly, as both arthropod communities as well as insectivorous bird species have been shown to decline globally (Hallmann et al., 2017; Dirzo et al., 2014; Van Klink et al., 2020; Wagner et al., 2021; Møller, 2020; Stokke et al., 2021; European Bird Census Council, 2019), the present results emphasizes the importance of identifying and quantifying the components of variation shaping the relationships between arthropod communities and life history traits in insectivorous avian species.

There were temporal effects in the arthropod communities in our study areas such that abundance and biomass both had an increase during the house sparrow breeding season (Table 2-3, Figure 3). Late in the season (late July-middle of August) there was evidence for a decrease in arthropod abundance, while the arthropod biomass continued to increase for the duration of the study period (Table 2-3, Figure 3). This might suggest that there is a shift towards bigger species of arthropods available late in the breeding season. Other studies have found that arthropods seem to vary throughout the seasons (Jahn et al., 2010; Møller, 2019; D'Souza et al., 2021). For instance, the size and abundances of arthropods differed during the breeding season among arthropod taxa (Jahn et al., 2010). The present study found a spatial effect in arthropod biomass between different habitat types, with higher arthropod biomass on farm islands, but no evidence for a difference in arthropod abundance (Table 2-3, Figure 3). Arthropod abundance is often found to be highly correlated to arthropod biomass and similar relationship between abundance and biomass could be expected at this study system as well (Vereecken et al., 2021; Kinsella et al., 2020). This indicates that the composition of the arthropod community could be different depending on habitat type. Guo et al. (2020) showed that arthropod diversity in China differed between farmland and semi-natural habitat types. Another study from Belgium observed that the abundance of arthropods was higher in farmlands compared to forest clear-cuts while the body size of arthropods was higher in clear-cuts (Hollander et al., 2015). Hollander et al. (2015) suggested that farmland management may induce different conditions for food quality and quantity for insectivorous birds compared to production forests.

The metabarcoding results showed that Tipuloidea, Chironomidae, Scathophagidae, and Lepidoptera were frequently present in the diet of house sparrow fledglings (Table 4). Nevertheless, Scathophagidae had a low abundance in the malaise traps compared to the other four taxa (Table 4), while Tipuloidea, Chironomidae and Lepidoptera were abundant in both the traps and faeces. Thus, there were both a high availability and consumption of these taxa in 2017 suggesting that the malaise traps were adequate in collecting major important taxa present in the fledgling diet. While Hymenoptera and Plecoptera had high abundances in the malaise traps which indicates a high availability in the environment, they were sparsely found in the faeces samples which may be an indicator that the house sparrow does not prefer these taxa. The findings from the malaise traps and metabarcoding suggest that flying arthropods may be a major part of the fledgling diet. This also corresponds well with results from a preliminary video survey of house sparrow feeding rates where prey composition was assessed in our study area (Lazarus et al., 2021, unpublished results). Previous research on house sparrows also supports the importance of flying arthropods as well, where the groups of Lepidoptera and Diptera is mentioned to be an important component of the nestling diet (Vincent, 2005; Seel, 1969; Anderson, 2006). However, Vincent (2005) and Seel (1969) mentioned that spiders and caterpillars in addition to flies (Diptera) were important prey in the house sparrow diet.

Despite having taxa that contributes to the fledgling diet in malaise traps, it should be noted that the samples are partly biased due to the lack of data on non-flying arthropods such as spiders and Lepidoptera in their larva stage, which might not be well represented by using a malaise trap (Anderson, 2006: Nielsen et al., 2017). Even though flying arthropods are important for fledgling diet, it would therefore be interesting to use pitfall traps together with malaise traps. Császár et al. (2018) suggested that adding a roof on funnel pitfall traps is an efficient method for capturing ground beetles and spiders by limiting small vertebrates and litter falling into the trap while simultaneously lowering the escape rates of beetles. Frass traps is a method used to collect faecal matter from caterpillars by placing frass-nets under trees (Visser et al., 2006). This method has been suggested to be a good method for estimating caterpillar biomass and have been used in multiple studies (Visser et al., 2006; Verboven et al., 2001; Zandt, 1994), and may be a useful approach to add to the Helgeland project in future studies to gain more knowledge about larvae that is likely underrepresented by just using malaise traps. By implementing one or two non-malaise traps which also demand minimal maintenance and that passively collect arthropods could give more information about the arthropod availability and arthropod biomass on the islands with less bias toward flying arthropods.

Despite temporal variation in the arthropod community and the presence of the taxa in the diet neither arthropod biomass nor abundance had any evidence for influencing the number of fledglings. This in contrast to other studies which have shown that food availability and arthropod biomass influenced the number of clutches, nestling survival, in addition to different measures of reproductive success which were positively related to food availability (Julseth, 2019; Grüebler et al., 2010; Grames et al., 2023). A positive effect of food availability on nestling survival has been found in a few studies (Grüebler et al., 2010; Seress et al., 2020), others have not discovered an effect of arthropod abundance on insectivorous birds (Imlay et al., 2017). A study in Canada by Imlay et al. (2017) suggested that the effect arthropod abundance had on nestling survival in barn swallows, tree swallows (*Tachycineta bicolor*) and cliff swallows (*Petrochelidon pyrrhonota*) might have varied geographically. One reason why the number of house sparrow fledglings in the clutches were not influenced by the abundance or biomass of the sampled arthropod community could be because the arthropod availability might be well above sufficient for raising the chicks and consequently not affect the nestling survival. In such a case, other limiting factors, such as nest quality and environmental conditions, might have higher impact on life history traits in the house sparrow population (Newton, 1980; Imlay et al., 2017; Dunn et al., 2011). Alternatively, parents might attempt to compensate for limits in food availability by increasing the effort put into searching and providing food to prevent fledgling mortality. Such compensating food provisioning behaviour has been documented in previous studies (Rakhimberdiev et al., 2015; Dobbs et al., 2007; Sinkovics et al., 2021). For instance, Sinkovics et al. (2021) showed that great tits in urban areas fed their chicks with smaller prey items but compensated by having higher feeding rates than parents in forest sites. A corresponding mechanism in the present study might explain why arthropod abundance and arthropod biomass did not influence the number of fledglings produced.

Both body mass and body size were positively related to arthropod abundance and arthropod biomass (Table 7-10, Figure 5-6), but with no clear evidence for the relationship between arthropod biomass and fledgling body mass during early nestling stages (Table 8A, Figure 5C). Still, the general pattern suggests that fledgling weight and tarsus length increased as arthropod availability increased throughout the entire nestling stage. Other studies have also found a corresponding positive effect on both body mass and tarsus length with increasing arthropod availability in birds (Samplonius et al., 2016; García-Navas & Sanz, 2011; Orłowski et al., 2017; Seress et al., 2018). Additionally, Seress et al. (2012) found that different habitat types have been shown to result in both different size of prey items and to affect the house sparrow body size when comparing rural and urban areas (Seress et al., 2012). For instance, limitations in the preferred nestling diet are thought to be responsible for the decline in fledgling body mass in great tits and reproductive success in cities compared to the forest sites in Hungary (Seress et al., 2018). The present study revealed no evidence for a difference in the effect of arthropod biomass between habitat types for fledgling body mass, but the effect of arthropod biomass on tarsus length was stronger on non-farm islands (Figure 6C-D). A possible explanation for such a pattern could be that body size (i.e., tarsus length) is a stable morphological trait compared to body weight. Accordingly, in Pennsylvania, USA it has been shown that the early nutrition in young song sparrows (*Melospiza melodia*) affected the growth rates and where the effect on skeletal size in young birds was carried over into adulthood (Searcy et al., 2004).

Arthropod biomass was found to be higher at farm islands (Table 3A and B, Figure 3B). However, this did not seem to translate into the expected differences in house sparrow populations, but rather the opposite pattern was found, where the non-farm populations produced more fledglings, and achieved longer tarsus lengths (Table 5, 6, 10, Figure 4, 6). One likely explanation for the contradicting pattern is that the observed peak in arthropod biomass at farm islands but not arthropod abundance (Figure 8) was a consequence of the increase of big arthropod species that emerged late in the season that the house sparrow has no or little preference for. Thus, the expected effect of higher arthropod biomass during the breeding season on farm-islands would not necessarily affect the house sparrow fledglings. Accordingly, Nell et al. (2023) showed that the available arthropod species with high biomass were not necessarily present in the diet of coastal cactus wrens in California, USA. Other studies have also shown that fledgling diet in insectivorous birds differs throughout the season (Arnold et al., 2010; Evans et al., 1997; Blondel et al., 1991). For instance, in a study of blue tits in Scotland it was observed that the broods raised earlier in the season were provided by a different diet than the broods raised later in the season (Arnold et al., 2010). Thus, as the phenology and composition of the arthropod community develops throughout the breeding season it is likely that also the composition of the diet provided to the fledglings changed which need to be considered when interpreting the results.

Another possibility for the difference in the effect of arthropods on fledgling morphology in the present study could indirectly be associated by differences in nest quality. The quality of nesting sites might differ between farm and non-farm islands, where nest boxes are used at non-farm islands and natural cavities in barns and cowsheds are more frequently used at farm islands. This could influence the fledgling survival to be higher at non-farm islands despite the biomass being higher at farm islands. Thus, Fargallo et al. (2001) reported that birds using nest boxes produced more Eurasian kestrel (*Falco tinnunculus*) fledglings than the breeding pairs using holes in manmade buildings in Spain. Møller (2010) reported that bird populations that had indoor nests had a lower nest predation rate in Denmark and Ukraine. It has also been shown in Canada that tree swallow pairs that used nesting boxes were significantly more successful at producing fledglings than the pairs that used non-human influenced sites (Norris et al., 2018), while Sudyka et al. (2022) argue that human made nest boxes provided less efficient thermoregulation compared to natural cavities in Poland. Another factor that needs to be considered when interpreting the results is that some farms involved in the study have had renovations in some years by improving and expanding the buildings and some farms have in later years closed the husbandry. Ringsby et al. (2006) suggested that the extinction of a house sparrow subpopulation at Ytre Kvarøy in Helgeland, Norway was a result from closing the farm production on the island. These kinds of disturbances and changes at the farm islands might have contributed to an increased stress level for the house sparrows at some farm islands and consequently increased the fledgling mortality. This is supported by previous studies that have shown how nestling survival in birds tends to decrease when experiencing high level of disturbances (Watson et al., 2021; Kight & Swaddle, 2007).

Another factor to consider which may potentially influence body sizes between farm and non-farm populations is the differences in the spatial distribution of nest sites between farm, and non-farm habitats. The house sparrows at non-farm islands were more spatially spread out in a larger area covered by the village compared to farm populations where house sparrow populations were aggregated due to their association to the barns. Thus, higher local densities at farms could be related to a lower availability of territories, which could affect life history traits such as fledgling body size in the studied farm populations, compared to non-farm populations. Accordingly, Wilkin et al. (2006) showed that great tits with small territories had smaller clutches and less body weight compared to bigger territories in the United Kingdom.

The present study revealed that the availability of arthropods (i.e., abundance and biomass) in early (i.e., 0-5 days old) and late nestling stages (i.e., 6-10 days old) had similar effects on fledgling morphology and reproductive success (Table 5-10). Even though the parents of house sparrow fledglings have been shown to gradually shift their offsprings diet from being based on arthropods in the early nestling stage towards a diet consisting of higher frequencies of seeds and grains at a later stage (Vincent, 2005; Anderson, 2006), this present study did not identify the consequences of such a potential change in the fledgling diet. In blue tits in Spain, it has been found that the parents feeding strategies and type of food items changed with nestling age by prioritising different species of caterpillars and by eating other taxa when caterpillars were scarce (García-Navas et al., 2012). The results indicates that arthropods were important for the development of the house sparrow nestlings throughout both nestling stages included in this study. In addition to age dependent diet of house sparrow nestlings, the diet might be different among broods raised later in the breeding season compared to broods raised in early breeding season. For instance, Tremblay et al. (2003) showed that insectivorous birds change their diet during the season, and that the variation in peak food availability influenced both fledgling mass and success by studying blue tits in Corsica, France.

This study focused on the overall availability of arthropods, its seasonal change and effect on house sparrow nestlings, as well as which taxa that were found in the diet of house sparrow nestlings. To aid conservation of arthropods and insectivorous species a more in-depth knowledge about the nestling diet throughout the season is needed to better understand the interaction between the arthropods and the house sparrow, perhaps by identifying and monitoring assumed important arthropods. Thus, future studies should investigate how individual variation in nestling's arthropod diet changes throughout the season by using metabarcoding technique of faecal samples and link this knowledge on how it affects individual body size and probability of survival to fledgling stages as well as to recruitment. Additionally, the arthropod measures during all data analyses were not including non-flying insects which can create an underrepresentation of some taxonomic groups assumed to be important such as caterpillars (Vincent, 2005; Anderson, 2006).

It may also be interesting to further investigate how specific environmental factors could influence the food availability and how this would consequently relate to measures of reproductive success and morphological traits in the house sparrow population, such as temperature, precipitation, and wind strength. Climate change is suspected to be a partial driver of the observed insect declines (IPES, 2019; CBD, 2022; Wagner et al., 2021; Cardoso et al., 2020; Sánchez-Bayo & Wyckhuys, 2019). In some cases, climate change may interfere with predator-prey interactions causing phenological mismatch (Burgess et al., 2018; Visser et al., 1998). However, multi-brooded species are expected to not be particularly susceptible for this type of temporal mismatch because they depend on food availability throughout the breeding season in order to produce multiple clutches (Dunn et al., 2011). Nonetheless, the importance of environmental factors such as temperature and precipitation which influence the arthropod community has been shown to be important in the present study system influencing the size and survival of fledglings (Ringsby et al., 2002). Additionally, previous studies have also been shown to influence brood size, nestling condition, and nestling mass in other insectivorous bird species (Donald et al., 2001; Cox et al., 2019).

Environmental conditions experienced during the nestling stage, such as food availability, might be carried over to influence adult survival and adult reproductive success. Previous studies such as Pepke et al. (2023) has shown that the early-life environment influenced adult house sparrows in our study population through effects on telomere dynamics. Accordingly, Eastwood et al. (2019) showed that early-life environment affected telomere length, which influenced adult survival and reproductive success in the Australian purple-crowned fairy-wren (*Malurus coronatus coronatus*). Future studies might therefore want to add environmental factors in the analyses to better analyse how such factors in combination with arthropod abundance influence the prey-predator interactions.

Conclusions

This study contributes with important knowledge on how variation in arthropod availability impact life history traits in local populations of house sparrows in northern Norway. Arthropod abundance and biomass increased throughout the breeding season and had a positive impact on fledgling body mass and fledgling body size, but no evidence for influencing parental reproductive success. Habitat types (i.e., farm habitats and non-farm habitats) influenced both the arthropod community and the house sparrow population, through higher arthropod biomass in farm habitats, as well as higher reproductive success and body sizes in non-farm habitats. Reports of insect declines and declines in other house sparrow populations sheds light on the importance of understanding the effect of the ecological interaction between trophic levels, especially considering climate change affecting the phenology of populations. Future studies might want to investigate in further detail about how the arthropod composition at the islands changes through season in relation to the arthropod diet of the house sparrow to provide greater knowledge about the differences between habitat types and age differences in diet in addition to shed light on how the environment could influence the predator-prey interactions observed in this study.

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Tables

Table 1: An overview of the eight islands that had malaise traps used for collecting the arthropods and the island habitat types (i.e., farm or non-farm) at Helgeland. Each subpopulation of house sparrows had one or two malaise traps, where some islands had two subpopulations (i.e., north population and south population). Year shows the years each malaise trap site was active.

Island	Location of site	Year	Habitat Type
Gjerøy	South	2017, 2018, 2019	Farm
Gjerøy	North	2019	Farm
Hestmannøy	South	2017, 2018, 2019	Farm
Hestmannøy	North	2017, 2018, 2019	Farm
Træna	-	2017, 2018, 2019	Non-Farm
Sleneset	-	2017, 2018, 2019	Non-Farm
Selvær	-	2017, 2018, 2019	Non-Farm
Lovund	-	2017, 2018, 2019	Non-Farm
Indre Kvarøy	-	2017, 2018, 2019	Farm
Nesøy	-	2019	Farm

Table 2: All parameter estimates after hypothesis testing with LRT when analysing the variation in arthropod abundances in malaise traps at Helgeland from 2017-2019 using a GLMM fitted with a negative binomial distribution. The explanatory variables included were week, week^2, year, habitat type (i.e., farm or non-farm), and the interaction between week and year. The site of malaise traps was included as a random effect where each malaise trap site corresponds to the site of local house sparrow populations. However, the presented table does not include the seasonal change in abundance depending on habitat type (i.e., week x habitat type) as no evidence for such relationship was present (see results). For each fixed effect the table shows the parameter estimates, their standard errors and 95% confidence intervals. Week was mean-centred so that the intercept is at the middle of the season.

			95% Confidence interval	
	Estimate	Std. Error	Lower	Upper
Intercept	6.5304	0.1687	6.1998	6.8611
Week	0.1374	0.0101	0.1176	0.1571
Week^2	-0.0095	0.0011	-0.0117	-0.0072
Year 2018	0.0118	0.0831	-0.1510	0.1747
Year 2019	0.0964	0.0812	-0.0628	0.2557
Non-farm	-0.2263	0.2435	-0.7035	0.2510
Week x 2018	0.0652	0.0143	0.0372	0.0932
Week x 2019	-0.0738	0.0132	-0.0996	-0.0479
σ_{Site}	0.3623			

Table 3: All parameter estimates after hypothesis testing with LRT when analysing the variation in arthropod biomass (g) in malaise traps at Helgeland from 2017-2019 using a GLMM fitted with a gaussian distribution. The explanatory variables included were week, week^2, year, habitat type (i.e., farm or non-farm), interaction between week and year, and an interaction between week and habitat type. The location of malaise traps was included as a random effect where each malaise trap site corresponds to the site of local house sparrow populations. However, the presented table does not include the nonlinear change over the season (i.e., week$^{\wedge 2}$) as no evidence for such relationship was present (see results). For each fixed effect the table shows the parameter estimates, their standard errors and 95% confidence intervals. Week was mean-centred so that the intercept is at the middle of the season.

			95% Confidence interval	
	Estimate	Std. Error	Lower	Upper
Intercept	0.4731	0.0879	0.3008	0.6455
Week	0.0670	0.0072	0.0530	0.0811
Year 2018	0.0151	0.0537	-0.0902	0.1203
Year 2019	0.0481	0.0526	-0.0550	0.1512
Non-farm	-0.1790	0.1249	-0.4239	0.0658
Week x 2018	0.0108	0.0094	-0.0075	0.0292
Week x 2019	-0.0127	0.0086	-0.0295	0.0041
Week x Non-Farm	-0.0282	0.0073	-0.0425	-0.0138
σ_{Site}	0.1801			
$\sigma_{Residual}$	0.4757			

Table 4: The table provides an overview of the taxa collected in malaise traps in relation to the number of samples from metabarcoding of fledgling faeces in 2017. Taxa is the taxonomic group in the metabarcoding data that corresponded to the taxonomic group in the malaise trap data. Samples is the number of samples with a species DNA sequence found out of eight possible occurrences at the assigned taxonomic level. Total Abundance is the abundance of an arthropod in the malaise traps at the islands Hestmannøy and Træna in 2017.

Taxa	Taxonomic level	Total Abundance	Samples
Diptera	Order	-	-
Tipuloidea	Super family	14348	8
Chironomidae	Family	9693	8
Scathophagidae	Family	9	7
Rhagionidae	Family	88	5
Psychodidae	Family	771	5
Bibionidae	Family	964	5
Scatopsidae	Family	188	2
Empididae	Family	783	2
Tabanidae	Family	1	2
Calliphoridae	Family	0	2
Syrphidae	Family	28	1
Culicidae	Family	3	1
Hemiptera	Order	-	-
Aphididae	Family	112	3
Lepidoptera	Order	46931	6
Geometridae	Family	1664	6
Nymphalidae	Family	2	1

Coleoptera	Order	464	2
Carabidae	Family	0	3
Staphylinidae	Family	134	2
Curculionidae	Family	23	1
Araneae	Order	1100	4
Hymenoptera	Order	10052	2
Plecoptera	Order	2965	1
Trichoptera	Order	109	1

Table 5: All parameter estimates of how the number of house sparrow fledglings was affected by the variation in arthropod abundances during early nestling stages (0-5 days, Table 5A) and during late nestling stages (6-10 days, Table 5B) after hypothesis testing with LRT of interactions to get precise estimates. GLMM's were fitted with a poisson distribution where the parameters are presented on log scale. The arthropod abundance was collected from malaise traps at eight local islands at Helgeland from 2017-2019. The explanatory variables included were year, arthropod abundance during either early (Table 5A) or late (Table 5B) nestling stages, and habitat type (i.e., farm or non-farm). The identity of the islands was included as a random effect. However, the presented table does not include the effect arthropod abundance had on the number of fledglings depending on habitat type (i.e., abundance x habitat type) as no evidence for such relationship was present (see results). For each fixed effect the table shows the parameter estimates, their standard errors and 95% confidence intervals, where the parameter estimates for abundance are given in units of 1000.

A) The effect of arthropod abundance during early nestling stages (0-5 days after hatching) on number of fledglings

			95% Confidence interval	
	Estimate	Std. Error	Lower	Upper
Intercept	0.7966	0.0612	0.6764	0.9165
Year 2018	-0.0849	0.0609	-0.2042	0.0344
Year 2019	0.0877	0.0667	-0.0430	0.2183
Abundance	0.0126	0.0591	-0.1032	0.1283
Non-farm	0.5166	0.0571	0.4048	0.6284
σ_{Island}	0.00005			

B) The effect of arthropod abundance during late nestling stages (6-10 days after hatching) on number of fledglings

			95% Confidence interval	
	Estimate	Std. Error	Lower	Upper
Intercept	0.7963	0.0611	0.6766	0.9161
Year 2018	-0.0856	0.0609	-0.2050	0.0339
Year 2019	0.0883	0.0664	-0.0419	0.2185
Abundance	0.0189	0.0639	-0.1063	0.1441
Non-farm	0.5171	0.0564	0.4066	0.6276
σ_{Island}	0.00005			

Table 6: All parameter estimates of how the number of house sparrow fledglings was affected by the variation in arthropod biomass (g) during early nestling stages (0-5 days, Table 6A) and during late nestling stages (6-10 days, Table 6B) after hypothesis testing with LRT of interactions to get precise estimates. GLMM's were fitted with a poisson distribution where the parameters are presented on log scale. The arthropod biomass was collected from malaise traps at eight local islands at Helgeland from 2017-2019. The explanatory variables included were year, arthropod biomass during either early (Table 6A) or late (Table 6B) nestling stages, and habitat type (i.e., farm or non-farm). The identity of the islands was included as a random effect. However, the presented table does not include the effect arthropod biomass had on the number of fledglings depending on habitat type (i.e., biomass x habitat type) as no evidence for such relationship was present (see results). For each fixed effect the table shows the parameter estimates, their standard errors and 95% confidence intervals.

A) The effect of arthropod biomass during early nestling stages (0-5 days after hatching) on number of fledglings

			95% Confidence interval	
	Estimate	Std. Error	Lower	Upper
Intercept	0.8016	0.0657	0.6728	0.9304
Year 2018	-0.0859	0.0614	-0.2062	0.0344
Year 2019	0.0882	0.0666	-0.0422	0.2187
Biomass	-0.0095	0.0643	-0.1355	0.1165
Non-farm	0.5078	0.0661	0.3783	0.6373
σIsland	0.00003			

B) The effect of arthropod biomass during late nestling stages (6-10 days after hatching) on number of fledglings

			95% Confidence interval	
	Estimate	Std. Error	Lower	Upper
Intercept	0.8010	0.0644	0.6747	0.9272
Year 2018	-0.0857	0.0612	-0.2058	0.0343
Year 2019	0.0884	0.0665	-0.0419	0.2187
Biomass	-0.0102	0.0718	-0.1509	0.1306
Non-farm	0.5088	0.0634	0.3845	0.6330
σ_{Island}	0.00004			

Table 7: All parameter estimates of how fledgling body mass (g) in house sparrows was affected by the effect of variation in arthropod abundances during early nestling stages (0-5 days, Table 7A) and during late nestling stages (6-10 days, Table 7B) after hypothesis testing with LRT for interactions to get precise estimates. GLMM's were fitted with a gaussian distribution with the random effect including brood ID nested in islands. The arthropod abundance was collected from eight local island islands at malaise traps at Helgeland from 2017-2019. The explanatory variables included were year, arthropod abundance during either early (Table 7A) or late (Table 7B) nestling stages, and habitat type (i.e., farm or non-farm). However, the presented table does not include the effect arthropod abundance had on fledgling body mass depending on habitat type (i.e., abundance x habitat type) as no evidence for such relationship was present (see results). For each fixed effect the table shows the parameter estimates, their standard errors and 95% confidence intervals is included, where the parameter estimates for abundance are given in units of 1000.

A) The effect of arthropod abundance during early nestling stages (0-5 days after hatchin) on fledgling body mass (g)

			95% Confidence interval	
	Estimate	Std. Error	Lower	Upper
Intercept	26.4952	0.6409	25.2391	27.7513
2018	-1.6229	0.3763	-2.3605	-0.8852
2019	0.1737	0.4200	-0.6495	0.9969
Abundance	1.0181	0.4259	0.1834	1.8529
Non-farm	0.6633	0.7815	-0.8684	2.1950
$\sigma_{Brood:Island}$	2.7266			
σ_{Island}	0.9314			
$\sigma_{Residual}$	3.2652			

B) The effect of arthropod abundance during late nestling stages (6-10 days after hatching) on fledgling body mass (g)

			95% Confidence interval	
	Estimate	Std. Error	Lower	Upper
Intercept	26.4982	0.6380	25.2477	27.7486
2018	-1.6522	0.3777	-2.3923	-0.9120
2019	0.2497	0.4187	-0.5709	1.0702
Abundance	0.9619	0.4739	0.0330	1.8908
Non-farm	0.6194	0.7759	-0.9014	2.1401
$\sigma_{Brood:Island}$	2.7343			

σ_{Island}	0.9232
σ_{Residual}	3.2651

Table 8: All parameter estimates of how fledgling body mass (g) in house sparrows was affected by the effect of variation in arthropod biomass (g) during early nestling stages (0-5 days, Table 8A) and during late nestling stages (6-10 days, Table 8B) after hypothesis testing with LRT for interactions to get precise estimates. GLMM's were fitted with a gaussian distribution with the included random effect being brood ID nested in islands. The arthropod biomass was collected from malaise traps at eight local islands at Helgeland from 2017-2019. The explanatory variables included were year, arthropod biomass during either early (Table 8A) or late (Table 8B) nestling stages, and habitat type (i.e., farm or non-farm). However, the presented table does not include the effect arthropod biomass had on fledgling body mass depending on habitat (i.e., biomass x habitat type) as the relationship present was not significant ($p > 0.05$) (see results). For each fixed effect the table shows the parameter estimates, their standard errors and 95% confidence intervals.

A) The effect of arthropod biomass during early nestling stages (0-5 days after hatching) on fledgling body mass (g)

			95% Confidence interval	
	Estimate	Std. Error	Lower	Upper
Intercept	26.3781	0.6431	25.1176	27.6386
2018	-1.5137	0.3832	-2.2648	-0.7626
2019	0.3542	0.4226	-0.4741	1.1825
Biomass	0.6361	0.4259	-0.1986	1.4708
Non-farm	0.7495	0.7862	-0.7914	2.2904
$\sigma_{\text{Brood:Island}}$	2.747			
σ_{Island}	0.909			
σ_{Residual}	3.264			

B) The effect of arthropod biomass during late nestling stages (6-10 days after hatching) on fledgling body mass (g)

			95% Confidence interval	
	Estimate	Std. Error	Lower	Upper
Intercept	26.2387	0.6442	24.9760	27.5013
2018	-1.4559	0.3805	-2.2017	-0.7101
2019	0.4037	0.4199	-0.4193	1.2267

Biomass	1.2670	0.4869	0.3128	2.2213
Non-farm	0.9334	0.7863	-0.6078	2.4745
$\sigma_{\text{Brood:Island}}$	2.7260			
σ_{Island}	0.9127			
σ_{Residual}	3.2644			

Table 9: All parameter estimates of how fledgling body size (i.e., tarsus length in mm) in house sparrows were affected by the effect of variation in arthropod abundances during early nestling stages (0-5 days, Table 9A) and during late nestling stages (6-10 days, Table 9B) after hypothesis testing with LRT for interactions to get precise estimates. GLMM's were fitted with a gaussian distribution with the random effect included were brood ID nested in islands. The arthropod abundance was collected from malaise traps at eight local islands at Helgeland from 2017-2019. The explanatory variables included were year, arthropod abundance during either early (Table 9A) or late (Table 9B) nestling stages, and habitat type (i.e., farm or non-farm island). However, the presented table does not include the effect arthropod abundance had on fledgling body size depending on habitat type (i.e., abundance x habitat type) as no evidence for such relationship was present (see results). For each fixed effect the table shows the parameter estimates, their standard errors and 95% confidence intervals, where the parameter estimates for abundance are given in units of 1000.

A) The effect of arthropod abundance during early nestling stages (0-5 days after hatching) on fledgling body size (mm)

			95% Confidence interval	
	Estimate	Std. Error	Lower	Upper
Intercept	18.9512	0.1960	18.5671	19.3354
2018	-0.5868	0.1174	-0.8168	-0.3568
2019	0.0338	0.1309	-0.2226	0.2903
Abundance	0.4193	0.1326	0.1594	0.6791
Non-farm	0.4442	0.2383	-0.0228	0.9111
$\sigma_{\text{Brood:Island}}$	0.8894			
σ_{Island}	0.2822			
σ_{Residual}	0.9054			

A) The effect of arthropod abundance during late nestling stages (6-10 days after hatching) on fledgling body size (mm)

			95% Confidence interval	

	Estimate	Std. Error	Lower	Upper
Intercept	18.9527	0.1972	18.5661	19.3393
2018	-0.5994	0.1178	-0.8303	-0.3684
2019	0.0637	0.1305	-0.1921	0.3195
Abundance	0.4141	0.14853	0.1229	0.7052
Non-farm	0.4270	0.2398	-0.0429	0.8969
$\sigma_{Brood:Island}$	0.8923			
σ_{Island}	0.2849			
$\sigma_{Residual}$	0.9054			

Table 10: All parameter estimates of how fledgling body size (i.e., tarsus length in mm) in house sparrows were affected by the effect of variation in arthropod biomass (g) during early nestling stages (0-5 days, Table 10A) and during late nestling stages (6-10 days, Table 10B) after hypothesis testing with LRT for interactions to get precise estimates. GLMM's were fitted with a gaussian distribution with the random effect included were brood ID nested in islands. The arthropod biomass was collected from malaise traps at eight local islands at Helgeland from 2017-2019. The explanatory variables included were year, arthropod biomass during either early (Table 10A) or late (Table 10B) nestling stages, habitat type (i.e., farm or non-farm), and the effect arthropod biomass had on fledgling body size depending on habitat type (i.e., biomass x habitat type). For each fixed effect the table shows the parameter estimates, their standard errors and 95% confidence intervals.

A) The effect of arthropod biomass during early nestling stages (0-5 days after hatching) on fledgling body size (mm)

			95% Confidence interval	
	Estimate	Std. Error	Lower	Upper
Intercept	18.9287	0.1967	18.5431	19.3142
2018	-0.5255	0.1184	-0.7576	-0.2935
2019	0.0919	0.1305	-0.1639	0.3477
Biomass	0.1372	0.1432	-0.1435	0.4179
Non-farm	0.6925	0.2468	0.2087	1.1762
Biomass x Non-farm	1.0804	0.3417	0.4108	1.7500
$\sigma_{Brood: Island}$	0.8830			
σ_{Island}	0.2765			
$\sigma_{Residual}$	0.9052			

B) The effect of arthropod biomass during late nestling stages (6-10 days after hatching) on fledgling body size (mm)

			95% Confidence interval	
	Estimate	Std. Error	Lower	Upper
Intercept	18.8921	0.2031	18.4941	19.2901
2018	-0.5166	0.1178	-0.7475	-0.2857
2019	0.1085	0.1299	-0.1460	0.3630
Biomass	0.3061	0.1699	-0.0270	0.6392
Non-farm	0.6537	0.2512	0.1614	1.1461
Biomass x Non-farm	0.9549	0.3518	0.2653	1.6444
$\sigma_{Brood:Island}$	0.8776			
σ_{Island}	0.2923			
$\sigma_{Residual}$	0.9052			

Figures

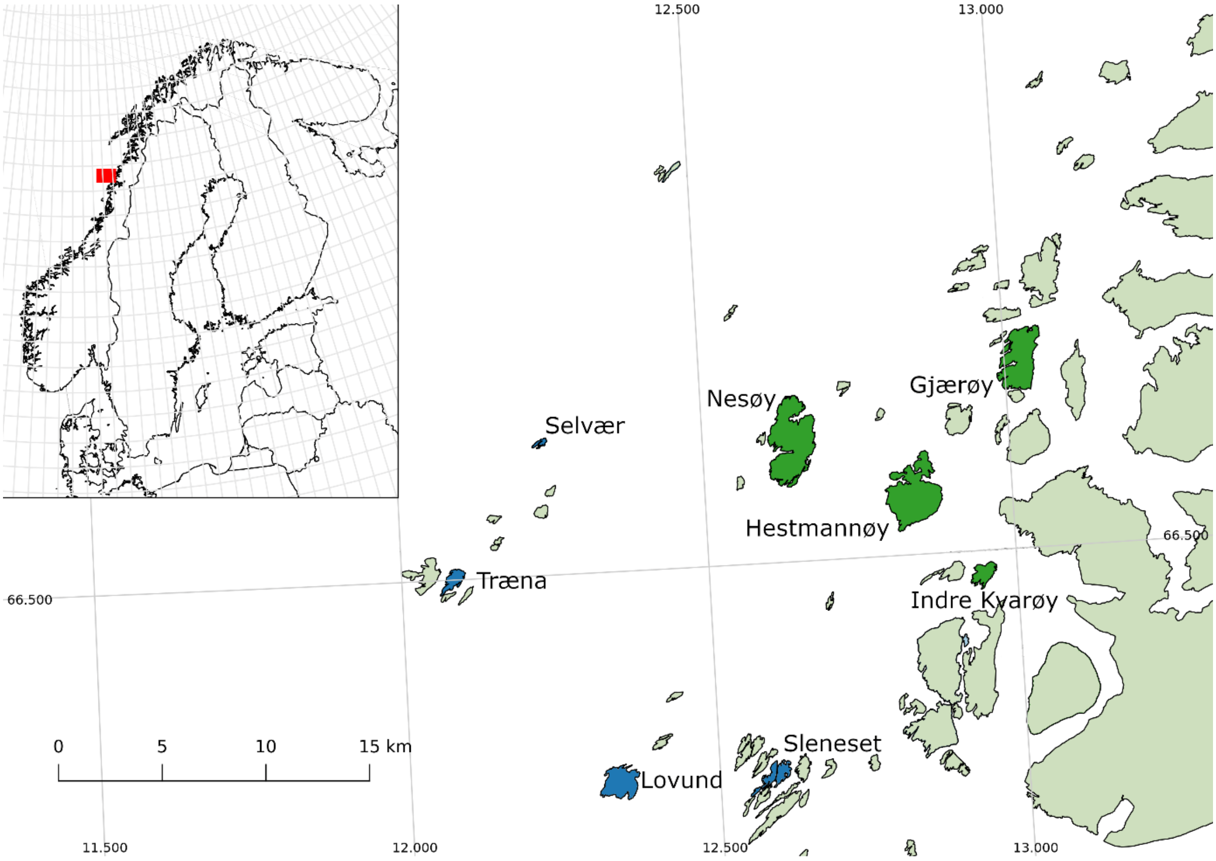

Figure 1: A map over the study area and the specific islands visited during 2017-2019 at the archipelago Helgeland in northern Norway. The islands coloured in dark green were islands with farming activities and the ones coloured in blue were islands without farming activities. The islands included were Selvær (non-farm), Træna (non-farm), Lovund (non-farm), Sleneset (non-farm), Gjerøy (farm), Nesøy (farm), Hestmannøy (farm), and Indre Kvarøy (farm).

Figure 2: The setup of the malaise traps (SLAM, standard type II) that was used to collect the arthropod data in this study. The sloped white roof guided the arthropods to the container at the top of the trap with 96% ethanol. Photo: Margrete Saugestad (Sleneset, 2022).

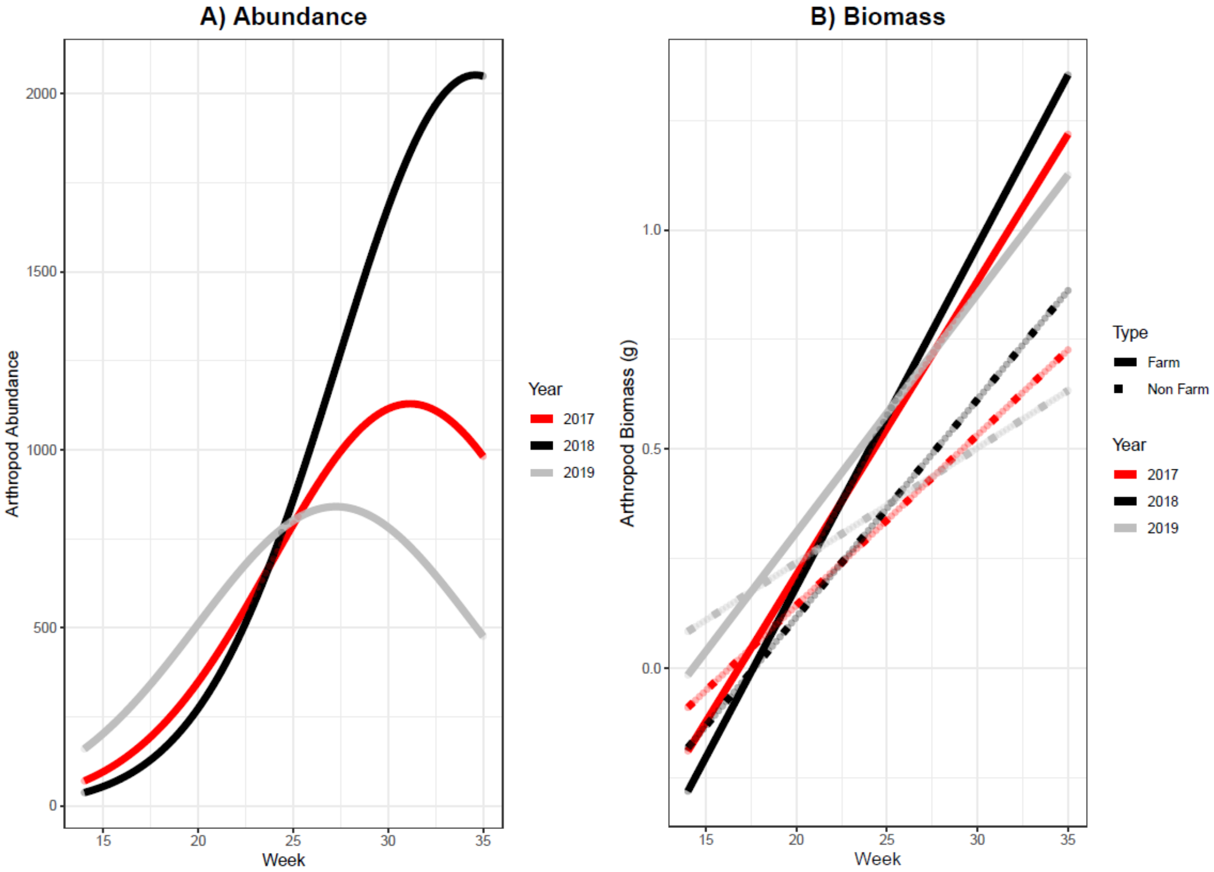

Figure 3: Prediction of the seasonal change (over weeks) in A) arthropod abundance and B) arthropod biomass (g) for three different years and two different habitat types (only biomass). The figures are based on GLMMs fitted with negative binomial (A) and gaussian distribution (B), see materials and Table S2 for further details.

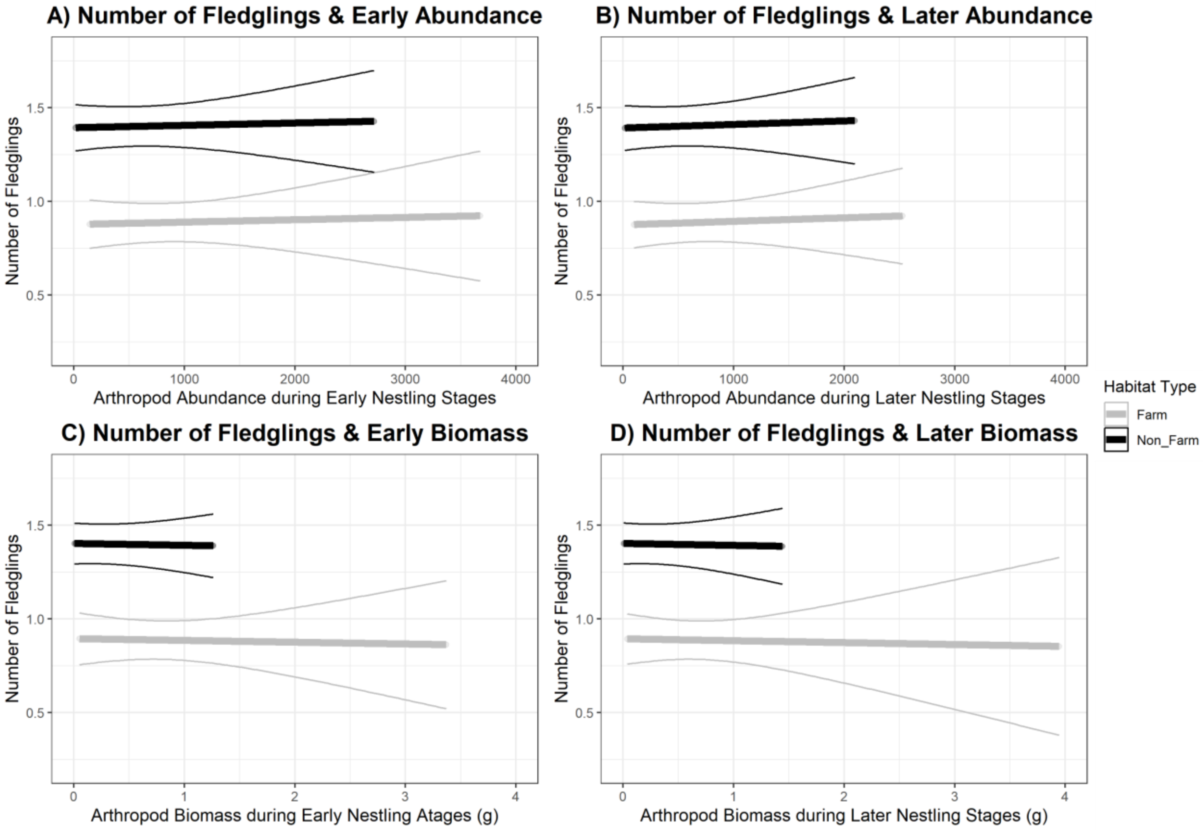

Figure 4: Predictions of how the number of fledglings was influenced by A) arthropod abundance during early nestling stages, B) arthropod abundance during later nestling stages, C) arthropod biomass (g) during early nestling stages, and D) arthropod biomass (g) during later nestling stages, in regard to habitat type in 2019. Where early nestling stages is the age interval between 0-5 days, and later nestling stages is the interval between 6-10 days. The figures are based on GLMMs fitted with a poisson distribution, where the response variable is on a log scale (see Table S3). The area around the regression line indicates the 95% confidence interval.

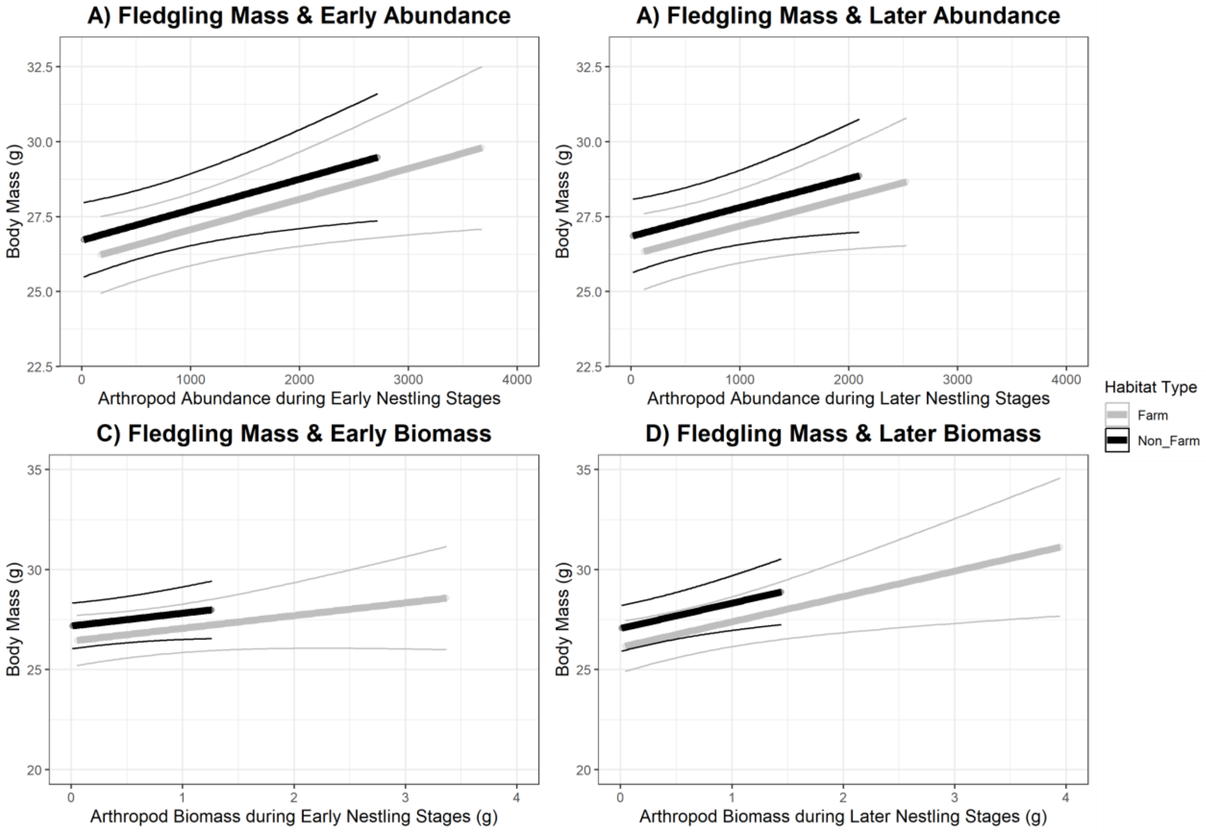

Figure 5: Predictions of how fledgling body mass (g) was influenced by A) arthropod abundance during early nestling stages, B) arthropod abundance during later nestling stages, C) arthropod biomass (g) during early nestling stages, and D) arthropod biomass (g) during later nestling stages, in regard to habitat type in 2019. Where early nestling stages is the age interval between 0-5 days, and later nestling stages is the interval between 6-10 days. The figures are based on GLMMs fitted with a normal distribution (see Table S4). The area around the regression line indicates the 95% confidence interval.

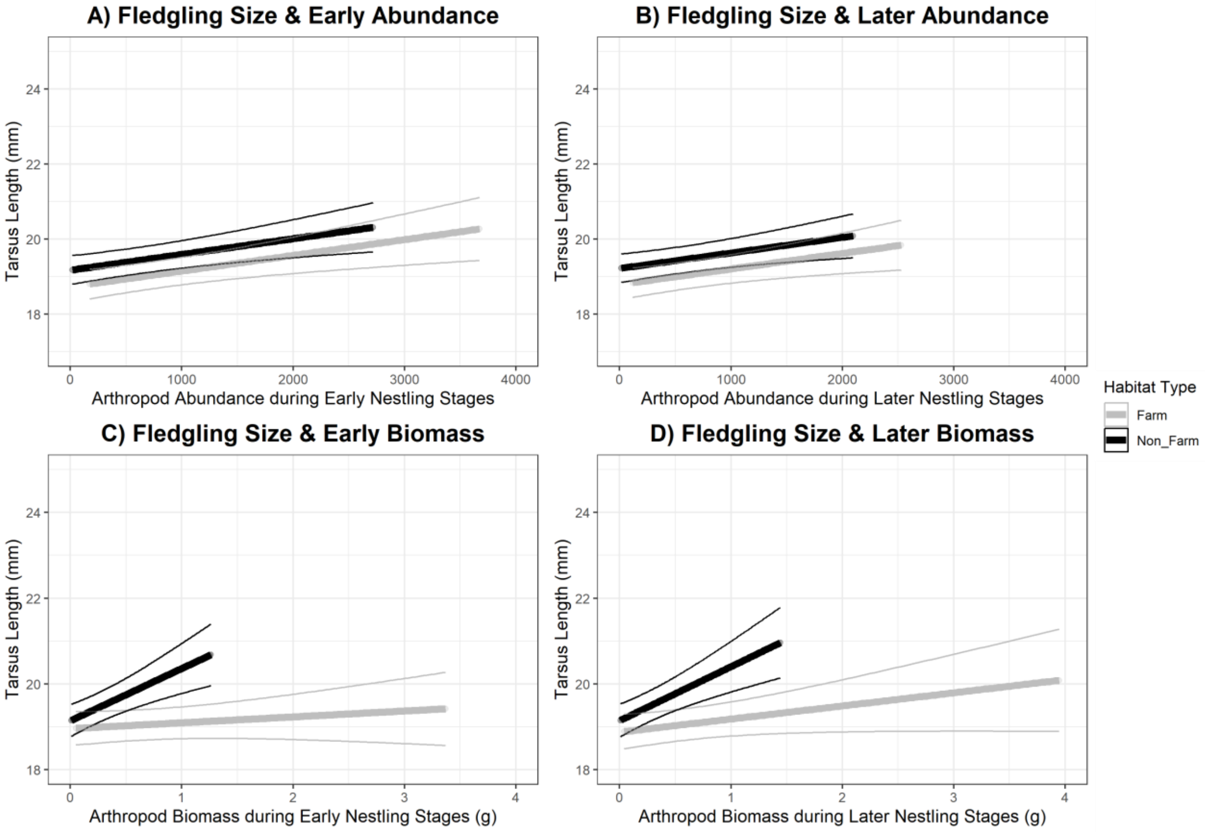

Figure 6: Predictions of how fledgling tarsus length (mm) as a measure of fledgling body size was influenced by A) arthropod abundance during early nestling stages, B) arthropod abundance during later nestling stages, C) arthropod biomass (g) during early nestling stages, and D) arthropod biomass (g) during later nestling stages, in regard to habitat type in 2019. Where early nestling stages is the age interval between 0-5 days, and later nestling stages is the interval between 6-10 days. The figures are based on GLMMs fitted with a normal distribution (see Table S5). The area around the regression line indicates the 95% confidence interval.

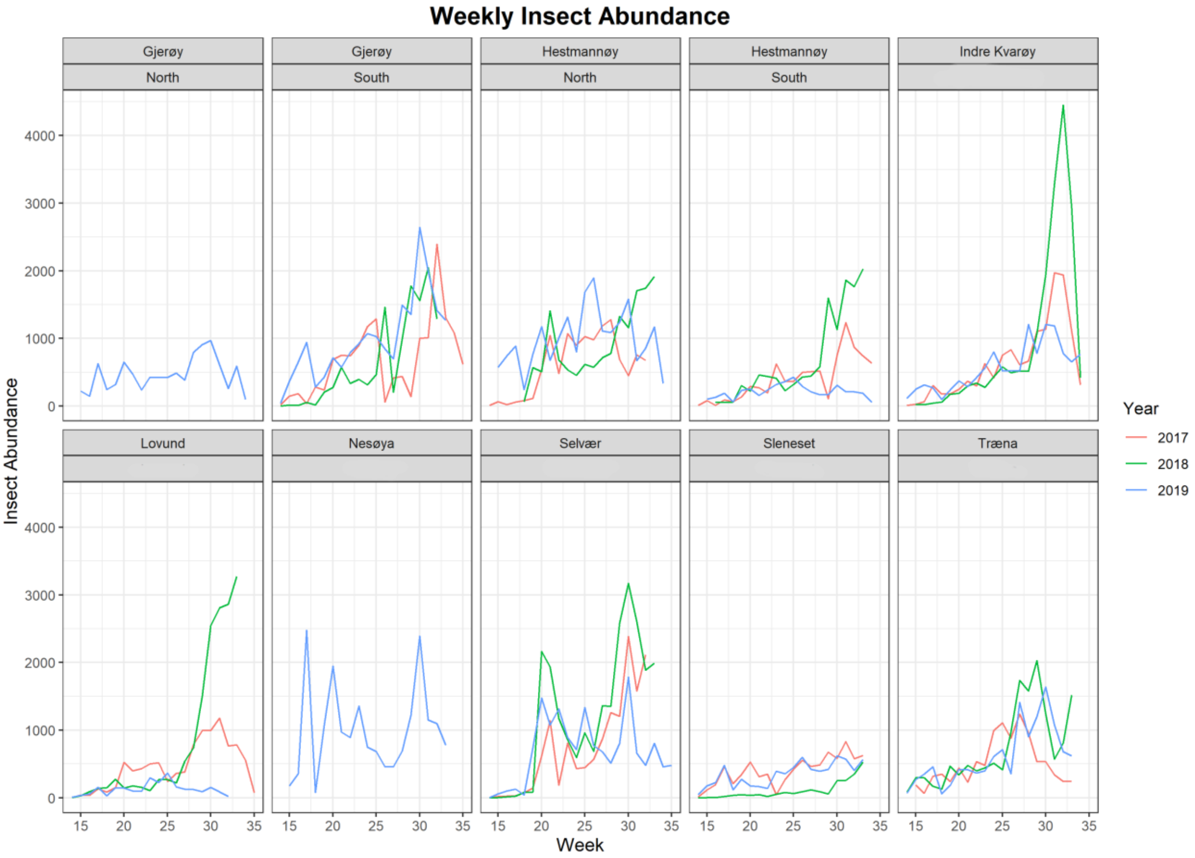

Figure 7: Shows the observed trends in arthropod abundance at the different islands among weeks from 2017-2019 at Helgeland. This figure based on the arthropod data before any statistical analyses. The x-axis are the week numbers ranging from 14-35 (April-August), and the y-axis shows the number of individuals of arthropods collected in the malaise traps located at the different islands.

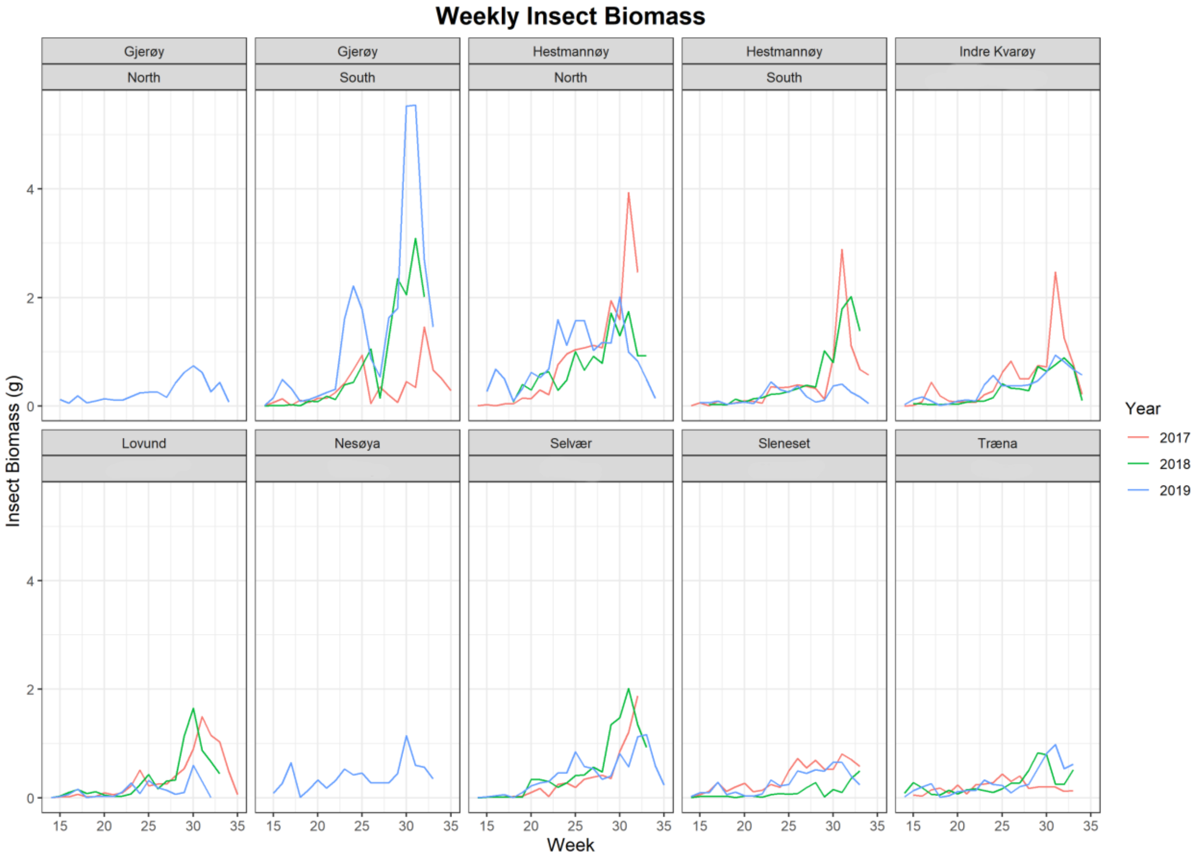

Figure 8: Shows the observed trends in arthropod biomass (g) at the different islands among weeks from 2017-2019 at Helgeland. This figure is based on the arthropod data before any statistical analyses. The x-axis are the week numbers ranging from 14-35 (April-August), and the y-axis shows the arthropod biomass (g) collected at the malaise traps located at the islands.

Supplementary materials

Table S1: An overview of the number of house sparrow broods on each island for the three years the analysis of reproductive success is based on at Helgeland. Location of site differentiate between malaise traps sites if there were multiple traps by classifying them based on the location of the trap on the island (north or south of the island). The islands were separated into farm or non-farm islands (i.e., habitat type) depending on farming activity.

Island	Location of site	Habitat type	2017	2018	2019
Nesøy	-	Farm	-	-	10
Træna	-	Non-farm	33	40	21
Selvær	-	Non-farm	14	33	9
Gjerøy	South	Farm	1	11	7
Gjerøy	North	Farm	-	-	8
Hestmannøy	South	Farm	0	8	7
Hestmannøy	North	Farm	38	41	61
Indre kvarøy	-	Farm	20	16	12
Lovund	-	Non-farm	20	27	5
Sleneset	-	Non-farm	23	44	21

Table S2: The global GLMMs used when analysing the variation in arthropod abundance and biomass in malaise traps at Helgeland from 2017-2019. Where GLMM for arthropod abundance were fitted with a negative binomial and GLMM for arthropod biomass were fitted with a gaussian distribution. In all models the malaise traps site was included as a random factor. Explanatory variables included were week, week^2, year, habitat type (i.e., farm island or non-farm), in addition to the interaction between week and habitat type (i.e., week x habitat type), and week and year (i.e., week x year).

	Response	Fixed effect	Random effect	Distribution
Abundance	Weekly abundance	Week, week^2, year, habitat type, interaction between year and week, interaction between habitat type and week	Malaise Site	Negative binomial
Biomass	Weekly biomass	Week, week^2, year, habitat type, interaction between year and week, interaction between habitat type and week	Malaise Site	Gaussian

Table S3: The global GLMMs used when analysing how variation in arthropod abundance and biomass in malaise traps at Helgeland from 2017-2019 influenced the number of fledglings in the house sparrow. Where the GLMMs were fitted with a poisson distribution, and had island included as a random factor. All models had identical explanatory variables except for the arthropod measure. The four arthropod measures included: abundance 5 (arthropod abundance during early nestling period), abundance 10 (arthropod abundance during late nestling period), biomass 5 (arthropod biomass during early nestling period), and biomass 10 (arthropod biomass during late nestling period). The explanatory variables included were year, habitat type (i.e., farm island or non-farm) and one of the four arthropod measures, in addition to an interaction between habitat type and the arthropod measure (i.e., arthropod measure x habitat type).

	Response	Fixed effect	Random effect	Distribution
Early abundance	Fledglings	Year, abundance 5, habitat type, interaction between abundance 5 and habitat type	Island	Poisson
Later abundance	Fledglings	Year, abundance 10, habitat type, interaction between abundance 10 and habitat type	Island	Poisson
Early biomass	Fledglings	Year, biomass 5, habitat type, interaction between biomass 5 and habitat type	Island	Poisson
Later biomass	Fledglings	Year, biomass 10, habitat type, interaction between biomass 10 and habitat type	Island	Poisson

Table S4: The global GLMMs used when analysing how variation in arthropod abundance and biomass in malaise traps at Helgeland from 2017-2019 influenced the fledgling body mass in the house sparrow, where the body mass was standardized to an 11-day old fledgling. The GLMMs were fitted with a gaussian distribution and had brood ID nested in islands included as a random factor. All models had identical explanatory variables except for the arthropod measure. The four arthropod measures included: abundance 5 (arthropod abundance during early nestling period), abundance 10 (arthropod abundance during late nestling period), biomass 5 (arthropod biomass during early nestling period), and biomass 10 (arthropod biomass during late nestling period). The explanatory variables included were year, habitat type (i.e., farm island or non-farm) and one of the four arthropod measures, in addition to an interaction between habitat type and the arthropod measure (i.e., arthropod measure x habitat type).

	Response	Fixed effect	Random effect	Distribution
Early abundance	Body mass	Year, abundance 5, habitat type, interaction between abundance 5 and habitat type	Island/brood	Gaussian
Later abundance	Body mass	Year, abundance 10, habitat type, interaction between abundance 10 and habitat type	Island/brood	Gaussian
Early biomass	Body mass	Year, biomass 5, habitat type, interaction between biomass 5 and habitat type	Island/brood	Gaussian
Later biomass	Body mass	Year, biomass 10, habitat type, interaction between biomass 10 and habitat type	Island/brood	Gaussian

Table S5: The global GLMMs used when analysing how variation in arthropod abundance and biomass in malaise traps at Helgeland from 2017 to 2019 influenced the fledgling tarsus length in the house sparrow, where the tarsus length was standardized to an 11-day old fledgling. The GLMMs were fitted with a gaussian distribution and had brood ID nested in islands included as a random factor. All models had identical explanatory variables except for the arthropod measure. The four arthropod measures included: abundance 5 (arthropod abundance during early nestling period), abundance 10 (arthropod abundance during late nestling period), biomass 5 (arthropod biomass during early nestling period), and biomass 10 (arthropod biomass during late nestling period). The explanatory variables included were year, habitat type (i.e., farm island or non-farm) and one of the four arthropod measures, in addition to an interaction between habitat type and the arthropod measure (i.e., arthropod measure x habitat type.

	Response	Fixed effect	Random effect	Distribution
Early abundance	Tarsus length	Year, abundance 5, habitat type, interaction between abundance 5 and habitat type	Island/brood	Gaussian
Later abundance	Tarsus length	Year, abundance 10, habitat type, interaction between abundance 10 and habitat type	Island/brood	Gaussian
Early biomass	Tarsus length	Year, biomass 5, habitat type, interaction between biomass 5 and habitat type	Island/brood	Gaussian
Later biomass	Tarsus length	Year, biomass 10, habitat type, interaction between biomass 10 and habitat type	Island/brood	Gaussian

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