

Variability in double brooding of the great tit (*Parus major*) across polluted and resource-poor area

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Master's thesis**Subject:** Biology / MDP Biosciences – Evolutionary Biology**Author(s):** Lasanthi Kanthika Wijayathunge Arachchige**Title:** Variability in double brooding of the great tit (*Parus major*) across polluted and resource-poor area**Supervisor(s):** Dr. Tapio Eeva,**Number of pages:** 36 pages**Date:** 13.07.2025

Environmental changes such as climate change and human-induced pollution can alter breeding phenology and reproductive success in natural ecosystems. Long-term studies on monitoring reproductive performance in a highly polluted area are important to measure the environmental quality of a particular area. Harjavalta copper smelter is a significant point source of pollution in southwest Finland, which emits copper, nickel, lead, cadmium, arsenic, mercury, zinc, as well as sulphur dioxide to the surrounding environment. In this study, we investigated the probability of double brooding in great tit (*Parus major*) along a pre-determined pollution gradient surrounding the smelter to identify factors that affect the decision to start a second breeding attempt.

The pollution gradient was categorized into two parts according to the distance from the copper smelter (polluted zone <2.5km and control zone >2.5-15km). These areas further included multiple nest box sites, and data were collected up to the site level for 33 years. Generalized linear mixed models were used to analyse the data.

Population density was the major significant factor and negatively associated with the probability of double brooding, followed by the timing of breeding (first egg laying date of the 1st brood), whereas probability between polluted and control zones was not statistically significant. However, a positive relationship between first brood success (measured with the number of fledglings) and the likelihood of having a second brood was observed. The second brood probability showed a slightly negative trend over the study period. Contrary to some other life-history parameters documented in earlier studies, there was no significant impact of distance zone, suggesting that pollution is not an influential factor on the probability of multiple brooding. This study provides insights into density-dependent reproductive decisions and performance of great tits and suggests that higher local competition for resources is one of the major factors shaping the life-history decisions of great tits.

Key words: *Parus major*, second broods, environmental pollution, timing of breeding, reproduction strategies,

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1 Introduction

Avian breeding ecology is a complex process which controlled by a variety of ecological factors such as resource availability, climatic conditions, and anthropogenic disturbances (Betts et al., 2022; Northrup et al., 2019). In evolutionary perspective, one important life-history decision is whether to breed once or multiple times per breeding season. Multiple brooding is specially chosen in high-quality habitats that supply sufficient resources that can be used by birds to invest lower cost to produce more offspring (Nagy & Holmes, 2004). Multiple brooding may be beneficial for an organism as it has the potential to enhance reproductive output and fitness. Previous studies have shown that species capable of multiple brooding can raise their fecundity by elevating their capacity for passing on genes into the next generation (Cornell & Williams, 2016).

Starting a second breeding attempt during a single breeding period is a challenging decision which is influenced by a variety of ecological, behavioural, and physiological factors. Resource availability, especially food availability, plays a pivotal role in multiple brooding. Previous studies have confirmed that the probability of starting a second brood has a strong positive relationship with good quality habitats with adequate food supplies, indicating the adaptive nature of reproductive methods in response to resource availability (L. Q. Fan et al., 2017). Predation pressure can also be considered as another important factor that alters the reproductive strategies, where birds may attempt to trade off the second brood to lower the risk of losing their total reproductive investment (Carro et al., 2014). On the other hand, the quality of individuals is also a critical factor. High-quality individuals are equipped with stronger foraging ability and higher access to resources, which increases their probability of having second broods (Cornell & Williams, 2016).

1.1 Anthropogenic impacts on breeding of birds

Breeding phenology of birds is influenced by anthropogenic impacts, such as climate change or environmental pollution, by altering environmental conditions and food availability. These factors altogether can change the timing of breeding attempts, length of breeding season, and success (Both et al., 2019; Halupka et al., 2023; Reed et al., 2013). Human-induced environmental modifications, such as industrial expansion and urbanization, have significant influence on the natural environment, causing habitat changes and pollution emissions that can potentially have adverse effects on avian reproductive ecology (Rhind, 2009). Many studies investigate the causes for decline of global bird populations. The major reasons identified were habitat loss and changes of

habitat quality driven by land-use change due to agricultural and industrial expansions (Brandolin et al., 2016; Habib et al., 2007).

1.1.1 Impact of climate change

Numerous studies have investigated the impact of climate change on birds, including breeding ecology, and found a number of important life-history aspects affected, such as timing and duration of breeding season, success rates, and population dynamics (Halupka et al., 2023; Newson et al., 2009; Parmesan, 2006). Warming temperatures and alterations in seasonal patterns, such as early spring conditions, change the phenology of the environment, whereas many species advance their breeding according to local climatic conditions (Weiskopf et al., 2020). However, this advancement in breeding phenology does not occur consistently through all the trophic levels, resulting in the phenology of prey species typically advancing quicker than that of predator species (Bründl et al., 2020). This mismatch of the breeding season of birds and their prey abundance has significant consequences, since the availability of food sources, in other words, abundance of prey species during the breeding period, may no longer be well aligned with the demand of breeding bird populations (Bründl et al., 2020).

It is important to note that avian breeding ecology is differently impacted by climate change according to the species, habitat types, and elevation. Studies have found that species inhabiting higher elevations are more susceptible to climate change since environmental conditions are rapidly changing in higher elevations, and the bird species have lower capacity to adapt to rapid changes (Weiskopf et al., 2020). Furthermore, studies suggest that short-distance migrants are adapting to the rapid environmental changes faster than species migrate through long distances. The timing of migration and duration of migratory season have been advanced due to warm spring conditions (Lehikoinen et al., 2019; Youngflesh et al., 2023). Reproductive success is influenced by various environmental stressors because of climate change. Warming climate can cause thermal stress, which can negatively impact on egg viability and nestling survival rates in species that are behaviourally less adapted to cope with elevated temperatures (Ardia et al., 2006; Churchill et al., 2023; La Sorte et al., 2019).

1.1.2 Impact of environmental pollution

Environmental pollution is another frequently underestimated hazard to bird populations in various ways. Contaminants such as heavy metals, pesticides, and other industrial wastes can decrease habitat quality, disrupt food chains, and have a direct influence on bird health and reproductive

performance (Kight & Swaddle, 2007; Rhind, 2009). Numerous studies indicate that pollution has a negative impact on bird population, diversity, and breeding. For example, in a study of eastern bluebirds (*Sialia sialis*), researchers discovered that breeding success and nestling condition were negatively impacted by anthropogenic activities (Kight & Swaddle, 2007).

Furthermore, environmental degradation and land-use change caused the decline of insect pollinator diversity and abundance, such as bees, which are critical to the health of natural ecosystems (Basu & Cetzal-Ix, 2018). Lowering insect abundance has a direct negative impact on food availability of insectivorous birds, which is one of the major determinants of the decision to initiate a second breeding attempt (Jackson & Cresswell, 2017; Seress et al., 2020).

Microplastics (MPs) are one of the important groups of environmental contaminants. Studies revealed that different types of microplastics, including polyethylene and polyethylene terephthalate, are accumulated in the gastrointestinal tracts of six bird species, including tree swallows and adult migratory birds. The researchers suggest that MPs may enter the birds through their dietary intake, particularly through predation on insects (Hoang & Mitten, 2022). The consumption of microplastics by birds leads to oxidative stress in multiple organs, decreases body weight, and modifies biochemical indicators, suggesting possible detrimental effects on their physiological functions (de Souza et al., 2022). Experimental studies have shown that microplastic ingestion could impact sex hormones, which are essential for reproductive function (Monclús et al., 2022). Although these studies don't show the direct impact of microplastics on double brooding, altered hormone levels can weaken reproductive performance in the next breeding event.

A review paper deeply discussed the effects of current pesticide usage on wild birds and revealed that the chemicals containing in pesticides possess a direct impact on the fitness of the wild birds. Pesticides containing azole, organochlorine, organophosphate, carbamate, pyrethroid, and neonicotinoid were identified as chemicals with the potential to disrupt reproductive endocrine function and impair thyroid and gonad hormones, which are influenced by cross-regulation of these hormones during reproduction. The influence of hormonal changes, such as gonadotropins (LH, FSH), and sex steroids, can impact on overall reproductive cycle, including gonadal development, folliculogenesis, and the ovulation processes, resulting decrease in clutch size or complete reproductive failure (Mohanty, 2024).

The current study is focused on the environment around the Harjavalta copper-nickel smelter located in south-west Finland, which has been contributing significantly to Finland's industrial output and economy since 1945. However, Harjavalta copper smelter is a well-known example for a

point-source of industrial pollution, including heavy metal emissions such as copper, nickel, lead, cadmium, arsenic, mercury, zinc, as well as sulphur dioxide and particulate matter, light and noise pollution (Kiikkilä, 2003).

Previous studies have reported heavy metal accumulation in birds in polluted environments. Elevated amounts of heavy metals were found in the tissues of birds, which can contribute to health-related issues, including decreased reproductive success and higher mortality rates (Berglund et al., 2015; Turzańska-Pietras et al., 2018). The main route of heavy metals to insectivorous birds is invertebrate prey species such as insects. For example, a study carried out in the Harjavalta area revealed bioaccumulation of cobalt, arsenic, copper, iron, nickel, zinc, lead, and mercury in common wasp (*Vespula vulgaris*) species (Skaldina et al., 2020).

Researchers carrying out long-term research in and around the Harjavalta area have suggested that heavy metal exposure and higher emissions of the copper smelter have resulted in poor-quality and low-productive habitats, which leads to lower local survival rates of pied flycatchers (*Ficedula hypoleuca*) (Eeva & Lehikoinen, 1998). Furthermore, *F. hypoleuca* are primarily insectivorous and inhabit in polluted area, ingesting invertebrate food rich with heavy metals, which has an impact on their calcium metabolism, resulting in decreased reproductive success. On the other hand, Great tit (*Parus major*) nestlings were under stress due to lower food availability as well as lower food quality (Eeva et al., 2003; Eeva & Lehikoinen, 2004).

The surrounding pollution combined with the contamination and habitat degradation have made it difficult to find good quality breeding and foraging grounds for birds living in the particular area (Eeva et al., 2012). Environmental pollution could affect different species in different ways, potentially leading to declines in avian species and general biodiversity in the Harjavalta region. Indeed, some studies have shown reduced species diversity and population density in areas with high pollution, especially in the vicinity of the copper smelter (Eeva et al., 2003). Again, the potential role of changed probability of second nesting as an explanatory factor, has remained unstudied.

Understanding the processes by which environmental stressors, such as contamination from industry, influence breeding performance of birds, including the initiation of second broods, is important for assessing the ecological impacts of human activity on avian populations.

1.2 Great tit (*P. major*) as a model species for the environmental conditions

The great tit (*P. major*) (Picture 1) is a widely studied, important model organism for studying breeding behaviour because of its widespread distribution, high breeding densities, and finally, well-documented breeding biology (Maziarz et al., 2015). Another advantage is great tit's inhabits both natural and anthropogenically altered landscapes and ability to nesting in man-made nest boxes, making it an ideal species for comparative studies (Barton et al., 2023).



Picture 1: Great tit (*Parus major*). Source: <https://ebird.org/species>

One prominent characteristic of great tit for being in focus in breeding ecology studies is the facultative multiple breeding behaviour displayed by some individuals, which allows them to produce a second brood within the same breeding season after successfully fledging the chicks from the first brood (Verboven & Verhulst, 1996a).

The purpose of this study is to examine the probability of great tits commencing a second brood in the pollution gradient surrounding the Harjavalta copper smelter. The region has been categorised into two parts, polluted zone and control zone, according to the distance from the copper smelter. The temporal changes in the probability of breeding twice during the breeding season will be examined from the long-term research data collected by the research group, from the viewpoint of climate variations and other environmental changes. Furthermore, I will investigate whether the success of the first nest increases the chance of establishing a second nest.

By addressing these objectives, this study aims to enhance our knowledge about the impact of industrial pollution and other environmental stresses on life-history strategies of birds, specifically the tendency for repeated breeding attempts during a single breeding season. Such findings are critical for understanding the reasons behind the population declines and developing conservation

measures to mitigate the effects of anthropogenic disturbances on bird populations and preserve biodiversity in human-altered environments.

2 Methodology

2.1 Study area

The research area is in Harjavalta, which surrounds a Finnish copper smelter. Located in southwestern Finland (61.32005° N, 22.121895° E). The Harjavalta industrial complex has been operated since 1945 and is considered one of the major point sources of metal emissions in Finland (Kiikkilä, 2003) This smelter mainly produces copper, nickel, and sulphuric acid.

The forest habitat of the study area mainly consists of coniferous trees, dominated by Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), and several deciduous species, including birch (*Betula pendula* and *B. pubescens*). The forest understory vegetation reflects clear signs of industrial pollution stress in the contaminated area, characterized by reduced plant species diversity and density relative to the control area (Salemaa et al., 2001).

The climate of the respective area is typical of the southern boreal zone, which consists of cold winters and mild summers. The mean annual temperature is approximately 5°C. During the breeding season (April – July), average monthly temperatures vary between 5-20°C (Pirinen et al., 2012)

2.2 Data collection method

2.2.1 Study design

Data for this study were collected from 1991 to 2023, over 33 years. The focus area was further categorized into two separate zones (Fig. 1) according to proximity to the smelter: polluted zone (within 2.5km of the smelter) and control zone (>2.5 km from the smelter), adhering to the gradient method applied in prior ecological research in this area (Eeva et al., 2009; Eeva & Lehikoinen, 1998). Within these two regions, 25 nest box sites, each containing 20-60 nest boxes, were established. The number of active sites varies among the years. Wooden nest boxes with inner dimensions of L 12cm × W 12cm × H 20cm and 32mm entrance hole were mounted on tree trunks 2m above ground level while maintaining approximately 30 - 40 m distance between the nest boxes (Eeva & Lehikoinen, 1995).

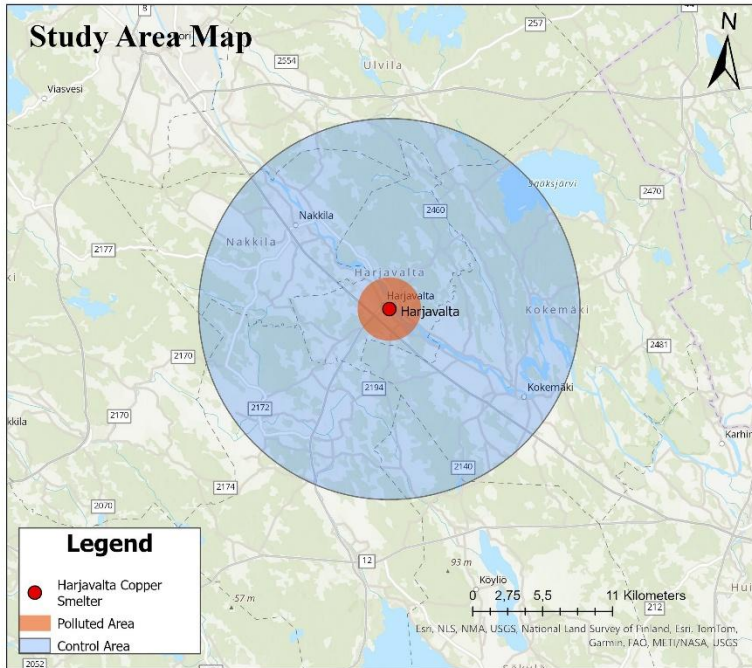


Figure 1: Map of the study area showing Harjavalta copper smelter, polluted area and control area

The nest box sites show varying degrees of metal pollution levels, with greater concentrations of arsenic, copper, nickel, lead, and zinc found in the soil closer to the emission source (Deromea & Lindroos, 1998; Ruiz et al., 2017). The number of active nest box sites was not similar in each year. For example, new sites have been established after forest clear-cuttings.

The nest boxes were observed during the breeding season (April-August). Monitoring commenced in late April and was conducted with weekly visits to assess nest box occupancy and breeding parameters. When a nest was discovered in a building phase, more frequent visits were often arranged to precisely record the dates of the first eggs and the size of the clutches. The first egg-laying date was calculated back from the number of unincubated eggs, assuming that birds lay one egg per day, as they normally do. Hatching date was estimated by measuring the wing length of recently hatched chicks and comparing those values to the existing wing growth curve of this species from the same area (See the supplement in Eeva et al., 2020).

2.2.2 Recording breeding parameters

For each breeding attempt, the following data were recorded. First egg laying date (standardized as days from January 1st), clutch size (total number of eggs laid), hatching date (when the first egg hatched), number of hatchlings, number of fledglings, and occurrence of a second brood.

A nesting attempt was categorized based on the timing of egg-laying. Depending on the phenology of the year, the clutches laid before 26th May were considered as first broods. Clutches laid in late May or early June are considered as replacement nests. Finally, nests were considered as “true” second broods after the nestlings from the earliest first broods fledged in each nest box site. Fledgling success was calculated as the proportion of hatchlings that successfully fledged from each nest box site. However, in this method, late nests can be categorized as replacement nests (e.g. a new nest appeared soon after the nesting failure in the neighbouring nest box).

2.2.3 Habitat characterization

Vegetation surveys were conducted at each nest box site to characterize the habitat structure. The abundances of the three dominant species, Scots pine, Norway spruce, and birch, were visually estimated within a 50-meter radius around each nest box. Tree abundance was ranked on a semi-quantitative scale from 0 to 3, where: 0 = not present, 1 = Present but rare, 2 = common, 3 = dominant. The mean of these scores was calculated annually for each study plot.

2.3 Data analysis

The original data set included 457 records from 1991 to 2023. A collection of 368 records from nest box sites located within 15 km radius involving 14525 nests was taken for this analysis. Each nest box sites were numbered, and the breeding data were recorded at nest box site level, to make analysis at site level without focusing on breeding parameters of individual parents. Out of 368 records, 105 incidents didn't have any second brood. Initially, the data were entered into Microsoft Excel. Table 1 presents the variables used in the statistical analysis

Table 1: Description of parameters used in statistical analysis

The table shows the parameters and their descriptions. The data was arranged according to the following set of parameters

Parameter	Description
Year	Calendar year of data collection (1991-2023)
Zone	Categorical variable indicating pollution level (zone1 = polluted area <2.5km from copper smelter, zone2 = control area >2.5km from copper smelter)
Site	Identity of nest box site (25 nest box sites were included)
Boxes	Number of nest boxes at each site (ranging between 20-60)
Distance	Distance (km) from the copper smelter
First	Annual count of first brood at each nestbox site
Second	Annual count of second brood at each nestbox site
Laying date	Average first egg-laying date (day of year) for first brood at each site

Parameter	Description
Fledgling number 1	Average number of fledglings produced in first broods at each site
Fledgling number 2	Average number of fledglings produced in second broods at each site
Density	Derived variable representing breeding density at each site (proportion (%) of nest boxes with 1st nest)

the statistical analysis was performed with R version 4.4.2 and SAS software to assess the variation in the probability of initiating a second brood along the pollution gradient. The analysis will focus on

- 1.) Identifying whether there is a significant difference in the likelihood of starting a second brood between birds nesting in polluted versus control areas.
- 2.) Investigate the temporal change of the probability of double brooding
- 3.) Assess the relationship between first brood success and the probability of producing a second brood
- 4.) Examine the role of vegetation composition (pine, spruce, and birch abundance) in the likelihood of having a second attempt.

To investigate the factors affecting the probability of second brood, I used generalized linear models (GLMMs) set up in R using the `glmer` function from the `lme4` package. The model was fitted with binomial error distribution and logit link function. The response variable was a two-column matrix of second versus first broods, representing the binary outcome of whether a second brood occurred. The fixed effects included in the model were Zone (distinguishing between polluted and control areas), Year (to account for long-term temporal trends), laying date (reflects first egg laying date of each site) Fledgling number1 (average number of fledglings produced in first brood), and population density (the nest box occupation % of 1st broods per site, representing local competition). The variable Year was rescaled by converting calendar year (1999, 2000, 2001,...) to sequential integers (1-33), for example, 1=1999, 2=2000, etc. This conversion keeps the original relationship between years while lowering numerical instability caused by the large values in the original scale (Bolker et al., 2009). Site was considered a random effect to control for repeated observations within the same location over time. The model was fitted using the Laplace approximation with the `bobyqa` optimizer. This method was adopted because it accounts for both fixed and random variation and is suitable for long-term, hierarchical ecological datasets. The predicted probabilities were calculated for the model using the `predict()` function with `type =`

“response”. These prediction values present the model's estimated probability of double brooding for each observation. Predicted values were inserted as a separate variable in the dataset for further visualisation. The R code for my final model was the following:

```
additive_model <- glmer(  
  cbind(Second, First) ~ Zone + Year_scaled + Laying date + Fledgling number1 + Density + (1 |  
  Site),  
  data = sbrood_clean,  
  family = binomial,  
  control = glmerControl(optimizer = "bobyqa"))
```

Habitat parameters (Abundance scores of pine, birch, and spruce) were not included in the final model since the tree species were not significantly associated with the response variable and did not improve the model fit. However, this data was used in data visualizations to examine the potential ecological patterns.

3 Results

The data with 368 annual observations from 20 nest box sites (179 records from the polluted zone and 189 records from the control site) were used to interpret results. Among all observations, 71.47% nest box sites recorded second nests (72.62% in the polluted zone and 70.37% in the control zone, respectively).

Table 2 provides the summary statistics for the model. The random effect of the model, Site, showed low variance 0.018 and SD =0.13, meaning low variation between sites in the probability of double brooding, suggesting our fixed effects captured most relevant ecological factors and validates spatial design of the study. Model fit indices (AIC = 1032, BIC = 1059, log-likelihood = -509). Residual diagnostics showed no strong deviations from homogeneity (median = -0.17, interquartile range -1.58 to 3.66) indicating fair balance between model complexity and explanatory power.

Table 2: Summary of the generalized model results and their interpretation.

Total number of 368 records, including 179 observations from the polluted zone, 189 observations from the control zone

Predictor	Estimate	Standard error	Z value	P	Interpretation
(Intercept)	2.648	1.547	1.711	1.087	
Zone	0.138	0.143	0.963	p = 0.335	No significant effect of the pollution zone.
Year	-0.007	0.006	-1.042	p = 0.298	Not significant, weak negative trend over time.
Laying date	-0.029	0.012	-2,383	p = 0.017	Significant negative effect.
Fledgling number	0.036	0.030	1.204	p = 0.228	Not significant
Density	-0.042	0.007	-5.896	p = 3.72×10 ⁻⁹	Highly significant. Higher nest density reduces the likelihood of having a second brood

Among the fixed effects, population density and egg laying date were statistically significant. Lower p-value ($p < 0.001$) and the negative estimate (-0.042) suggest that a higher density of breeding birds reduces the likelihood of initiating a second brood. This likely reflects intraspecific competition or resource limitation in denser populations. First egg laying date shows a significant negative effect ($p < 0.05$) with a negative estimate (-0.029), indicating late breeders possess lesser probability of having a second brood. The other predictors, Zone, Year, and fledgling number were not statistically significant.

3.1 Temporal trends of second brood probability in polluted and control zones

The polluted zone (within 2.5 km of the smelter, in red) and the control zone (beyond 2.5 km, in blue), spanning the years 1991 to 2023 is shown in Figure 2. Each point corresponds to an annual observation at a given site, and the smoothed trend lines with 95% confidence intervals provide an estimate of the overall trend within each zone.

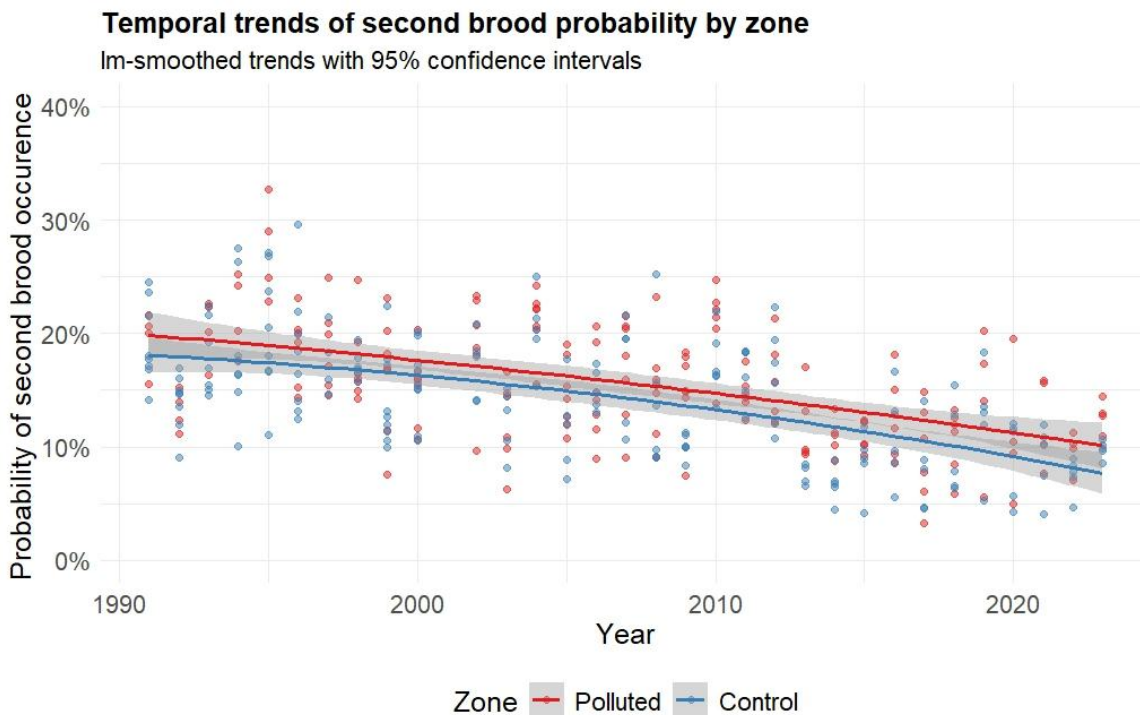


Figure 2: Long-term temporal trends in the probability of second brood occurrence across two zones. Red regression line represents the polluted zone, and the blue regression line represents the control zone of the model's predicted values with the surrounding grey colour. Sample size = 368 observations

The results show a general decline (nearly 10% units) in second brood probability over time in both zones. This suggests that environmental conditions, especially chronic exposure to pollution, may not be the main reason for declining second brood probability.

3.2 Relationship between first brood success and probability of occurrence of second brood

The figure below (Figure 3) illustrates that the overall trend showing a slightly positive relationship between first brood success and second brood probability in both zones. Although first brood success was not statistically significant ($p > 0.05$), this finding is well aligned with the idea that

better initial breeding outcomes may signal higher individual quality or favourable local conditions. So, they pay additional reproductive effort to lay a second clutch of eggs.

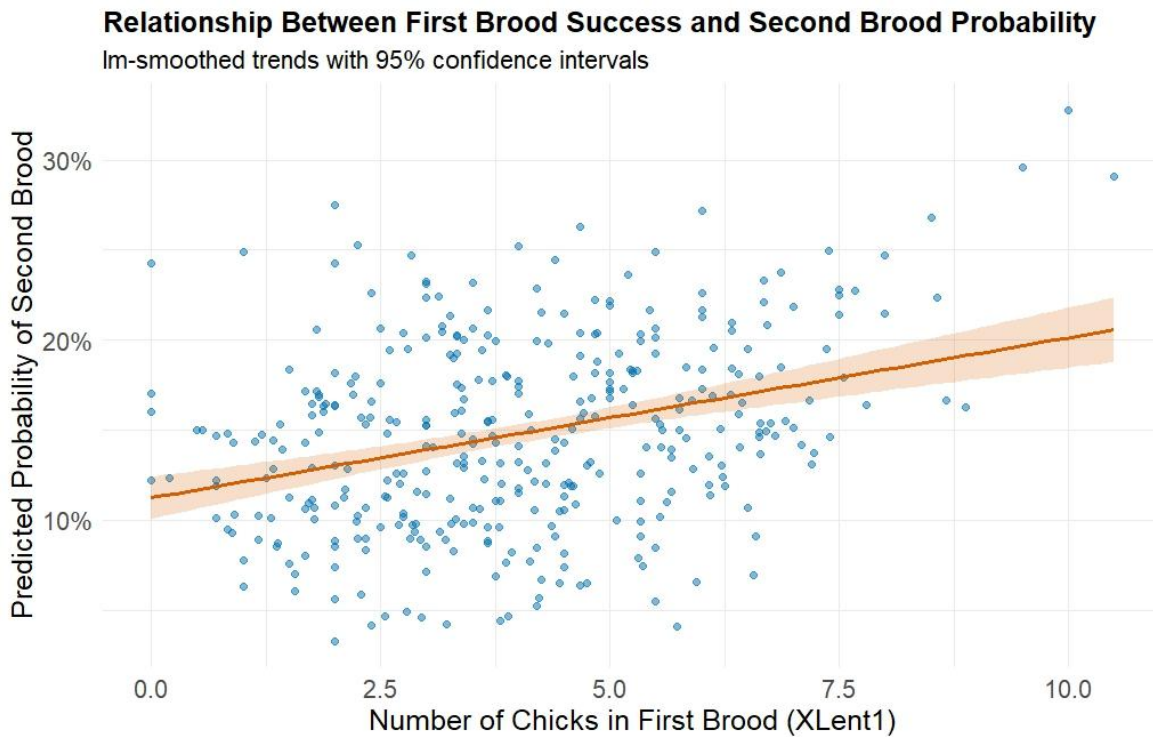


Figure 3: Relationship between the average number of fledglings in the first brood in a nest box site and the probability of second brood occurrence. The red regression line shows linear trend with the surrounding light-red coloured 95% confidence level. Sample size = 368 observations.

3.3 Relationship between density of nests and second brood probability

The density of great tits in nest box sites showed a highly significant impact on the probability of double brooding ($p < 0.001$). Figure 4 clearly shows a gradual decline in the probability of having a second brood in both polluted and control zones when the nest density rises. This would suggest intraspecific competition for the resources.

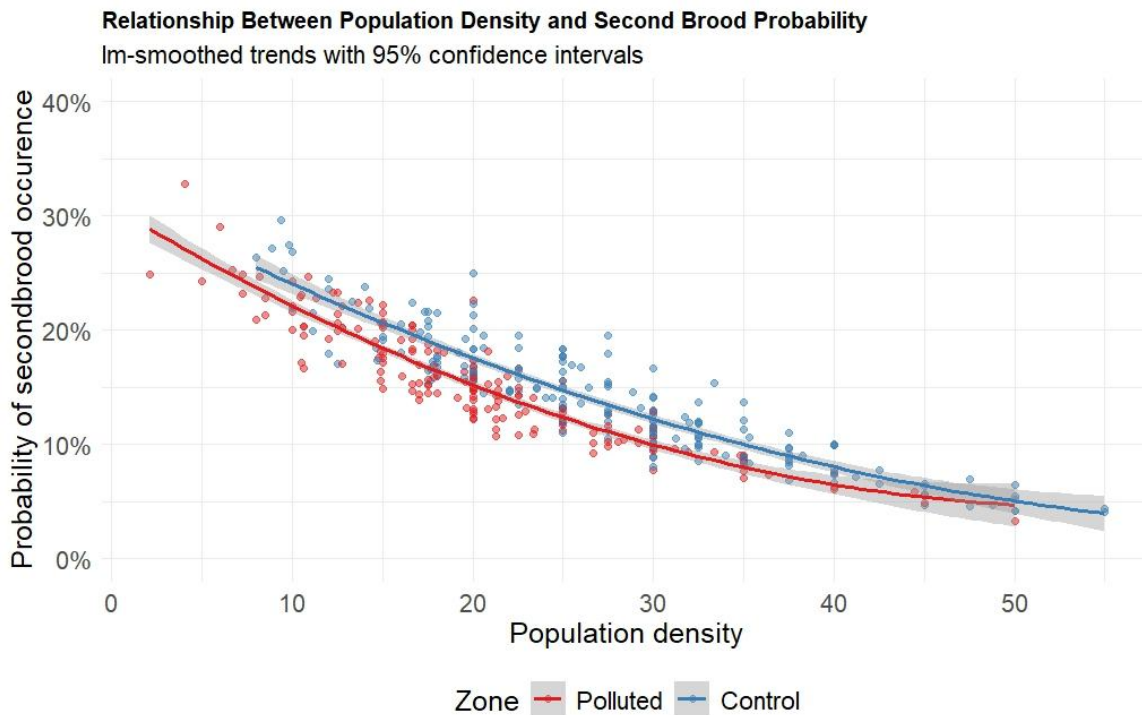


Figure 4: Relationship between the great tit nest density and the probability of second brood occurrence. The red regression line represents polluted zone, while blue regression line represents control areas smoothed trend with the surrounding grey coloured 95% confidence level. Sample size = 368 observations.

3.4 Impact of vegetation of the nest box site on the probability of having a second brood

The vegetation parameters were not statistically significant. Here, I explored the relationship between the abundance of common tree species (birch, pine and spruce) and the predicted probability of having a second brood

As shown in Figure 5, birch is a relatively common tree species. The proportion of birch trees in most observations concentrated around ranking number 2. There is a slight increase in the probability of double brooding in areas where the birch trees are more abundant. Interestingly, the probability of a second brood in the control zone is slightly higher than that of the polluted zone.

Pine was the dominant plant species at most sites. The abundance score of pines in most sites is concentrated near the score value of 3. Figure 6 suggests a negative association between the dominance of pine in the habitat and the occurrence of second broods. This trend was evident in both polluted and control zones. In other words, as the proportion of pine increases, birds are less likely to initiate a second breeding attempt.

Spruce was the comparatively least abundant tree species in most sites. The results as shown in Figure 7, indicate minimal increase of probability of the second brood with the spruce abundance.

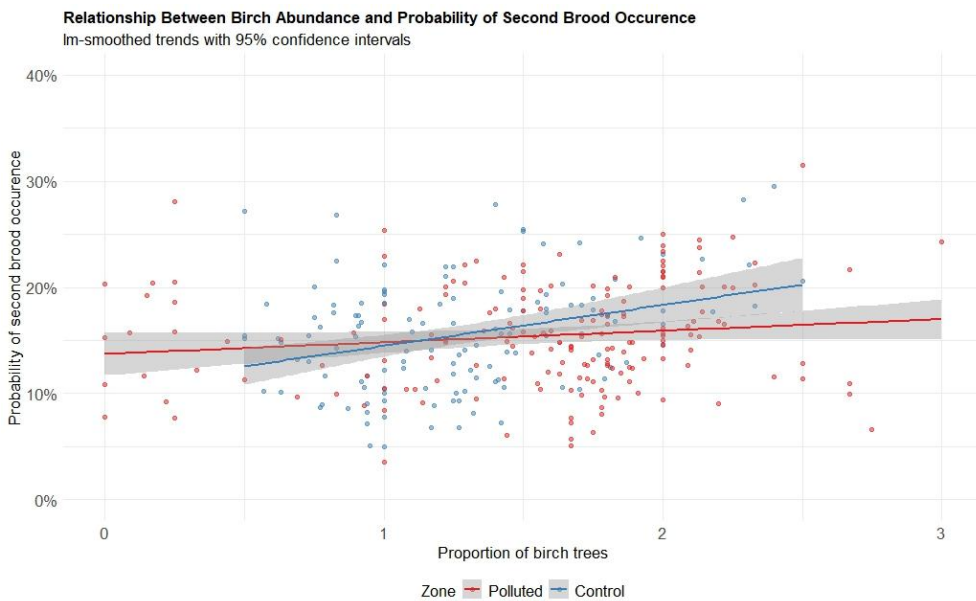


Figure 5: Relationship between birch tree abundance and the probability of occurrence of second brood in polluted and control areas. The red regression line represents the polluted zone, and the blue regression line represents the control zone of the model's predicted values with the surrounding grey coloured 95% confidence level. Sample size = 368 observations

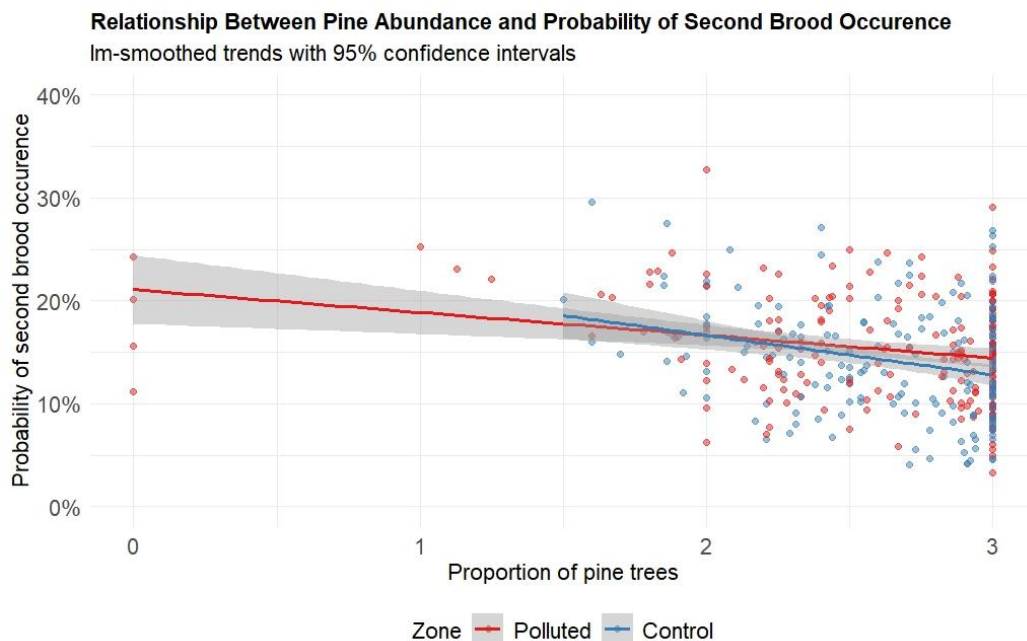


Figure 6: Relationship between pine tree abundance and the probability of occurring second brood in polluted and control areas. The red regression line represents the polluted zone, and the blue regression line represents the control zone of the model's predicted values, surrounding grey coloured 95% confidence level. Sample size = 368 observations.

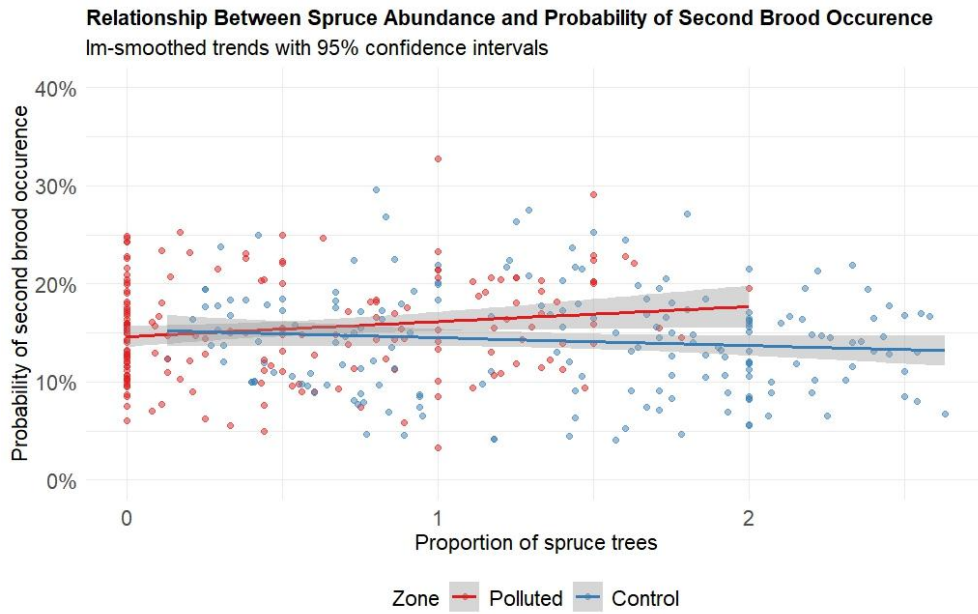


Figure 7: Relationship between spruce tree abundance and the probability of occurrence of second brood in polluted and control areas. The red regression line represents the polluted zone, and the blue regression line represents the control zone of the model's predicted values, surrounding grey coloured 95% confidence level. Sample size = 368 observations.

4 Discussion

The number of reproductive attempts in a breeding season is an important factor of fecundity and individuals' fitness of a multiple-brooded species. Since the double brooding is facultative, the second reproduction attempt can be changed with the environmental conditions (Williams, 1966). According to the life-history theory, when reproductive investment is high, there is a trade-off between present and future reproductive efforts. The purpose of this study was to assess the factors influencing on second brood probability of great tits along the pollution gradient.

4.1 Impact of nest density

The results of this study show that breeding density was the strongest predictor of second brood probability (Figure 4). A possible explanation for this might be intraspecific competition for resources, limiting multi-brooding. Great tits are territorial (Both & Visser, 2000) and mainly insectivorous passerines, nestling diet consisting primarily of caterpillars, followed by spiders and other invertebrates, making caterpillars a critical source of survival (Naef-Daenzer et al., 2000). When the local population density increases, the demand for the prey increases, resulting local competition. A strong relationship between food availability and breeding success of great tits has been reported by a study, tested food limitation hypothesis through a experimental set up offer supplementary diet (meal worms) to great tit nestlings. That study found that the supplemented nestlings had larger body size and enhanced survival rate. Another interesting result was that nestlings of supplemented broods in human-altered habitats had equal body size and survival rate to nestlings of forest control great tit broods (Seress et al., 2020). When the resources are poor in the territory and competition is higher, parents have to invest more energy in parental provisioning, which can result in reduced probability of a second breeding attempt, as the “cost of reproduction hypotheses” predicts (Tremblay et al., 2005; Williams, 1966).

Another study shows density-dependent clutch size reduction in central European great tit populations (Sasvári et al., 1992) and this negative relationship suggests that competition for resources limits multi-brooding. A 27-year data set on savannah sparrows (*Passerculus sandwichensis*) also revealed that high local breeding density resulted decreased probability of second brooding, declined seasonal fledging success, and increased nest predation rate (Woodworth et al., 2017).

Harjavalta copper smelter and the surrounding area have been studied by our research group since 1991. There was a gradual increase in great tit nest density by three times (0.8/ha to 2.4/ha) from 1991 to 2011 (Eeva & Lehikoinen, 2013). Pied flycatchers (*Ficedula hypoleuca*) and blue tits (*Cyanistes caeruleus*) also nest in the nest boxes provided in the area and have been continuously monitored.

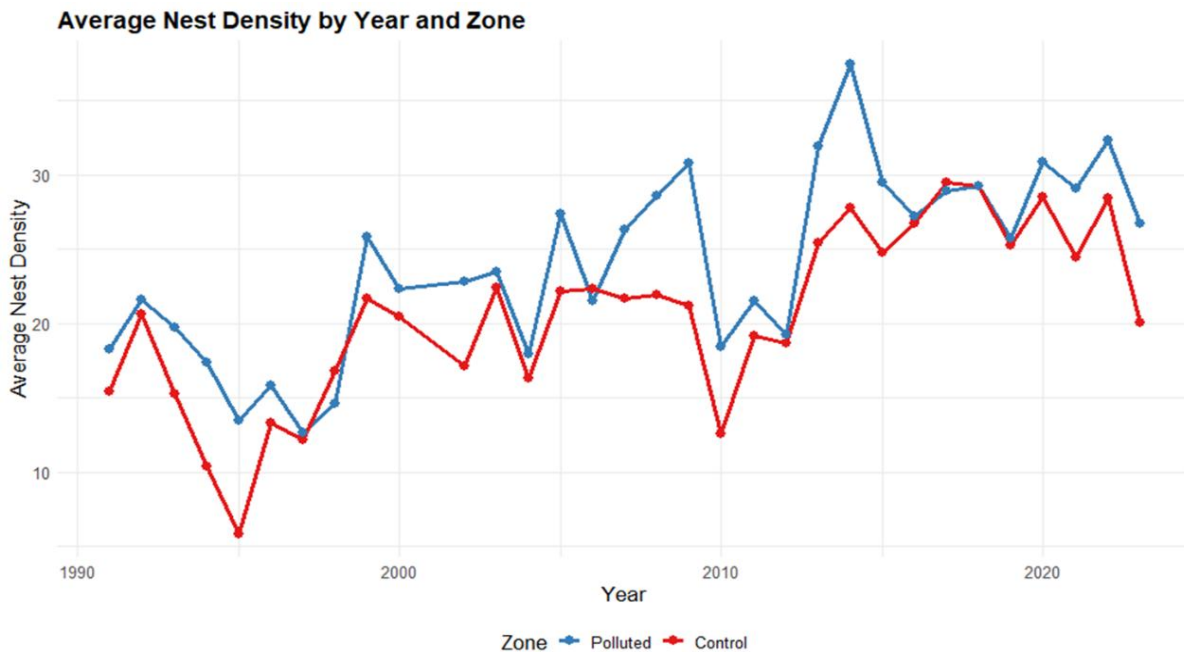


Figure 8: Temporal changes in average nest density (average number of occupied nests per nest box site) of great tits in the study area. Red line represents the control zone, and blue line represents the polluted zone

What can be seen in the long-term data of this great tit population is general temporal pattern of rising of the nest density of great tits (Figure 8). Therefore, reduced probability of second broods likely reflects increased population density and more intense interspecific competition.

4.2 Timing of breeding and temporal trends

This study detects a significant relationship between the first egg-laying date and the probability of the occurrence of double brood. In other words, early laying birds tend to be more likely to commence a second breeding attempt. This finding is aligned with previous studies about the “date hypothesis,” suggesting that the first egg laying date for the season has a significant impact on reproductive success (Verboven & Verhulst, 1996). To date, several studies have indicated that early breeding is beneficial because the timing of breeding synchronizes with food availability (peak abundance of caterpillars) and increases the probability of multiple brooding (Barba et al., 1995; Hinks et al., 2015; Nomi et al., 2018).

Another key factor is climate change. Warming climate has altered the timing of breeding. Rock sparrow (*Petronia petronia*) in the Alpine region has extended the length of the breeding season by approximately 1.5 days per year during 1991 – 2013, and this expansion caused to increase the frequency of laying second clutch from 14% to 25%. However, there was no significant trend of laying date of the first clutch over the period (Mingozzi et al., 2022)

Great tits egg laying date of first clutch advanced by 2.2 days in the polluted area in Harjavalta within 20 years (Eeva & Lehikoinen, 2013). An experimental study tested date hypotheses using tree swallows (*Tachycineta bicolor*) revealed late-breeding individuals facing seasonal decline in resources tend to have lesser reproductive success than the early-breeders (Harriman et al., 2017). When resources are lacking in the habitats, parents may invest more in post-fledgling care of the first breeding attempt and trade off second broods to ensure quality rather than quantity (Grüebler & Naef-Daenzer, 2010). Another explanation is individual variation and the age of the parents (often called “individual quality hypothesis”). Studies showed that early breeders are more competent and experienced, and the age of the males positively correlated to commencing second brood (Nomi et al., 2018) Quality individuals may start breeding early and commence a second breeding attempt in the same season.

4.3 Impact of pollution

The most unexpected finding to emerge from the analysis is absence of a significant different in the probability of double brooding in two zones around polluting industry, as seen in Figure 2. However, the findings of current study do not support the previous research regarding heavy metal pollution impact on avian breeding. This result might be explained by the fact that intense density–dependent effect may overshadow the impact on pollution (zone effect).

Another explanation is that great tits may have improved adaptations to tolerate local environmental pollution. Several studies concluded that industrial pollution has direct negative impact on arthropod abundance (Gbarakoro et al., 2015; Tóth et al., 2023). This can affect to breeding performance through lowered food availability in breeding season rather than direct toxicity (McPeck, 2008). Moreover, Harjavalta copper smelter has reduced emissions of heavy metals and sulphur dioxide from 50 tons to 0.4 tons from 1990 to 2009 by installing new filters, causing reduced heavy metal accumulation in liver tissues of great tits and pied flycatchers (Berglund et al., 2012). Great tit and pied flycatchers improved their breeding success after decreasing the emission from the copper smelter. This is probably because rehabilitation of the vegetation and insect abundance (Eeva and Lehikoinen, 2000). A similar study done in Portugal investigated slow

recovery of heavy metal concentrations in pine needles, followed by great tit breeding success in an industrial polluted area (Costa et al., 2017)

4.4 Impact of first brood success

Current results show statistically non-significant relationship between the number of fledglings from first brood and the probability of the second brood. Figure 3 shows that there has been a steady rise in the probability of laying a second clutch when the birds had a higher number of fledglings from the first clutch. There is around 11% predicted probability of initiating a second brood when a poor number of chicks (1-2) fledged, and it reaches up to 25% when a higher number of fledglings (9-10) are produced.

This outcome is not aligned with the “cost of reproduction hypotheses,” which says higher parental investment in the first brood lowers the probability of having a second brood (Williams, 1966). An experimental study showed that parents incubating higher number of eggs in the first breeding attempt had to invest more in parental care in the nestling and fledgling periods. This depleted their energy reserves and they are less likely to initiate or care for a second clutch (De Heij et al., 2006)

Our findings supported the “individual quality hypotheses,” suggested that variation of intrinsic quality such as genetic traits, physiological conditions, caused the difference of survival and reproductive success among different individuals (Badger et al., 2023; Q. Fan et al., 2021). High-quality parents hold better foraging ability compared to poorer breeders and save energy by provisioning nestlings in more effective ways (Lescroël et al., 2010). Age of the female may be playing a role in determining the probability of a second brood. Adult great tit females tend to lay eggs earlier with larger clutch sizes when compared to young females (Jarvinen, 1991). On the other hand, females that laid first clutch early and had larger first clutch and raised nestlings with higher body mass were more likely to have a second brood (Verboven & Verhulst, 1996). However, Interplay of habitat quality, synchronized breeding time with food availability and individual quality is important to have successful first brood and initiate a second brood.

4.5 Impact of vegetation

Pine was the most abundant tree species in our research area, followed by birch and spruce. Although abundance of tree species was excluded from the final statistical model since lack of significance ($p > 0.5$), tree abundance was plotted against the probability of having a double brood as exploratory visualizations. Pine showed a slightly negative relationship with the probability of

multi-brooding (Figure 6), whereas spruce showed no clear relationship (Figure 7), and birch indicated positive relationship (Figure 5).

It seems possible that these results are due to the ecological characteristics of the three species. Caterpillar biomass is a crucial factor of the reproductive success of great tits as it is the major dietary component of great tit nestlings (Naef-Daenzer et al., 2000; Rytönen & Krams, 2003). Tree species that accommodate higher caterpillar abundance in early spring are likely better for breeding great tits. These results match those observed in earlier study carried out in northern Finland which found the great tits enhance the foraging in birch (*Betula* spp.) trees up to 88% when they are having nestlings. The leaf arrangement of birch creates favourable conditions for gleaning caterpillars (Rytönen & Krams, 2003). In contrast to deciduous trees like birch, that has early caterpillar peaks, coniferous trees like pine, caterpillars become more abundant later in the season. In that sense, birches might enable birds to start breeding earlier (Burger et al., 2012). Pine is less favourable to arthropod communities. Additionally, in pine-rich areas, structural simplicity of the vegetation may also reduce cover and microhabitat diversity (Atemasov et al., 2024). Microclimatic changes influence on phenology of caterpillars and vegetation development could be a determining factor for breeding success (Massa et al., 2004).

4.6 Limitations of the study

This study offers some important insights into the factors associated with the probability of multi-brooding in a polluted area. Due to practical constraints, the individual bird identification could not be done for most breeding pairs, instead, annual numbers of 1st and 2nd broods per nest box site was considered as units for statistical analyses and to visualize the impact of site-specific population density on double-brooding.

The study is limited by lack of information on nestling condition, post-fledgling survival, which may be influenced differently by the environmental stressors. Although we assessed vegetation parameters such as pine, birch, and spruce, potentially important factors, such as predation pressure and food availability, were not directly taken into account. Studies show that predation pressure is an important determinant of reproductive performance, including the probability of multiple-brooding (Hua et al., 2014).

4.7 Conclusion

This long-term study with a continuous dataset for 33 years was analysed to identify factors influencing the probability of second broods along the pre-determined pollution gradient in Harjavalta copper smelter. The analysis confirmed that the production of second brood in great tits is more strongly associated with nest density than pollution level. The second major finding is the relationship between the first egg-laying date and the probability of second brood occurrence. Early breeders tend to initiate a second breeding attempt, which aligns with the studies confirming date hypotheses. Further studies could assess the long-term effect of exposure to pollutants by combining multiple ecological factors, highlighting ecological complexity and adaptation of the avian populations.

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6 Reference

- Ardia, D. R., Cooper, C. B., & Dhondt, A. A. (2006). Warm temperatures lead to early onset of incubation, shorter incubation periods and greater hatching asynchrony in tree swallows *Tachycineta bicolor* at the extremes of their range. *Journal of Avian Biology*, *37*(2), 137–142. <https://doi.org/10.1111/j.0908-8857.2006.03747.x>
- Atemasov, A., Atemasova, T., Atemasov -VNKarazin, A., & Atemasova -VNKarazin, T. (2024). Breeding bird communities of the pine forests in the forest-steppe zone. *The Journal of V. N. Karazin Kharkiv National University. Series*, *42*, 4–21. <https://doi.org/10.26565/2075-5457-2024-1>
- Badger, J. J., Bowen, W. D., Den Heyer, C. E., & Breed, G. A. (2023). Individual Quality Drives Life History Variation in a Long-Lived Marine Predator. *American Naturalist*, *202*(3), 351–367. <https://doi.org/10.1086/725451>
- Barba, E., Gil-Delgado, J. A., & Monrós, J. S. (1995). The Costs of Being Late: Consequences of Delaying Great Tit *Parus major* First Clutches. *Journal of Animal Ecology*, *64*(5), 642–651. <https://about.jstor.org/terms>
- Barton, M. G., Henderson, I., Border, J. A., & Siriwardena, G. (2023). A review of the impacts of air pollution on terrestrial birds. *Science of the Total Environment* *873*. 162136. <https://doi.org/10.1016/j.scitotenv.2023.162136>
- Basu, S. K., & Cetzal-Ix, W. (2018). Call of the wild: conservation of natural insect pollinators should be a priority. *Biodiversity* *19*(3–4), 240–243. Taylor and Francis Ltd. <https://doi.org/10.1080/14888386.2018.1523747>
- Berglund, Å. M. M., Rainio, M. J., & Eeva, T. (2012). Decreased metal accumulation in passerines as a result of reduced emissions. *Environmental Toxicology and Chemistry*, *31*(6), 1317–1323. <https://doi.org/10.1002/etc.1814>
- Berglund, Å. M. M., Rainio, M. J., & Eeva, T. (2015). Temporal trends in metal pollution: Using bird excrement as indicator. *PLoS ONE*, *10*(2). <https://doi.org/10.1371/journal.pone.0117071>
- Betts, M. G., Yang, Z., Hadley, A. S., Smith, A. C., Rousseau, J. S., Northrup, J. M., Nocera, J. J., Gorelick, N., & Gerber, B. D. (2022). Forest degradation drives widespread avian habitat and population declines. *Nature Ecology and Evolution*, *6*(6), 709–719. <https://doi.org/10.1038/s41559-022-01737-8>
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J. S. S. (2009). Generalized linear mixed models: a practical guide for ecology and

evolution. *Trends in Ecology and Evolution*, 24(3), 127–135.

<https://doi.org/10.1016/j.tree.2008.10.008>

Both, C., Ubels, R., & Ravussin, P. A. (2019). Life-history innovation to climate change: can single-brooded migrant birds become multiple breeders? *Journal of Avian Biology*, 50(5).

<https://doi.org/10.1111/jav.01951>

Both, C., & Visser, M. E. (2000). Breeding Territory Size Affects Fitness: An Experimental Study on Competition at the individual level. *Journal of Animal Ecology*, 69(6), 1021–1030.

<https://www.jstor.org/stable/2647162>

Brandolin, P. G., Blendinger, P. G., & Cantero, J. J. (2016). From relict saline wetlands to new ecosystems: Changes in bird assemblages. *Ardeola*, 63(2), 329–348.

<https://doi.org/10.13157/arla.63.2.2016.ra7>

Bründl, A. C., Sallé, L., Lejeune, L. A., Sorato, E., Thiney, A. C., Chaine, A. S., & Russell, A. F. (2020). Elevational Gradients as a Model for Understanding Associations Among

Temperature, Breeding Phenology and Success. *Frontiers in Ecology and Evolution*, 8.

<https://doi.org/10.3389/fevo.2020.563377>

Burger, C., Belskii, E., Eeva, T., Laaksonen, T., Mägi, M., Mänd, R., Qvarnström, A., Slagsvold, T., Veen, T., Visser, M. E., Wiebe, K. L., Wiley, C., Wright, J., & Both, C. (2012). Climate change, breeding date and nestling diet: How temperature differentially affects seasonal changes in pied flycatcher diet depending on habitat variation. *Journal of Animal Ecology*,

81(4), 926–936. <https://doi.org/10.1111/j.1365-2656.2012.01968.x>

Carro, M. E., Mermoz, M. E., & Fernández, G. J. (2014). Factors affecting the probability of double brooding by Southern House Wrens. *Journal of Field Ornithology*, 85(3), 227–236.

Churchill, J. E., Birker, M. L. M., Versteegh, M., Altamirano, T. A., Vásquez, R. A., & Komdeur, J. (2023). The delayed effect of climatic conditions on pre-fledging nestling haematocrit in a

suboscine species in Patagonia. *Journal of Avian Biology*, 2023(9–10).

<https://doi.org/10.1111/jav.03056>

Cornell, A., & Williams, T. D. (2016). Individual quality and double-brooding in a highly

synchronous songbird population. *Auk*, 133(2), 251–260. <https://doi.org/10.1642/AUK-15-165.1>

Costa, R. A., Gomes, T., Eira, C., Vaqueiro, J., & Vingada, J. V. (2017). Great tit response to decreasing industrial heavy metal emissions. *Ecotoxicology*, 26(6), 802–808.

<https://doi.org/10.1007/s10646-017-1811-6>

- De Heij, M. E., Van Den Hout, P. J., & Tinbergen, J. M. (2006). Fitness cost of incubation in great tits (*Parus major*) is related to clutch size. *Proceedings of the Royal Society B: Biological Sciences*, 273(1599), 2353–2361. <https://doi.org/10.1098/rspb.2006.3584>
- De Souza, S. S., Freitas, Í. N., Gonçalves, S. de O., Luz, T. M. da, Araújo, A. P. da C., Rajagopal, R., Balasubramani, G., Rahman, M. M., & Malafaia, G. (2022). Toxicity induced via ingestion of naturally-aged polystyrene microplastics by a small-sized terrestrial bird and its potential role as vectors for the dispersion of these pollutants. *Journal of Hazardous Materials*, 434. <https://doi.org/10.1016/j.jhazmat.2022.128814>
- Deromea, J., & Lindroos, A.-J. (1998). Effects of heavy metal contamination on macronutrient availability and acidification parameters in forest soil in the vicinity of the Harjavalta Cu-Ni smelter, SW Finland. *Environmental Pollution*, 99(2), 225–232. [https://doi.org/https://doi.org/10.1016/s0269-7491\(97\)00185-1](https://doi.org/https://doi.org/10.1016/s0269-7491(97)00185-1)
- Eeva, T., Lehikoinen, E. Recovery of breeding success in wild birds. *Nature* 403, 851–852 (2000). <https://doi.org/10.1038/35002672>
- Eeva, T., Belskii, E., Gilyazov, A. S., & Kozlov, M. V. (2012). Pollution impacts on bird population density and species diversity at four non-ferrous smelter sites. *Biological Conservation*, 150(1), 33–41. <https://doi.org/10.1016/j.biocon.2012.03.004>
- Eeva, T., Espín, S., Sánchez-Virosta, P., & Rainio, M. (2020). Weather effects on breeding parameters of two insectivorous passerines in a polluted area. *Science of the Total Environment*, 729. <https://doi.org/10.1016/j.scitotenv.2020.138913>
- Eeva, T., Hakkarainen, H., & Belskii, E. (2009). Local survival of pied flycatcher males and females in a pollution gradient of a Cu smelter. *Environmental Pollution*, 157(6), 1857–1861. <https://doi.org/10.1016/j.envpol.2009.01.015>
- Eeva, T., & Lehikoinen, E. (1995). Egg shell quality, clutch size and hatching success of the great tit (*Parus major*) and the pied flycatcher (*Ficedula hypoleuca*) in an air pollution gradient. *Oecologia*, 3(102), 312–323. <https://doi.org/https://doi.org/10.1007/BF00329798>
- Eeva, T., & Lehikoinen, E. (1998). Local survival rates of the pied flycatchers (*Ficedula hypoleuca*) and the great tits (*Parus major*) in an air pollution gradient. *Ecoscience*, 5(1), 46–50. <https://doi.org/10.1080/11956860.1998.11682445>
- Eeva, T., & Lehikoinen, E. (2004). Rich calcium availability diminishes heavy metal toxicity in Pied Flycatcher. *Functional Ecology*, 18(4), 548–553. <https://doi.org/10.1111/j.0269-8463.2004.00875.x>

- Eeva, T., & Lehikoinen, E. (2013). Density effect on great tit (*Parus major*) clutch size intensifies in a polluted environment. *Oecologia*, *173*, 1661–1668. <https://doi.org/10.1007/s00442-013-2732-6>
- Eeva, T., Lehikoinen, E., & Nikinmaa, M. (2003). Pollution-induced nutritional stress in birds: An experimental study of direct and indirect effects. *Ecological Applications*, *13*(5), 1242–1249. <https://doi.org/10.1890/01-5375>
- Fan, L. Q., Chen, G. L., Da, X. W., Luo, J. J., Xian, L. L., Ren, Q. M., Xie, Y. Y., & Du, B. (2017). Seasonal variation in food availability influences the breeding strategy of White-collared Blackbirds *Turdus albocinctus* on the Tibetan Plateau. *Ibis*, *159*(4), 873–882. <https://doi.org/10.1111/ibi.12506>
- Fan, Q., Mingju, E., Wei, Y., Sun, W., & Wang, H. (2021). Mate choice in double-breeding female great tits (*Parus major*): Good males or compatible males. *Animals*, *11*(1), 1–17. <https://doi.org/10.3390/ani11010140>
- Gbarakoro, T. N., Oneche, E., & Umeozor, C. O. (2015). Impact of Heavy Metals on Species Richness, Abundance and Vertical Distribution of Soil Microarthropods in Waste Dump Sites at Delta Steel Company, Warri, Nigeria. *International Journal of Environment and Resource*, *4*(0), 9. <https://doi.org/10.14355/ijer.2015.04.002>
- Grüebler, M. U., & Naef-Daenzer, B. (2010). Fitness consequences of timing of breeding in birds: Date effects in the course of a reproductive episode. *Journal of Avian Biology*, *41*(3), 282–291. <https://doi.org/10.1111/j.1600-048X.2009.04865.x>
- Habib, L., Bayne, E. M., & Boutin, S. (2007). Chronic industrial noise affects pairing success and age structure of ovenbirds *Seiurus aurocapilla*. *Journal of Applied Ecology*, *44*(1), 176–184. <https://doi.org/10.1111/j.1365-2664.2006.01234.x>
- Halupka, L., Arlt, D., Tolvanen, J., Millon, A., Bize, P., Adamík, P., Albert, P., Arendt, W. J., Artemyev, A. V., Baglione, V., Bañbura, J., Bañbura, M., Barba, E., Barrett, R. T., Becker, P. H., Belskii, E., Bolton, M., Bowers, E. K., Bried, J., ... Halupka, K. (2023). The effect of climate change on avian offspring production: A global meta-analysis. *Proceedings of the National Academy of Sciences of the United States of America*, *120*(19), e2208389120. <https://doi.org/10.1073/pnas.2208389120>
- Harriman, V. B., Dawson, R. D., Bortolotti, L. E., & Clark, R. G. (2017). Seasonal patterns in reproductive success of temperate-breeding birds: Experimental tests of the date and quality hypotheses. *Ecology and Evolution*, *7*(7), 2122–2132. <https://doi.org/10.1002/ece3.2815>

- Hinks, A. E., Cole, E. F., Daniels, K. J., Wilkin, T. A., Nakagawa, S., & Sheldon, B. C. (2015). Scale-Dependent Phenological Synchrony between Songbirds and Their Caterpillar Food Source. *The American Naturalist*, *186*(1). <https://doi.org/10.5061/dryad.n6g3q>
- Hoang, T., & Mitten, S. (2022). Microplastic accumulation in the gastrointestinal tracts of nestling and adult migratory birds. *Science of the Total Environment*, *838*. <https://doi.org/10.1016/j.scitotenv.2022.155827>
- Hua, F., Sieving, K. E., Fletcher, R. J., & Wright, C. A. (2014). Increased perception of predation risk to adults and offspring alters avian reproductive strategy and performance. *Behavioral Ecology*, *25*(3), 509–519. <https://doi.org/10.1093/beheco/aru017>
- Jackson, P., & Cresswell, W. (2017). Factors determining the frequency and productivity of double brooding of Barn Owls *Tyto alba*. *Bird Study*, *64*(3), 353–361. <https://doi.org/10.1080/00063657.2017.1363716>
- Jarvinen, A. (1991). A meta-analytic study of the effects of female age on laying-date and clutch-size in the Great Tit *Parus major* and the Pied Flycatcher *Ficedula hypoleuca*. *Ibis* *133*(1), 62–67. <https://doi.org/10.1111/j.1474-919X.1991.tb04811.x>
- Kight, C. R., & Swaddle, J. P. (2007). Associations of anthropogenic activity and disturbance with fitness metrics of eastern bluebirds (*Sialia sialis*). *Biological Conservation*, *138*(1–2), 189–197. <https://doi.org/10.1016/j.biocon.2007.04.014>
- Kiikkilä, O. (2003). Heavy-metal Pollution and Remediation of Forest Soil around the Harjavalta Cu-Ni Smelter, in SW Finland. *Silva Fennica*, *37*(3). <https://doi.org/10.14214/sf.497>
- La Sorte, F. A., Fink, D., & Johnston, A. (2019). Time of emergence of novel climates for North American migratory bird populations. *Ecography*, *42*(6), 1079–1091. <https://doi.org/10.1111/ecog.04408>
- Lehikoinen, A., Lindén, A., Karlsson, M., Andersson, A., Crewe, T. L., Dunn, E. H., Gregory, G., Karlsson, L., Kristiansen, V., Mackenzie, S., Newman, S., Røer, J. E., Sharpe, C., Sokolov, L. V., Steinholtz, Å., Stervander, M., Tirri, I. S., & Tjørnløv, R. S. (2019). Phenology of the avian spring migratory passage in Europe and North America: Asymmetric advancement in time and increase in duration. *Ecological Indicators*, *101*, 985–991. <https://doi.org/10.1016/j.ecolind.2019.01.083>
- Lescroël, A., Ballard, G., Toniolo, V., Barton, K. J., Wilson, P. R., O', P., Lyver, B., & Ainley, D. G. (2010). Working less to gain more: when breeding quality relates to foraging efficiency. *Ecology*, *91*(7), 2044–2055. <http://www.jstor.org/stable/25680458>
- Massa, B., Lo Valvo, F., Margagliotta, B., & Lo Valvo, M. (2004). Adaptive plasticity of blue tits (*Parus caeruleus*) and great tits (*Parus major*) breeding in natural and semi-natural insular

- habitats. *Italian Journal of Zoology*, 71(3), 209–217.
<https://doi.org/10.1080/11250000409356574>
- Maziarz, M., Wesołowski, T., Hebda, G., & Cholewa, M. (2015). Natural nest-sites of Great Tits (*Parus major*) in a primeval temperate forest (Białowieża National Park, Poland). *Journal of Ornithology*, 156(3), 613–623. <https://doi.org/10.1007/s10336-015-1169-6>
- McPeck, M. A. (2008). Ecological factors limiting the distribution and abundances of Odonata. In A. Córdoba-Aguilar (Ed.), *Dragonflies and damselflies: Model organisms for ecological and evolutionary research* (pp. 51–62). Oxford University Press.
- Mingozzi, T., Storino, P., Venuto, G., Massolo, A., & Tavecchia, G. (2022). Climate warming induced a stretch of the breeding season and an increase of second clutches in a passerine breeding at its altitudinal limits. *Current Zoology*, 68(1), 9–17.
<https://doi.org/10.1093/cz/zoab029>
- Mohanty, B. (2024). Pesticides exposure and compromised fitness in wild birds: Focusing on the reproductive endocrine disruption. In *Pesticide Biochemistry and Physiology* (Vol. 199). Academic Press Inc. <https://doi.org/10.1016/j.pestbp.2024.105800>
- Monclús, L., McCann Smith, E., Ciesielski, T. M., Wagner, M., & Jaspers, V. L. B. (2022). Microplastic Ingestion Induces Size-Specific Effects in Japanese Quail. *Environmental Science and Technology*, 56(22), 15902–15911. <https://doi.org/10.1021/acs.est.2c03878>
- Naef-Daenzer, L., Naef-Daenzer, B., & Nager, R. G. (2000). Prey selection and foraging performance of breeding Great Tits *Parus major* in relation to food availability. *Journal of Avian Biology*, 31(2), 206–214. <https://doi.org/10.1034/j.1600-048X.2000.310212.x>
- Nagy, L. R., & Holmes, R. T. (2004). Factors influencing fecundity in migratory songbirds: Is nest predation the most important? *Journal of Avian Biology*, 35(6), 487–491.
<https://doi.org/10.1111/j.0908-8857.2004.03429.x>
- Newson, S., Mendes, S., Crick, H., Dulvy, N., Houghton, J., Hays, G., Hutson, A., Macleod, C., Pierce, G., & Robinson, R. (2009). Indicators of the impact of climate change on migratory species. *Endangered Species Research*, 7(May), 101–113. <https://doi.org/10.3354/esr00162>
- Nomi, D., Yuta, T., & Koizumi, I. (2018). Facultative multiple breeding as a female conditional strategy in Japanese tits: partner's quality affects the initiation of second clutches. *Ecological Research*, 33(2), 479–485. <https://doi.org/10.1007/s11284-018-1565-5>
- Northrup, J. M., Rivers, J. W., Yang, Z., & Betts, M. G. (2019). Synergistic effects of climate and land-use change influence broad-scale avian population declines. *Global Change Biology*, 25(5), 1561–1575. <https://doi.org/10.1111/gcb.14571>

- Parmesan, C. (2006). Ecological and Evolutionary Responses to Recent Climate Change. *Annual of Ecology, Evolution and Systematics*, 37(2006), 637–669.
<https://doi.org/10.2307/annurev.ecolsys.37.091305.30000024>
- Pirinen, P., Simola, H., Aalto, J., Kaukoranta, J.-P., Karlsson, P., & Ruuhela, R. (2012). *Tilastoja Suomen ilmastosta 1981-2010*. <http://hdl.handle.net/10138/35880>
- Reed, T. E., Jenouvrier, S., & Visser, M. E. (2013). Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. *Journal of Animal Ecology*, 82(1), 131–144. <https://doi.org/10.1111/j.1365-2656.2012.02020.x>
- Rhind, S. M. (2009). Anthropogenic pollutants: A threat to ecosystem sustainability? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1534), 3391–3401.
<https://doi.org/10.1098/rstb.2009.0122>
- Ruiz, S. R., Espín, S., Sánchez-Virosta, P., Salminen, J. P., Lilley, T. M., & Eeva, T. (2017). Vitamin profiles in two free-living passerine birds under a metal pollution gradient – A calcium supplementation experiment. *Ecotoxicology and Environmental Safety*, 138, 242–252. <https://doi.org/10.1016/j.ecoenv.2016.12.037>
- Rytkönen, S., & Krams, I. (2003). Does foraging behaviour explain the poor breeding success of great tits *Parus major* in northern Europe? *Journal of Avian Biology*, 34(3), 288–297.
<https://doi.org/10.1034/j.1600-048X.2003.03041.x>
- Salemaa, M., Vanha-Majamaa, I., & Derome, J. (2001). Understorey vegetation along a heavy-metal pollution gradient in SW Finland. *Environmental Pollution*, 112(3), 339–350.
[https://doi.org/10.1016/s0269-7491\(00\)00150-0](https://doi.org/10.1016/s0269-7491(00)00150-0)
- Sasvári, L., Orell, M., Sasvairi, L., Sasvairi, M. O., Orell, L., & Sasvdri, L. (1992). Breeding Success in a North and a Central European Population of the Great Tit *Parus major*. *Ornis Scandinavica*, 23(1), 96. <http://www.jstor.org/stable/3676432> .
- Seress, G., Sándor, K., Evans, K. L., & Liker, A. (2020). Food availability limits avian reproduction in the city: An experimental study on great tits *Parus major*. *Journal of Animal Ecology*, 89(7), 1570–1580. <https://doi.org/10.1111/1365-2656.13211>
- Skaldina, O., Cizek, R., Peräniemi, S., Kolehmainen, M., & Sorvari, J. (2020). Facing the threat: common yellow jacket wasps as indicators of heavy metal pollution. *Environmental Science and Pollution Research*, 27(23), 29031–29042. <https://doi.org/10.1007/s11356-020-09107-2>
- Tóth, Z., Dombos, M., & Hornung, E. (2023). Urban soil quality deteriorates even with low heavy metal levels: An arthropod-based multi-indices approach. *Ecological Applications*, 33(4).
<https://doi.org/10.1002/eap.2848>

- Tremblay, I., Thomas, D., Blondel, J., Perret, P., & Lambrechts, M. M. (2005). The effect of habitat quality on foraging patterns, provisioning rate and nestling growth in Corsican Blue Tits *Parus caeruleus*. *Ibis*, *147*(1), 17–24. <https://doi.org/10.1111/j.1474-919x.2004.00312.x>
- Turzańska-Pietras, K., Chachulska, J., Polechońska, L., & Borowiec, M. (2018). Does heavy metal exposure affect the condition of Whitethroat (*Sylvia communis*) nestlings? *Environmental Science and Pollution Research*, *25*(8), 7758–7766. <https://doi.org/10.1007/s11356-017-1064-1>
- Verboven, N., & Verhulst, S. (1996). Seasonal Variation in the Incidence of Double Broods: The Date Hypothesis Fits Better than the Quality Hypothesis. *Journal of Animal Ecology*, *65*(3), 264–273. <https://doi.org/10.2307/5873>
- Weiskopf, S. R., Rubenstein, M. A., Crozier, L. G., Gaichas, S., Griffis, R., Halofsky, J. E., Hyde, K. J. W., Morelli, T. L., Morissette, J. T., Muñoz, R. C., Pershing, A. J., Peterson, D. L., Poudel, R., Staudinger, M. D., Sutton-Grier, A. E., Thompson, L., Vose, J., Weltzin, J. F., & Whyte, K. P. (2020). Climate change effects on biodiversity, ecosystems, ecosystem services, and natural resource management in the United States. *Science of the Total Environment*, *733*, 137782.. <https://doi.org/10.1016/j.scitotenv.2020.137782>
- Williams. (1966). Natural Selection, the Costs of Reproduction, and a Refinement of Lack's Principle. *The American Naturalist*, *100*(916), 687–690. <https://doi.org/10.1086/282461>
- Woodworth, B. K., Wheelwright, N. T., Newman, A. E. M., & Norris, D. R. (2017). Local density regulates migratory songbird reproductive success through effects on double-brooding and nest predation. *Ecology*, *98*(8), 2039–2048. <https://doi.org/10.1002/ecy.1911>
- Youngflesh, C., Montgomery, G. A., Saracco, J. F., Miller, D. A. W., Guralnick, R. P., Hurlbert, A. H., Siegel, R. B., LaFrance, R., & Tingley, M. W. (2023). Demographic consequences of phenological asynchrony for North American songbirds. *Proceedings of the National Academy of Sciences of the United States of America*, *120*(28). <https://doi.org/10.1073/pnas.2221961120>

Tools and Resources Used in the Research and Writing Process

AI powered tools

Keenious - To find relevant research papers

Sci space - To find research papers and summarize them using a synthesis table

Copilot- To understand technical terms and parts of research papers

Chat GPT - To generate an outline for the introduction as a reference to build my own outline.

Compare and contrast different statistical methods.

Other websites (without AI)

Grammarly (word-plugin free version) - To correct grammar, spelling, and punctuation.

www.powerthesaurus.org/ - Thesaurus website

www.phrasebank.manchester.ac.uk – Academic phrasebank