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The effect of arthropod availability on reproductive phenology and success in a multi-brooded passerine *Passer domesticus*

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Abstract

Arthropods are an important protein source during the early growth and development of many small tetrapods, including the nestlings of many passerine bird species. The seasonal variation of arthropod communities is therefore expected to be an important factor influencing the breeding phenologies and reproductive success of such species, as parents must time their breeding attempts to ensure high availability of food for their young. Anthropogenic environmental changes are now reported to cause both arthropod declines and trophic mismatches in ecosystems worldwide. It is therefore vital that the influence of arthropod communities on reproduction at higher trophic levels becomes better understood, not least to improve conservation efforts. In this study, arthropod communities were sampled using Malaise traps and quantified according to abundance, biomass, taxonomic richness, and taxonomic diversity in an archipelago off the coast of northern Norway that constitutes the habitat of a metapopulation of house sparrows (*Passer domesticus*). The data collection was carried out throughout the breeding season. The effects of these arthropod community characteristics on the number of house sparrow clutches laid per week as well as on nestling mortality were then investigated using generalised linear mixed models. Arthropod biomass, and especially arthropod biomass two weeks following egg laying, positively affected the number of clutches laid per week. There was also some support for a negative effect of arthropod biomass on nestling mortality. These findings shed light on an aspect of reproductive phenology and success that has previously received little attention in the context of multi-brooded species and underscores the necessity of including trophic interactions in population studies.

Sammendrag

Leddyr er en viktig proteinkilde under den tidlige veksten og utviklingen til mange små tetrapoder, derunder reirungene til mange arter av spurvefugler. Sesongvariasjonen i leddyrsamfunn forventes derfor å være en viktig faktor som spiller inn på hekkefenologi og reproduktiv suksess hos slike arter, da foreldre må hekke på et tidspunkt som sikrer ungenes mattilgang. Det rapporteres nå om nedganger i leddyrbestander og trofiske fenologiske avvik (mismatches) forårsaket av antropogene miljøforandringer i økosystemer over hele verden. Det er derfor svært viktig å utvikle en bedre forståelse av leddyrsamfunns innvirkning på reproduksjon på høyere trofiske nivåer, ikke minst i bevaringsøyemed. I denne studien ble leddyrsamfunn kvantifisert med hensyn til tallrikhet, biomasse, taksonomisk rikhet og taksonomisk mangfold ved bruk av Malaise-feller på en øygruppe utenfor kysten av Nord-Norge som utgjør habitatet til en metapopulasjon av gråspurv (*Passer domesticus*). Datainnsamlingen ble foretatt gjennom en enkelt hekkesesong. Effekten av samfunnsegenskapene på antall kull lagt per uke samt dødelighet hos reirungene ble så undersøkt ved hjelp av generaliserte lineære mixed effects-modeller. Leddyrbiomasse, og særlig leddyrbiomassen to uker etter egglegging, hadde en positiv effekt på antall kull lagt per uke. Det ble også funnet noe støtte for en negativ effekt av leddyrbiomasse på dødelighet hos reirungene. Disse funnene belyser et aspekt ved reproduktiv fenologi og suksess som tidligere har fått lite oppmerksomhet når det gjelder arter som legger flere kull i løpet av en sesong, og understreker nødvendigheten av å inkludere trofiske interaksjoner i populasjonsstudier.

Introduction

Phenology, the timing of seasonal events such as breeding, flowering in plants, and annual migrations in many bird species, is important in many ecological and evolutionary processes (Forrest & Miller-Rushing 2010). The phenologies of primary producers, often determined by abiotic factors such as photoperiod or temperature, can give rise to complex dynamics at the community level. Species that depend on plants for nutrition must be adapted to seasonal variation in food availability, and higher levels in the trophic chain are affected in turn (Parmesan 2006; Both *et al.* 2009a; Forrest & Miller-Rushing 2010; Ovaskainen *et al.* 2013). Many small terrestrial tetrapod species are dependent on arthropods as a protein source during the early development of their young. For instance, positive relationships between arthropod availability and various measures of reproductive success and timing of breeding have been reported in passerine birds (Bryant 1975; Blancher & Robertson 1987; Perrins & McCleery 1989; Perrins 1991; Dias & Blondel 1996; Naef-Daenzer & Keller 1999; Burger *et al.* 2012; Møller 2013; Samplonius *et al.* 2016), lizards (Ballinger 1977), and bats (Arlettaz *et al.* 2001). Reports of long-term declines of arthropod communities from Germany between 1989 and 2016 (Hallmann *et al.* 2017) and from Puerto Rico between 1976 and 2012 (Lister & Garcia 2018) have recently been cause for much concern among conservationists. In a recent review article, Sánchez-Bayo and Wyckhuys (2019) found dramatic declines across a large range of insect taxa and geographical zones (but see Komonen, Halme and Kotiaho 2019). Reduced numbers of arthropod prey may be one substantial factor explaining declines of passerine bird populations in recent decades (Pettersson *et al.* 1995; Benton *et al.* 2002; Summers-Smith 2003; Newton 2004; Goulson 2014; Lister & Garcia 2018), but there is still a lack of knowledge about how temporal and spatial variation in arthropod community structure may affect the reproductive success and local phenology of passerine bird species.

Life history theory assumes that phenotypic traits including traits relating to phenology are heritable and shaped by adaptive evolution through an interaction between intrinsic and extrinsic factors (Stearns 2000). In this context, "intrinsic factors" refers to trade-offs between different life history traits (see Stearns 1989 for a detailed review) as well as genetic constraints on adaptation (Hansen & Houle 2008), while "extrinsic factors" are environmental factors, such as weather conditions and food availability, that influence survival and reproduction. It follows that individuals subject to seasonally variable environments should match their life cycles to this predictable variation in environmental conditions in order to

maximize their reproduction and survival at each life stage, and that failure to do so (phenological mismatch) entails a cost in terms of reduced fitness (Parmesan 2006; Visser & Gienapp 2019). Examples include reduced survival in snowshoe hares (*Lepus americanus*) in Montana, USA, who mistime moulting (Zimova, Mills & Nowak 2016) and increased metabolic effort in parent blue tits (*Parus caeruleus*) in Corsica and southern France whose breeding was asynchronous with prey abundance (Thomas *et al.* 2001). The individual costs of mismatch can have great consequences at the population level. For instance, Møller, Rubolini and Lehikoinen (2008) found that failure to adjust the timing of spring migration to rising temperatures is associated with population declines in migratory birds, and Visser *et al.* (1998) demonstrated that phenological mismatch led to increased selection pressure on the laying date of great tits (*Parus major*) towards restored synchrony with prey species.

Arthropod populations are subject to large seasonal fluctuations, especially in temperate and arctic habitats where low winter temperatures pose particular challenges for the survival of poikilothermic organisms (Wolda 1988; Danks 2004). In these habitats, arthropods normally undergo diapause during the winter months. Species that are dependent on arthropod prey for their young are expected to time their breeding to maintain synchrony with prey populations. An example of this dynamic is seen in the great tit populations in Wytham Woods in England and on the Hoge Veluwe in the Netherlands. In these populations, parent birds feed their nestlings caterpillars, whose abundance is closely linked to leaf emergence on oak trees (van Balen 1973; Perrins & McCleery 1989; Perrins 1991; van Noordwijk, McCleery & Perrins 1995; Visser *et al.* 1998). As the energy demands of the nestlings are highest when they are 9-10 days old, it is crucial for parent tits to use environmental cues in order to predict the occurrence of the caterpillar peak and start their reproduction in advance (Perrins 1991). The mean times of caterpillar peaks have shifted towards earlier dates as a result of rising temperatures (Visser *et al.* 1998; Cresswell & McCleery 2003). In Wytham Woods, the great tits have maintained synchrony by shortening the incubation period to expedite hatching and avoid phenological mismatch (Cresswell & McCleery 2003). On the Hoge Veluwe, a similar shortening of the incubation period was found, but here the change was insufficient to fully compensate for the earlier arrival of the caterpillar peak (Visser *et al.* 1998; Visser, Holleman & Gienapp 2006; Ramakers, Gienapp & Visser 2019). A similar mismatch between breeding phenology and prey abundance was also found in pied flycatchers (*Ficedula hypoleuca*) in the same area (Samplonius *et al.* 2016). It is predicted that such phenological decoupling between trophic levels will become more common across a range of organismal groups as global

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temperatures continue to rise, and that this may have dramatic consequences including population reductions and even extinctions (Hughes 2000; Visser & Both 2005; Both *et al.* 2009a; Cahill *et al.* 2013; Visser & Gienapp 2019).

Multiple brooding is a life history strategy where resources are allocated to several reproductive attempts within a single breeding season (Lack 1947). The choice of multiple versus single brooding may in some instances be viewed as a case of the life history trade-off between number and quality of offspring (Smith & Fretwell 1974). For a given clutch size, the annual reproductive success (ARS) of an individual can be maximized either by increasing the number of clutches laid or by increasing the within-clutch nestling survival (Verhulst, Tinbergen & Daan 1997). In facultative multi-brooders, multiple brooding tends to increase ARS, making the number of broods per breeding season an important fitness metric in these species (Bryant 1979; Smith & Marquiss 1995; Weggler 2006; Husby, Kruuk & Visser 2009; Hoffmann, Postma & Schaub 2015; Cornell & Williams 2016). Since each clutch only represents a portion of a multi-brooded individual's potential ARS, it is thought that multi-brooded species should start laying earlier than single-brooded species and keep producing broods for as long as conditions allow (Klomp 1970; Crick, Gibbons & Magrath 1993). Single-brooding appears to be favoured by natural selection in circumstances where environmental conditions constrain the length of the breeding season to a shorter window (Martin 1987; Weggler 2006), as is the case for great tits dependent on highly seasonal caterpillars. Indeed, Husby, Kruuk and Visser (2009) found a decline in the proportion of double-brooding great tits in the Netherlands over a 50-year period, possibly related to the increasing phenological mismatch between lay dates and the caterpillar peak in the same period.

Arthropods occupy a huge range of ecological niches, each of which may be affected by seasonal variation in unique ways. The composition of the whole arthropod community is therefore expected to change continually between the emergence of the first active species in spring and the disappearance of the last in autumn (Høye & Forchhammer 2008). It is expected that multi-brooded populations are much less dependent on a few, temporally limited prey species than single-brooded populations (Halupka, Dyrcz & Borowiec 2008; Both *et al.* 2009b; Samplonius *et al.* 2016), but specific arthropod taxa may still be crucial at different times in the course of a breeding season (Brambilla & Rubolini 2009). For instance, for house sparrows (*Passer domesticus*) in Oxford, England, the main food items provided to

nestlings have been found to change from dipterans to aphids as the breeding season progresses (Seel 1969), and likewise from caterpillars to flying insects for pied flycatchers in the Netherlands (Samplonius *et al.* 2016). As increased temperatures and altered weather patterns associated with climate change are likely to affect arthropod phenological responses (Høye & Forchhammer 2008), it is now more important than ever to study the temporal and spatial dynamics of arthropod communities in order to understand the breeding phenology and reproductive success of multi-brooded species that are dependent on them as a food source during early development.

In an archipelago in northern Norway, an insular metapopulation of house sparrows has been studied using capture-mark-recapture methods since 1993 (Ringsby, Sæther & Solberg 1998; Ringsby *et al.* 1999; Ringsby *et al.* 2002). It has previously been shown that the onset of breeding is highly asynchronous between populations in this system (Ringsby *et al.* 2002; Johansen 2018). Inter-island differences in arthropod community structure may contribute to this asynchrony. Thus, directly quantifying the spatiotemporal variation of the arthropod communities in the archipelago becomes necessary in order to gain an understanding of the processes underlying variation in local house sparrow breeding phenology and nestling survival.

In the present study, Malaise traps were used to continuously sample arthropods in the habitats of eight house sparrow populations on seven islands during a single breeding season. The aim of this initial part of the study was to describe both the spatial variation of arthropod communities between different sites as well as their seasonal development through the breeding season. Spatial heterogeneity in community structure may arise as a consequence of environmental heterogeneity as well as biotic factors (Borcard, Legendre & Drapeau 1992; Pickett & Cadenasso 1995). Island systems are ideal for studying such spatial variation in terrestrial communities because islands can be viewed as discrete habitat patches with clearly defined edges (Forman & Godron 1981). Seasonally, it is expected that communities will undergo major changes between the beginning and the end of the house sparrow breeding season, arising from the different phenological responses to seasonal changes in habitat productivity in the different taxonomic groups comprising the community. The arthropod communities were characterised on a weekly basis according to abundance, biomass, taxonomic richness, and taxonomic diversity (see Materials and methods for further definitions). Richness and diversity are hypothesised to be important in this context because

nestlings require a range of different nutrients in their diets (Murphy 1996), and as different arthropod taxa may differ in terms of their nutrient composition (Schowalter & Crossley Jr 1983; Arnold *et al.* 2010), some variation in prey taxa may be beneficial (Karasov 1985; Boag 1987; Mills *et al.* 1991). The data gathered on arthropod community characteristics were used to test two main hypotheses:

1. *House sparrows match their breeding time according to temporal variation in defining characteristics of the arthropod community.*

Since arthropods are crucial prey for nestlings, it can be assumed that house sparrows time their laying so that the arthropod community characteristics (abundance, biomass, richness, or diversity) during the nestling period are favourable for fledgling production. Since the incubation time for house sparrows is around two weeks, the *lag effect hypothesis* thus states that the number of clutches laid each week is best predicted by arthropod community characteristics two weeks following laying. This hypothesis implies that sparrows employ an adaptive strategy of using some environmental cue, e.g. temperature, to anticipate future conditions (Frederiksen *et al.* 2004; Visser, Holleman & Gienapp 2006). Alternatively, the *current effect hypothesis* states that the number of clutches laid per week can be predicted by the arthropod community characteristics concurrent with laying. If other environmental cues are not reliable predictors of future conditions, using current conditions as a guide may be the best strategy available to the sparrows. These alternative strategies have somewhat different ecological implications. A lag effect strategy will allow greater synchrony between the nestling period and peaks in arthropod community characteristics and is expected if peaks are short-lived. A current effect strategy may allow for greater plasticity in response to annual variation in environmental conditions, as it does not rely on the association between the arthropod community and a proximate environmental cue (Visser, Holleman & Gienapp 2006).

2. *House sparrow nestling mortality can be predicted by variation in defining characteristics of the arthropod community.*

Given that arthropods are crucial as a protein source during the early nestling stage, high abundance, biomass, richness or diversity of arthropod prey species is predicted to result in reduced mortality (Anderson 1977; Reed, Jenouvrier & Visser 2013). Specifically, higher

measures of these community characteristics during the first five days after hatching are expected to reduce mortality during the nestling period, as the first five days are when mortality is highest. Throughout this five-day period, nestlings are completely dependent on arthropod prey (Kalmbach 1940).

Materials and methods

Study species

The house sparrow is the world's most widely distributed passerine bird species (Anderson 2006). Commensal with humans, it is socially monogamous (Anderson 2006) and breeds in colonies (Summers-Smith 1954). In northern Norway, the house sparrow breeding season lasts from early May until mid-August (Ringsby, Sæther & Solberg 1998), with each pair laying up to three clutches consisting of 5 eggs on average (Ringsby, Sæther & Solberg 1998; Westneat *et al.* 2014). Natal dispersal rates range from around 10% up to around 50% (Altwegg, Ringsby & Sæther 2000; Pärn *et al.* 2012). Although largely granivorous as adults (Kalmbach 1940; Hammer 1948; Gavett & Wakeley 1986), nestlings are exclusively fed arthropods immediately after hatching, with the proportion of plant matter gradually increasing with nestling age (Kalmbach 1940; Klvaňová *et al.* 2012).

Study area

This study was conducted on an archipelago off the coast of northern Norway (Figure 1). Seven islands were included in the study: Hestmannøy, Gjerøy, Indre Kvarøy, Husøy, Sleneset, Lovund, and Selvær. Hestmannøy has two distinct house sparrow populations, one on the north side and one on the south side of the island – hereafter Storselsøy (north) and Hestmona (south). These islands form part of a larger system where house sparrows have been studied using capture-mark-recapture methods since 1993 (Ringsby, Sæther & Solberg 1998). In previous studies, the islands in the system have often been divided into two distinct types characterized by the presence or absence of dairy farms (Ringsby *et al.* 2002; Pärn *et al.* 2012). On islands with farms, house sparrows live in close association with these, most often breeding in nests located inside barns and cowsheds. Here, adults forage on grains and cattle-feed in addition to food items available in the surrounding natural habitat. On islands where dairy farms are absent, sparrows most often breed in nest-boxes, and sunflower seeds provided by residents compose a significant part of their diets, especially during the winter months. Of the islands included in the present study, Hestmannøy and Gjerøy are farm islands and Husøy, Sleneset, Lovund, Selvær and Indre Kvarøy are no-farm islands. However, due to low house sparrow breeding activity on Gjerøy and Hestmona, these sites were not included in the analyses concerning house sparrow reproductive output, leaving Storselsøy as the only farm site.

Data collection

All data included in this study were collected during the spring and summer of 2017. Arthropod data were collected between April 6th and August 31st, using eight Malaise traps (Matthews & Matthews 1971) placed in central locations in the habitats of local house sparrow populations (Figure 2). Although Malaise traps are primarily developed to capture flying insects, other invertebrates may also be collected. In Malaise traps, arthropods are funnelled into a bottle containing 96% ethanol, where they are then preserved. Bottles in the Malaise traps were collected and immediately replaced once per week (dates and times of insertion and collection were noted in all cases to correct for discrepancies in the number of sampling days). One trap was placed on each island except Hestmannøy, where the distinct house sparrow populations at Storselsøy and Hestmona required one trap at each site. For a complete list of taxa caught in the Malaise traps during the study period, see table A12 (in Appendix). Note that two of these, Gastropoda and Oligochaeta, are not arthropods but molluscs and annelids, respectively. However, for the sake of simplicity the term arthropods is used throughout this study.

In order to collect data on house sparrow reproductive success, each site was searched for active nests on a weekly basis. The number of eggs laid in each nest was recorded, and the laying date (date of the first egg laid in the brood) was either determined exactly (when the brood was found during laying) or estimated based on hatch date and the median incubation time of 11 days from the penultimate egg (Kvalnes *et al.* 2013). When finding nestlings, hatch date was estimated based on visual assessment of nestling age (Kvalnes *et al.* 2013). All nestlings were marked with a numbered metal ring and a unique combination of three coloured plastic rings. Each nest was visited when chicks were 8-13 days old, and the number of fledglings alive was recorded. Fledglings were then individually measured for morphological traits, and blood samples were taken for molecular genetic analyses (Ringsby, Sæther & Solberg 1998; Sæther *et al.* 1999). For the purposes of this study, nestling mortality was calculated using the proportion of eggs that resulted in fledglings. Thus, the effect of any unfertilised eggs could not be separated from mortality in the egg (for house sparrows in Oxfordshire, England, Seel (1968) estimated that 92% of eggs were fertilised).

Arthropod community characteristics: abundance, biomass, diversity and richness

Each weekly sample from the Malaise traps was sorted into taxonomic groups using stereomicroscopy with a magnification range of 6.3x to 40x. Insects were identified to family wherever possible, and order or suborder when family could not easily be determined by morphological identification. Non-insect invertebrates were identified to class or subclass (e.g. Oligochaeta, Gastropoda, and Arachnida). In one case only (*Bombus*) were individuals identified to the genus level. Due to their minute size, two taxa were assumed to be unimportant as house sparrow food sources and were therefore excluded completely from all analyses. These taxa were Acari (mites and ticks) and Thysanoptera (thrips). The arthropod communities were quantified according to four measures: total arthropod abundance, total arthropod dry biomass, arthropod diversity, and arthropod taxonomic richness.

All individuals caught in each trap in a given week were counted, and this number was used to represent the weekly total arthropod abundance (N) on each island.

To estimate arthropod biomass (B), one weekly sample of each taxon was taken out, weighed to an accuracy of 10^{-5} gram, and placed in a drying cupboard at 70 ºC, where they were left to dry for about 48 hours. The samples were then weighed again, and the drying process was resumed for another 24 hours, after which the samples were weighed a third time. Since no significant changes in mass were observed between the last two measurements, the mean of the last two measurements were taken to represent the dry biomass of each sample. These numbers were then divided by the number of individuals in the sample to obtain an average individual dry biomass for each taxon (the number of individuals in these samples ranged from 1 to 1983 with mean 121.58 and median 23). Finally, the number of individuals of each taxon in each weekly sample was multiplied by the average dry biomass for its taxon to obtain an estimated biomass (in grams) of each taxon per site per week. To avoid bias, the weekly samples selected for this step contained individuals that were considered to be representative specimens of the taxon in question.

To account for variation in the time intervals between sample collections, the biomass and abundance measures were standardized by dividing the totals by the number of days the trap had been active, so that the measure used in the analyses was the daily mean value for each week.

The Shannon diversity index was used (Magurran 2013) to estimate the weekly diversity (H)

of the arthropod community:

$$H = -\sum_{i=1}^{S} p_i ln(p_i)$$

where S is the total number of taxa present in the sample and p_i is the proportion of individuals in the sample belonging to taxon i. Thus, Shannon's diversity index accounts for both the total number of taxa and each taxon's proportional representation in the sample – increasing taxonomic richness and increasing equitability will both lead to a higher value of H.

The taxonomic richness (T) of the communities was estimated by counting the number of taxa present in each weekly sample.

Statistical analyses

The statistical analyses were performed in the statistical software R (R Core Team 2018), using generalized linear mixed models (GLMM) fitted with the package glmmTMB (Brooks *et al.* 2017). GLMMs are mixed effects models that allow for the residuals of the response variables to have distributions other than Gaussian (Zuur *et al.* 2009). This is accomplished by specifying the distribution of the data, which gives a link function $g(\mu) = \eta$ describing the relationship between the mean μ of the response variable y and the linear predictor η. The model parameters in a GLMM are estimated using maximum likelihood. Besides *fixed* effects, whose effect on the mean of the response variable is estimated by the model, a GLMM allows the inclusion of *random* effects, for which only the variance of the effect on the mean of the response variable is estimated. Using GLMMs was considered appropriate for this study for two reasons. One is that the response variables, number of clutches laid per week and nestling mortality, were expected to follow a Poisson distribution and a binomial distribution, respectively. The other reason is that the structure of the data, with clutches nested within study site and week, necessitated the inclusion of random intercepts for study site and week in all models to account for non-independence.

An important assumption of multiple regression techniques is that the explanatory variables included in a model are not highly correlated, in which case the problem of multicollinearity arises (Graham 2003). In the data set used for the present study, substantial correlations between variables were present (see Appendix Table A11). All arthropod measures were also highly correlated with temperature, which was not included as an explanatory variable in any

model for this reason.

Due to the multicollinearity of the explanatory variables, a set of candidate models was constructed to investigate each hypothesis regarding the effect of the arthropod community on sparrow reproduction according to the general structure

$$\eta = \alpha + \beta x + s_i + w_j$$

where α is the intercept, β is the effect of one of the arthropod measures x (either total abundance N, total biomass B, Shannon diversity H, or taxonomic richness T), s_i is the random intercept for study sites $i = (1, 2, …, k)$ assumed to be $N \sim (0, \sigma_s^2)$, and w_j is the random intercept for weeks $j = (1, 2, …, 18)$ assumed to be $N \sim (0, \sigma_w^2)$. To investigate whether there was any non-linearity in the relationships between the response and each predictor variable, candidate models including a second-order term x^2 were also included. Finally, a model was constructed that included only the intercept and the random factors.

To assess the effect of arthropod community characteristics on the number of clutches laid on each site per week, several candidate GLMMs were fitted according to the general structure outlined above, with the assumption of a Poisson distributed response variable. However, there were more zero-counts (weeks wherein no clutches were laid) than the expectation under a Poisson distribution, which would cause overdispersion in a regular Poisson GLMM. For this reason, a two-part, zero-altered Poisson model was fitted where zeroes are assumed to be generated by a separate process to the one generating non-zero counts (Zuur *et al.* 2009). Such an assumption is justified in the case of the present study because the zero-inflation stems at least in part from the fact that measurements started before the beginning of the breeding season and ended after the end of the breeding season.

In addition to the current effect of each community measure at the time of laying, lag effects were modelled whereby the value of each measure two weeks following laying was used as the explanatory variable (see Introduction for the rationale behind testing both current and lag effects). Towards the end of the breeding season on some islands, the arthropod sampling period did not extend to two weeks beyond the last laid clutches. These clutches, 3 in total, were excluded from all analyses in order to allow for meaningful model comparisons, but this did not greatly affect the parameter estimates of the models. 17 candidate models were constructed – current and lag effects of each of the four arthropod measures (N, B, H, T), with and without a second-order term, and finally a model containing only the intercept and random effects.

To investigate the effect of arthropod community characteristics on nestling mortality, GLMMs were fitted with a binomial distribution with a complementary log-log link. The response variable in these models was the proportion of nestlings not surviving to the fledgling stage. To control for the effect of season, clutch number (i.e. whether the clutch was the first, second, or third in its nest) was included in all models as a factor, thus giving the model structure

$$\eta = \alpha + \beta_1 second + \beta_2 third + \beta_3 x + \beta_4 x^2 + s_i + w_j$$

where α is the intercept for the first clutch, β_1 and β_2 are the effects of the second and third clutches respectively, β_3 is the effect of one of the arthropod measures x (N, B, H, T) during the first five days following hatching, β_4 is the second-order effect of the arthropod measure x, and s_i and w_j are the random intercepts for study sites and weeks respectively. The measures were standardized within clutch numbers, so that the value used for each measure was the difference from the mean value within each clutch number. Again, non-linear effects were considered in separate models, giving a total of nine candidate models.

To evaluate which of the candidate models best predicted the response variable, they were evaluated according to the corrected Akaike Information Criterion (AIC_c) (Burnham & Anderson 2002) using the R package AICcmodavg (Mazerolle 2019):

$$AIC_c = -2\log(L(\theta)) + 2K \left(\frac{n}{n - K - 1}\right)$$

where $log(L(\theta))$ is the maximum likelihood, K is the number of model parameters, and n is the sample size. Using this criterion, each model can be assigned a relative score, and the model with the lowest AIC_c score is considered to be the best-supported model, given the data and the alternative models. Common statistical practice is to consider models with AIC_c scores within 2 of the best-supported model equally well supported (Burnham & Anderson 2002). In addition to the AIC_c score, models are assigned Akaike weights (w), which sum to 1 and signify the likelihood that the model is the actual best model in the set (Burnham & Anderson 2002). Finally, the Akaike weight of the top model was divided by the Akaike weight of each subsequent model in the set to give the evidence ratio (ER) for each model.

Results

Arthropod community characteristics in time and space

The number of arthropod individuals caught per week during the study period ranged from 9 (Hestmona, week 16) to 2362 (Selvær, week 30) (Figure 3a). Across all sites, arthropod abundance increased throughout the season, from a mean of 91 individuals caught in week 15 (n = 7 traps, SD = 50) to a mean of 1089 individuals caught in week 33 (n = 6 traps, SD = 716). Especially notable peaks in abundance were observed on Selvær, Gjerøy, and Indre Kvarøy after week 30 (Figure 3a).

Arthropod dry biomass per week during the study period ranged from 0.004 grams (Indre Kvarøy, week 14) to 4.032 grams (Storselsøy, week 31) (Figure 3b). Across sites, mean biomass increased from 0.046 grams in week 15 (n = 7 traps, SD = 0.022) to 1.430 grams in week 33 (n = 6 traps, SD = 1.07). The increase was particularly steep between mid-July and early August, with a peak of 1.996 in week 31 (n = 8 traps, SD = 1.257, see Figure 3b). Some of this increase in biomass can be attributed to the effect of the superfamily Tipuloidea (crane flies), which was among the largest arthropods caught and which increased markedly in number after week 30 on all sites except Sleneset and Husøy (Appendix Figure A12).

The number of taxa caught in one week ranged from three (Indre Kvarøy, week 14) to 30 (Hestmona, week 23) (Figure 3c). Across sites, the mean taxonomic richness of the arthropod communities increased from 6.571 taxa in week 15 (n = 7 traps, SD = 1.272) until reaching a plateau around 24.286 in week 26 (n = 7 traps, SD = 4.498, see Figure 3c). The Shannon diversity index indicated a general trend of higher diversity late than early in the season, with a small drop around week 20 (Figure 3c). Generally, there was great variation in abundance, biomass and diversity between sites in the last part of the study period (see Figure 3).

Effect of arthropod communities on number of clutches laid per week

Across the six sites with sufficiently high breeding activity (see Study area in Materials and methods), a total of 184 clutches were laid (Figure 4), of which 181 were included in the analyses (the remaining 3 clutches were excluded because the lag effect could not be modelled, see Statistical analyses in Materials and methods).

The highest ranked model explaining the variation in the number of clutches laid per week included a linear positive lag effect of total biomass as the only fixed effect (Table 1). Thus, there was an increase in the number of clutches laid per week with increasing biomass two weeks later ($\beta = 2.968$, CI = [0.585, 5.351], Table 2a and Figure 5a). The probability that this

model was the actual best model in the set at explaining the data was 21.8% (w_1, Table 1).

The second highest ranked model included an uncertain linear positive lag effect of taxonomic richness ($\beta = 0.037$, CI = [-0.001, 0.075]). There was a probability of 9.5% that this model was the actual best model in the set (w_2, Table 1). The highest ranked model was more than twice as likely to be the best model as the second-ranked model ($ER_2 = 2.17$, Table 1).

Three other candidate models had $\Delta AIC_c \leq 2$, all of which had some permutation of total biomass or taxonomic richness as explanatory variables (see Table 1). The model ranked fifth indicated that there was a linear positive effect of current biomass on the number of clutches per week ($\beta = 3.609$, CI = [0.058, 7.159], Table 2b and Figure 5b). This model was more than two times less likely to be the best model than the highest ranked model ($ER_5 = 2.53$, Table 1). The parameter estimates of the models ranked third and fourth were all uncertain, with confidence intervals overlapping zero (model 3: $\beta_T{}^2 = -0.004$, $CI_T{}^2 = [-0.009, 0.001]$, model 4: $\beta_{BL}{}^2 = 3.473$, $CI_{BL}{}^2 = [-5.509, 12.455]$).

Effect of arthropod communities on nestling mortality

163 clutches were included in these analyses. Out of 787 eggs, 465 fledglings were alive at the last nest visit, giving a mean nestling mortality across all sites of 0.409.

The highest ranked model explaining the variation in mortality between broods included a negative effect of total biomass as the only fixed factor in addition to clutch number, indicating reduced nestling mortality with increasing biomass (Table 3). As the parameter estimate for biomass marginally included zero, these results only indicate an uncertain trend for nestling mortality to decrease with increasing available arthropod biomass ($\beta = -0.343$, CI = [-0.726, 0.041], Table 4 and Figure 6).

Three other candidate models had $\Delta AIC_c \leq 2$ (Table 3), all of which had confidence intervals for the parameter estimates that overlapped zero. The second highest ranked model only had clutch number as a fixed factor. The model ranked third included a positive effect of total abundance on mortality ($\beta = 0.095$, CI = [-0.055, 0.246]), and the model ranked fourth included a non-linear negative effect of biomass ($\beta_B{}^2 = -0.154$, CI = [-0.263, 0.571]).

Discussion

The present study suggests that the substantial spatial and seasonal variation in arthropod biomass present in the study area (Figure 3b) can predict the timing of breeding in local house sparrow populations (Tables 1 and 2, Figure 5). Accordingly, the results suggest that house sparrows synchronise the nestling period with anticipated high levels of food availability, as has previously been shown in single- and double-brooded passerine species (Visser, Holleman & Gienapp 2006). This result is important because such phenological synchrony has previously been thought to be less relevant to multi-brooded species with longer breeding seasons (Verboven, Tinbergen & Verhulst 2001). A negative relationship between arthropod biomass and nestling mortality was also found (Figure 6). Although this result was less certain (CI = [-0.726, 0.041], Table 4), it does point towards an important role of arthropod communities in influencing reproductive success. No strong support was found for effects of abundance, taxonomic richness, or taxonomic diversity in either analysis. The present study complies with earlier literature demonstrating the significance of arthropod communities to population dynamics at higher trophic levels (Bryant 1975; Ballinger 1977; Martin 1987; Pettersson *et al.* 1995; Visser *et al.* 1998; Arlettaz *et al.* 2001; Cresswell & McCleery 2003; Both *et al.* 2009a; Pearce-Higgins *et al.* 2010; Møller 2013; Lister & Garcia 2018).

When studying the role of arthropods as a food source, it is vital that appropriate sampling methods are applied (Hutto 1990), and a fundamental assumption of this study is that there is substantial overlap between the arthropod taxa sampled and those captured by house sparrows to feed nestlings. The data used in these analyses were collected using Malaise traps (Malaise 1937). Due to differences in life history and behaviour, different taxa and life-stages are not equally likely to be caught in these traps. Malaise traps are flight-intercept traps and thus primarily trap flying taxa and life-stages, they are furthermore known to be somewhat biased towards the insect orders Diptera and Hymenoptera (Matthews & Matthews 1971; Diserud, Stur & Aagaard 2013; Sheikh *et al.* 2016). In the present study, dipterans make up 34% of identified taxa (17 out of 50, see Appendix Table A12), 66.9% of the total individuals, and 63.8% of the total arthropod biomass. There is also a risk of underestimating the arthropod abundance or mischaracterising the taxonomic composition of the community at a site if the trap is not ideally placed (Matthews & Matthews 1971), since arthropod distributions may be patchy even at quite small scales (Weaver 1995; Maudsley, Seeley & Lewis 2002). Even though care was taken to place traps in comparable locations on each site, some noise due to small-scale habitat variation cannot be ruled out, especially since only one trap was placed at

each site.

Previous studies suggest that the taxonomic composition of house sparrow nestling diets varies between populations (Hammer 1948; Seel 1969; Anderson 1978; Gavett & Wakeley 1986; Klvaňová *et al.* 2012). While several studies based on analyses of stomach contents or faecal sacs find that Coleoptera (beetles) constitute the largest part of house sparrow nestling diet (Gavett & Wakeley 1986; Klvaňová *et al.* 2012), these findings may be biased as hard coleopteran body parts are more likely to pass intact through the digestive system and are thus easier to identify than those of other invertebrates. In particular, the findings of Seel (1969) suggest that this is the case, since Coleoptera constituted a smaller percentage of the total in (undigested) crop contents than in stomach contents. Due to the large amount of inter-population variation found in the literature, the dietary composition of house sparrows in this metapopulation was unclear at the outset of the present study. However, based on field observations of foraging parents, tipuloids were suspected to be of importance. DNA metabarcoding techniques can be used to determine the species composition in the diets of insectivorous birds by analysing faecal matter (Jedlicka, Sharma & Almeida 2013), thus somewhat mitigating the problem of unequal digestibility of different prey taxa (but not eradicating it completely – see Nielsen *et al.* 2018, Deagle *et al.* 2019, and Mata *et al.* 2019). To determine which taxa were most important in nestling diets, a pilot study was conducted using DNA metabarcoding techniques on faecal samples taken from 29 nestlings from 14 nests on Hestmannøy and 54 nestlings from 17 nests on Husøy in the period from May to August of 2017. Preliminary results suggest that nestling diet in the study area was dominated by Diptera, and particularly by Tipulidae, with Lepidoptera being the second most common order (Ringsby, Kvalnes & Fossøy, unpublished results). Generally, the taxa found in nestling faeces correspond well with those found in Malaise trap samples. Insects dominate, although it is not possible to determine the life-stages at which they are caught. As discussed above, Diptera made up substantial proportions of the total biomass, abundance, and taxa in the Malaise trap samples. Lepidoptera, however, was less well represented. This is in line with previous studies finding that Malaise traps are not the best type of trap for sampling this order (Nielsen *et al.* 2018). In addition, based on the nestling provisioning habits of a number of passerines including house sparrows (Anderson 1978; Visser, Holleman & Gienapp 2006; Arnold *et al.* 2010; Burger *et al.* 2012; Samplonius *et al.* 2016) it seems likely that at least some species of Lepidoptera (and possibly other orders, e.g. Coleoptera) are primarily captured at the caterpillar stage in the focal population. The abundance of this life-stage

cannot be quantified by Malaise trapping. Based on the preliminary DNA metabarcode findings discussed above in conjunction with the seasonal development of tipuloid abundance in the study area (Appendix Figure A12), it may be hypothesised that Tipulidae is a particularly important prey taxon during the last part of the breeding season. Some other taxa or life-stages may well be similarly important during the earlier part of the season. However, the pilot study did not have a sufficiently high sample size to detect any such seasonal variation with certainty.

There was support for an effect of arthropod biomass on the number of clutches laid per week (Table 2, Figure 5). Both the current and lag effect hypotheses found some support, the latter more so than the former. This lends support to the hypothesis that house sparrows could be using environmental cues other than current arthropod biomass to determine when to lay. This strategy would allow the sparrows to take full advantage of periods of high arthropod biomass by ensuring nestlings hatch as soon as high-biomass periods arrive, rather than delaying laying and running the risk of missing a crucial window of opportunity. This is in line with previous research on other passerines (Visser, Holleman & Gienapp 2006). The precise nature of the proximate cues used to initiate laying in the focal metapopulation remains somewhat unclear. One previous study of the factors influencing onset of breeding (i.e. the timing of the first clutch only) found that both onset of spring and population density had different effects depending on habitat type (Johansen 2018). Cues may be based on the current state of the arthropod community, i.e. laying is initiated when some arthropod biomass threshold is reached but well in advance of the optimal levels for rearing nestlings, or on the ontogenetic stage of some important taxon. Alternatively, some other environmental cue not directly related to arthropod community characteristics may be used. In other passerine populations, temperature and photoperiod have been found to act as cues to initiate laying (Lofts & Murton 1968; Meijer et al. 1999; Sharp 2005; Visser, Holleman & Gienapp 2006; Dickey, Gauthier & Cadieux 2008; Phillimore et al. 2016). Sparrows may even use different cues at different stages of the breeding season, as it is not obvious that arthropod taxa emerging at different times are subject to the same phenological drivers (Searle et al. 2013; Forrest 2016). A reliance on environmental cues to predict future arthropod biomass may leave populations vulnerable to changing environments (Helm et al. 2013), as with the great tits on the Hoge Veluwe. These birds are suggested to use March and April temperatures as cues to begin laying, since these have historically been reliable predictors of the later April and May temperatures that are the actual drivers of the caterpillar abundance increase. However,

climate change has affected temperatures in these periods unequally, resulting in phenological mismatch (Visser *et al.* 1998; Visser, Holleman & Gienapp 2006; Ramakers, Gienapp & Visser 2019).

The highest ranked model of the effect of arthropod communities on nestling mortality suggested a trend towards a negative effect of arthropod biomass (Table 4, Figure 6). This result is in agreement with the findings of Anderson (1977), who demonstrated that house sparrow fledgling success in Missouri, USA, was significantly greater in years with emergence of superabundant cicadas than in non-emergence years. However, the model that only included an intercept and clutch number was ranked second and had an evidence ratio of 1.62, suggesting that the quantified arthropod community characteristics had limited explanatory value for nestling mortality (Table 3). This would be a somewhat surprising result, given the crucial role of arthropod prey during the nestling stage known from the literature (Kalmbach 1940; Klvaňová *et al.* 2012), but one reason contributing to the low AIC_c score of this model may simply be that it has the fewest parameters (Burnham & Anderson 2002). Since clutch number increases through the season, it may be that the model is not able to separate the effects of the arthropod communities from the effect of clutch number. However, if the statistical effect of arthropod communities was very clear in the data, this should not be a problem. It may be that arthropod abundance and biomass in the habitat, even when relatively low, are already so high that food limitation is not an important factor for nestling survival. In other words, the functional response may have plateaued so that further increases in food availability do not lead to increased foraging efficiency in parent house sparrows (Holling 1959). Interestingly, the apparent effect of arthropod biomass on the timing of laying may contribute to obscuring the relationship between mortality and biomass by reducing the variation in arthropod biomass between broods. Given that most clutches are synchronised with periods of relatively high arthropod biomass, the fitness consequences of *not* being synchronised might be less apparent in the data than they would have been if timing of laying was random (Haller & Hendry 2014). As discussed above, the inclusion of all arthropod taxa (except Acari and Thysanoptera, see Materials and methods) in the analysis without distinguishing between important and unimportant prey taxa means that some portion of the variation in biomass is likely to be irrelevant to house sparrows. It is also possible that some important prey taxa are not adequately represented in the data due to the sampling methods used. Furthermore, since arthropod community characteristics during the first five days following hatching were calculated on the basis of weekly samples, within-week

variation in community characteristics is not reflected in the data. It has previously been shown that bad weather conditions during the nestling period negatively affect recruitment in the focal metapopulation, very likely through an effect on arthropod activity (Ringsby *et al.* 2002). These factors may have contributed to increase the uncertainty of the effects estimated in the models by obscuring the actual relationships.

The phenological dynamics that have been explored in this study present an exciting area for future research. A logical next step involves expanding our knowledge of house sparrow provisioning behaviour in the metapopulation and focusing on the most important prey taxa in future studies. In addition to further analysis of DNA metabarcode results, a promising avenue in this regard involves obtaining video footage of foraging parent house sparrows and performing evaluations of both the amount of food brought and the taxonomic identity of the arthropod prey. Other methods of arthropod sampling in addition to Malaise traps may also be considered. Based on data from a single year, it is not possible to say with certainty whether the focal house sparrow metapopulation is affected by disruptions like the phenological mismatch reported by Visser *et al.* (1998). It is therefore vital that data on arthropod communities is integrated into longitudinal population studies of insectivorous animals, not least because this would enable an investigation of the potential role of food availability in producing the different phenological responses of multi-brooded and single-brooded species to climate change documented elsewhere (Dunn & Møller 2014). Studies of this kind may also be complemented by experimental work, e.g. food supplementation studies, as has been done by Peach *et al.* (2018).

The present study represents an important step on the way to developing an understanding of the role played by arthropod community variation in shaping the reproductive phenologies of multi-brooded passerines, complementing previous work by Visser *et al.* (1998), Perrins (1991), and others (Bryant 1975; Blancher & Robertson 1987; Dias & Blondel 1996; Naef-Daenzer & Keller 1999; Burger *et al.* 2012; Møller 2013; Samplonius *et al.* 2016), as well as identifying some of the ecological mechanisms behind the variation in reproductive phenology in a house sparrow metapopulation. In conclusion, this study illustrates the importance of directly including seasonal and spatial arthropod community dynamics in investigations of the breeding phenology and reproductive success of animals that depend on these communities as a food source, an aspect that has often been neglected in past studies. In light of the ongoing climate change and biodiversity crises, both of which may be expected to disrupt these important ecological interactions between trophic levels, further development of

this field of knowledge is now crucial.

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Tables

Table 1 AIC_c ranking table for GLMMs modelling the effects of arthropod communities on the number of clutches laid per week in an insular metapopulation of house sparrows off the coast of northern Norway during the breeding season of 2017. In all models, site and week were included as random factors. Explanatory variables included are arthropod dry biomass (B), arthropod taxonomic richness (T), Shannon diversity (H), and total arthropod abundance (N), as well as the above after a two-week lag (B_L, T_L, H_L, and N_L, respectively). AIC_c score relative to the highest-ranked model (ΔAIC_c), Akaike weight (w_i), and evidence ratio (ER_i) are listed for each model.

Rank	Model parameters	ΔAIC_c	w_i	ER_i
1	$\mathbf{B_L}$	**0**	**0.218**	**1**
2	T_L	1.55	0.101	2.17
3	$T + T^2$	1.67	0.095	2.3
4	$B_L + B_L{}^2$	1.68	0.094	2.32
5	B	1.85	0.086	2.53
6	H	2.04	0.079	2.78
7	$N + N^2$	2.32	0.068	3.19
8	T	2.43	0.065	3.37
9	$H + H^2$	2.60	0.059	3.67
10	$T_L + T_L{}^2$	3.50	0.038	5.76
11	$B + B^2$	3.80	0.033	6.67
12	H_L	4.86	0.019	11.35
13	N_L	5.45	0.014	15.22
14	N	5.45	0.014	15.26
15	$N_L + N_L{}^2$	6.17	0.010	21.89
16	$H_L + H_L{}^2$	7.04	0.006	33.83
17	Intercept	29.87	< 0.001	3056012

Table 2 All parameter estimates from the models ranked a) 1st and b) 5th in the AIC_c comparison of GLMMs using arthropod community measures to explain the number of clutches laid per week in an insular metapopulation of house sparrows in an archipelago located off the coast of northern Norway during the breeding season of 2017. The fixed effects included are arthropod dry biomass two weeks following laying (B_L) and arthropod dry biomass at the time of laying (B). The models were fitted with random intercepts for site and week. The estimates for the zero-inflation model components (ZI) of each model are also listed.

	Parameter	Estimate	95% confidence interval	
			Lower	Upper
a) **Model 1**	Intercept	0.342	-0.397	1.081
	β_{BL}	2.968	0.585	5.351
	σ^2_{site}	0.000	-	-
	σ^2_{week}	0.572	0.114	2.875
	Intercept$_{ZI}$	-0.925	-1.701	-0.148
b) **Model 5**	Intercept	0.573	0.028	1.117
	β_B	3.609	0.058	7.160
	σ^2_{site}	0.000	-	-
	σ^2_{week}	0.354	0.087	1.439
	Intercept$_{ZI}$	-0.699	-1.270	-0.128

Table 3 AIC_c ranking table for the candidate GLMMs modelling the effects of arthropod communities on variation in mortality between broods in an insular metapopulation of house sparrows off the coast of northern Norway during the breeding season of 2017. In all models, site and week were included as random factors. Explanatory variables included are total arthropod dry biomass (B), arthropod taxonomic richness (T), Shannon diversity (H), total arthropod abundance (N), and clutch number (CN). AIC_c score relative to the highest-ranked model (ΔAIC_c), Akaike weight (w_i), and evidence ratio (ER_i) are listed for each model.

Rank	Model parameters	ΔAIC_c	w_i	ER_i
1	**B + CN**	**0**	**0.302**	**1**
2	CN	0.96	0.187	1.62
3	N + CN	1.63	0.133	2.26
4	$B + B^2 + CN$	1.66	0.131	2.3
5	T + CN	2.89	0.071	4.25
6	H + CN	2.90	0.071	4.27
7	$N + N^2 + CN$	3.69	0.048	6.33
8	$H + H^2 + CN$	4.46	0.032	9.3
9	$T + T^2 + CN$	5.04	0.024	12.4

Table 4 All parameter estimates from the highest ranked model in the AIC_c comparison of GLMMs using arthropod community measures to explain the variation in fledgling mortality between broods in an insular metapopulation of house sparrows in an archipelago located off the coast of northern Norway during the breeding season of 2017. The fixed effects included are arthropod dry biomass during the five days following hatching (B) and clutch number (CN). The model was fitted with random intercepts for site and week.

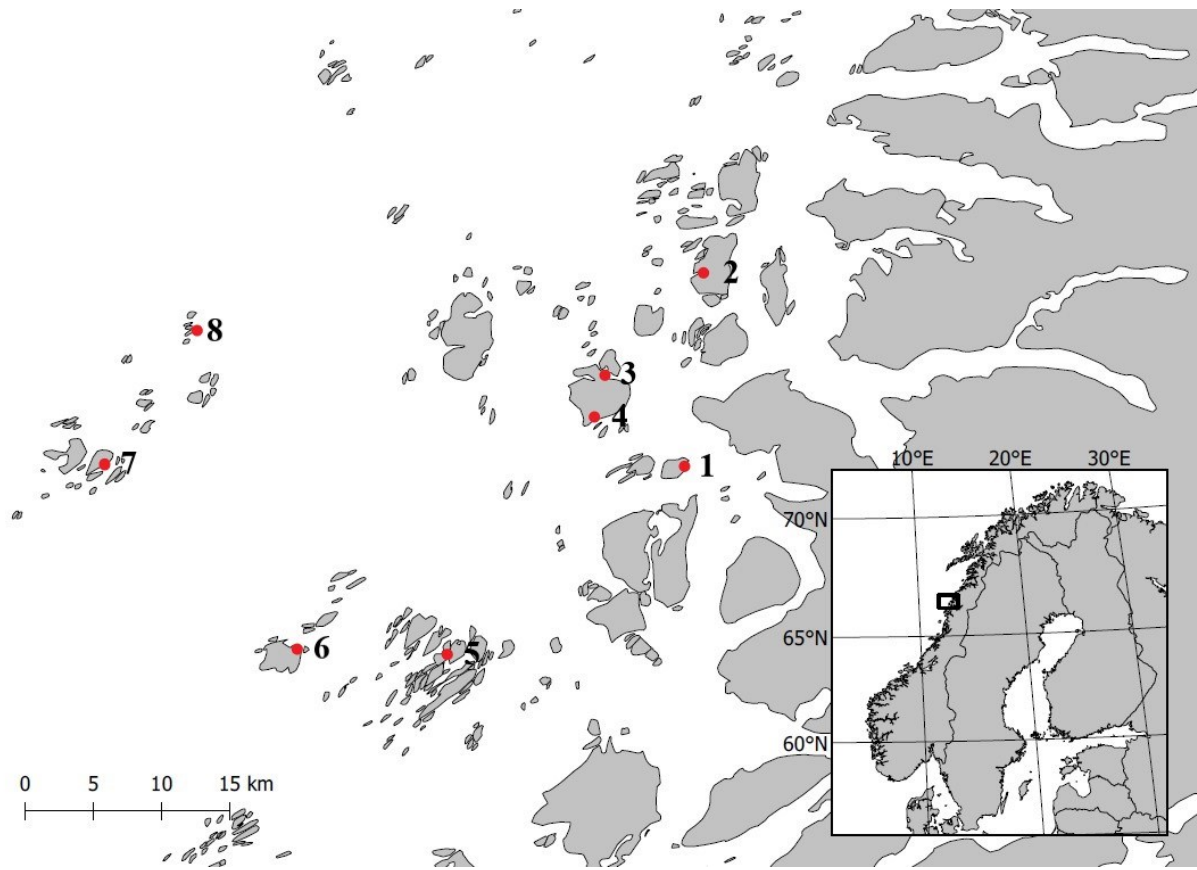| Parameter	Estimate	95% confidence interval	
		Lower	Upper
Intercept	-0.650	-1.134	-0.167
β_B	-0.343	-0.726	0.041
β_{CN2}	-0.092	-0.539	0.355
β_{CN3}	0.105	-0.544	0.755
σ^2_{site}	0.175	0.044	0.688
σ^2_{week}	0.126	0.029	0.548

Figures

Figure 1 Map of the study area consisting of seven islands and its location within Norway. The eight sites where arthropod sampling took place between early April to mid-August 2017 are marked with red dots and labelled as follows: Indre Kvarøy (**1**), Gjerøy (**2**), Storselsøy (**3**), Hestmona (**4**), Sleneset (**5**), Lovund (**6**), Husøy (**7**), Selvær (**8**). Map courtesy of Thomas Kvalnes, modified by the author.

Figure 2 A Malaise trap of the type used to collect arthropods in an archipelago in northern Norway during the house sparrow breeding season of 2017. The funnel arthropods into a bottle at the top containing 96% ethanol, where they are then preserved. Photo: Mary Ngo, Selvær 2019.
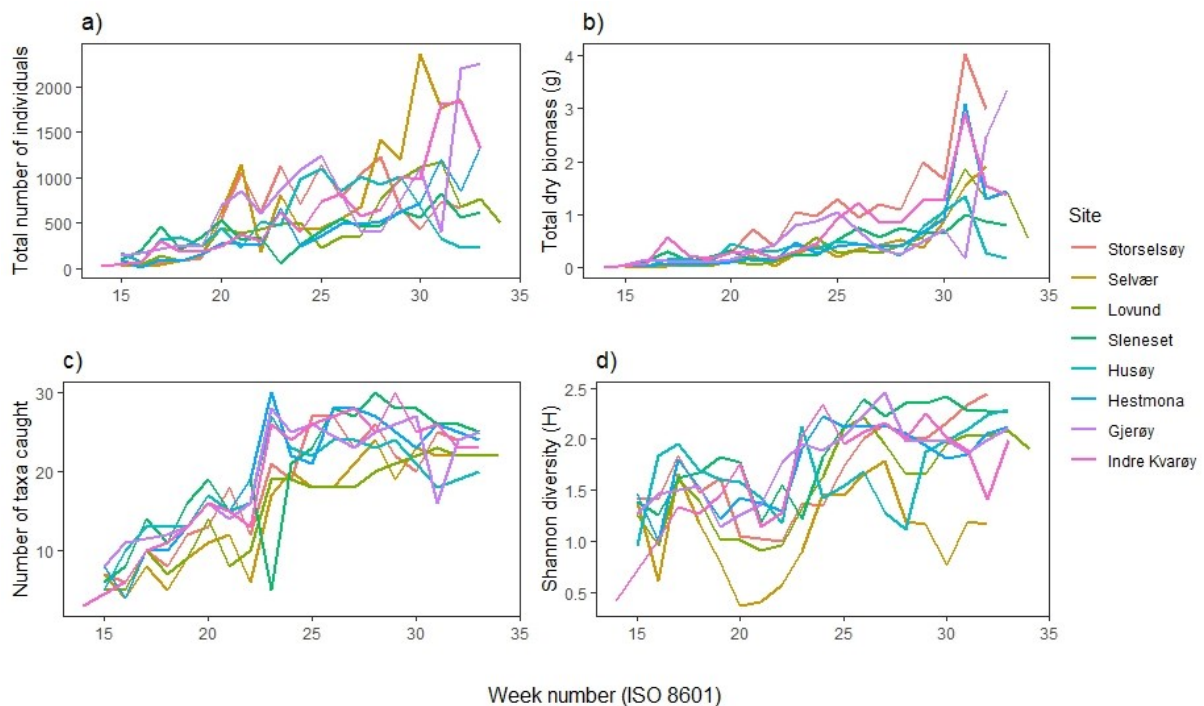

Figure 3 Seasonal variation in community structure among eight sites distributed across seven islands in an archipelago located off the coast of northern Norway in the period from early April to mid-August 2017. Variation is shown as a) arthropod abundance, b) arthropod dry biomass, c) taxonomic richness, measured as the total number of taxa caught per week, and d) Shannon diversity index (*H*). For further details, see Materials and methods above.
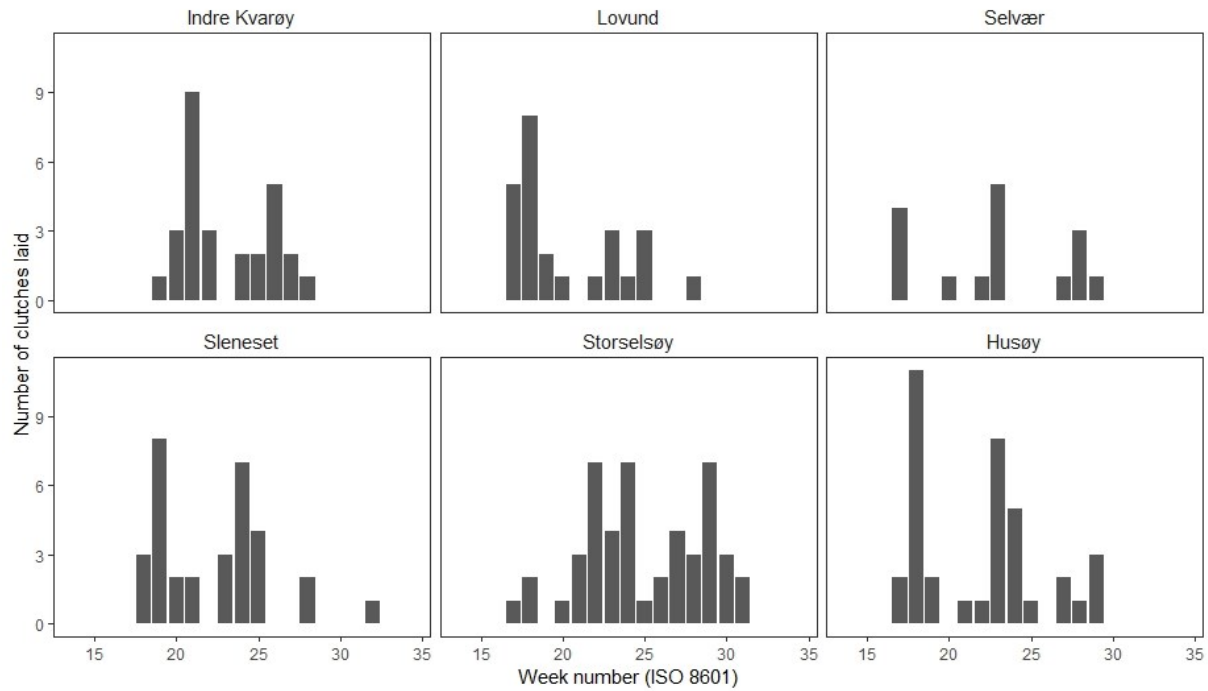
Figure 4 Number of clutches laid in a metapopulation of house sparrows across six sites on six islands in an archipelago located off the coast of northern Norway in the period from early April to mid-August 2017. Clutches were counted in the week during which the first egg was laid.
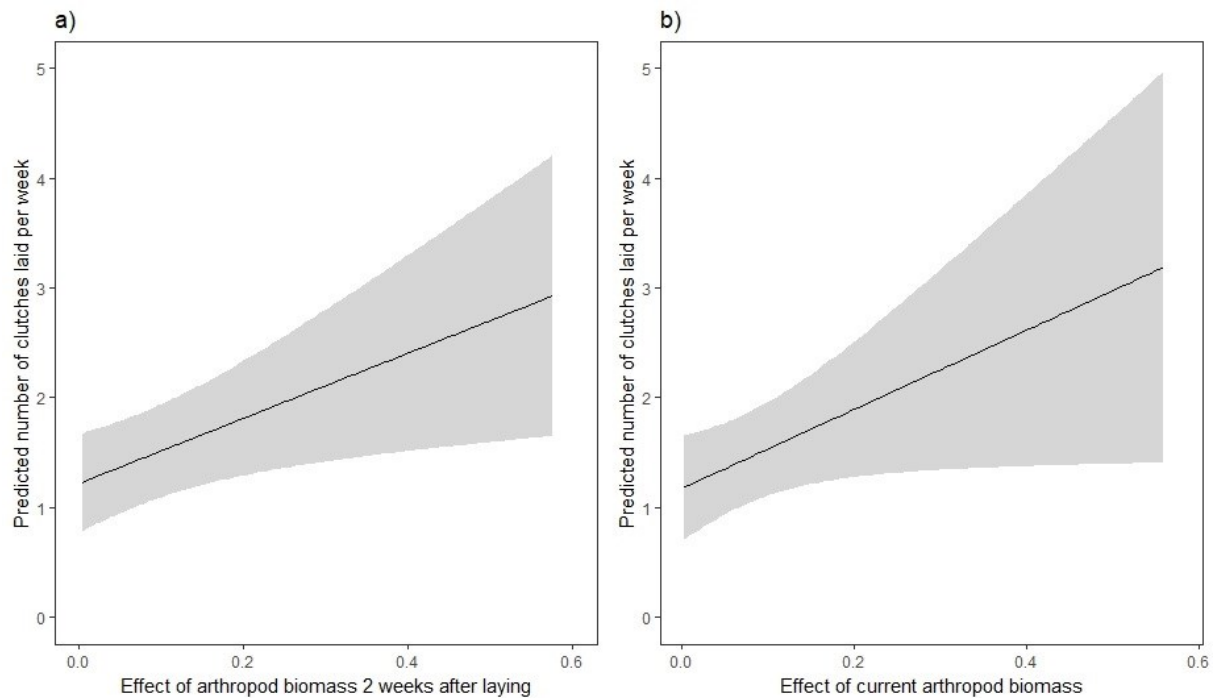
Figure 5 Predicted number of clutches laid per week in a metapopulation of house sparrows in an archipelago located off the coast of northern Norway with increasing arthropod biomass a) two weeks following laying and b) concurrently with laying. The shaded areas indicate the 95% confidence interval.
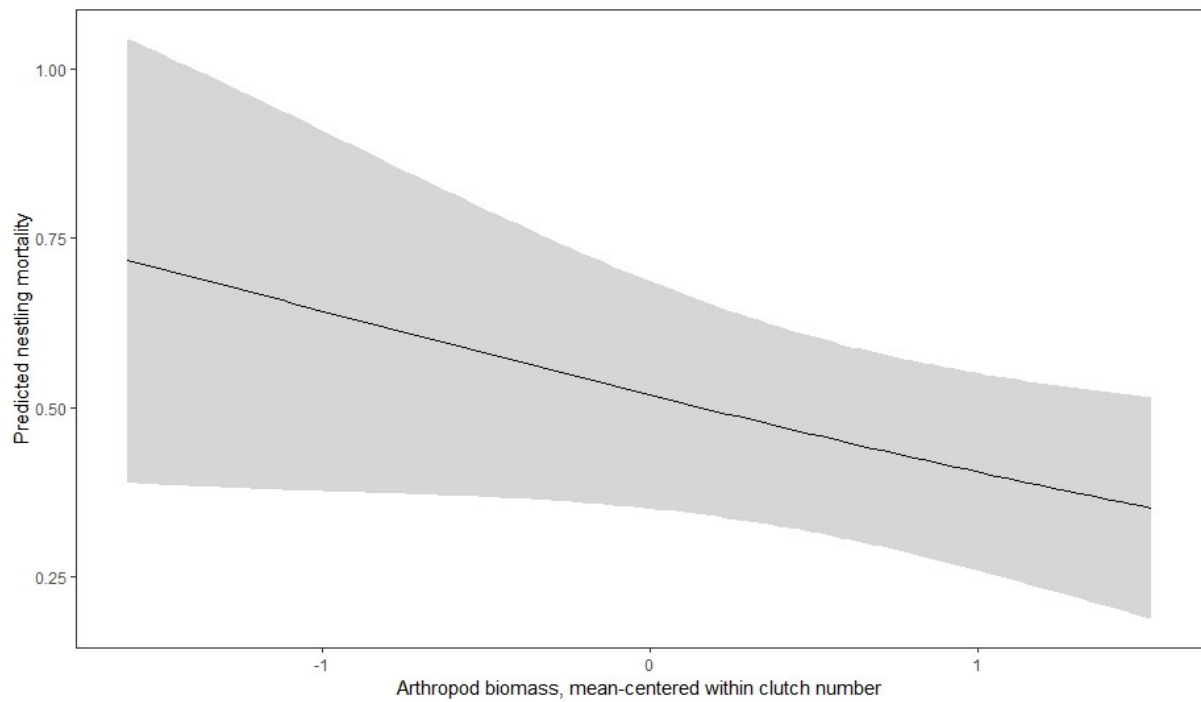
Figure 6 Predicted effect of increasing arthropod biomass on house sparrow nestling mortality in an archipelago located off the coast of northern Norway. The shaded area indicates the 95% confidence interval.

Appendix

Table A11 Pearson product-moment correlation coefficients and their corresponding p-values for arthropod community characteristics used as explanatory variables. The explanatory variables tested are total arthropod abundance (N), total arthropod dry biomass (B), Shannon diversity (H), and arthropod taxonomic richness (T). The sample size for all pairs is 165, and the compared values each correspond to the estimated catch during a single five-day period.

	N	**B**	**H**	**T**
N	-	p < 0.001	p = 0.44	p < 0.001
B	0.38	-	p < 0.001	p < 0.001
H	0.06	0.53	-	p < 0.001
T	0.50	0.46	0.81	-

Table A12 A complete list of all taxa that were caught in 8 Malaise traps on seven islands in an archipelago in northern Norway during the house sparrow breeding season of 2017. In addition to each taxon's scientific name, its taxonomic level, the order and class to which it belongs, and the first and last week that it appeared (the week when the sample was collected) are listed. In one case, marked *, two taxa are combined due to the difficulty of morphological identification.

Taxon	**Level**	**Order**	**Class**	**First seen (week)**	**Last seen (week)**
Anisopodidae	Family	Diptera	Insecta	15	34
Aphididae	Family	Hemiptera	Insecta	22	34
Arachnida	Class	NA	Arachnida	15	34
Bibionidae	Family	Diptera	Insecta	23	34
Bombus	Genus	Hymenoptera	Insecta	19	33
Brachycera (indet.)	Suborder	Diptera	Insecta	14	34
Cantharidae	Family	Coleoptera	Insecta	23	33
Carabidae	Family	Coleoptera	Insecta	30	30
Chironomidae	Family	Diptera	Insecta	15	34
Chrysomelidae	Family	Coleoptera	Insecta	17	23
Chrysopidae	Family	Neuroptera	Insecta	24	31
Coccinellidae	Family	Coleoptera	Insecta	22	28
Coleoptera (indet.)	Order	Coleoptera	Insecta	18	33
Collembola	Subclass	NA	Entognatha	14	34

Culicidae	Family	Diptera	Insecta	27	27
Curculionidae	Family	Coleoptera	Insecta	15	32
Diplopoda	Class	NA	Diplopoda	32	32
Elateridae	Family	Coleoptera	Insecta	22	32
Empididae	Family	Diptera	Insecta	20	34
Ephemeroptera (indet.)	Order	Ephemeroptera	Insecta	22	22
Formicidae	Family	Hymenoptera	Insecta	17	33
Gastropoda	Class	NA	Gastropoda	22	33
Geometridae	Family	Lepidoptera	Insecta	15	33
Hemerobiidae	Family	Neuroptera	Insecta	19	34
Heteroptera (indet.)	Suborder	Hemiptera	Insecta	16	34
Homoptera	Suborder	Hemiptera	Insecta	15	34
Hymenoptera (indet.)	Order	Hymenoptera	Insecta	17	34
Ichneumonidae	Family	Hymenoptera	Insecta	17	34
Lepidoptera (indet.)	Order	Lepidoptera	Insecta	16	34
Muscidae/ Calliphoridae*	Family	Diptera	Insecta	15	33
Mycetophilidae	Family	Diptera	Insecta	15	34
Nematocera (indet.)	Suborder	Diptera	Insecta	14	34
Neuroptera (indet.)	Order	Neuroptera	Insecta	26	33
Nymphalidae	Family	Lepidoptera	Insecta	29	29
Oligochaeta	Subclass	NA	Clitellata	32	33
Plecoptera (indet.)	Order	Plecoptera	Insecta	15	32
Psocoptera (indet.)	Order	Psocoptera	Insecta	23	34
Psychodidae	Family	Diptera	Insecta	15	34
Rhagionidae	Family	Diptera	Insecta	24	29
Scathophagidae	Family	Diptera	Insecta	15	33
Scatopsidae	Family	Diptera	Insecta	18	34

Siphonaptera (indet.)	Order	Siphonaptera	Insecta	19	28
Staphylinidae	Family	Coleoptera	Insecta	15	34
Symphyta (indet.)	Suborder	Hymenoptera	Insecta	20	33
Syrphidae	Family	Diptera	Insecta	23	32
Tabanidae	Family	Diptera	Insecta	29	32
Tipuloidea	Super-family	Diptera	Insecta	16	34
Trichoptera (indet.)	Order	Trichoptera	Insecta	22	34
Ulidiidae	Family	Diptera	Insecta	27	33
Vespidae	Family	Hymenoptera	Insecta	22	30

Table A13 Descriptive statistics of observed nestling mortality in house sparrow clutches laid on six sites on six islands in an archipelago located off the coast of northern Norway throughout the breeding season of 2017, by clutch number (i.e. whether the clutch is the first, second or third clutch laid at that nest site in the season).

Clutch number	Sample size	Mean nestling mortality	SE
1	78	0.383	0.039
2	68	0.403	0.043
3	17	0.579	0.089

Table A14 Sample sizes of first, second, and third clutches on all six sites with house sparrow breeding activity in an archipelago located off the coast of northern Norway during the breeding season of 2017. Clutches listed here are those in which at least one egg hatched.

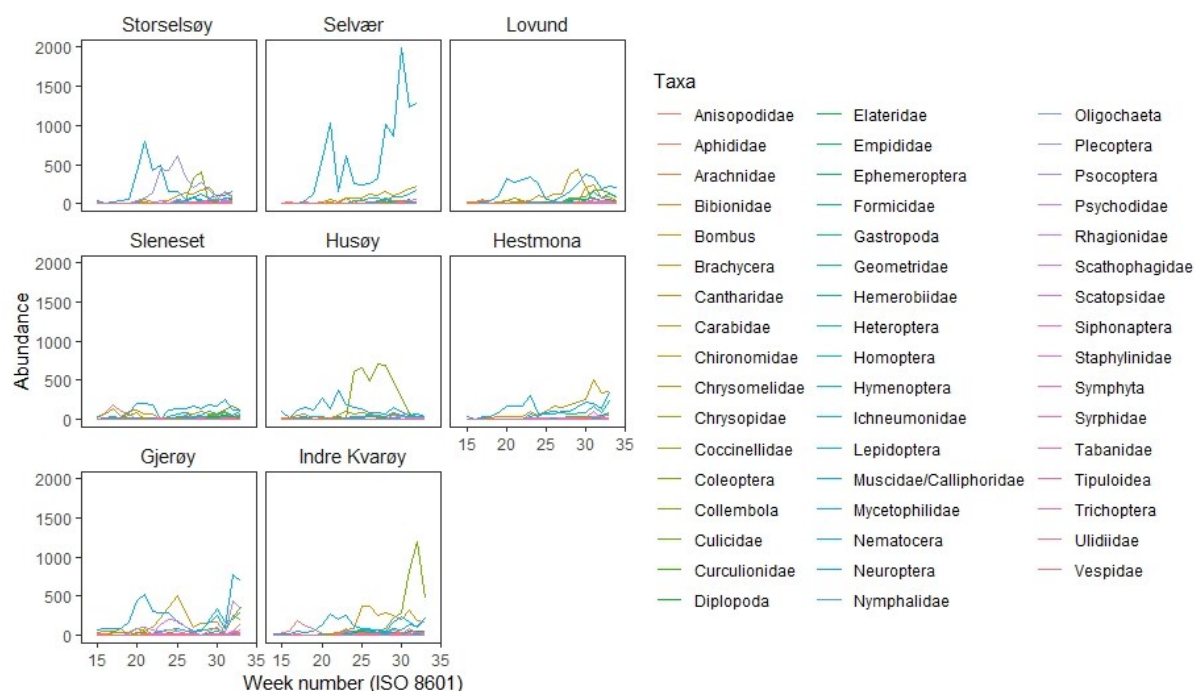| Site	First clutches	Second clutches	Third clutches	Total
Indre Kvarøy	11	11	0	22
Lovund	16	8	0	24
Selvær	7	5	3	15
Sleneset	15	12	1	28
Storselsøy	13	18	12	43
Husøy	16	14	1	31

Figure A11 Variation in arthropod abundance divided by taxon across eight sites on seven islands in an archipelago located off the coast of northern Norway in the period from early April to mid-August 2017. The y-axis denotes the number of individuals caught. For further details, see Materials and methods above.
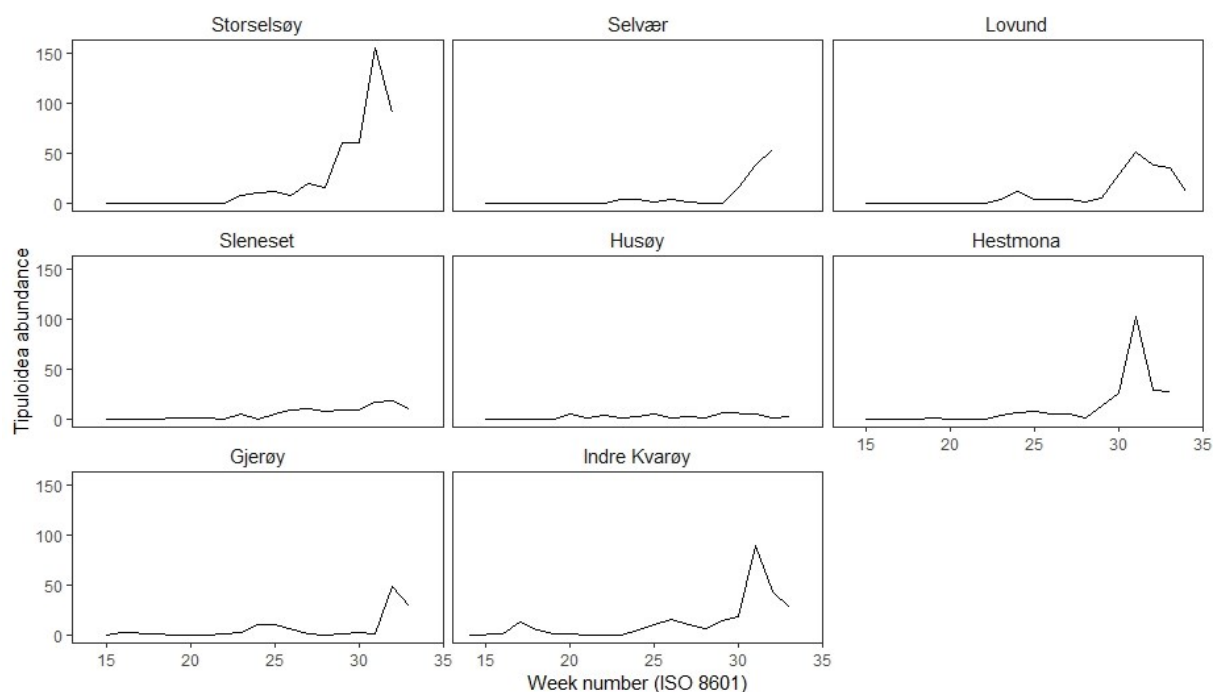

Figure A12 Variation in the abundance of the superfamily Tipuloidea (crane flies) across eight sites on seven islands in an archipelago located off the coast of northern Norway in the period from early April to mid-August 2017. The y-axis denotes the number of individuals caught. For further details, see Materials and methods above.