Spatio-temporal dynamics in breeding occurrence of passerine birds in subarctic birch forest

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BIO-3950 Master thesis in Biology, Northern Populations and Ecosystems
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Abstract

The three box-nesting passerine bird species pied flycatcher, great tit and common redstart breed at their distributional limit in Troms, Northern Norway. Access to food and favourable weather conditions is expected to be of importance for the birds´ breeding population dynamics. In the same area, geometrid moth larvae experience cyclic population outbreaks at approx. 10 year intervals, constituting a superabundant and potentially important source of food for insectivorous birds during the breeding season. To assess if the birds´ breeding population dynamics could be explained by moth larval densities and summer temperatures, we conducted yearly inspections of nest box occupancy and moth larval counts during a period of 13 years at 12 study sites, and obtained temperature measurements from nearby weather stations. Results from GLMM models with a logit link function suggested a moderate positive numerical response of the bird community to high moth larval densities. The response was species specific, with the great tit showing the most consistent response – indicating that this species is probably more dependent on moth larvae during breeding season than the other two bird species. The bird community also showed a positive numerical response the year after high summer temperatures, likely because it caused higher breeding success and subsequent higher return rates of breeding birds. It was concluded that the focal bird community was positively affected by high moth larval densities and summer temperatures, but that other factors were probably also limiting on breeding population densities due to the moderate response.

Key words: *Ficedula hypoleuca, Parus major, Phoenicurus phoenicurus*, *Operophtera brumata, Epirrita autumnata, Agriopis aurantiaria*, moth larvae, temperature, breeding population dynamics, numerical response.

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1 Introduction

The size of a population is dependent on the demographic processes of birth, death and migration (Begon et al. 2006). These processes can be affected by several factors, such as access to food and other resources, competition from other species, predation and parasitism or disease, intraspecific interactions and environmental disturbances (Newton 1998, Sinclair and Krebs 2002). Different populations and species can be structured to different degrees by these factors, and it is debated whether bottom-up or top-down control is more important. It is suggested by Sinclair and Krebs (2002) that the primary limitation to the growth rate of a population is food, possibly modified by the other factors. This is also proposed to apply for bird populations, and there is reason to believe that sufficient access to food is especially important during the breeding season. Breeding birds need food for the development of eggs, for the incubation period, to feed their nestlings, and to stay alive themselves while doing so (Lundberg and Alatalo 1992).

An important source of food for passerine birds during the breeding season is lepidoptera larvae. This has been shown by multiple studies, among others by Sanz (1998), who found in a comparative study that lepidoptera larvae was the prey type most frequently given to nestlings of pied flycatcher (*Ficedula hypoleuca*). This is confirmed in a study by Burger et al. (2012), which also revealed that nestlings of pied flycatcher receiving more larvae experienced better growth. Some species of lepidoptera larvae experience occasional mass outbreaks (Myers and Cory 2013, Tenow 1972), leading to a periodically superabundant source of food for insectivorous birds. The relationship between these outbreaks and population density of passerine birds have been investigated in several studies. The population density of some bird species have been shown to be quite strongly coupled to the population cycles of geometrid moth larvae, e.g. the relationship between *Epirrita autumnata* and brambling (*Fringilla montifringilla*) (Enemar et al. 2004, Hogstad 2000, Lindström et al. 2005), while others show a weaker relationship, or no relationship at all (Enemar et al. 2004). A numerical response can happen in two ways, either directly through immigration of birds to an area of high larval density, or with a delayed effect if the demographic processes reproductive success or survival is affected (Newton 1998).

There are many species of passerine birds living in the mountain birch forest of Northern Norway. Some of them are resident year-round, others only during breeding season. Three of the species having Northern Norway as an important breeding area, are the great tit (*Parus*

major), the pied flycatcher, and the common redstart (*Phoenicurus phoenicurus*). This area is at the northern distribution limit for all three species (Hagemeijer and Blair 1997, Hauge 1994, Lifjeld 1994). They became more common in the area during the 20th century, and at least for the great tit this is suggested to be explained by a rise in winter temperatures (Haftorn 1971). The great tit in the area is a partial and short-range migrant (Haftorn 1971), while the pied flycatcher and the redstart are long-range migrants, and spend winter in Africa north of the Sahara (Hogstad 1994, Lifjeld 1994). All three species are insectivorous during the breeding season, with various caterpillars as an important part of the nestlings´ diet (Haftorn 1971, Slagsvold 1975). They are also frequent inhabitants of nest boxes, but have some differences concerning their breeding strategy – e.g. that the great tit has clutches of almost twice the size of the other two species (Haftorn 1971, Lundberg and Alatalo 1992, Perrins 1979).

Northern Norway and Fennoscandia also represent the northern distributional limit of three species of geometrid moth: *E. autumnata, Operophtera brumata* and *Agriopis aurantiaria.* These species experience population outbreaks at intervals of approximately 10 years, and their larvae emerge and forage on birch leaves for 4-8 weeks in spring (Jepsen et al. 2011). *E. autumnata* is a native species, while *O. brumata* has expanded its distribution northwards into the area in the end of the 19th century (Tenow 1972). In recent decades, both species have expanded their outbreak range, meaning the geographical area where they experience population outbreaks (Jepsen et al. 2008). *A. aurantiaria* invaded this region quite recently, the first outbreak being recorded in 2004-2006. These expansions are probably happening as a response to warmer springs allowing earlier hatching of eggs and consequently better match with budburst (Jepsen et al. 2011), and/or milder winters that allow better survival of eggs (Ammunét et al. 2012, Jepsen et al. 2008). The large outbreaks of geometrid moths in the birch forests of Northern Norway constitute a large source of food for the insectivorous birds breeding in the area.

Spring temperature normally has an influence on both moth and bird phenology. Hatching and development of moth larvae happen earlier and faster with higher temperatures (Ayres and MacLean Jr 1987, Embree 1970, Jepsen et al. 2011). Warmer springs can lead to earlier onset of breeding for the birds (Visser et al. 2009), and warm summers have been found to increase breeding success (Thingstad et al. 2006). Cold weather and precipitation during the nestling phase can be negative for the birds´ breeding success, e.g. if the female needs to spend more time on the nest and less time feeding the nestlings (Perrins 1979). Poor breeding success has

been shown for both the great tit and the pied flycatcher in northern latitudes in a cold and rainy summer, even though the redstart managed well (Hildèn et al. 1982).

Based on 13 years of observations of artificial nest boxes at 12 study sites in Northern Norway, I will examine to what extent the breeding population dynamics of the three passerine bird species at their northern distribution margin can be explained by the cyclic population dynamics of geometrid moth larvae, and inter-annual variation in spring temperature. The questions that will be addressed in this study, for each bird species separately and for the three species combined (i.e. considered as a community), are: 1) Are the birds´ breeding populations responding numerically to moth population dynamics? 2) Are the birds´ responses species specific? 3) Does temperature influence breeding density?

I expect that the birds´ breeding populations will experience a positive response to high densities of moth larvae. Due to differences between the three bird species, I predict that their responses will differ, and that the great tit will have the strongest response to more abundant food. This assumption is based on the larger clutch size of the great tit, and that earlier studies have found that it seems more dependent on caterpillars in the diet than the other two species (Cholewa and Wesolowski 2011, Haftorn 1971, Slagsvold 1975). Temperature is expected to have a positive effect on breeding density, based on other studies finding low temperatures and bad weather to be negative, and warm summers to increase breeding success (Hildèn et al. 1982, Perrins 1979, Thingstad et al. 2006). A response could be either direct, to larval densities or temperatures the same year, or delayed, to larval densities or temperatures the previous year. A direct response is expected if more birds settle to breed in an area of high moth larval densities or good weather conditions, while a delayed response is expected if such conditions increases breeding success and the subsequent return rate (i.e. a demographical response).

2 Methods

2.1 Study area and design

The study is part of an ongoing project for long-term monitoring of geometrid moth population dynamics, and is therefore based on an already established study design. The monitoring project has been carried out since 1999 by the Birchmoth research group at UiT – the Arctic University of Norway, and the Norwegian Institute for Nature Research.

The study is conducted in sub-arctic mountain birch (*Betula pubescens*, spp. *czerepanovii*) forest in northern Norway, Troms county (69°30´ to 70°03´N; 18° to 20°E). Because of the proximity to the coast, the climate is oceanic, with small differences between summer and winter temperature (Ims et al. 2004, Moen 1998). The normal mean temperature between 1961 and 1990 was -4.4 ℃ and 11.8 ℃ in January and July, respectively (MET Norway, 2017).
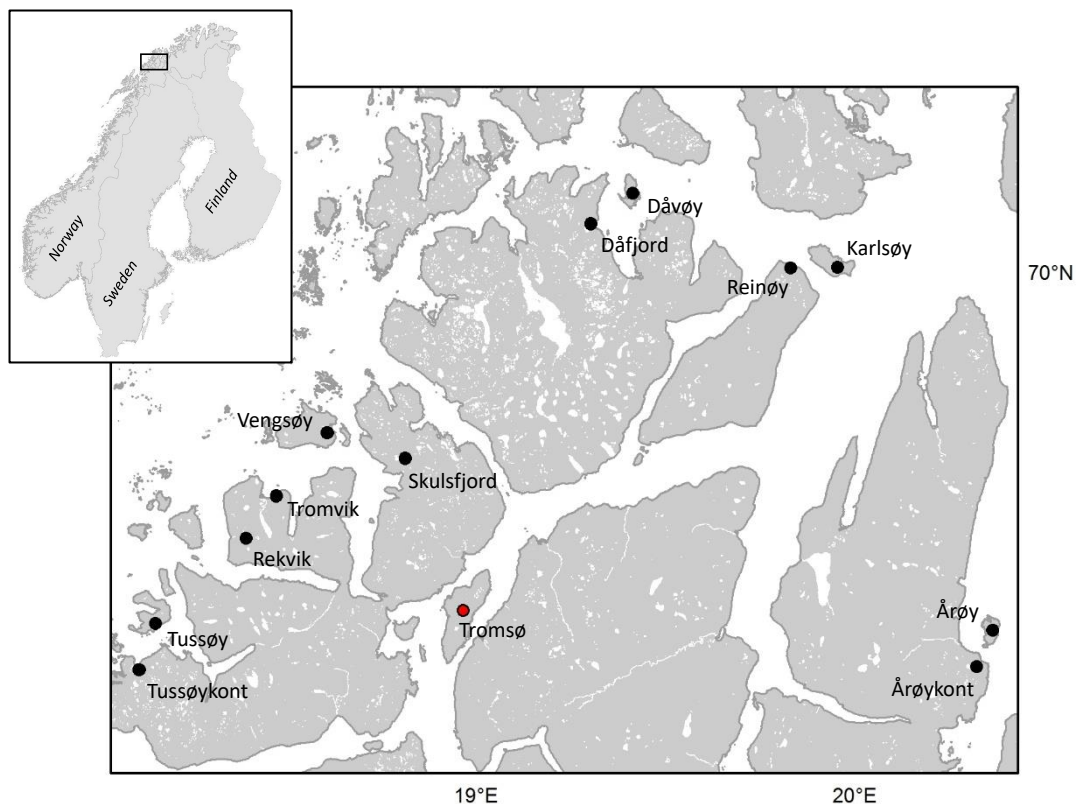
Figure 1: Map of the study area, showing the location of the 12 study sites (black dots) in the coastal district of Troms county. The design was already established for monitoring of moth density, and the 6 island-mainland transect pairs will in this study be treated as 12 separate replicates.

The study design was made up of 12 study sites, organized spatially in 6 pairs (Figure 1), with one site on the mainland or a large island, and one site on a smaller island. This was a part of

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the already established study design, and the 6 pairs were in this study instead treated as 12 separate replicates. The two sites in each pair were separated by a distance of 4 to 9 km, and at least 1.5 km of open sea or treeless mountain habitat, and different pairs were separated by a minimum of 13 km (Ims et al. 2004).

In 1999, a 1.8 km long transect containing 10 permanent sampling stations was established at all 12 study sites. The sampling stations provided specific locations for monitoring of moth density, placed every 200 m along the transect line. Nest boxes were installed at all stations in April 2004. Each station had two nest boxes placed approximately 2 m above ground, in parallel with the transect approximately 20-30 m from the midpoint of the station, depending on the availability of trees of sufficient size to mount the boxes on. The boxes had a dimension of 25 (h) * 14 (w) * 14 (d) cm, and were painted in a grey colour that did not stand out between the trunks of the birch trees. The three focal bird species have differing preferences regarding hole size of the nest boxes. The pied flycatcher usually prefers a smaller hole of approximately 30 mm, probably to avoid predation (Lundberg and Alatalo 1992). The great tit normally uses the same type of box, while the redstart is more likely to nest in a box with a wider hole: 40 mm or larger (Vedum 1996). To facilitate nesting attempts from all three species, the two boxes in one sampling station had holes of different sizes – one of 32 mm and one of 50 mm in diameter. Broken boxes with large holes were in some cases replaced by a box with a small sized hole, this resulted in a change in hole size for 7 boxes. In the transect located on Reinøy, all boxes had small holes from 2009 because they also took part in another study design (10 boxes changed size).

2.2 Study species

The pied flycatcher is a small passerine bird, with a length of approximately 13 cm (Haftorn 1971). It is a long distance migratory species, with the breeding population distributed across Europe in summer, while overwintering in Africa north of the equator. It occurs in forests across most parts of Norway (Haftorn 1971). It breeds in natural holes in trees, and can nest in all types of forest as long as there are suitable holes (Lifjeld 1994). It is easily studied during breeding season, because it often prefers artificial nest boxes over natural holes (Lundberg and Alatalo 1992). The pied flycatcher is mainly insectivorous. Among the food most commonly fed to nestlings are lepidoptera larvae (Lundberg and Alatalo 1992), but it seems to adapt its diet to the type of habitat and the conditions where it lives (Bösenberg 1964, read in Slagsvold 1975). It raises only one brood per season, which is normally fed by both

parents. The female lays one egg per day, in the study area normally in the first half of June, until the final clutch size of approximately 5-7 eggs is reached. The eggs are incubated for 13-15 days, and the nestlings remain in the nest for approximately 16 days before fledging (Haftorn 1971).

The great tit is also a small passerine bird, of approx. 15 cm (Haftorn 1971). It is predominantly resident or short distance migratory, and is often attracted to areas near people in winter, where there is better access to food (Hauge 1994). It is distributed across Europe, Asia and Northwest Africa, and occurs in most parts of Norway (Haftorn 1971). It is mainly insectivorous in summer, while depending more on seeds and fruits in winter (Haftorn 1971). It mainly feeds its nestlings with different caterpillars, more independently of habitat type than the pied flycatcher (Royama 1970, Slagsvold 1975, van Balen 1973). The great tit normally nests in natural holes, but in resemblance with the pied flycatcher, this species also frequently uses artificial nest boxes when they are available. Sometimes the whole breeding population in an area breeds in nest boxes (Perrins 1979). The female lays 8-13 eggs, one per day, in this study area up to two weeks earlier than the other two bird species in the study (Schott 2013). The eggs are incubated for 14-15 days after the last egg is laid, and the nestlings remain in the nest for 18-22 days after hatching, fed by both parents. The fledged young are fed and watched by their parents for 2-4 weeks (Haftorn 1971).

The common redstart is a passerine bird about 14.5 cm long. It is widespread across most parts of Norway during summer, density being a little lower on the west coast. Similar to the pied flycatcher it is a long distance migratory species, travelling long distances between their breeding grounds in Northwest Africa, West Asia and most parts of Europe, and wintering areas in North Africa (Haftorn 1971, Hogstad 1994). The diet consists mainly of insects, and lepidoptera larvae makes up a part of nestling diet, but the importance of it varies between studies (Haftorn 1971, Sedlacek et al. 2007). The clutch of 6-7 eggs are normally laid, one each day, during the first three weeks of June in the study area. The eggs are incubated for approximately 11-13 days before hatching, and the nestlings remain in the nest for 14-17 days before fledging. The young are fed by both parents in the nest, and for 2-3 weeks after fledging (Haftorn 1971, Hogstad 1994).

The most abundant species of geometrid moths in the study area are the autumnal moth (*E. autumnata*), the winter moth (*O. brumata*), and the scarce umber moth (*A. aurantiaria*). The larvae of these species hatch approximately at the same time as bud burst of the mountain

birch, which is their main host tree, in spring. The larvae then forage on the foliage of the trees for 4-6 weeks, before falling to the ground and pupating. Their population dynamics are characterized by cyclic outbreaks with approximately 10 year intervals, and in periods of outbreak densities, they can cause severe defoliation and forest damage (Tenow 1972).

2.3 Data collection

The transects were visited once per summer, normally in late June or early July. The timing of the visit depended on the phenology of the larvae, because it is important that the majority of the larvae are in their 3rd-4th instar when they are counted (Ims et al. 2004). It is also important to visit stations at approximately the same stage of development each year, to make results comparable between years regarding both moth and bird numbers.

To estimate moth density, we randomly cut off and collected 10 live branches of mountain birch of about arm length ($\approx$ 80 cm), from trees within approx. 30 m from the station. The branches were shaken in a large plastic box until all larvae had fallen off. The larvae were sorted by species, and counted. The total count for all 10 branches was used as a measure of moth density specific for each station.

Nest boxes were inspected at the same time as larval density was measured. It was registered whether or not the box was occupied. If occupied, we determined the species present, and counted the number of eggs and chicks. Identification of species can be done from the appearance of the nest (Figure 2). The great tit builds their nest on a base of moss, using wool and hair as insulation (Perrins 1979). The common redstart usually builds their nests of grass and roots, insulating it with large feathers (Haftorn 1971). The nest of the pied flycatcher often has a base of bark of birch or pine, or dead leaves. The insulation commonly consists of dry grass. The nests of the pied flycatcher and the common redstart can be relatively similar, other than the feathers used for insulation in the redstart nest (Lundberg and Alatalo 1992). Signs of predation were recorded, along with other factors which could render boxes unavailable for breeding (e.g. damage to the box or occupation by bumblebees).

Figure 2: The appearance of the birds´ nests can be used for identification of the individual species. From left to right: Pied flycatcher, great tit, and common redstart.

Temperature data from three weather stations in Tromsø, with altitudes ranging from 8 to 100 m.a.s.l., were collected from the MET Norway.

2.4 Statistical analyses

Because of the binary response variable (nest box occupied or not), and the need to include both fixed and random effects, I chose to use generalized linear mixed models (GLMMs) with a binomial distribution and a logit link function (Bolker et al. 2009).

The response variable to be included in the analysis was occupancy of nest boxes. This is a binary variable, with the possible outcomes on box level being occupied or unoccupied. The box was categorized as occupied if it contained either eggs or chicks. Data were aggregated by location and year so the response variable became the proportion of occupied boxes of the total number of available boxes per transect. The data were also separated according to hole size of the nest boxes, since the birds did not utilize the boxes with different hole sizes similarly. A box was defined as available if it was possible for a bird to use it for nest building (93% of the boxes across all years and localities), meaning that it should be in one piece and attached to the tree, and unoccupied by other species (e.g. bumblebees). The proportion of occupied nest boxes is expected to be a good index of the birds´ breeding population density.

The two main predictor variables of interest were moth larval density and spring temperature. Since moth density could influence current-year breeding density both via direct and delayed responses from the birds, two larvae variables were included: one for moth density in year t (the same year as the rest of the data), and one for density in year t-1. The two time-lagged

moth density predictors were not included simultaneously in the same models because they were strongly correlated (VIF $\approx$ 4, Pearson r = 0.86), since it should be avoided to have two highly collinear variables in the same model (Zuur et al. 2010). The two most common moth species (*O. brumata* and *E. autumnata*) were also strongly correlated, and were therefore lumped into one common density predictor along with the less common *A. aurantiaria.* This is also biologically justified, because the breeding dynamics of the birds are expected to be influenced by the total availability of moth larvae. The moth variables were transformed to natural logarithms for easier visualisation, because the data extended across several orders of magnitude (Withlock and Schluter 2015). Two temperature variables (temperature in year t and t-1) were also included, to account for the possibility that also temperature could have both direct and delayed effects on the density of the birds´ breeding population. These two variables were not substantially correlated (VIF $\approx$ 1, Pearson r = -0.32), and were therefore included simultaneously in the models. Temperatures were calculated as means of temperature measurements from the three weather stations in Tromsø, operated by MET Norway, for the periods of 15/05 - 15/06, and 15/06 – 15/07. The first period was used to examine the direct effect of temperature in year t, because the birds most commonly start breeding in this period, while the second interval was used to explore the effect of temperature in year t-1, because it was expected to have a larger impact on the chicks´ survival and potentially the next year´s return rate (i.e. the delayed response).

In addition to the main predictor variables, some other factors were included as covariates in the models to control for their possible biasing influence on the response variable. The effects of these variables were not themselves of interest in this study. The proportion of boxes occupied by the same species the preceding year was included as a predictor variable (i.e. covariate), because the size of the breeding population in one year is likely to partly depend on the size of the breeding population the year before. Interspecific competition was also included, by adding the proportion of boxes occupied by the other two species possibly competing for nest sites and food. For boxes with small holes, the redstart was left out as a competing species, as it very rarely used these boxes. In addition to the predictor variables already listed, it was necessary to account for possible unknown differences between the 12 study sites. This was accomplished by including site as a random intercept, thus meaning that the analyses of the fixed predictors (i.e. moth larval density and temperature) focus on the effects of the temporal variation in these predictors, corrected for time-invariant site differences.

The GLMMs were fitted using the *glmer* function in the *lme4* library in R (Bates et al. 2015). Two full models were made for each combination of bird species and nest box type (Table 1). The moth variables were kept in separate models, while all models contained both temperature variables, and the covariates interspecific competition and density of the species of interest in the year before, in addition to site as a random intercept. Predictions were made from the GLMM-models, where the effects of the different larvae- and temperature variables on proportions of occupied nest boxes were estimated. This was done by keeping the other variables constant at their mean values.

The amount of the total variation that could be attributed to between-year and between-site effects was estimated by carrying out an analysis of deviance of a binomial-logistic model for each of the bird models, with year and site as categorical predictor variables. For the log transformed moth larvae densities, site and year effects are calculated as mean squares from a linear model.

Table 1: The combination of variables in the different models. Log(moths) t = log (moth larval density year t). Log(moths) t-1 = log (moth larval density year t-1) Bird.sp. t-1 = occupancy by the focal bird species year t-1. PF = pied flycatcher. GT = great tit. CR = common redstart. Temp t= temperature year t. Temp t-1 = temperature year t-1. Site = site as random effect.

Species	Box type	Log(moths) t	Log(moths) t-1	Bird.sp. t-1	PF	GT	CR	Temp t	Temp t-1	Site
PF	Small	x		x		x		x	x	x
PF	Small		x	x		x		x	x	x
PF	Large	x		x		x	x	x	x	x
PF	Large		x	x		x	x	x	x	x
PF	All	x		x		x	x	x	x	x
PF	All		x	x		x	x	x	x	x
GT	Small	x		x	x			x	x	x
GT	Small		x	x	x			x	x	x
GT	Large	x		x	x		x	x	x	x
GT	Large		x	x	x		x	x	x	x
GT	All	x		x	x		x	x	x	x
GT	All		x	x	x		x	x	x	x
CR	Large	x		x	x	x		x	x	x
CR	Large		x	x	x	x		x	x	x
CR	All	x		x	x	x		x	x	x
CR	All		x	x	x	x		x	x	x
ALL	Small	x		x				x	x	x
ALL	Small		x	x				x	x	x
ALL	Large	x		x				x	x	x
ALL	Large		x	x				x	x	x
ALL	All	x		x				x	x	x
ALL	All		x	x				x	x	x

I also wanted to further examine the distribution of birds between the two different box types, and to check if there was a "spillover"-effect between the boxes, i.e. whether birds started to use the suboptimal boxes with large holes more often when the preferred box type with small holes was saturated. This was done by specifying a GLM-model with a binomial distribution and a logit link function, with the proportion of occupied boxes with large holes for each of the bird species as a response variable, and the empirical logit of the proportion of occupied boxes with small holes by the whole bird community as a predictor variable. The box type with small holes was used as the predictor because it was the preferred box type for the two most common birds: the pied flycatcher and the great tit. Similar models, but with occupancy by each individual species as predictor variables, were also made to examine the different bird

species´ use of the two box types, and if there were a "spillover"-effect also based the occupancy of their own species. The empirical logits were estimated by the *empLogit* function in the *binomTools* package (Christensen and Hansen 2011).

The data were checked for influential single observations using the *influence* and *sigtest* functions in the *influence.ME* package (Nieuwenhuis et al. 2012). None of the single observations seemed largely influential. The GLMM-models were checked for overdispersion, which was roughly estimated by determining the sum of squared Pearson residuals, subsequently comparing it to the residual degrees of freedom, as suggested by Bolker (2015). The models for pied flycatcher in small boxes, for common redstart in both box types, and the models for the whole bird community were a little overdispersed, and this was taken into account when interpreting the results. Multicollinearity between the variables in the models was inspected by the *corvif* function (Zuur et al. 2009), to calculate variance inflation factors (VIFs). Variables with a VIF-value above 3 were considered problematic (Zuur et al. 2010). This was generally no problem for the models, except for the larvae variables for time t and t-1 (see above). Confidence intervals for parameter estimates and predictions were calculated as $\pm1.95\times$SE of the value of the estimated value on the scale of the link function, and backtransformed to response scale when necessary. The variance of the random effects was not included in the confidence intervals on predictions from the GLMMs as suggested by Bolker (2015). All plots were made using the *ggplot2* package (Wickham 2009), and data analyses were carried out using R version 3.2.2 (R Core Team 2015).

3 Results

3.1 Variation in the predictor variables

Two peaks in moth larval density were apparent across the sites during the course of the study – one around 2004, and one larger in the years around 2014 (Figure 3). Although there was some variation in larval density between the sites (especially in the size and timing of the first peak; Figure 3), the amount of variation between years was approx. 7 times higher (Table 2).
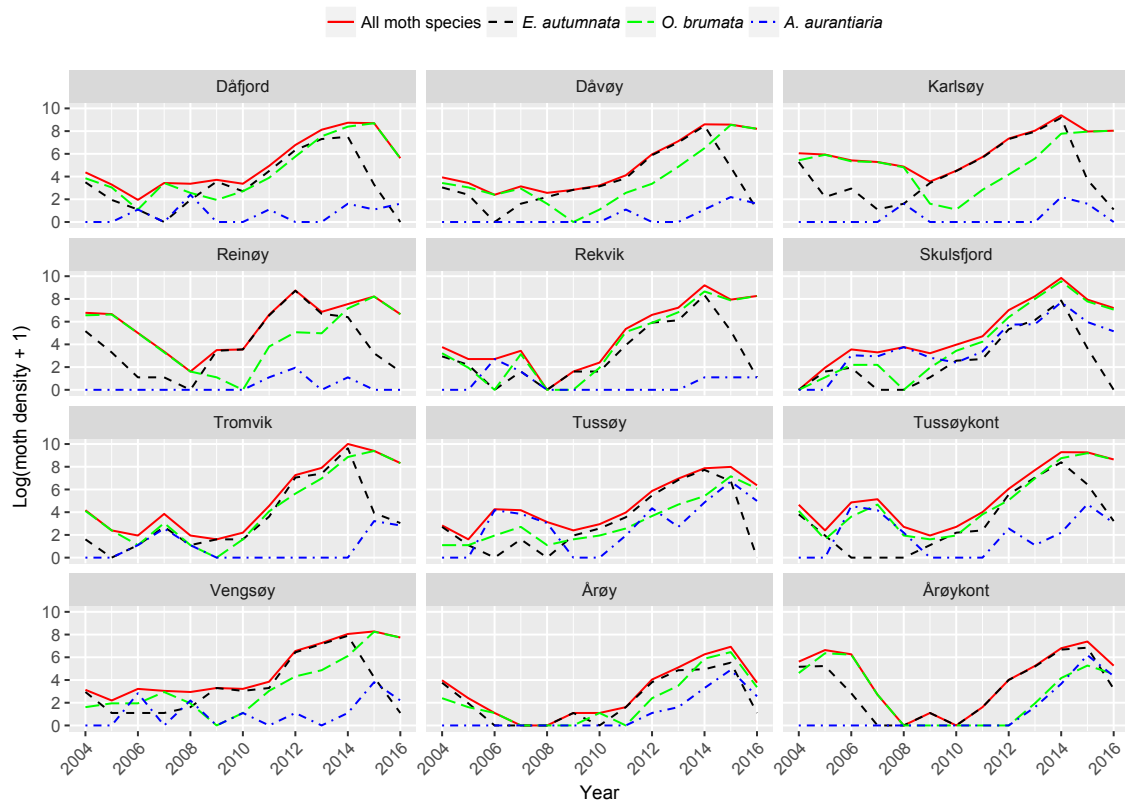
Figure 3: Moth density for each study site (log scale). The density is measured as the sum of larvae for all stations in a transect.

The mean spring temperature (in the period 15/05-15/06) in the study area (Figure 4) fluctuated between 6°C and 11.5°C over the 13-year study period, with the spring in 2013 standing out as markedly warmer than in the other years. The mean summer temperature (15/06-15/07) fluctuated between 9.4°C and 13.2°C.
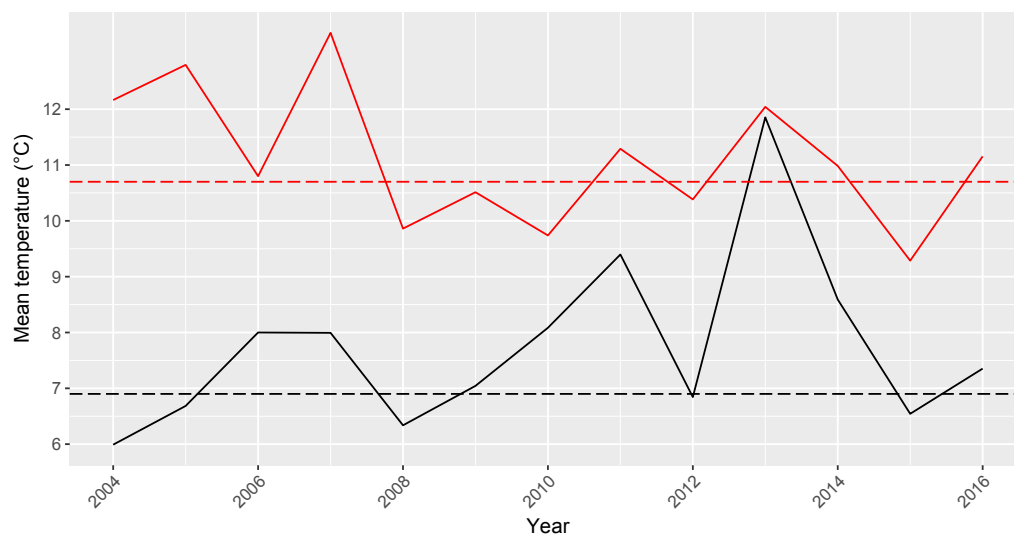
Figure 4: Mean temperatures in the study area in the periods 15/05 - 15/06 (black, solid line) and 15/06 - 15/07 (red, solid line), and normal temperature for the two periods (dotted lines). Because normal temperatures were available for only one of the three weather stations used in the study, the plot is restricted to display mean temperatures from this station, but the temperatures were highly similar in all three stations.

3.2 Variation in nest box occupancy

Table 2: The number and proportion of nest boxes occupied by the different bird species across all years (n=13) and study sites (n=12), as well as the amount of the total variation in nest box occupancy and moth larval density could be attributed to additive effects of year and site. The year and site effects on the nest box occupancies are given as deviances obtained from binomial-logistic models, whereas the year and site effects on log-transformed larval density are given as mean squares obtained from a linear model.

Species	Nest box	Number	Proportion	Dev. year	Dev. site	Dev. residual
Pied flycatcher	Small	700	0.45	54.80	225.93	223.86
Pied flycatcher	Large	114	0.08	50.30	68.83	126.91
Pied flycatcher	All	814	0.28	51.21	215.56	165.92
Great tit	Small	193	0.12	19.23	72.42	182.86
Great tit	Large	108	0.08	36.39	51.94	133.55
Great tit	All	301	0.10	29.45	105.70	186.13
Common redstart	Small	40	0.03	28.51	39.87	67.91
Common redstart	Large	111	0.08	25.88	31.92	173.07
Common redstart	All	151	0.05	40.98	48.77	190.33
All	Small	933	0.60	60.78	251.86	239.51
All	Large	333	0.24	45.93	84.07	206.35
All	All	1266	0.43	58.97	244.34	224.00
Moth larvae (log)				718.19	103.66	171.94

Overall nest box occupancy varied between species (Table 2), and between the boxes with small and large holes. The pied flycatcher was overall the most common bird in the nest boxes, occupying close to one third of the boxes across all years and sites. It was primarily found in the box type with small holes, while there was a significant tendency for its

occupancy of large-hole boxes to increase with total (i.e. all bird species, slope: 0.19 [95% CI: 0.01-0.26], p < 0.001) and its own occupancy of boxes with small holes (slope 0.18 [95% CI: 0.09-0.28], p < 0.001; Figure 5). The great tit was overall found in 10 % of the boxes. This species was quite evenly distributed between the two box types (Table 2). Its occupancy of large-hole boxes increased significantly with the total (slope: 0.22 [95% CI: 0.15-0.30], p < 0.001) and its own occupancy of small-hole boxes (slope: 0.13 [95% CI: 0.05-0.21], p = 0.002; Figure 5). The common redstart was the least common occupant of the nest boxes – overall found in 5 % of all nest boxes. Occupancy by redstart of small-hole boxes was omitted from further analyses due to small sample size (Table 2). Its occupancy of large-hole boxes was not related to the total occupancy of small-hole boxes (slope: -0.01 [95% CI: -0.09 – 0.07], p = 0.841), while there was a significant relationship between its own occupancy of the two box types (slope: 0.20 [95% CI: 0.12-0.29], p < 0.001; Figure 5).
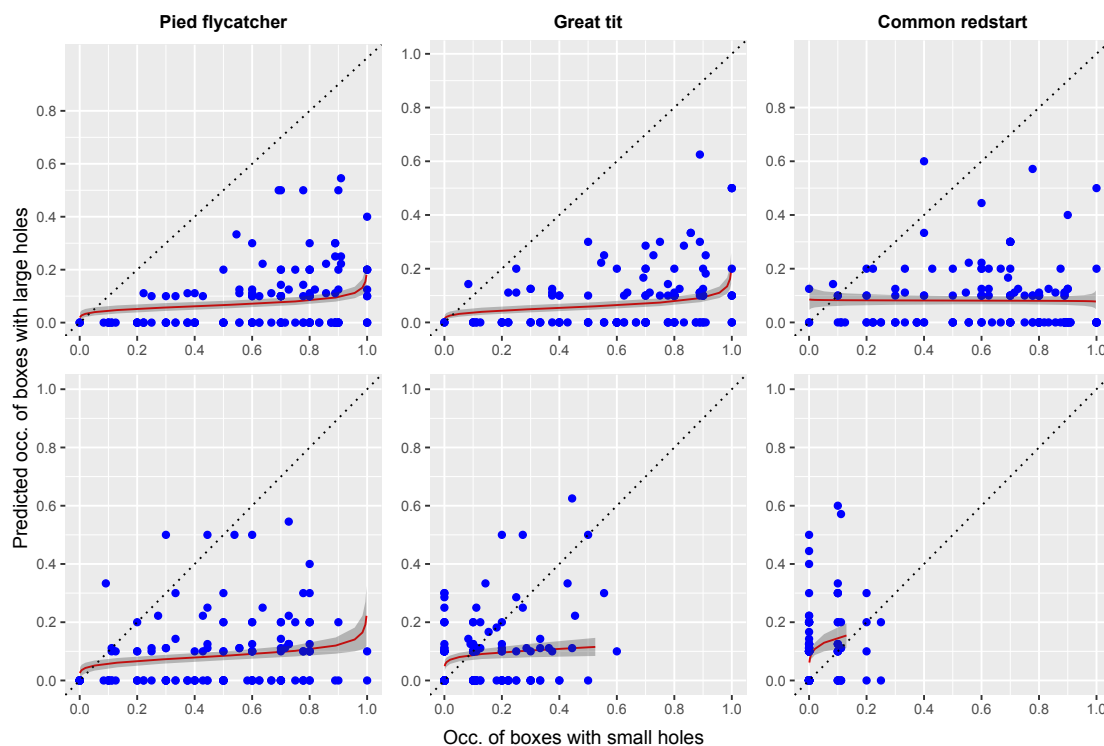
Figure 5: Observed (dots) and predicted (red lines) relations between occupancy of nest boxes with large (response) and small (predictor) entrance holes. Upper panels: the predictor is total occupancy of all birds in small-hole nest boxes. Lower panels: the predictor is the species´ own occupancy of small-hole nest boxes. The predictions are from logistic models with 95 % confidence intervals (shaded areas). 1:1 stippled lines are included to show difference from equal use of the two box types.

The proportion of occupied boxes varied both spatially and temporally in the study period (Table 2). For boxes with small holes, differences between sites explained approximately 4

times more of the total variance than differences between years, in all cases except for the common redstart. For boxes with large holes, the difference in the amount of variance attributed to site and year was less distinct. The amount of total variance explained by site and year was of approximately equal size for boxes with small and large holes, indicating that the contribution of temporal effects was higher for large-hole than for small-hole boxes.

Figure 6 and 7 shows the variation in nest box occupancy for boxes with small and large holes, respectively. Overall occupancy of boxes with large holes had a peak around 2014 in several localities, which seemed to correspond approximately with the largest peak in larval density. This peak was less clear for boxes with small holes. Occupancy of small-hole boxes by pied flycatchers in Reinøya was high in the beginning of the study period, but decreased distinctly from 2009. This is probably an artefact of the number of boxes with small holes at the transect being doubled this year, in addition to 60 boxes of the same type becoming available at different altitudes in the area, due to establishment of another study.
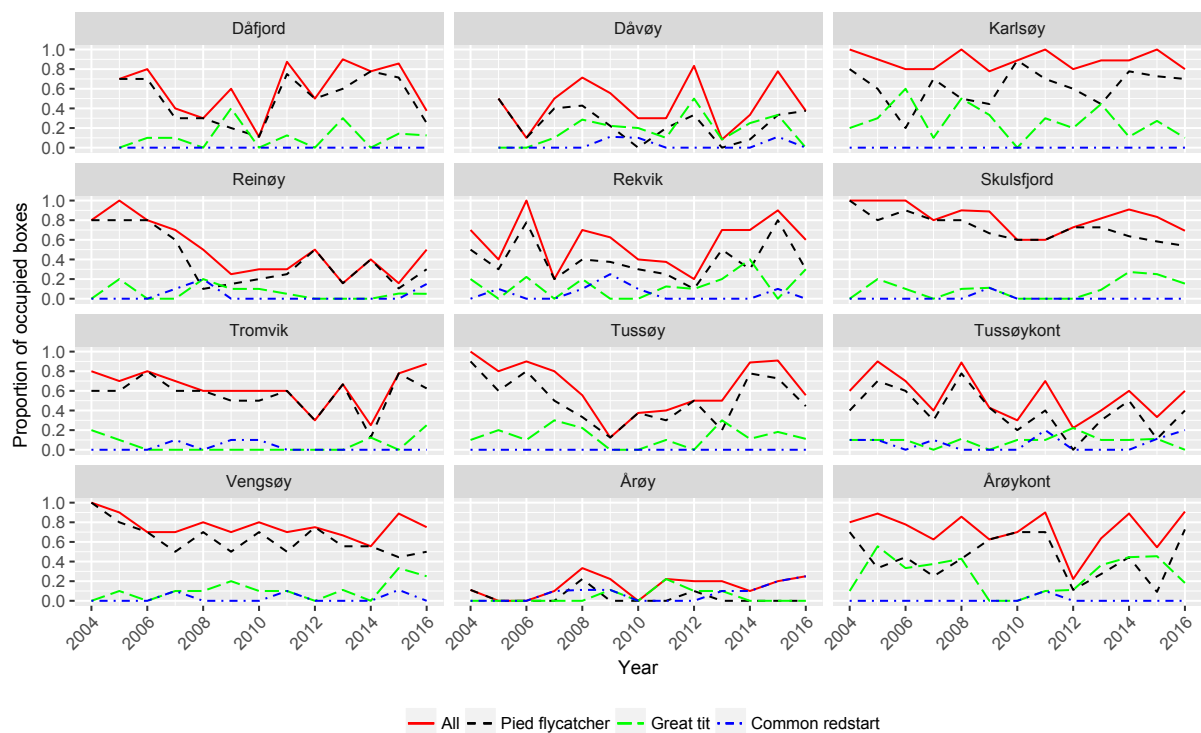
Figure 6: Proportion of occupied small-hole nest boxes for each study site.
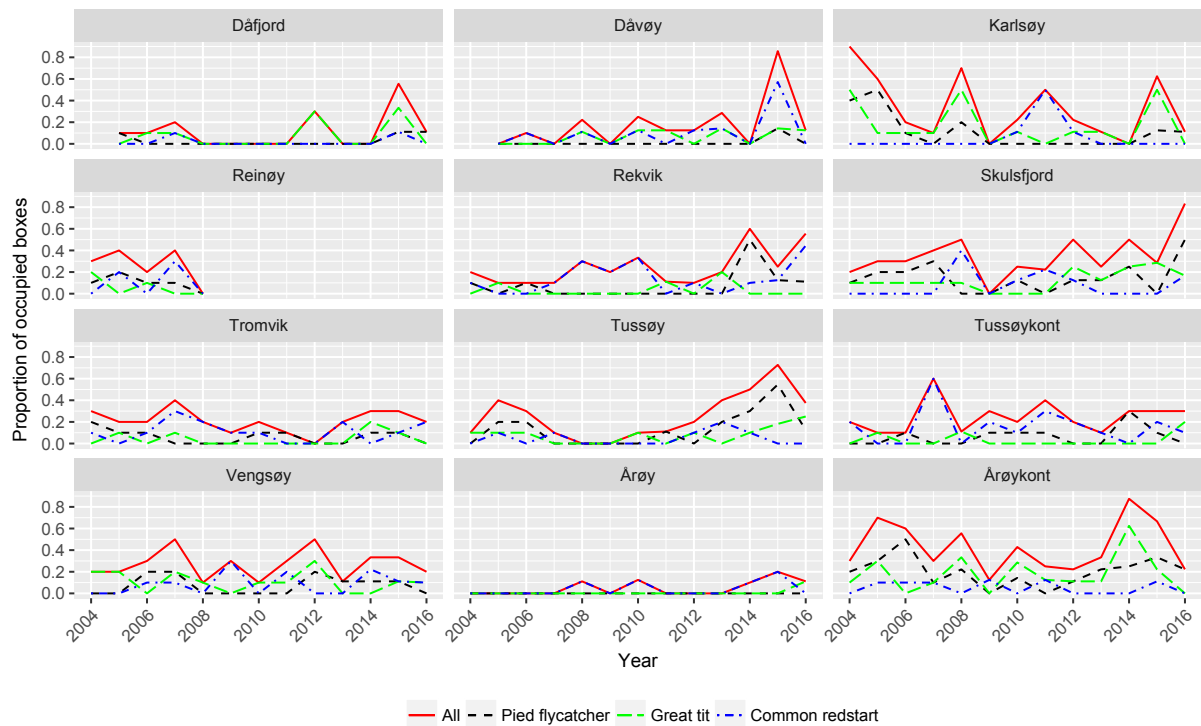
Figure 7: Proportion of occupied large-hole nest boxes, for each study site. Because all boxes had small holes in Reinøy from 2009, no occupancy of large-hole boxes was recorded after that.

3.3 Predictors of nest box occupancy

Table 3: The effects of the four predictor variables larval density in year t and t-1, and temperature in year t and t-1, on nest box occupancy. Effect sizes are shown as odds ratios with 95 % confidence intervals in brackets. Significant results are highlighted in bold. Temperature effects are obtained from the models with larval density in year t.

Species	Hole size	Larvae density year t	Larvae density year t-1	Temp. year t	Temp. year t-1
All	Small	1.028 [0.979 - 1.079]	**1.056 [1.006 - 1.109]**	0.941 [0.862 - 1.027]	**1.204 [1.086 - 1.336]**
All	Large	**1.189 [1.122 - 1.261]**	**1.173 [1.103 - 1.248]**	**0.851 [0.759 - 0.951]**	1.081 [0.957 - 1.220]
All	All	**1.082 [1.046 - 1.119]**	**1.083 [1.047 - 1.121]**	**0.931 [0.872 - 0.992]**	**1.111 [1.035 - 1.193]**
PF	Small	1.023 [0.973 - 1.076]	1.041 [0.990 - 1.094]	0.989 [0.905 - 1.080]	**1.209 [1.090 - 1.342]**
PF	Large	**1.234 [1.119 - 1.363]**	**1.192 [1.072 - 1.328]**	0.983 [0.817 - 1.172]	**1.338 [1.097 - 1.639]**
PF	All	**1.056 [1.015 - 1.099]**	**1.054 [1.013 - 1.097]**	0.978 [0.909 - 1.050]	**1.139 [1.048 - 1.239]**
GT	Small	**1.198 [1.033 - 1.190]**	**1.123 [1.043 - 1.207]**	0.965 [0.853 - 1.089]	**1.162 [1.003 - 1.304]**
GT	Large	**1.174 [1.062 - 1.298]**	**1.167 [1.055 - 1.292]**	**0.767 [0.621 - 0.929]**	1.044 [0.849 - 1.287]
GT	All	**1.141 [1.079 - 1.208]**	**1.151 [1.086 - 1.221]**	**0.902 [0.812 - 0.999]**	1.126 [0.998 - 1.270]
CR	Large	1.078 [0.984 - 1.179]	1.056 [0.966 - 1.154]	0.852 [0.714 - 1.005]	**0.828 [0.686 - 0.996]**
CR	All	1.003 [0.931 - 1.078]	1.020 [0.950 - 1.094]	**0.834 [0.714 - 0.964]**	**0.792 [0.674 - 0.929]**

Larval density in year t was found to have positive effects on the pied flycatcher, the great tit, and occupancy on the community level (i.e. the three species combined, Table 3). The great tit showed the most consistent response across both box types. On community level and for the pied flycatcher, this response was only significant for boxes with large holes and the two

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box types combined. The delayed effects of larval density in year t-1 were similar to the direct effects, except that the effect on occupancy of small-hole boxes on community level was marginally significant.

At community level, the predicted proportion of occupied boxes (Figure 8) of both types increased from minimum 0.32 (95% CI: 0.25-0.41) at the lowest moth larval density, to 0.51 (95% CI: 0.42-0.60) at the highest moth larval density in the time series. Equivalent minimum and maximum predictions for the great tit was 0.05 (95% CI: 0.03-0.08) and 0.16 (95% CI: 0.11-0.23), while they were 0.19 (95% CI: 0.13-0.27) and 0.29 (95% CI: 0.20-0.40) for the pied flycatcher.
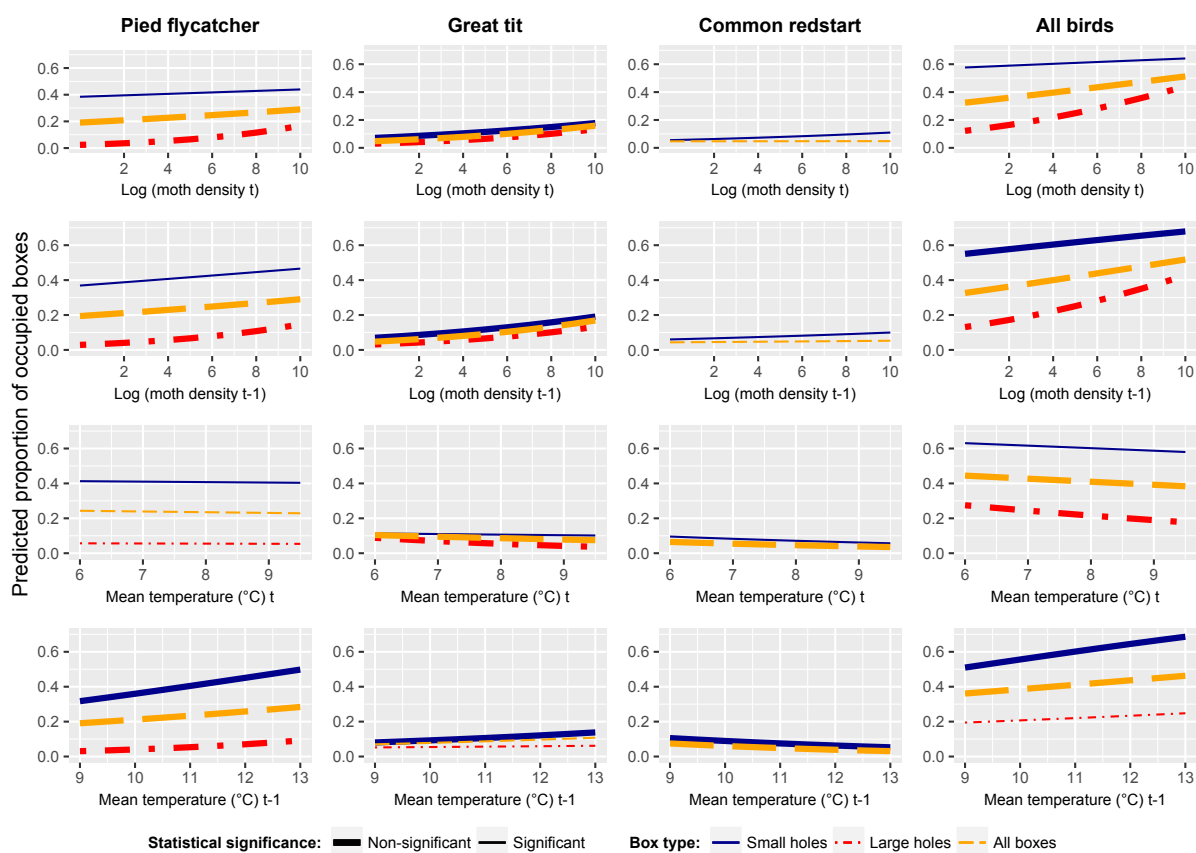
Figure 8: The predicted effects of the four variables moth density in year t and t-1, and temperature in year t and t-1, on the proportion of occupied nest boxes. The effects of the other predictor variables are kept constant at their mean values. Significant effects are shown with bold lines. Confidence intervals were left out to improve the readability of the plots, but confidence intervals for predictions at minimum and maximum values of statistically significant predictors can be found in section 3.

Spring temperatures in year t had a slight negative influence on nest box occupancy for all three bird species (Table 3). The effect was significant for great tits in large-hole boxes, and for the combination of both box types. The effect was also significant on community level and for common redstart in both box types, but these effects seemed dependent on the high

temperatures in 2013, and were not significant when this year was removed. The proportion of both box types combined occupied by great tit was predicted (Figure 8) to decrease from max. 0.14 (95% CI: 0.08-0.23) at the lowest mean temperature, to min. 0.06 (95% CI: 0.03-0.11) at the highest mean temperature measured in the time series. The equivalent predictions for great tit in large-hole boxes were max. 0.09 (95% CI: 0.05-0.14) and min. 0.04 (95% CI: 0.02-0.06).

Summer temperatures in year t-1 was found to have significant positive effects on community level for both box types combined, and boxes with small holes (Table 3). The pied flycatcher showed a significant response across both box types, while the great tit responded only marginally significantly in small-hole boxes. The common redstart showed a significant but weak negative response to increased summer temperatures for both box types, and in boxes with large holes. At community level, the proportion of occupied boxes was predicted (Figure 8) to increase from minimum 0.36 (95% CI: 0.29-0.44) at the lowest mean temperature, to maximum 0.46 (95% CI: 0.38-0.55) at the highest mean temperature measured in the study period for both box types combined. The equivalent predictions for the pied flycatcher in both box types were min. 0.19 (95% CI: 0.13-0.28) and max. 0.28 (95% CI: 0.20-0.38), while they were 0.08 (95% CI: 0.05-0.13) and 0.14 (95% CI: 0.09-0.21) for the great tit in small-hole boxes. For the common redstart, the predicted proportion of occupied boxes of both types combined decreased from 0.07 (95% CI: 0.05-0.11) to 0.03 (95% CI: 0.02-0.05).

The covariates competition and last year´s occupancy had variable effects among bird species and box types, suggesting no consistent effects of competitors and last year´s breeding density on the breeding population in the current year (Appendix A).

4 Discussion

The main purpose of the study was to see whether the breeding population density of passerine birds at the northern limit of their distribution range was affected by the cyclic outbreaks of moth larvae occurring regularly in the area, and by the temperature variation between years. The whole box nesting bird community was found to show a moderate numerical response to high moth densities. It was not possible to establish whether the numerical response was direct or delayed, as effect sizes were approximately equal, and the larval variables were highly correlated. The responses were species specific, with the great tit responding positively in both box types, the pied flycatcher only in boxes with large holes, and the redstart not at all. The density of the whole breeding population responded negatively to increased spring temperatures in the year of the study, while the effect of summer temperatures in year t-1 had a positive influence on the breeding density of the bird community in both box types combined. The pied flycatcher showed the most consistent positive response across both box types, while the redstart responded slightly negatively.

4.1 Effects of moth larval density

The breeding population of the whole bird community showed a positive numerical response to moth larvae outbreaks. For the whole community in both box types combined, the nest box occupancy at peak larval density was predicted to be 17 % higher than what it was at minimum larval density, which should be considered as a rather moderate numerical response to a tenfold increase in larval density on log scale. This suggests that high moth larval density and consequential good access to food during the breeding season is important and positive for the breeding density of this bird community, and was according to my prediction. The response was species specific, which was also expected due to interspecific differences.

The pied flycatcher´s response was statistically significant only for its occupancy of boxes with large holes. This box type has been shown by both literature (Lundberg and Alatalo 1992, Vedum 1996) and my results (Table 2, Figure 5), to be a subordinate box type for the pied flycatcher, possibly because of higher predation pressure in such boxes (Järvinen 1990). The occupancy of the subordinate box type was higher in years when a high proportion of small boxes was occupied, suggesting a "spillover"-effect when densities and probably also competition in boxes with small holes was high. This might indicate that high densities of moth larvae are not essential for the pied flycatcher to breed, but that a superabundant access to food as caused by moth outbreaks could increase the breeding density to higher levels than

normal, as shown for other species of birds and moths (Holmes et al. 1986, Lindström et al. 2005).

The great tit utilized the two box types relatively equally, and responded positively to increased larval density across both hole sizes. This suggests that moth larvae might be more important for the great tit during breeding season than for the other two species, which responded less consistently or not at all. The explanation for this might be that the great tit is a larvae specialist during the breeding season (Royama 1970, van Balen 1973, Wilkin et al. 2009), and probably to a higher extent than the other two species (Cholewa and Wesolowski 2011). The great tit also has larger clutches which require abundant access to food (Perrins 1991), and might therefore be more vulnerable to food shortages than the other two species, which normally have smaller clutches.

The breeding density of the common redstart in boxes with large holes showed no response to increased larval density. This was also assumed in advance, as the importance of lepidoptera larvae in the redstart´s nestling diet has been found to differ between studies (Haftorn 1971, Sedlacek et al. 2007), and was the most frequent food type given to nestlings in only 35 % of the studies in the review by Cholewa and Wesolowski (2011). This is lower than for the other two species (42 % for the pied flycatcher and 75 % for the great tit). It could therefore be assumed that access to moth larvae is not essential for the redstart to breed. The low sample size for redstart could make the results for this species less reliable than for the other two species.

The fact that breeding took place also in years of very low densities of moth larvae indicates that none of the birds are critically dependant on this source of food to breed. Strong predation pressure on moth larvae by birds has been found in a study by Pepi et al. (2017), which was conducted in the same study area. No connection was found between bird predation pressure and occupancy of nest boxes, presumably because the inhabitants of the nest boxes constitute only a small part of the passerine bird community in the area, and that there are other species possibly predating moth larvae more heavily. This study supports that finding, as the long-term numerical response of the box-nesting bird community to moth larval density was significant, but probably not strong enough to largely reduce and control moth density.

4.2 Direct or delayed response to moth larval density?

A positive response to high moth larval density could be caused by both direct and delayed effects. To account for this, two different larvae variables were included in the analyses. The direct effect was measured by larval density in year t, while the delayed effect was measured by larval density in year t-1. High collinearity was detected between these two variables. According to Zuur et. al. (2010), this could be solved by excluding one of the collinear variables from the model, to avoid possibly disturbed relationships and inflated p-values preventing detection of statistically significant effects. The decision of which variable to exclude could be taken on the basis on VIF-values, or knowledge of the biological system under study (Zuur et al. 2010). In this study, both moth larvae variables were of biological interest, and it was difficult to distinguish *a priori* which variable that was most important. To be able to test for the effects of both variables, they were added to the models one at a time. Analyses showed that the effect sizes of both variables were of approximately equal size. Based on this, it is difficult to make conclusions about one of the variables being more important than the other. It could also be argued that a proportion of birds do not attempt to breed until their second year, but the inclusion of larval density in year t-2 did not clarify the difference between direct and delayed effect much, and the variables were still too highly correlated to include in the models simultaneously. At least for the pied flycatcher, quite many birds breed already in their first year (Lundberg and Alatalo 1992), and the inclusion of larval density in year t-1 in the models was expected to be sufficient to capture a response.

It can be argued that both direct and delayed effects are plausible explanations for the patterns observed in this study. A delayed, or demographic, effect could be present if the birds experience higher breeding success in years of moth outbreaks, leading to a higher return rate in the following year (Holmes et al. 1986, Newton 1998). Nestlings of pied flycatcher have shown a higher return rate as breeding birds when food was provisioned during nestling phase (Verhulst 1994), and a long term study of pied flycatchers found higher nestling survival in years of high *E. autumnata* densities (Nyholm 2011). The success of great tit clutches was also related positively to larval density (Verboven et al. 2001). High proportions of the great tit showed high breeding site fidelity in a study in Oxford, especially when having bred successfully the year before (Harvey et al. 1979). Other passerine birds are found to be positively correlated to the density of *E. autumnata* one or two years earlier, suggesting a delayed response through increased reproductive success (Enemar et al. 2004). These findings suggest that a delayed density response could be expected for the birds in the study.

Passerine birds have also been shown to respond directly to increased moth larval density. Several studies have shown that the brambling (*F. montifringilla*) responds directly to high moth larval densities, probably due to their nomadic behaviour (Enemar et al. 2004, Hogstad 2000). I am not aware of any studies on the focal species of the present study concerning their ability to spatially track peaks in food availability. A study by Mantyla et al. (2015) found that pied flycatchers were not able to find the nesting site that provides most food for their young, but there were some uncertainties attached to this result. The possibility that the birds in this study could show a direct response should therefore not be rejected.

Both direct and delayed numerical responses to food availability have been shown for passerine birds in previous studies. Because of the difficulties separating the effects in this study, no conclusion about one or the other being more important could be made. Based on stronger support for the presence of delayed effects of moth larval density on the focal species in literature, I assume that such effects might be more important in the study system, but a combination of both is also possible.

4.3 Effects of temperature

The response to higher spring temperatures could also be direct or delayed. This was tested by including temperatures both from year t and t-1 in the models. Increased spring temperature (mean temperature between 15/05 and 15/06) in year t was found to have a slight negative effect on breeding population density, which was significant for the whole community, the great tit and the common redstart in both box types combined. This result was quite unexpected, as it was anticipated that breeding density would increase with temperature. The effect of temperature in year t seems largely driven by an extraordinary warm spring in 2013, when nest box occupation was also low, possibly explained by other factors than temperature. If 2013 was removed from the data, the only significant result left was the slight negative effect on the great tit´s breeding density in both box types combined, and in large-hole boxes. High temperatures in early spring might induce an earlier start of breeding (Visser et al. 2009), and a warm spring would normally indicate a warm breeding season. Yet, this is not always the case, and periods of cold weather after hatching could be detrimental for the chicks (Ludwig et al. 2006) and eggs (Järvinen and Väisänen 1984). A higher rate of abandoned nests with lower temperatures has also been shown for the pied flycatcher (Nyholm 2011). When temperature is measured as a mean for a long period, such cold spells might not be captured, and the effect of higher mean temperature could therefore look falsely negative. Other ways of measuring temperature could be more appropriate for the purpose. The fact that

the great tit in our study area already initiates breeding up to 2 weeks earlier than the other two species in the study (Schott 2013), might make it more exposed to cold spells early in season, and possibly explain why it is the only species showing a significant negative response after removal of observations from 2013.

Warmer summers (mean temperature between 15/06 and 15/07) in year t-1 had a positive influence on the breeding population of the whole community, especially in small-hole boxes. Occupancy by the whole community across both box types was predicted to increase by 10% from the lowest to the highest measured mean temperature, which was weaker than the response to larval densities. The response was consistent across both box types for the pied flycatcher, while it was weaker and only marginally significant for great tit in small-hole boxes. The redstart showed a slightly negative response to warmer summers. The positive response could be caused by increased breeding success in years of higher summer temperatures, with subsequent higher return rates the following year. Previous studies on the pied flycatcher in Scandinavian ecosystems have found that breeding success was positively correlated to June temperatures, and that the size of the breeding population in one year was positively correlated to the number of fledged young in the following (Nyholm 2011, Thingstad et al. 2006). The 37-year study by Enemar et al. (2004) showed similar results for a community of passerine birds in Swedish Lapland. These findings indicate that the effect of temperature might indeed be delayed, and the results of this study corresponded to those findings. The reason why the redstart showed a weak negative response, could be because of low sample size. The weaker and more inconsistent response seen for the great tit could perhaps be explained by an inappropriate choice of temperature interval, since it often breeds earlier than the other two focal species. It could also be that the breeding success of the great tit is less affected by temperatures during the breeding season. It has been shown that experimental cooling of great tit nests did not impair the great tit´s breeding success, probably because the females were able to compensate for the cooling (Álvarez and Barba 2014).

The moderate numerical responses to moth larvae densities and temperatures indicate that there are probably also other factors limiting the number of breeding birds in the study area, such as access to other resources, predation, parasitism or disease, or environmental disturbances (Newton 1998). A large part of the total variation in nest box occupancy rates was connected to variance between sites, indicating that different factors attributed to habitat quality are important in determining breeding population size. If most of the variation in nest box occupancy at some study sites are explained by time-invariant between-site effects, e.g. in

an especially advantageous or poor habitat, this could reduce the explanatory power of more site-invariant factors, such as the moth larval densities and temperature measured in this study. This could perhaps make the size of the response across all study sites smaller. Other factors that could explain the spatial variation between sites was not in the scope of this project, which focused primarily on the factors that could determine the temporal dynamics of the focal bird community. Some unexplained variation indicates that there were also other factors not controlled for that affected breeding densities.

How differences between habitats affects the breeding population densities for box-nesting passerine birds in subarctic mountain birch forests could be an interesting subject for future research, and the spatially extensive design of this study could be suitable for the purpose. The monitoring of breeding bird density should continue in the future, to get a longer time series that cover more moth larvae outbreaks. It could also be interesting to visit the nest boxes more frequently during the breeding season, to allow determination of e.g. the breeding success (i.e. number of fledged young). Such data would permit investigations on the relationship between moth larval density and the breeding success the same year, and not only via the increased return rate that could be captured by the snapshot of the system obtained when visiting only once. It would also allow for a measure of predation rate, which has been found to influence breeding success in pied flycatcher (Nyholm 2011). This would, however, be much more time-consuming than the present procedure. It would also be interesting to examine whether the whole bird community of passerine birds in the study area shows a stronger numerical response to larval density than the moderate response found for the box-nesting birds. This was also suggested by Pepi et al. (2017), to see if a relationship could be established between the whole insectivorous bird community and the larval predation rate.

5 Conclusion

The large, regular outbreaks of moth larvae in subarctic birch forest constitutes an important source of food for breeding birds in spring. A moderate numerical response to outbreak densities of moth larvae was found for the box nesting bird community in this study. The response was species specific, and the great tit appeared to be most dependant on moth larvae, with a positive response for the density of the whole breeding population. The pied flycatcher seemed less dependent on access to moth larvae, but apparently increased its breeding density to higher than normal in outbreak years. This was indicated by an increased use of a less optimal nesting sites in years of high moth larvae densities, probably due to higher competition for its main nesting sites in these years. The common redstart did not respond, either because it is less dependent on moth larvae, or because the low sample size made it hard to detect a response.

Analyses were not able to answer whether the numerical response was caused by direct or delayed effects. Earlier studies suggest that the delayed, demographic effects might be more important in this system, but a combination of the two is also possible. The moderate response, with breeding also in years of low moth density, indicates that none of the birds are critically dependent on moth larvae as a source of food during the breeding season.

Spring temperature did unexpectedly have a negative direct effect on breeding density of the bird community, even though it was only rarely statistically significant. This could perhaps be caused by cold spells not captured by the chosen variable. The delayed effect of temperature was moderately positive, probably due to warm summers causing higher breeding success, and higher return rate of breeding birds in the following year.

The moderate numerical responses to both larval densities and temperature suggest that both temperature and access to food is important for the breeding population density of this bird community, but that there are also other factors determining and limiting the population size.

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Appendix

Appendix A

Table A.1: The parameter estimates in the form of odds ratios, 95 % confidence intervals, and p-value for all variables and models.

Model	Variable	Oddsratio	2,5% CI	97,5% CI	P-value
FLS-S1	lmoths	1.023	0.973	1.076	3,77E-01
	fls.p.lag	1.793	0.998	3.229	5,09E-02
	kj.p	0.121	0.044	0.331	4,31E-05
	temp	0.989	0.905	1.080	8,07E-01
	temp.lag1	1.209	1.090	1.342	3,50E-04
FLS-S2	lmoths.lag1	1.041	0.990	1.094	1,15E-01
	fls.p.lag1	1.811	1.012	3.247	4,57E-02
	kj.p	0.110	0.039	0.302	2,11E-05
	temp	0.994	0.911	1.083	8,84E-01
	temp.lag1	1.214	1.094	1.348	2,61E-04
FLS-B1	lmoths	1.234	1.119	1.363	2,46E-05
	fls.p.lag1	8.903	1.517	50.298	1,32E-02
	kj.p	2.184	0.309	14.473	4,21E-01
	rst.p	0.440	0.041	3.608	4,66E-01
	temp	0.983	0.817	1.172	8,52E-01
	temp.lag1	1.338	1.097	1.639	4,05E-03
FLS-B2	lmoths.lag1	1.192	1.072	1.328	1,17E-03
	fls.p.lag1	5.604	0.870	34.996	6,37E-02
	kj.p	2.967	0.427	19.369	2,58E-01
	rst.p	0.577	0.057	4.526	6,17E-01
	temp	1.061	0.890	1.254	4,90E-01
	temp.lag1	1.363	1.118	1.671	2,23E-03
FLS-1	lmoths	1.056	1.015	1.099	6,71E-03
	fls.p.lag1	2.228	1.023	4.872	4,38E-02
	kj.p	0.441	0.145	1.329	1,46E-01
	rst.p	0.485	0.111	2.063	3,31E-01
	temp	0.978	0.909	1.050	5,40E-01
	temp.lag1	1.139	1.048	1.239	2,29E-03
FLS-2	lmoths.lag1	1.054	1.013	1.097	8,83E-03
	fls.p.lag1	2.051	0.942	4.480	7,04E-02
	kj.p	0.440	0.144	1.333	1,47E-01
	rst.p	0.461	0.105	1.960	2,98E-01
	temp	0.993	0.925	1.065	8,47E-01
	temp.lag1	1.139	1.048	1.238	2,21E-03

Model	Variable	Oddsratio	2,5% CI	97,5% CI	P-value
KJ-S1	lmoths	1.198	1.033	1.190	3,89E-03
	kj.p.lag1	0.538	0.143	1.976	3,51E-01
	fls.p	0.288	0.121	0.669	4,03E-03
	temp	0.965	0.853	1.089	5,68E-01
	temp.lag1	1.162	1.003	1.304	4,48E-02
KJ-S2	lmoths.lag1	1.123	1.043	1.207	1,86E-03
	kj.p.lag1	0.448	0.116	1.684	2,36E-01
	fls.p	0.276	0.116	0.639	2,87E-03
	temp	0.990	0.877	1.112	8,70E-01
	temp.lag1	1.171	1.011	1.357	3,39E-02
KJ-B1	lmoths	1.174	1.062	1.298	1,53E-03
	kj.p.lag1	0.049	0.004	0.429	8,68E-03
	fls.p	4.907	0.635	35.307	1,16E-01
	rst.p	0.014	0.001	0.193	2,79E-03
	temp	0.767	0.621	0.929	8,55E-03
	temp.lag1	1.044	0.849	1.287	6,75E-01
KJ-B2	lmoths.lag1	1.167	1.055	1.292	2,50E-03
	kj.p.lag1	0.043	0.004	0.380	6,39E-03
	fls.p	6.299	0.864	43.078	6,13E-02
	rst.p	0.0159	0.001	0.218	3,56E-03
	temp	0.816	0.665	0.982	3,73E-02
	temp.lag1	1.062	0.865	1.307	5,60E-01
KJ-1	lmoths	1.141	1.079	1.208	3,85E-06
	kj.p.lag1	0.366	0.089	1.507	1,64E-01
	fls.p	0.679	0.227	2.019	4,86E-01
	rst.p	0.188	0.019	1.628	1,37E-01
	temp	0.902	0.812	0.999	4,98E-02
	temp.lag1	1.126	0.998	1.270	5,21E-02
KJ-2	lmoths.lag1	1.151	1.086	1.221	2,36E-06
	kj.p.lag1	0.286	0.067	1.204	8,78E-02
	fls.p	0.657	0.218	1.961	4,51E-01
	rst.p	0.168	0.017	1.481	1,16E-01
	temp	0.938	0.846	1.035	2,05E-01
	temp.lag1	1.134	1.006	1.277	3,79E-02

Model	Variable	Oddsratio	2,5% CI	97,5% CI	P-value
RST-B1	lmoths	1.078	0.984	1.179	1,02E-01
	rst.p.lag1	0.200	0.023	1.456	1,27E-01
	kj.p	0.016	0.001	0.235	3,99E-03
	fls.p	0.336	0.034	2.563	3,16E-01
	temp	0.852	0.714	1.005	6,44E-02
	temp.lag1	0.828	0.686	0.996	4,77E-02
RST-B2	lmoths.lag1	1.056	0.966	1.154	2,23E-01
	rst.p.lag1	0.190	0.021	1.382	1,15E-01
	kj.p	0.017	0.001	0.254	4,81E-03
	fls.p	0.388	0.040	2.930	3,82E-01
	temp	0.876	0.735	1.028	1,18E-01
	temp.lag1	0.827	0.684	0.994	4,41E-02
RST-1	lmoths	1.003	0.931	1.078	9,45E-01
	rst.p.lag1	0.660	0.049	7.747	7,45E-01
	kj.p	0.112	0.009	1.244	7,63E-02
	fls.p	0.423	0.102	1.752	2,28E-01
	temp	0.834	0.714	0.964	1,67E-02
	temp.lag1	0.792	0.674	0.929	4,18E-03
RST-2	lmoths.lag1	1.020	0.950	1.094	5,76E-01
	rst.p.lag1	0.695	0.053	8.016	7,74E-01
	kj.p	0.094	0.008	1.023	5,41E-02
	fls.p	0.395	0.096	1.636	1,94E-01
	temp	0.835	0.716	0.962	1,59E-02
	temp.lag1	0.798	0.678	0.934	5,25E-03

Model	Variable	Oddsratio	2,5% CI	97,5% CI	P-value
ALL-S1	lmoths	1.028	0.979	1.079	2,75E-01
	allbirds.lag1	1.004	0.951	1.059	8,92E-01
	temp	0.941	0.862	1.027	1,74E-01
	temp.lag1	1.204	1.086	1.336	4,21E-04
ALL-S2	lmoths.lag1	1.056	1.006	1.109	2,69E-02
	allbirds.lag1	1.000	0.948	1.055	1,00E+00
	temp	0.944	0.866	1.028	1,84E-01
	temp.lag1	1.208	1.089	1.340	3,40E-04
ALL-B1	lmoths	1.189	1.122	1.261	6,23E-09
	allbirds.lag1	0.970	0.893	1.052	4,66E-01
	temp	0.851	0.759	0.951	5,05E-03
	temp.lag1	1.081	0.957	1.220	2,08E-01
ALL-B2	lmoths.lag1	1.173	1.103	1.248	3,54E-07
	allbirds.lag1	0.949	0.872	1.031	2,17E-01
	temp	0.902	0.806	1.004	6,26E-02
	temp.lag1	1.089	0.965	1.228	1,65E-01
ALL-1	lmoths	1.082	1.046	1.119	5,75E-06
	allbirds.lag1	1.024	0.996	1.053	9,56E-02
	temp	0.931	0.872	0.992	2,90E-02
	temp.lag1	1.111	1.035	1.193	3,61E-03
ALL-2	lmoths.lag1	1.083	1.047	1.121	5,09E-06
	allbirds.lag1	1.018	0.990	1.047	2,18E-01
	temp	0.951	0.893	1.013	1,18E-01
	temp.lag1	1.110	1.034	1.192	3,94E-03