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# Abstract

Inbreeding depression (a decrease in individual fitness caused by inbreeding) has been observed in a wide range of species, but its mechanisms remain unclear. In addition, this topic tends to be studied in captive populations, where ecological determinants of fitness are difficult to evaluate. In this study, I investigated the impact of inbreeding on onset of breeding in a natural metapopulation of house sparrows (*Passer domesticus*), a multi-brooded passerine. I used linear mixed effects models and Cox proportional hazards models, and selected the best performing models using AIC-based model comparison. Individual onset of breeding (lay date of the first egg of the first clutch of the season) was better predicted by models which include maternal experience, habitat, and population density. Females with a higher inbreeding coefficient did not lay their first clutch of the season later than less inbred birds. The deviation of a female's onset of breeding from the population's mean onset of breeding in a given year was better predicted by models which include cumulative degree days, habitat, maternal inbreeding, and the interaction between maternal inbreeding and cumulative degree days. More inbred females showed a smaller deviation from the mean lay date at colder temperatures. These results suggest that inbreeding does not affect mean lay date in this metapopulation, but that it has a temperature-dependent impact on variation in lay date, which deserves further exploration.



# Sammendrag

Innavlsdepresjon (en reduksjon i individuell fitness forårsaket av innavl) har blitt observert hos mange ulike arter, men mekanismene som gir innavlsdepresjon er fremdeles uklare. Innavl og innavlsdepresjon studeres vanligvis i populasjoner i fangenskap, hvor økologiske faktorene som påvirker fitness er vanskelige å evaluere. I denne studien undersøker jeg effekten av innavl på tidspunkt for hekkestart i en naturlig metapopulasjon av gråspurv (*Passer domesticus*), en spurvefugl som kan ha flere kull i løpet av en hekkesesong. Jeg brukte lineære miksede modeller og Cox proporsjonal hazard modell, og valgte de beste modellene ved å bruke AIC-basert modellsammenligning. Variasjon i individuell hekkestart (eggleggingsdato for første kulls første egg) ble best forklart av modeller som inkluderte morens erfaring, habitat-type og populasjonstetthet. Hunn-spurver med en høyere innavlskoeffisient la ikke sitt første kull senere i sesongen sammenlignet med mindre innavlede fugler. Variasjon i hunn-spurvers avvik fra en populasjons gjennomsnittlige hekkestart i et gitt år ble bedre forklart av modeller som inkluderte kumulative grad-dager, habitat-type, morens innavlsgrad, og interaksjonen mellom morens innavlsgrad og kumulative grad-dager. Mer innavlede hunn-spurver hadde et mindre avvik fra gjennomsnittlig eggleggingsdato ved kaldere temperaturer. Disse resultatene tilsier at innavl ikke har noen effekt på gjennomsnittlig hekkestart i denne metapopulasjonen, men at det har en temperatur-avhengig effekt på variasjon i eggleggingstidspunkt, noe som er verdt å utforske videre.





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And, of course, thanks to the generations of sparrows who, year after year, grumpily let us catch a glimpse of their world.



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# 1 Introduction

Inbreeding is caused by mating among close relatives (Keller et al., 2002). At the population level, this leads to an increase in homozygosity without a change in allele frequency. Inbred individuals have a higher than average proportion of homozygous loci, and this often negatively impacts fitness and fitness-related traits, a phenomenon called inbreeding depression. Inbreeding depression can have strong negative effects on population demography and increase extinction risk (O’Grady et al., 2006; Hedrick et al., 2016). Inbreeding depression is thought to be caused mainly by the expression of deleterious recessive or partially recessive alleles that are normally found at low frequency in a population (unmasking of genetic load), or by a lack of overdominance when heterozygotes enjoy higher fitness than homozygotes (Charlesworth et al., 1999; Lande, 1994; Roff, 2002; Charlesworth et al., 2009; Hedrick et al., 2016).

Inbreeding depression has mostly been studied in domesticated or captive species, in part due to the importance of this topic for agriculture and animal husbandry (e.g. Howard et al., 2017) and to captive animals being more readily available for study (Lacy et al., 1993). Studies of domesticated, captive animals are often easier to conduct; domesticated animals often show high levels of inbreeding due to artificial selection for desirable traits, while zoo animals are inbred due to a low number of available mates; their pedigrees are often well-documented, and they are easy to access and handle. By contrast, there has been much less research into the consequences of inbreeding depression in natural populations (Neaves et al., 2015). Yet, studies in well-fed, captive populations reveal little of the challenges faced by inbred individuals in natural environments (Bijlsma et al., 2000; Joron et al., 2003; Keller et al., 1994; Miller, 1994). Indeed, inbreeding depression tends to be stronger in wild populations compared to their captive zoo conspecifics (Crnokrak et al., 1999). Stressful environments are known to exacerbate inbreeding depression (Miller, 1994; Armbruster et al., 2005; de Boer et al., 2015); zoo animals are provided with abundant resources and shelter, and typically experience less stressful environments than their wild conspecifics, which could help explain their lower rates of inbreeding depression (Frankham, 2010). Higher inbreeding depression has been shown to increase

extinction risk in wild populations (Frankham, 2005). Given the current rate of decline of animal populations around the world (Hallmann et al., 2017; Lambertini, 2020; Rosenberg et al., 2019), there is an urgent need to better understand how shrinking or fragmented populations are affected by inbreeding (Keller et al., 2002). However, measuring inbreeding in wild populations has historically been difficult, due to the initial need to calculate it using pedigrees, which are difficult to obtain. In addition, mistakes in pedigrees can reduce their usefulness (e.g. Hammerly et al., 2013). Fortunately, genomic methods are becoming more accessible and make it possible to measure actual levels of homozygosity in wild individuals without a pedigree (Kardos et al., 2016).

Inbreeding depression tends to be stronger for life-history traits than for morphological traits (DeRose et al., 1999). In several bird species, inbreeding has been linked to reduced individual fitness due to lower hatching rates, lower chick survival, and lower offspring recruitment into the breeding population. Most studies to date have focused on hatching failure and, more generally, on the fate of the offspring of matings between relatives (Noordwijk et al., 1981; Spottiswoode et al., 2004; Jensen et al., 2007). For instance, a study in a population of great reed warblers (*Acrocephalus arundinaceus*) in Sweden showed that eggs were less likely to hatch when parents were genetically similar, that is, when the offspring have high inbreeding levels (Bensch et al., 1994). In a population of collared flycatchers (*Ficedula albicollis*), also in Sweden, inbreeding in the offspring of related parents led to increased rates of hatching failure as well as lower chick survival and recruitment (Kruuk et al., 2002).

Several studies have highlighted the need to explore the consequences of inbreeding throughout an individual's entire life cycle. In a cross-fostering experiment involving captive zebra finches (*Taeniopygia guttata*), most of the extra mortality caused by inbreeding occurred early in development, in the embryo stage; hatching failure, in this case, was not due to egg infertility but to low embryo survival (Hemmings et al., 2012). In a natural population of great tits (*Parus major*) in Belgium, individuals that mated with relatives did not experience any lifetime decrease in their reproductive success (Van de Casteele et al., 2003). However, in a population of the same species in England, the deleterious impact of inbreeding depression differed depending on life-history stages, with grand-offspring recruitment more strongly impacted than offspring recruitment (Szulkin et al., 2007). Therefore, matings between relatives did not impact these relatives' own lifetime reproductive success (LRS), but did reduce that of their inbred offspring.

Indeed, inbreeding depression can also increase based on environmental variables, for instance under situations of environmental stress (Pray et al., 1994; Armbruster et al., 2005; Cheptou et al., 2011). In British Columbia, a population of song sparrows (*Melospiza melodia*) was found to be more outbred following two population crashes due to harsh winter weather, indicating that inbred individuals suffered from particularly low fitness in these challenging circumstances (Keller et al., 1994). The impact of inbreeding on fitness in natural populations is therefore complex, and is likely to be dependent on many variables, highlighting the need to explore its impact on a variety of traits across the lifecycle in natural populations.

While many studies have investigated the fate of inbred offspring, the impact of inbreeding on the onset of breeding has received little attention, and onset of breeding is typically included in inbreeding studies as a predictor, rather than a response variable of interest (e.g. Van de Castele et al., 2003; White et al., 2015). Yet, in one insular population of song sparrows in British Columbia, females with a coefficient of inbreeding ( $F$ ) of 0.25 bred 7 to 17 days later than non-inbred females, depending on spring temperatures (Germain et al., 2016; Marr et al., 2006). This is a large difference, considering the short time window available for breeding in seasonal environments, and suggests that this topic deserves further scrutiny.

In seasonal environments, birds need to time the laying of their eggs in order for chick rearing to coincide with abundant food sources (Blondel et al., 1999; Lack, 1950; Lambrechts et al., 1997; Martin, 1987). Photoperiod has been proposed as a major cue for birds to time onset of breeding (Lambrechts et al., 1997), but cannot explain differences in onset of breeding across years in the same population, since it does not vary across years. In species that feed arthropods to their young, arthropod availability is an important determiner of breeding success (Naef-Daenzer et al., 2000; Verboven, N. et al., 2001). A mismatch between onset of breeding and arthropod availability can have a steep fitness cost for parents, due to poorer chick condition (Samplonius et al., 2016) or increased energy expenditure for the feeding parents (Thomas et al., 2001). Arthropods are ectotherms and their phenology depends directly on temperature (Frazier et al., 2006; Huey et al., 2001). Temperature is therefore an important predictor of onset of breeding in many bird species (Meijer et al., 1999; Shutt et al., 2019; Visser et al., 1998; Visser et al., 2006; Visser et al., 2009). More broadly, there is now a large body of evidence showing that climate change affects the timing of breeding in birds, with an overall trend for earlier breeding, indicating that breeding onset is shifting to track changes in peak arthropod abundance (Both et al., 2004; Møller et al., 2010).

Numerous studies have shown that delayed first clutches lead to lower offspring recruitment into the population, thus confirming the importance of onset of breeding in birds (see e.g. Verboven et al., 1998; Verhulst et al., 2008). In multi-brooded species, late breeding has consequences on offspring quality and clutch size as well as on total number of clutches (Westneat et al., 2009). For instance, a study of great tits showed that pairs whose breeding was delayed by house sparrows (*Passer domesticus*) attempting to nest in their nesting site had fewer offspring, and that these offspring were of lower quality (Barba et al., 1995). In a cross-fostering experiment in the same species, birds that raised their first brood late had a lower chance of a laying second clutch compared to birds that raised it early (Verboven et al., 1996). Therefore, delayed laying decreases the chance of further breeding attempts in the same season in multi-brooded birds (Lack, 1950). On the other hand, if a brood hatches too early, parents may have difficulty providing adequate nutrition to their chicks, and chick quality and survival are expected to decrease. Lower temperatures associated with early onset of breeding also increase the metabolic expenditure of the laying female, at a time when egg production already places increased energetic demands upon her (Salvante et al., 2010).

Arthropod availability and phenology are disrupted by anthropogenic climate change (Boggs, 2016). This puts many bird species at risk of experiencing trophic mismatch if they do not adjust their lay date accordingly (Durant et al., 2007; Visser et al., 1998; Visser et al., 2006). At the level of individuals, a failure to track changes in the timing of arthropod emergence may have a large impact on lifetime reproductive success. Therefore, if it is caused by inbreeding, delayed onset of breeding may contribute to inbreeding depression in these species.

In this study, I use data from a long-term study of a house sparrow metapopulation to explore whether inbreeding affects the timing of first clutches. House sparrows are multi-brooded and rely on arthropods to rear their chicks (Anderson, 2006). Timing of breeding is therefore crucial for annual and lifetime reproductive success in this species. The data analysed in this study were collected between 2003 and 2012 on 8 islands that are part of a larger island system. There is occasional natal dispersal between islands, but all breeding events happen within subpopulations, and most birds show some degree of inbreeding (Niskanen et al., 2020; Pärn et al., 2009). Inbreeding depression has been shown to occur in our study system, with higher coefficients of inbreeding associated with higher mortality and lower recruit production (Niskanen et al., 2020; Jensen et al., 2007; Billing et al., 2012). Crucially, inbreeding depression (more specifically here, the negative impact of a given unit of inbreeding on fitness components such as annual survival and recruit production)



shows both temporal and spatial consistency across populations (Niskanen et al., 2020). This makes it possible to investigate its consequences at the level of the metapopulation and thus to take advantage of a larger, more varied dataset, while controlling for spatiotemporal variation in onset of breeding.

I investigate the potential for more inbred individuals to experience greater trophic mismatch than their less inbred conspecifics by testing the following main hypotheses:

1. *Females with higher coefficients of inbreeding lay their first clutch later in the season, compared to females with lower coefficients of inbreeding.* As discussed above, delayed breeding in this species is likely to lead to lower offspring recruitment in the season, as it reduces the time available for raising successful second and third clutches.

2. *Females with higher coefficients of inbreeding deviate more from the population's mean onset of laying, compared to females with lower coefficients of inbreeding.* Effectively, this means that more inbred females should have difficulty tracking the most optimal breeding time, rather than merely shifting their onset of laying.



## 2 Methods

### 2.1 Study species

The house sparrow is a multi-brooded altricial passerine. House sparrows are sedentary and live and breed in colonies in close proximity with human settlements (Anderson, 2006; Ringsby et al., 2006). They show low dispersal; in our study system, less than 10% of individuals disperse, and nearly all of them do so before their first breeding attempt (Altwegg et al., 2000; Pärn et al., 2009; Tufto et al., 2005). House sparrows also display high nest site fidelity and often make use of nest boxes when these are provided, making it possible to closely track their breeding habits (Ringsby et al., 1998).

The diet of adult house sparrows consists mostly of grains, with seeds becoming important food sources in the autumn and winter months, and arthropods in spring and summer, during the breeding season (Anderson, 2006). By contrast, young nestlings are raised on a diet composed largely of arthropods (with estimates ranging from 70 to 100% of arthropod prey in the first five days); as nestlings grow older, the proportion of plant material in their diet increases (Anderson, 2006). Incubation lasts 11 days on average and chicks fledge about 13 to 14 days after hatching (Anderson, 2006; Ringsby et al., 1998; McGillivray, 1983). The interbrood interval (the time between the fledging of the last chick and the laying of the first egg of the next brood) is around 7 to 10 days (Anderson, 1994; McGillivray, 1983; Veiga, 1996). Therefore, the total time between a first and a second brood is estimated to be between 31 and 35 days.

In our study area, female house sparrows lay from one to three clutches each season, and each clutch is comprised of 4.6 eggs on average (Ringsby et al., 1998; Husby et al., 2006). The first eggs of the season are typically laid in early May, and the season ends in mid-August. House sparrows are socially monogamous, and pairs often form for the duration of the breeding season, although this is suspected to be mainly a consequence of nesting site fidelity (Anderson, 2006). Extra-pair paternity

has been demonstrated repeatedly in this species and varies considerably between populations (Veiga et al., 2000; Cordero et al., 1999; Griffith et al., 1999).

## 2.2 Study system and area

Sparrow populations in the Helgeland archipelago, which straddles the Arctic Circle off the coast of Norway (66°N, 13°E), have been studied since 1993 (Ringsby et al., 1998). The core of these efforts is the marking and subsequent re-capturing of individuals. When first caught, nestlings (approximately 11 days old), fledged juveniles and adults are marked with a numbered metal ring and a unique combination of three colored plastic rings, for future identification. For each island, the proportion of birds that are marked is very high (>90%) (Kvalnes et al., 2013).

The data were collected on 8 islands in the study system (see Figure A.1 for a map). On 5 of the islands (Aldra, Gjerøy, Hestmannøy, Indre Kvarøy, Nesøy), sparrow colonies are found on cattle farms, where they find shelter (“farm islands”). On the remaining 3 islands (Myken, Træna, and Selvær), there are no cattle farms, and birds live around villages where they may receive supplemental feeding from local residents (“non-farm islands”).

Data from 569 clutches, collected over 10 years (2003 - 2012), were included in the study. In 2003, data from only 5 of the islands (Aldra, Gjerøy, Hestmannøy, Indre Kvarøy, and Selvær) were available. The 2006 data for Indre Kvarøy were excluded, since concerns around disease in cattle that year delayed the data collection and many first clutches are likely to have been missed. Indeed, that year had the latest minimum lay date (day 147,  $n = 4$ ) across all Indre Kvarøy years, with the second latest being day 139 in 2003 ( $n = 3$ ).

## 2.3 Data collection procedure

On both types of islands, artificial nest boxes installed as part of the long-term sparrow study project are used every year by the birds to nest, but birds on farm islands also mainly nest inside of barns and cowsheds (Ringsby et al., 1998). During the reproductive season, nest boxes and barns are checked every few days to monitor egg laying efforts. Since females who have started laying usually lay one egg every day, lay date can be approximated with relatively high accuracy even if the initial observation took place a few days after the onset of laying. In cases when nestlings, rather than eggs, are observed, their age can be determined from morphological features and the lay date estimated (Husby et al., 2006).

## 2.4 Measure of inbreeding

As part of the overall monitoring of the study system, blood samples ( $25\mu\text{L}$ ) are routinely taken from the brachial vein of birds when they are first captured, either as 11-day-old nestlings or after fledging. Each female (mother) in the study was genotyped using a 200k SNP array (Lundregan et al., 2018), and a coefficient of inbreeding,  $F_{\text{GRM}}$ , was computed from these genetic data using the genomic relationship matrix (for more details, see Niskanen et al., 2020).  $F_{\text{GRM}}$  values were then standardized across the whole dataset to a mean of 0 and standard deviation of 1.  $F_{\text{GRM}}$  was used over pedigree-based measures of inbreeding as it provides a realized coefficient of inbreeding, whereas pedigrees can only estimate the expected coefficient of inbreeding. Pedigrees also require knowledge of all of an individual's grandparents, which in practice can be difficult to achieve. In addition, some studies have also shown that homozygosity can be a better predictor of inbreeding depression than pedigree (Hemmings et al., 2012; Niskanen et al., 2020).

## 2.5 Lay date and deviation in lay date

Lay date is defined as the number of the day on which the first egg in a clutch was laid, using the Julian calendar, where January 1<sup>st</sup> is coded as day 1. To reduce the risk of accidental inclusion of second clutches in the analysis, and since the time between the laying of the first egg of a clutch and that of the laying of the first egg of the next clutch is around 35 days, I excluded 5 clutches that had been laid more than 35 days after the mean lay date for the whole dataset. In addition, I also use a measure of the *deviation* in lay date, obtained by comparing an individual's lay date ( $LD$ ) to the mean lay date for the island that year ( $\overline{LDV}$ ):

$$LDV_{ij} = (LD_{ij} - \overline{LD}_j)^2$$

where  $i$  is an individual's breeding attempt, and  $j$  an island on a given year. Note that the average deviation is equal to the variance of lay date in the overall sample population:

$$\overline{LDV}_j = \frac{\sum (LD_{ij} - \overline{LD}_j)^2}{N_j}$$

## 2.6 Weather variables

Weather variables have previously been shown to be predictors of onset of breeding in house sparrows (Seel, 1968). Based on previous studies, including the work

of Johansen (2018), I use several measures of weather in the analyses to control for, and estimate the impact of, weather conditions. I did not include day length in the analyses, since there is very little latitudinal variation in the dataset and day length is therefore linearly correlated with date.

Mean April temperature and mean April precipitation were obtained from the Norwegian Meteorological Institute (2021) for the meteorological station on Myken. These values were retrieved using the Frost public API. Although Myken is located on the northern edge of the study system, previous work has shown a strong correlation between the Myken temperature records and those on Sleneset, on the southern edge of the study system (Ringsby et al., 2002). We can therefore assume that the Myken data are valid for the whole area covered by this study. Cumulative degree days and onset of spring were obtained from Johansen’s work (2018). Cumulative degree days were calculated using the “average” method described by Herms (2004). An average temperature for each day between January 1<sup>st</sup> and May 1<sup>st</sup> was calculated using the mean of the minimum and maximum temperatures. For each of these days, the number of degrees Celsius above a 5 degree threshold was then added, yielding the cumulative degree days for that year. For each year, onset of spring was defined as the day when green vegetation (as estimated by the normalized difference vegetation index provided by the Northern Research Institute) reached 70% of its mean July value (averaged across 13 years from 2000 to 2012).

I also extracted an additional variable from the above four measures of weather (mean April temperature, mean April precipitation, cumulative degree days, onset of spring) using principal component analysis. This variable accounts for 63% of the variance in the original weather variables, and is negatively correlated with warmer, wetter weather (see Figure A.3).

## 2.7 Other predictors

### 2.7.1 Population density

Population density has previously been shown to affect reproductive success in passerines (Ahola et al., 2012; Gustafsson, 1987). The population size for each island for each year was estimated based on counts of adult individuals at the start of the breeding season (non-farm islands) or on the number of marked adult individuals observed that year (farm islands) (Baalsrud et al., 2014). In our study system, there is a strong correlation between these two methods (Baalsrud et al., 2014; Jensen et al., 2013). For each island, a relative measure of population density for each year

was then obtained by subtracting the island’s mean population size from its annual population size (mean-centering). The population counts were conducted between 1993 and 2014, so the present analyses use only a subset of this data, and the mean of the relative population size across years for a given island is not necessarily zero.

### 2.7.2 Maternal age (mother’s experience)

Several studies have shown that one-year-old female house sparrows often breed later than older females, with some failing to breed at all during their first mating season (Anderson, 2006; Seel, 1968). Peralta-Sánchez et al. (2020) found an effect of maternal, but not paternal, age on lay date. Therefore, I have included maternal age category (one year old or older) as a binary variable in the analyses.

### 2.7.3 Habitat category

Years of experience suggest that, in our study system, birds on farm islands lay eggs several days later than on non-farm islands. These two habitats are clearly distinct: farm islands provide sparrows with shelter and a predictable source of food throughout the year in the form of cattle feed, and are assumed to be higher quality habitats (Pärn et al., 2012). The composition of the house sparrow diet is also known to vary depending on their environment, with farmland birds having more access to grain than village birds (Anderson, 2006). Given these observations, I have included habitat category (farm or non-farm) as a binary predictor in the analyses.

### 2.7.4 Clutch size

Finally, clutch size (the maximum number of eggs found in the nest) was considered but not included as a potential variable in the final models. Exploratory models containing clutch size predicted that for every additional egg, lay date decreases by 0.96 to 0.99 day (similar values were found by Johansen, 2018). This is what we expect since sparrows lay about one egg per day after the onset of laying (Anderson, 2006). In addition, directionality is difficult to establish here – do birds “plan” an earlier onset of laying when clutches are larger, or does earlier onset of laying lead them to lay larger clutches (i.e. does clutch size predict lay date or does lay date predict clutch size)? Taking these observations into consideration, and to reduce the risk of overparameterization, clutch size was therefore not considered in the final analyses.

## 2.8 Statistical analyses and variable selection

### 2.8.1 Linear models

First, I fitted linear mixed effects models to the data. Mixed models were chosen to account for any temporal and spatial heterogeneity in the dataset (see Ringsby et al., 2002), as well as to address issues of pseudoreplication since 165 females appear more than once in the dataset. All models therefore include female identity, island, and island-year as random factors.

Predictor variables were checked for multicollinearity, first using Pearson's  $r$  to detect correlations between variables and then computing the variance inflation factors (VIF) for selected models. I considered  $r$  values above 0.5 and VIFs above 3 to indicate problematic levels of collinearity (Graham, 2003). Due to collinearity, no more than one weather variable was ever included in the same model. In addition, year and population density were moderately correlated ( $r = 0.52$ ,  $df = 563$ ,  $p < .01$ ). Therefore, year was not included as a fixed effect in the analyses.

A total of 208 candidate models were included in the lay date and lay date deviation analyses. These were built using all possible combinations of the predictors mentioned above, as well as all possible interactions between  $F_{\text{GRM}}$  and these predictors. I did not include more than one interaction at a time to reduce the risk of overfitting and reduce the overall number of models being compared. The models were fitted using maximum likelihood (ML) rather than the package's default (REML), to allow for model comparison (Snijders et al., 2012; Hox et al., 2017). The models were then ranked according to AICc (AIC adjusted for small sample sizes) weights. Models within 2 AICc units of each other ( $\Delta\text{AICc} \leq 2$ ) were treated as equally likely given the dataset, while models with  $\Delta\text{AICc}$  scores above 2 were not considered further (Burnham et al., 2004). This first step allowed me to select a few candidate models for further investigation. When two candidate models differed only in whether they included  $F_{\text{GRM}}$  as a variable, they were compared using a likelihood ratio test (LRT), and the simplest model was preferred if the test statistic did not reach a significance level of 0.05 (Stephens et al., 2005).

### 2.8.2 Post-hoc analyses of lay date deviation

To better understand the shape of the degree days by inbreeding interaction uncovered by the lay date deviation analyses, I ran some further analyses, fitting



a similar model to the highest ranked lay date deviation model, but transforming the degree days variable to reflect other likely interaction patterns. I explored three possible relationships between degree days and inbreeding: a quadratic relationship, in which the more the degree day value deviates from the mean, the more inbreeding impacts the deviation in lay date (using the squared difference between mean degree days across all years and degree days that year), an exponential relationship, in which higher degree day values (warmer, earlier spring) have a disproportionately large positive impact on deviation in lay date at higher inbreeding levels (using degree days<sup>2</sup>), and a logarithmic relationship, in which lower degree day values (colder, later spring) have a disproportionately large negative impact on deviation in lay date at higher inbreeding levels (using  $\log_{10}$  degree days). To further check the shape of the interaction, I then fitted three models separately for the 5 years with degree days below 27 (lower half), and the 5 years with degree days above 27 (top half). These were the best model for deviation, a similar model without interaction, and a similar model without interaction or degree days. I then compared their estimates and AICc scores to those of the best model.

### 2.8.3 Cox proportional-hazards mixed effect models

Linear regression models require a baseline weather value, such as mean temperature in April, but a shifting window (e.g. last 30 days before laying) may be a more realistic predictor of lay date. An important limitation of using fixed time windows in these analyses is that these values are likely to be worse descriptions of reality as birds lay further from the 1<sup>st</sup> of May. For instance, in 2011, the mean April temperature was 4.0 degrees; a female laying on day 120 in 2007 experienced a mean temperature over the previous 30 days of 4.01 degrees, while this number was 5.30 for a female that laid on day 133. For these dates, the discrepancy between mean April temperatures and mean temperature for the 30 days preceding day 120 ranged from -0.5 degrees (in 2010) to 2.5 degrees (in 2006). Time-dependent Cox proportional-hazards models (henceforth Cox models) (Cox, 1972) are sometimes used in phenology studies to address this issue (e.g. in Boelman et al., 2017 or Templ, 2017). Values for a predictor can be specified for given time increments (e.g. daily) and over a given length of time (e.g. over 30 days before the event of interest; this is the time-dependency mentioned above) (Gienapp et al., 2005). Cox models are non-parametric, and thus have lower power overall than the linear models described above. However, if temperature is an important predictor of lay date, time-dependent analyses may give us more accurate predictor estimates than baseline analyses by reducing residual error. There is also some evidence that fe-

males may use temperature increase, rather than absolute temperature, as a cue for laying (Schaper et al., 2012). In addition, the use of survival analysis more accurately reflects the actual processes underlying lay date, as onset of breeding is then considered to be a daily decision rather than a target date.

To complement the linear regression models fitted for lay date, I ran a set of time-dependent Cox models. For the weather variable, I used mean daily temperatures for the 30 days before the lay date (data from the Norwegian Meteorological Institute, 2021). This number was chosen to make the variable comparable to the mean April temperature, since 30 is also the number of days in April. In addition, I also ran time-independent Cox models (using mean April temperature) to check the impact of time-dependency on the ranking of the models. A total of 80 models were compared in both the time-dependent and time-independent analyses. Model selection was performed in the same way as for linear models.

Proportional-hazards models are a type of survival analysis. As such, they estimate a hazard ratio, that is, the relative “risk” of an event occurring (in other words, the hazard ratio is a multiplier of the baseline “risk”). Here, estimates of fixed effects represent the impact of the predictor on the daily “risk” of egg-laying, with positive estimates increasing this “risk” and leading to earlier average lay date, and negative estimates decreasing it and leading to later average lay date.

## 2.9 Software

Analyses were conducted using R version 3.6.3 (R Core Team, 2020) and the `lme4` package version 1.1.23 (Bates et al., 2015) in R Studio version 1.3.1073 (RStudio Team, 2020). I made heavy use of tidyverse packages for data wrangling and graph production (Wickham et al., 2019). AICc values were computed using the `AICcmodavg` package version 2.3-1 (Mazerolle, 2020). Repeatability was calculated using the `rptR` package version 0.9.22 (Stoffel et al., 2017). The `coxme` package version 2.2-16 (Therneau, 2020) was used for mixed effects Cox models.

## 3 Results

### 3.1 Dataset

The distribution of lay date is shown in Figure A.2. The mean lay date across islands and years is 133.1 (13<sup>th</sup> May) (SD = 12.12, n = 569), with the earliest lay date being day 102 (12<sup>th</sup> April) on Gjerøy in 2010, and the latest mean lay date being day 163 (12<sup>th</sup> June) on Hestmannøy in 2003 (see Figure A.4). The mean lay date in non-farm island populations is 126.37 (n = 155), whereas it is 132.84 (n = 414) in farm island populations. The mean value for deviation in lay date is 150.62 (equivalent to 12.27 days), with little difference between habitats (farm: 147.78 or 12.16 days; non-farm: 158.22 or 12.58 days).

The mean non-standardised  $F_{\text{GRM}}$  across the metapopulation is 0.03. Notably, the population in Aldra shows much higher inbreeding levels, with a mean  $F_{\text{GRM}}$  of 0.09 (see Figure A.6). This is due to a population bottleneck that occurred prior to the start of this dataset in 2003.

Clutches from experienced mothers account for 281 out of 569 laying events (see Table A.1 and Table A.2 for a breakdown by island and year). The 569 clutches in this dataset were laid by 406 different individuals (see Table A.3). For a visual representation of the relative population density data, see Figure A.8.

Correlations between predictors are low, with the exception of correlations between weather variables (Figure A.3, see also Figure A.7).

## 3.2 Linear mixed models

### 3.2.1 Lay date

Eight models were retained by AICc (see Table 3.1). All include population density, habitat category, and experience as predictors. Inbreeding was present in half of these.

Table 3.1: AICc scores for lay date models. The parameters shown here are: lay date (LD),  $F_{\text{GRM}}$  (FG), interaction between mean April temperature and  $F_{\text{GRM}}$  (AT:FG), relative population density (PD), habitat category (HC), mother’s experience (EX), mean April temperature (AT), mean April precipitation (AP), principal component 1 of weather (W1).

Rank	Parameters	$\Delta\text{AICc}$	wAICc	ER
1	LD ~ PD + HC + EX + (RANDOM)	0	0.18	1
2	LD ~ PD + AT + HC + EX + (RANDOM)	0.06	0.17	1.03
3	LD ~ PD + AP + HC + EX + (RANDOM)	0.48	0.14	1.27
4	LD ~ <b>FG</b> + PD + AT + HC + EX + <b>AT:FG</b> + (RANDOM)	0.56	0.13	1.32
5	LD ~ <b>FG</b> + PD + AT + HC + EX + (RANDOM)	0.92	0.11	1.58
6	LD ~ <b>FG</b> + PD + HC + EX + (RANDOM)	0.99	0.11	1.64
7	LD ~ <b>FG</b> + PD + AP + HC + EX + (RANDOM)	1.54	0.08	2.16
8	LD ~ PD + W1 + HC + EX + (RANDOM)	1.82	0.07	2.49

Likelihood ratio tests do not support the inclusion of  $F_{\text{GRM}}$  ( $\chi^2(1) = 1.08$ ,  $p = 0.30$ ) nor of mean April temperature ( $\chi^2(1) = 2.01$ ,  $p = 0.16$ ), total April precipitation ( $\chi^2(1) = 1.60$ ,  $p = 0.21$ ), or the first weather PCA component ( $\chi^2(1) = 0.24$ ,  $p = 0.62$ ). Parameter estimates from the best performing model, model 1, are shown in Table 3.2.

The largest effect is that of habitat, with females from non-farm islands laying their first clutch around a week earlier than their farm-island conspecifics ( $\beta = -7.78$ , 95% CI [12.33, -2.98]). In addition, one-year-old females (“inexperienced” females) lay earlier than older females ( $\beta = 3.28$ , 95% CI [1.55, 5.01]). Finally, there is a weak negative effect of population density on lay date ( $\beta = -2.55$ , 95% CI [-5.23, 0.14]).

Model 6 (shown in Table 3.3) is similar to Model 1, with the addition of  $F_{\text{GRM}}$ . In this model, there is weak evidence that  $F_{\text{GRM}}$  ( $\beta = 0.49$ , 95% CI [-0.44, 1.42]) has a positive effect on lay date, suggesting that more inbred females lay slightly later than less inbred females.

Table 3.2: Best model for lay date (model 1)

Variable	Effect	$\beta$	CI		SD	VIF
			2.5%	97.5%		
Intercept	Fixed	133.81	130.85	136.88		
Population density	Fixed	-2.55	-5.23	0.14		1.03
Habitat (non-farm)	Fixed	-7.78	-12.33	-2.98		1.04
Experience (first year)	Fixed	3.28	1.55	5.01		1.00
Female ID	Random				3.66	
Island	Random				0.00	
Island that year	Random				7.02	
Residual	Random				9.10	

Table 3.3: Best model for lay date, with the addition of inbreeding (model 6)

Variable	Effect	$\beta$	CI		SD	VIF
			2.5%	97.5%		
Intercept	Fixed	133.73	130.79	136.79		
<b><math>F_{GRM}</math></b>	<b>Fixed</b>	<b>0.49</b>	<b>-0.44</b>	<b>1.42</b>		<b>1.01</b>
Population density	Fixed	-2.50	-5.16	0.16		1.03
Habitat (non-farm)	Fixed	-7.66	-12.18	-2.86		1.04
Experience (first year)	Fixed	3.22	1.48	4.95		1.01
Female ID	Random				3.55	
Island	Random				0.00	
Island that year	Random				6.96	
Residual	Random				9.14	

### 3.2.2 Deviation in lay date

Three models were retained based on AICc (see Table 3.4). All include  $F_{GRM}$ , population density, degree days and a degree days by  $F_{GRM}$  interaction. Likelihood ratio tests did not support the inclusion of experience ( $\chi^2(1) = 0.55$ ,  $p = 0.45$ ) or habitat category ( $\chi^2(1) = 0.14$ ,  $p = 0.71$ ).

Table 3.4: AICc scores for lay date deviation models. The parameters shown here are: lay date deviation (LDV),  $F_{GRM}$  (FG), interaction between cumulative degree days and  $F_{GRM}$  (DD:FG), relative population density (PD), cumulative degree days (DD), mother's experience (EX), habitat category (HC).

Rank	Parameters	$\Delta AICc$	wAICc	ER
1	LDV $\sim$ <b>FG</b> + PD + DD + <b>DD:FG</b> + (RANDOM)	0.00	0.54	1.00
2	LDV $\sim$ <b>FG</b> + PD + DD + EX + <b>DD:FG</b> + (RANDOM)	1.52	0.25	2.14
3	LDV $\sim$ <b>FG</b> + PD + DD + HC + <b>DD:FG</b> + (RANDOM)	1.93	0.21	2.63

The best model is presented in Table 3.5. Variance inflation factors are high for  $F_{\text{GRM}}$  (VIF = 4.19) and the  $F_{\text{GRM}}$  by degree day interaction (VIF = 4.22). This is due to the interaction term. In a similar model without the interaction term, the VIF for  $F_{\text{GRM}}$  is within acceptable limits (VIF = 1.00).

Table 3.5: Best model for deviation in lay date

Variable	Effect	$\beta$	CI		SD	VIF
			2.5%	97.5%		
Intercept	Fixed	138.68	74.10	202.36		
Population density	Fixed	11.74	-15.77	40.58		1.12
Degree days	Fixed	0.94	-0.60	2.58		1.14
<b><math>F_{\text{GRM}}</math></b>	<b>Fixed</b>	<b>-68.54</b>	<b>-7.24</b>	<b>-193.26</b>		<b>4.19</b>
<b><math>F_{\text{GRM}}:\text{Degree days}</math></b>	<b>Fixed</b>	<b>1.33</b>	<b>0.47</b>	<b>2.19</b>		<b>4.22</b>
Island	Random				50.00	
Island that year	Random				51.76	
Mother ID	Random				0.00	
Residual	Random				169.81	

This model includes weak evidence for a positive effect of relative population density on deviation in lay date ( $\beta = 11.74$ , 95% CI [-15.77, 40.58]). There is also evidence for an interaction between  $F_{\text{GRM}}$  and degree days (visualised in Figure 3.1), with more inbred birds showing stronger deviation from the population mean lay date with higher degree days values ( $\beta = 1.33$ , 95% CI [0.47, 2.19]). This model was further explored following the methods described in section 2.8.2. Of the three models with transformed degree days (quadratic, exponential and logarithmic), only the logarithmic model performed better than the best model, with an AICc score which was 1.56 points lower. The quadratic and exponential models had AICc scores larger than that of the original best model by 1.88 points and 9.86 points, respectively. When fitted to the warmer half of years only, the AICc scores of a model without degree days, with degree days, and with degree days and an inbreeding by degree days interaction were all within 2 units of one another. By contrast, the AICc score of the cold half model with an inbreeding by degree days interaction was lower than that of the model fitted to the complete dataset. The parameter estimate for the cold half of the dataset ( $\beta = 6.86$ , 95% CI [2.64, 11.09]) was also larger than that of the warmer half ( $\beta = 0.97$ , 95% CI [-0.43, 2.38]).

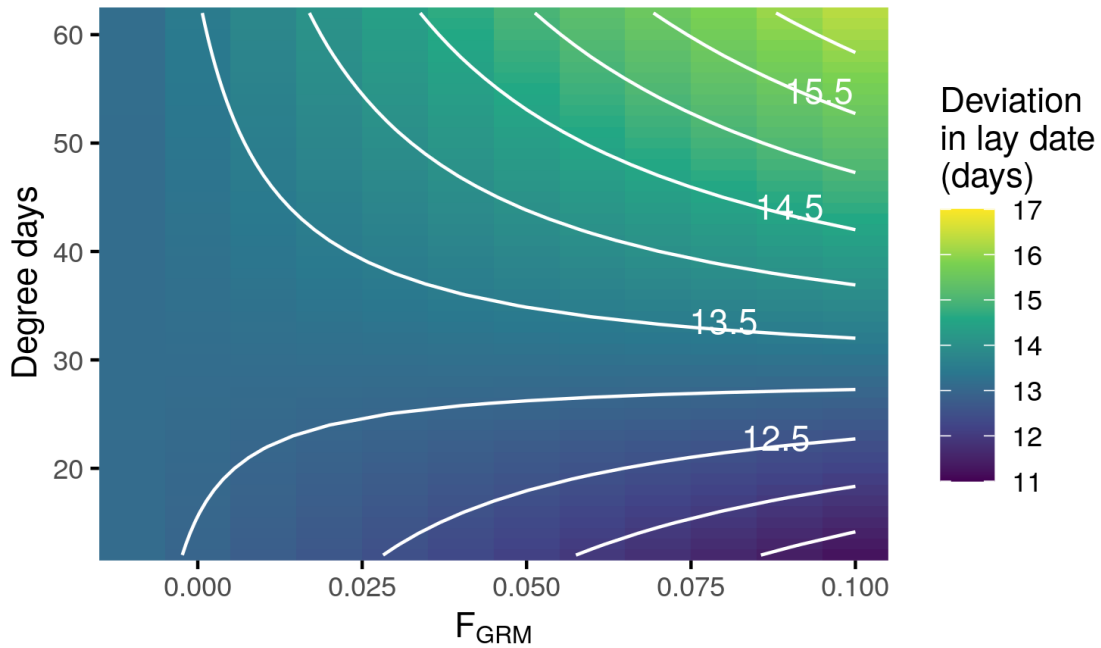


Figure 3.1: Interaction between  $F_{\text{GRM}}$  and deviation in lay date, based on predicted values when other predictors are kept constant. Non-standardised  $F_{\text{GRM}}$  and the square root of the deviation measure are presented for increased readability. The horizontal dashed line is the mean value for degree days across years.

### 3.3 Cox proportional hazards mixed-effect models

These analyses support the importance of the predictors found in the linear regression analyses (habitat, experience, density) (see Table 3.6). Overall, the inclusion of time-dependency has little impact on the ranking of models, and does not affect the two highest ranked models. However, a model including a temperature by  $F_{\text{GRM}}$  interaction is present in the best time-dependent models, whereas its time-independent equivalent does not meet the inclusion criterion based on  $\Delta\text{AICc}$ .

The best model (shown in Table 3.7) does not include inbreeding, and a likelihood ratio test between the first and second models does not justify including it ( $\chi^2(1) = 0, p = 0$ ). In the second best model (Table 3.8), there is very little evidence that inbreeding has a weak negative impact on daily risk of laying (hazard ratio: 0.95, 95% CI [0.85, 1.06]). As in the regression models, the impact of temperature is low, although confidence intervals are much narrower in the time-dependent models (see Table 3.7 for the values for temperature in the best time-dependent model; values from the equivalent time-independent model: hazard ratio: 1.18, CI [0.92, 1.52]), suggesting that time-dependent values are more reliable predictors of lay date.

Table 3.6: Comparison of AICc scores rankings for the top 5 time-dependent and time-independent Cox models. Models are ordered by time-dependent rank. The parameters shown here are: lay date (LD),  $F_{GRM}$  (FG), relative population density (PD), daily temperature in the time-dependent models or mean April temperature in the time-independent models (DT), habitat category (HC), mother's experience (EX), interaction between daily temperature or mean April temperature and  $F_{GRM}$  (DT:FG), interaction between relative population density and  $F_{GRM}$  (PD:FG), interaction between habitat category and  $F_{GRM}$  (HC:FG).

Rank (time-dep.)	Rank (time-ind.)	Variables	$\Delta AICc$ (time-dep.)	$\Delta AICc$ (time-ind.)
1	1	LD ~ PD + DT + HC + EX + (RANDOM)	0.00	0.00
2	2	LD ~ <b>FG</b> + PD + DT + HC + EX + (RANDOM)	1.24	1.01
3	5	LD ~ <b>FG</b> + PD + DT + HC + EX + <b>DT:FG</b> + (RANDOM)	1.83	2.31
4	3	LD ~ <b>FG</b> + PD + DT + HC + EX + <b>PD:FG</b> + (RANDOM)	2.07	1.79
5	4	LD ~ <b>FG</b> + PD + DT + HC + EX + <b>HC:FG</b> + (RANDOM)	2.37	2.21

Table 3.7: Best model for time-dependent Cox models. Hazard ratios represent the change to the daily risk per unit of the variable or for the category of the variable. Therefore, hazard ratios greater than 1 represent an increase in daily risk, whereas hazard ratios smaller than 1 represent a decrease in risk. Here, for instance, on a given day, non-farm females have a 2.29 times greater risk of laying than farm females.

Variable	Effect	Hazard ratio	CI		SD
			2.5%	97.5%	
Population density	Fixed	1.29	1.03	1.63	
Daily temperature	Fixed	1.10	1.05	1.15	
Habitat (non-farm)	Fixed	2.29	1.57	3.32	
Experience (inexperienced)	Fixed	0.74	0.61	0.89	
Island	Random				0.02
Island that year	Random				0.59
Mother ID	Random				0.02

Table 3.8: Second best model for time-dependent Cox models.

Variable	Effect	Hazard ratio	CI		SD
			2.5%	97.5%	
<b><math>F_{GRM}</math></b>	<b>Fixed</b>	<b>0.95</b>	<b>0.85</b>	<b>1.06</b>	
Population density	Fixed	1.29	1.02	1.61	
Daily temperature	Fixed	1.10	1.05	1.15	
Habitat (non-farm)	Fixed	2.26	1.55	3.30	
Experience (inexperienced)	Fixed	0.75	0.62	0.90	
Island	Random				0.06
Island that year	Random				0.58
Mother ID	Random				0.02



## 4 Discussion

These analyses do not show any clear evidence for an effect of inbreeding on mean lay date. The evidence that inbreeding influenced onset of lay date is weak, with a large confidence interval. Although the highest ranked model does not include it, inbreeding is present in some of the other highly ranked models. For lay date itself, the linear model that contains inbreeding in addition to the terms of the best model predicts that more inbred females laid slightly later (about half a day later for each increase of one standard deviation in  $F_{\text{GRM}}$ ). Similarly, the second best time-dependent Cox model estimates a hazard ratio under 1 for  $F_{\text{GRM}}$ , indicating a lower daily “risk” of laying an egg with higher inbreeding. These analyses show clear support for the influence of habitat, relative population density and female experience (based on age) on mean lay date, as demonstrated in previous studies in house sparrows as well as other passerines. Somewhat unexpectedly, weather variables did not seem to play a large role in onset of breeding in our population. However, in years when spring had been colder (as measured by cumulative degree days), more inbred females laid closer to the mean lay date than less inbred females. Population density was also found to have a large impact on variation in lay date.

Unlike in Germain et al. (2016) and Marr et al. (2006), there was no clear evidence for an impact of inbreeding on lay date itself in this dataset. However, these analyses were conducted in song sparrows, and are unlikely to be directly comparable. These two studies also did not investigate deviation from the mean population lay date. In the present analyses, in colder years (those with fewer cumulative degree days by the start of the breeding season), those females that were more inbred exhibited a *smaller* deviation from the population mean lay date. Based on AICc ranking of the models, inbreeding alone did not seem to impact variation in lay date. In the present dataset, the lack of evidence for an impact of inbreeding on lay date itself suggests that inbreeding did not negatively impact a female’s ability to reach breeding condition in time for the start of the breeding season. If inbred birds had simply been in worse physical condition and had needed more time to recover from the energetic demands of winter to breed, we expect that they would have laid eggs

later on average than less inbred birds.

In the lay date deviation analyses, the inbreeding by degree days interaction results requires cautious interpretation. As shown in Figure 3.1, the highest ranked model predicts that the deviation in lay date was smaller for inbred birds at low degree day numbers, but larger at high degree day numbers, with a crossing point around the mean degree day value for the 10 years under study. As a main effect,  $F_{GRM}$  had a strong negative impact leading to the small deviation values we observed at lower degree days in more inbred birds; each increase in one standard deviation in  $F_{GRM}$  reduced deviation in lay date by about 8 days. This is a non-intuitive result, and it is important to keep in mind that the degree days by inbreeding interaction included in the model is linear, but that the true interaction may have had a different shape. Post-hoc explorations of the best model suggest this. A better fit to the data was achieved after log-transforming the degree days variable, while models fitted to the warmer years in the dataset only did not differ in their AICc scores whether they included the inbreeding by degree days interaction or not. The effect of temperature on lay date deviation in inbred birds therefore appears to be stronger in colder years, and the interaction weakens with increasing degree days, so that there is in fact little difference in lay date deviation between low and high inbreeding females at warmer temperatures. These explorations lend further support to the idea that, in colder years, high  $F_{GRM}$  females did lay closer to the mean lay date than their less inbred conspecifics.

These results are difficult to reconcile with the existing literature on the impact of inbreeding on life-history traits. The lay date deviation analyses rely on the assumption that the mean lay date for a given island and year is optimal for long-term reproductive fitness. Under this assumption, more deviation in lay date in a subset of the population will lead to a fitness loss in this subset as fewer individuals lay close to the optimal lay date. While more inbred females did show more deviation in lay date in warmer years, in colder years, inbred females laid *closer* to the mean lay date than less inbred females. If the assumption that mean lay date is the optimal lay date holds, then inbred females were fitter than less inbred ones in colder years. While this is of course possible, it seems unlikely, especially considering that inbreeding depression has been shown across this study system. Another possibility is that some variation around the mean laying date is adaptive. In addition, as pointed out by Visser et al. (2019), a mismatch is not always a mistiming – in other words, a mismatch between onset of breeding and arthropod abundance may not always have negative fitness consequences. The composition of the diet of the chicks changes over time, with different types of arthropods being favoured depending on the chicks' age

(Julseth, 2019). By spreading out their lay date, parents could reduce competition for the kind of food most adequate for their chicks. In the highest ranked models for both mean lay date and deviation in lay date, high population density was associated with an earlier lay date and larger deviations from the mean lay date. This could be an adaptive mechanism to reduce breeding synchrony in the colony and thus reduce competition for the same food sources. Therefore, reduced deviation in lay date in inbred females at colder temperatures could have a negative impact on chick survival and contribute to their observed inbreeding depression (Niskanen et al., 2020). Alternatively, reduced deviation could have negative short-term impacts which are compensated by longer-term dynamics. In a four-decade study of great tits in the Netherlands, low fledgling numbers due to phenological mismatch were later compensated by lower competition (due to lower population density) and higher offspring recruitment rate (Reed et al., 2013). However, in the present study system, Johansen (2018) found that clutches that were laid early or late compared to the population mean produced more fledglings. Females that laid earlier also produced more fledglings over the whole breeding season. Therefore, greater lay date deviation may lead to increased annual reproductive success in this metapopulation.

Even assuming that some deviation in individual lay date from the population mean is neutral or advantageous, a proximate mechanism for the impact of degree days on this variation in inbred females is still required. Mean temperature did not have a strong impact on mean lay date in this population. Therefore, temperature was not used as a cue by females to trigger onset of laying (if it had been, models that include degree days would be ranked higher in the mean lay date comparisons). This eliminates any potential explanations that rely on the differing use of temperature-based cues by females of different inbreeding levels. It follows that, if temperature was not used as a cue, its effect on lay date variation was indirect. One obvious culprit is body condition. Laying eggs and rearing chicks is costly, and females need to have the required energy reserves to successfully reproduce. It has previously been shown that, in a large range of species, more inbred individuals tend to be of lower quality. Inbreeding depression is often stronger in stressful environments (Cheptou et al., 2011; Armbruster et al., 2005), and a long winter is certainly a stressful environment for sparrows. The fact that it is the degree days variable specifically, and not other, shorter-term measures of weather, that was associated with reduced lay date deviation in inbred birds is compatible with this interpretation. Exactly how poorer body condition could lead to reduced variation, however, is unclear. Notably, Marr et al. (2006) found some support for an interaction between temperature and mean lay date in which more inbred song sparrow females delayed their lay date more following warmer spring temperatures. At cold temperatures, the difference

between inbred and non-inbred females was lower, so that inbreeding depression was presumed to be weaker in colder years. These and the results presented here suggest that the relationship between lay date, inbreeding and temperature may not necessarily lead to inbreeding depression. Indeed, in their review of inbreeding depression in stressful environments, Armbruster et al. (2005) found that about a quarter of traits in published studies are not associated with more inbreeding depression under stressful conditions.

The weak role of weather variables in mean lay date, despite previous evidence of its influence on onset of breeding in this system, is another unexpected result. For instance, Pärn et al. (2012) found that an increase in one degree Celsius in the mean April and May temperatures led to birds breeding about 1 to 3 days earlier in the period from 1993 to 2008. The time-dependent Cox models have much narrower confidence intervals for daily temperatures 30 days prior to laying, compared to the time-independent models that use mean April temperature instead, indicating that the shifting window was a more accurate predictor of lay date than baseline temperatures. However, the effect size of the temperature variable is not larger in the time-dependent models. As noted in the Introduction, temperature is believed to be used as a proxy for arthropod abundance by many types of organisms that breed in seasonal environments, including passerines. However, the relative importance of photoperiod and temperature in onset of laying is still a subject of debate, although it is important to keep in mind that photoperiod cannot explain variation between years since it is entirely latitude-dependent. Some experimental set-ups have shown that photoperiod is much more important in determining lay date than temperature (Lambrechts et al., 1997).

A possible explanation for the limited impact of temperature on onset of breeding in this dataset is that other factors may take precedence in high latitude sparrow populations. In a 2016 paper, Phillimore et al. suggested that a photoperiod threshold may restrict the possibility for earlier breeding at higher latitudes. There is also some evidence that populations at high latitudes are more reliant on photoperiod than on other environmental cues (Schoech et al., 2007). Given how short the breeding season is in this study system, the risk of laying at too low temperatures may be worth taking. Weather variables could also be poor cues for arthropod abundance. In the same study system, in order to calculate degree days, Johansen (2018) had to lower the degree day threshold to 5 degrees Celsius, rather than 10 as is most commonly used for temperate environments, as spring temperatures were otherwise not warm enough for degree day accumulation by the time sparrows start laying. Yet, in a study in the same metapopulation, Julseth (2019) found that arthropod

biomass predicted the number of clutches laid in a given week, although with a short lag. It is therefore likely that sparrows use other cues as predictors for arthropod abundance.

While these results show that females with a high inbreeding coefficient laid around the same date as less inbred females, this does not contradict the findings of Niskanen et al. (2020), who found that inbreeding led to lower numbers of recruits into the population both annually and over the parent's lifetime. While inbreeding had little impact on mean lay date, the increased deviation in lay date at warm temperatures in inbred females means that these females did lay further from the mean lay date, although they laid too early or too late in equal proportions (see Figure A.5). Inbreeding could also still have negatively affected reproductive success, for instance by reducing egg size, clutch size, chick survival, total yearly and lifetime number of clutches, and so on. Deviation in lay date did also appear to be affected by inbreeding, and could also have impacted these.

As with other studies of inbreeding in natural populations, one limitation of these analyses was the narrow distribution of the inbreeding coefficient in the sample population. Ninety percent of individual  $F_{GRM}$  values lay between 0 and 0.10 (see Figure A.6). This makes it difficult to draw clear conclusions about the effect of very high inbreeding levels on lay date, especially considering the relatively high number of parameters included in the models given the sample size. Yet, high mean inbreeding can occur in this metapopulation, as exemplified by the high  $F$  values found on Aldra following a population bottleneck (Niskanen et al., 2020; Billing et al., 2012). A related point to consider is that individuals can only be present in our sample if they were healthy enough to reach breeding age and lay eggs. Those individuals that suffer from the most inbreeding depression are less likely to be alive long enough to be included in this type of sample, as exemplified by previous studies in this metapopulation that showed that more inbred fledglings were recruited at a lower rate (Jensen et al., 2007; Billing et al., 2012; Niskanen et al., 2020). This is inherent to the study of the effect of inbreeding on adult traits, and points to the importance of considering the effects of inbreeding across the whole life history.

While little work has been done to explore the consequences of inbreeding on lay date, this study shows that the consequences of inbreeding on lay date are worth investigating further. Most importantly, more studies are needed to confirm whether this is generalizable across other sparrow populations and in other species. For instance, analyzing a larger dataset in this metapopulation would allow us to obtain more precise confidence intervals and better understand the role of each predictor.

Crucially, future work should seek to uncover the effect of variation in lay date on lifetime reproductive success. This is necessary to establish whether differences in lay date contribute to inbreeding depression. In addition, this work does not take into account the phenotype of males. Male traits may affect how females respond to their environment. For instance, in grey jays (*Perisoreus canadensis*), females paired with older males adjust their lay date more at colder temperatures than those paired with young, less experienced males (Whelan et al., 2016). Notably, we know that males and females experience similar levels of inbreeding depression (Niskanen et al., 2020), so, should lay date be implicated in inbreeding depression, then the coefficient of inbreeding of males may also be an important predictor of variation in lay date. However, in their song sparrow study, Germain et al. (2016) found that the inbreeding level of males did not impact their female mates' lay date. Investigating partner effects on lay date may also improve our understanding of onset of breeding in this study system.

Genetic studies provide another avenue for further research, either through candidate gene studies, for instance of genes that impact melatonin production (Greives et al., 2012), or genome-wide association studies to uncover less obvious associations. However, these studies require very large sample sizes, especially if the trait is polygenic (i.e. influenced by many genes of small effect). In this study system, Bjerck (2016) was constrained in an exploration of this question by a low sample size and the absence of a large-effect locus. In great tits, Gienapp et al. (2017) could not find any association between onset of breeding and over 380 000 SNPs in 2249 individuals.

This thesis shows that, in a natural metapopulation of a multi-brooded passerine, inbreeding led to decreased deviation around the mean lay date of the first clutch of inbred females in colder years, and increased deviation in warmer years. However, there is no evidence for an impact of inbreeding on lay date itself in this dataset. This suggests that the effects of inbreeding on lay date were environment-dependent. Given the rather small effect size of this interaction, it is unlikely to have had a large impact on fitness, but it nonetheless deserves consideration in order to gain a broader view of the life-history traits that are impacted by inbreeding. The study of lay date presents additional difficulties compared to the traits that inbreeding depression studies most often concern themselves with, but this work shows that it is worth exploring.

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# A Appendix

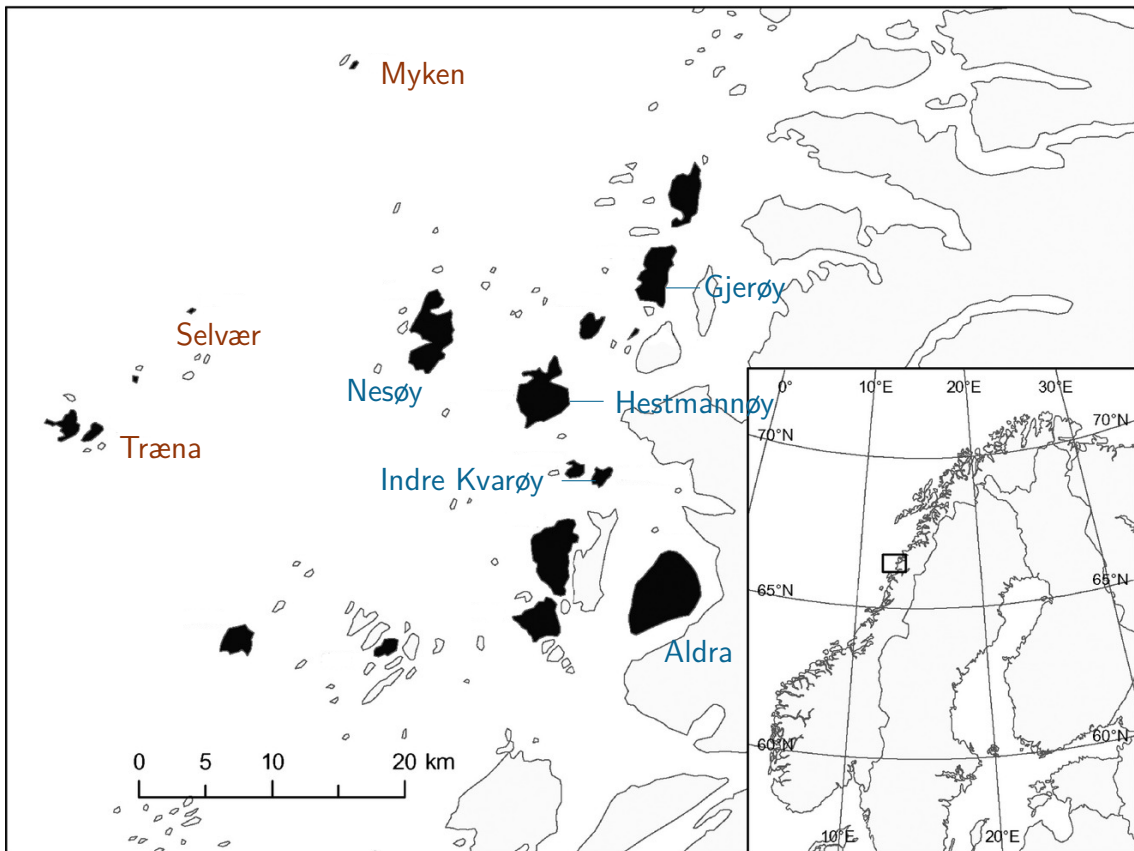


Figure A.1: Map of the study area. Islands filled in black are part of the overall metapopulation monitoring efforts by the Sparrow Group. The 8 named islands form this study's dataset, with red islands being non-farm islands and blue islands being farm islands. The weather data comes from the weather station on Myken.

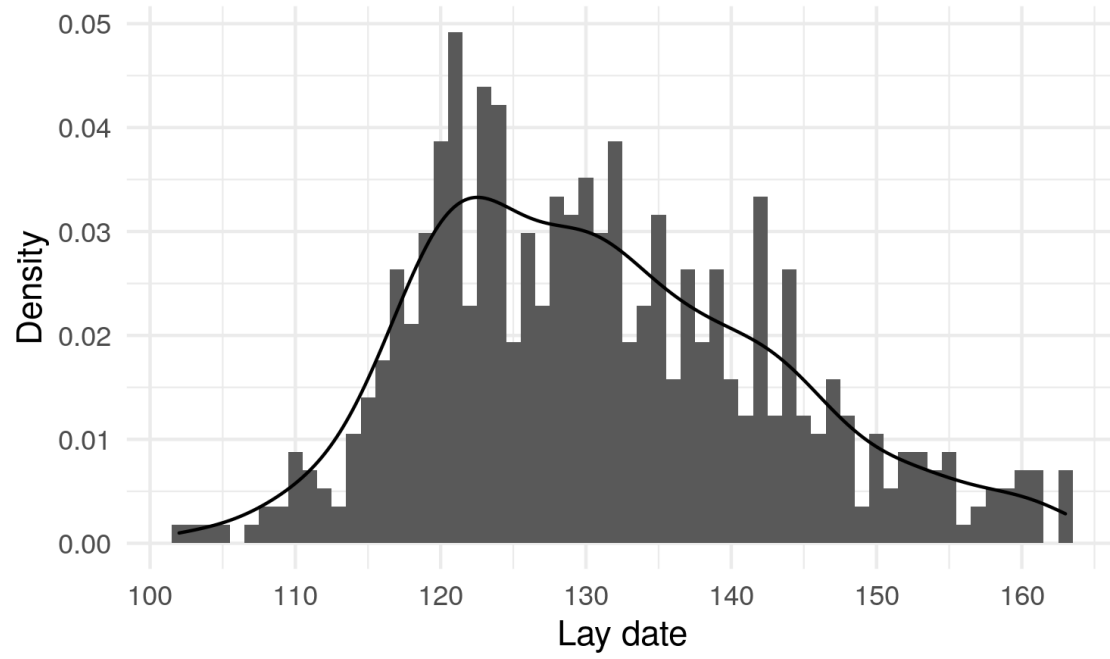


Figure A.2: Histogram and density plot of lay date. Lay date is expressed in Julian calendar days. There is a slight positive skew, as well as long tail to the right.



Figure A.3: Correlation matrix of the numerical variables used in the analyses. The intensity of the background colour reflects the strength of the association between the two variables, with red representing a positive association and blue a negative one.

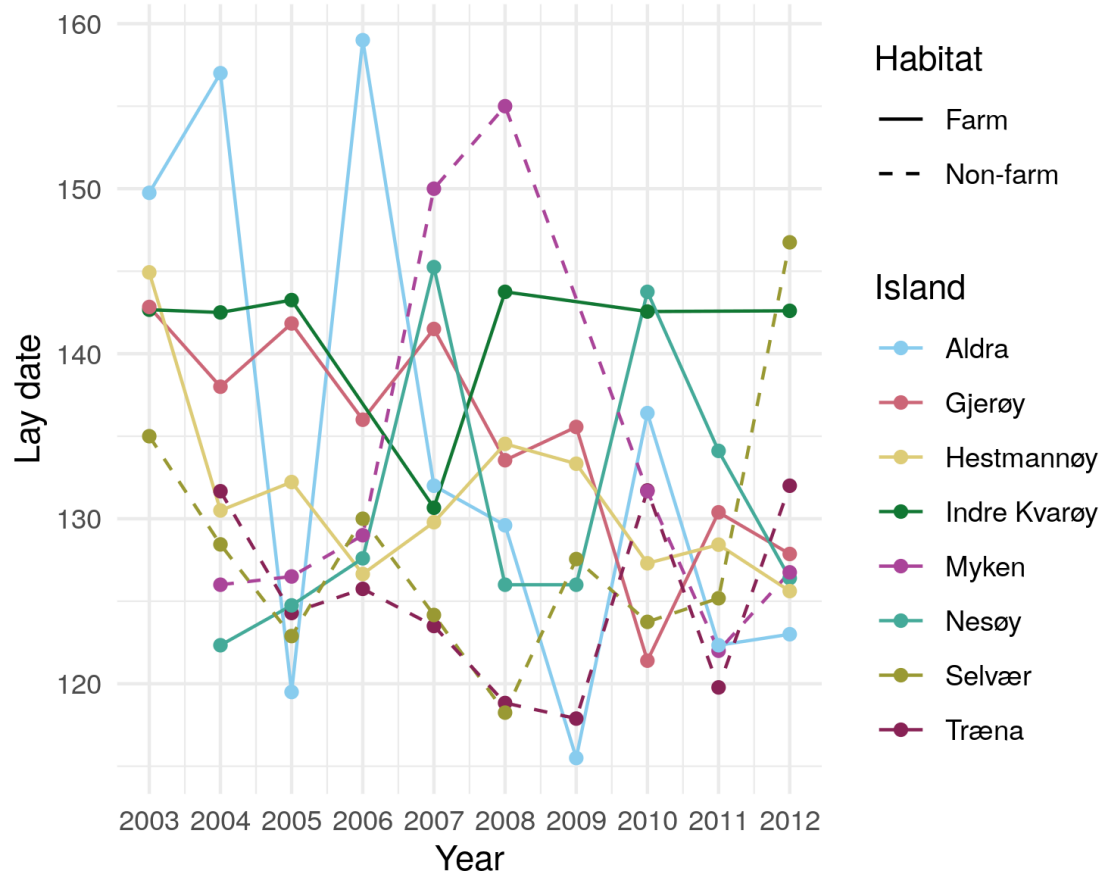


Figure A.4: Mean lay date in Julian calendar days across each island over time. Solid lines represent farm islands, and dashed lines represent non-farm islands.

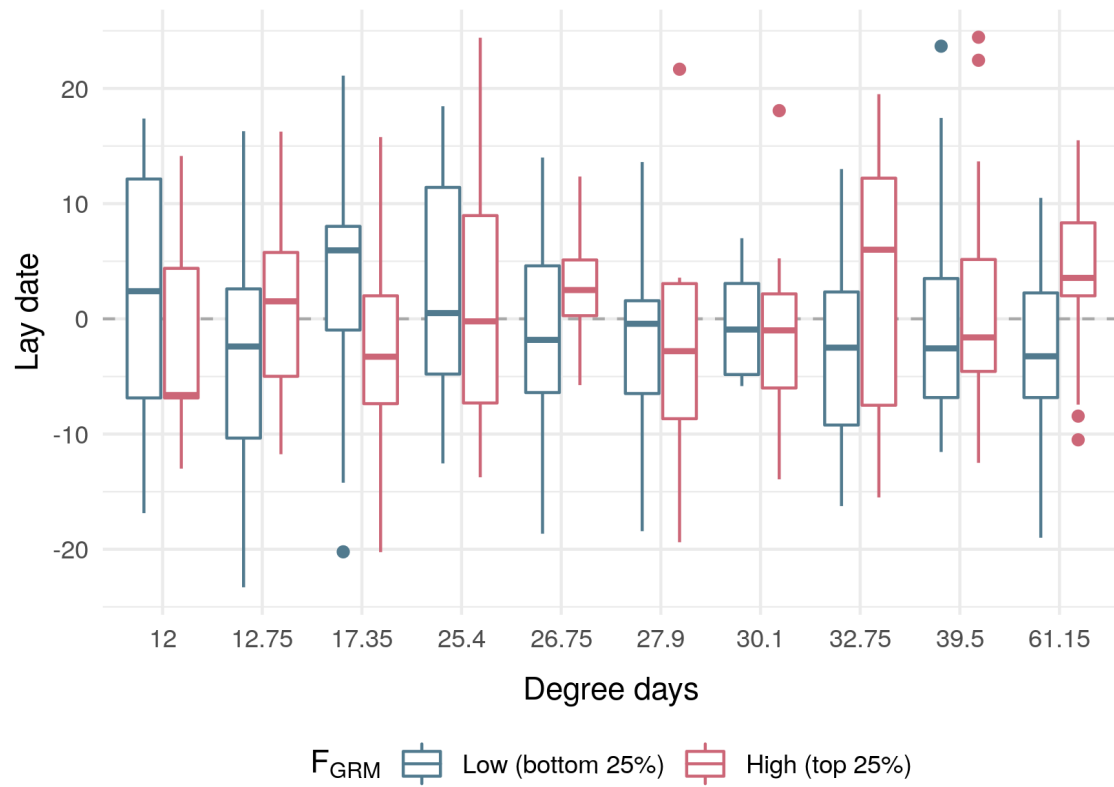


Figure A.5: Mean-centered lay date per degree days for females in the bottom 25% of  $F_{GRM}$  values (in blue), and those in the top 25% (in red). Lay date is centered around the population mean for each island and year. Degree days are plotted on an ordinal scale due to space constraints.

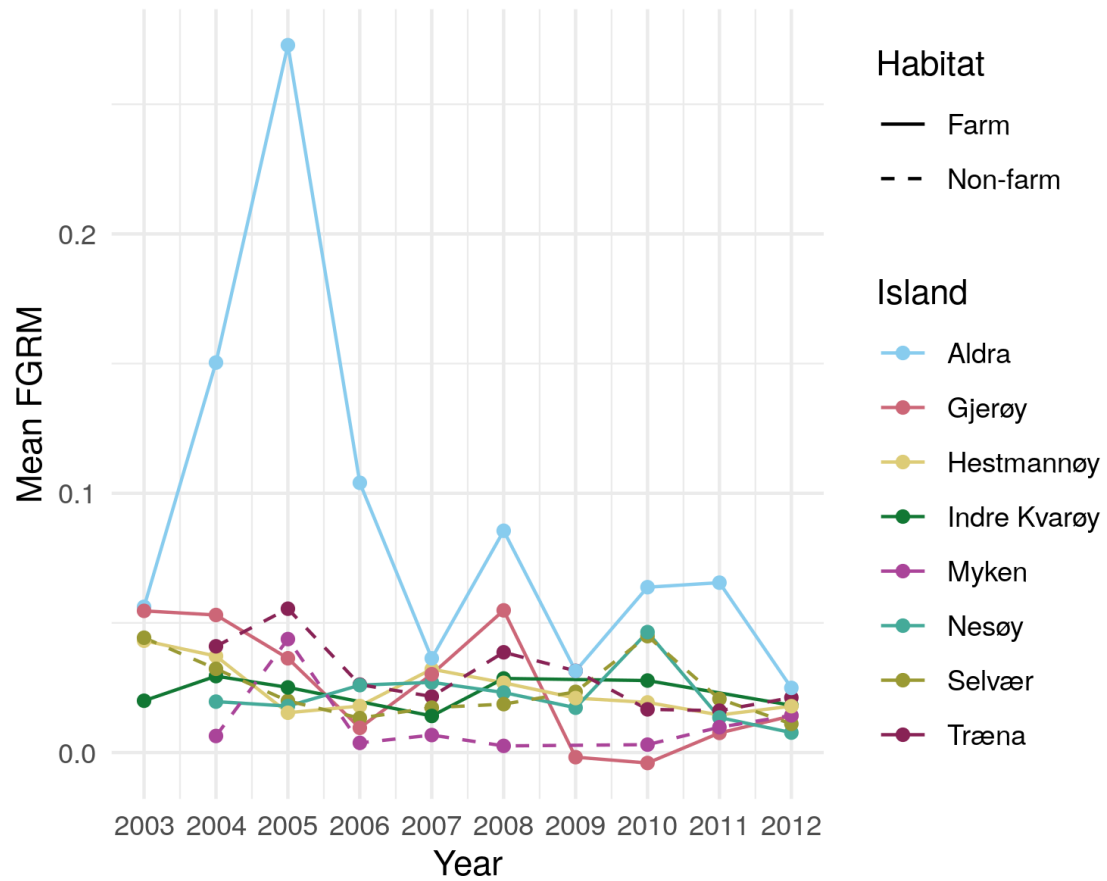


Figure A.6: Mean inbreeding ( $F_{GRM}$ ) across each island over time. Solid lines represent farm islands, and dashed lines represent non-farm islands.



Figure A.7: The distribution of inbreeding ( $F_{GRM}$ , non-standardised) against lay date, for each island. Negative  $F_{GRM}$  values correspond to outbred individuals.

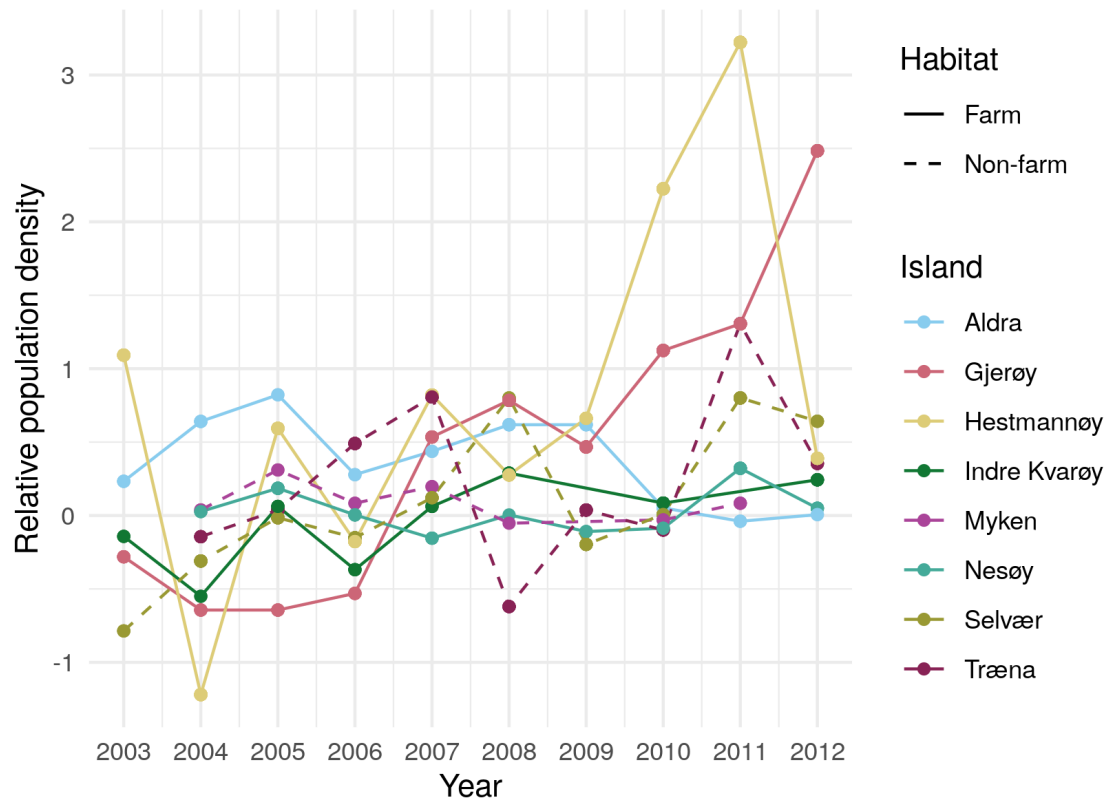


Figure A.8: Relative population density across islands over time. Relative population density was calculated based on the mean population size for each island between the years 1993-2014. Solid lines represent farm islands, and dashed lines represent non-farm islands.



Table A.1: Number of clutches from inexperienced and experienced mothers across islands. A female is considered inexperienced if she is laying at age 1, and experienced if she is at least 2 years old.

Island	Inexperienced	Experienced
Aldra	16	19
Gjerøy	44	68
Hestmannøy	94	92
Indre Kvarøy	22	17
Myken	16	3
Nesøy	17	25
Selvær	35	34
Træna	44	23
Total	288	281

Table A.2: Number of clutches from inexperienced and experienced mothers across years. A female is considered inexperienced if she is laying at age 1, and experienced if she is at least 2 years old.

Year	Inexperienced	Experienced
2003	18	12
2004	27	19
2005	29	27
2006	23	26
2007	24	30
2008	30	19
2009	35	33
2010	38	33
2011	37	44
2012	27	38
Total	288	281

Table A.3: Number of mothers with multiple recorded clutches in the dataset

Number of clutches	Number of individuals	Percentage of all individuals
1	299	73.65
2	68	16.75
3	23	5.67
4	15	3.69
5	1	0.25
Total	406	100