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Spatiotemporal variation in laying date and its impact on reproductive success in house sparrows (*Passer domesticus*)

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ABSTRACT

Timing of breeding is an important determinant of reproductive success for animals living in seasonal environments. Understanding the factors affecting reproductive processes are necessary to predict how populations may respond to future changes in the environment. In general, there is a shortage of studies investigating these processes in multi-brooded species in different habitat types. The aim of this study was to investigate the influence of demographic and environmental factors on the variation in timing of breeding and its consequences for reproductive success between two habitat types in a multi-brooded species, the house sparrow (*Passer domesticus*). Interestingly, the relationships between laying date of the first clutch and both onset of spring and population density depended on habitat type. Increased population density was associated with advanced laying dates in the no-farm populations where sparrows were more exposed to fluctuating weather and food availability, while no relationship was found in the farm populations where sparrows had access to shelter and food provided by farms. Onset of spring had no effect on laying date in the no-farm populations, and a weak negative effect in the farm populations. There were also differences in the effects of population density and season length on reproductive success between habitats. More fledglings were produced in the no-farm populations compared to the farm populations, especially at long season lengths. Reproductive success decreased with higher population densities only in the farm populations. The relationship between laying date and reproductive success were convex in both habitat types, with lower reproductive output in first clutches initiated around the mean laying date. The total production of fledglings through the season was higher for individuals starting their first clutches earlier than conspecifics. These results illustrate spatial variation in environmental and density dependent effects on reproductive traits. Also, several of the reproductive traits and strategies found in these house sparrow populations are in accordance with those found in other multi-brooded species, such as the importance of timing of breeding relative to conspecifics rather than timing to optimal conditions. This study underlines the importance of considering properties of the habitat and the reproductive strategy of a species when trying to understand how populations may respond to future climate change.

SAMMENDRAG

Tidspunkt for reproduksjon er en viktig determinant for reproduktiv suksess for dyr som lever i sesongmessige miljøer. Forståelse av faktorene som påvirker reproduktive prosesser er nødvendig for å kunne forutsi hvordan populasjoner kan komme til å reagere på fremtidige endringer i miljøet. Det er generelt en mangel på studier som undersøker slike prosesser i arter som kan legge flere kull per år i ulike habitattyper. Målet med denne studien var å undersøke innvirkningen av demografiske og miljømessige faktorer på variasjonen i hekketidspunkt og dets konsekvenser for reproduktiv suksess mellom to habitattyper i en art som kan legge flere kull per år; gråspurven (*Passer domesticus*). Et interessant funn var at forholdet mellom eggleggingsdato for det første kullet og både vårens ankomst og populasjonstetthet var avhengig av habitattype. Spurvene startet å hekke tidligere ved høyere populasjonstettheter i ikke-gårdspopulasjoner, hvor spurvene var mer utsatt for varierende vær og mattilgang, mens det ikke ble funnet noen sammenheng i gårdspopulasjonene hvor spurvene hadde tilgang til ly og mat fra gårder. Vårens ankomst hadde ingen effekt på eggleggingsdato i ikke-gårdspopulasjonene, og en svak negativ effekt i gårdspopulasjonene. Det var også forskjeller i effektene av populasjonstetthet og sesonglengde på reproduktiv suksess mellom habitater. Flere utfløyne unger ble produsert i ikke-gårdspopulasjoner sammenlignet med gårdspopulasjonene, spesielt ved lange sesonglengder. Reproduktiv suksess ble redusert ved høyere populasjonstetthet kun i gårdspopulasjonene. Forholdet mellom eggleggingsdato og reproduktiv suksess var konvekst i begge habitattyper, med lavere reproduktiv suksess i førstekull som ble startet omkring den gjennomsnittlige eggleggingsdatoen. Den totale produksjonen av utfløyne unger gjennom sesongen var høyere for individer som startet sine førstekull tidligere enn artsfrender. Disse resultatene illustrerer at det er romlig variasjon i miljø- og tetthetsavhengige effekter på reproduktive trekk. I tillegg er flere av reproduksjonstrekkene og strategiene som finnes i disse gråspurvpopulasjonene i samsvar med de som finnes i andre arter som kan legge flere kull per år, som for eksempel viktigheten av hekkestart i forhold til artsfrender i stedet for å hekke under optimale forhold. Denne studien understreker viktigheten av å ta egenskaper av habitatet og den reproduktive strategien til en art i betrakning når man prøver å forstå hvordan populasjoner kan respondere på fremtidige klimaendringer.

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INTRODUCTION

Phenology is the timing of seasonal activities in plants and animals, such as flowering in plants and breeding in animals (Walther *et al.* 2002). Timing of breeding is an important determinant of reproductive success for animals living in seasonal environments, where there is only a limited period of favourable conditions suitable for reproduction and growth (Perrins 1970; Cushing 1990; Verhulst and Tinbergen 1991; Landa 1992; Tejedo 1992; Brinkhof *et al.* 1993; Loe *et al.* 2005; Varpe *et al.* 2007; Ahola *et al.* 2012; Gienapp and Bregnballe 2012). Although breeding time has an additive genetic basis (Findlay and Cooke 1982; Price *et al.* 1988; Gharrett and Smoker 1993; Su *et al.* 1997; Sheldon *et al.* 2003), it may also be plastic in response to environmental conditions (Visser 2008; Husby *et al.* 2010). For birds living in temperate areas, shifts in photoperiod throughout the year stimulate physiological changes in hormones and reproductive organs (Cockrem 1995; Dawson *et al.* 2001; Dawson 2008). This leads to a physiological state in which breeding can begin, and prevents the occurrence of reproductive events out of season in response to short-term weather fluctuations (Cockrem 1995). However, onset of breeding is a highly variable trait, and hence, the exact initiation of breeding each year is assumed to be regulated by other environmental cues (Visser *et al.* 2004; Dawson 2008). For instance, temporally and spatially varying biotic and abiotic factors such as resource availability, weather conditions and the density of competitors have been shown to be of great importance for many species of birds during reproduction (Verhulst and Tinbergen 1991; Cockrem 1995; Naef-Daenzer *et al.* 2000; Dunn 2004; Visser and Both 2005; Dunn and Winkler 2010; Boulton *et al.* 2011; Ahola *et al.* 2012; Burger *et al.* 2012; Johansson *et al.* 2014).

According to life history theory, parents should time their breeding based on a balance between costs and benefits of reproducing at any given time in a way that maximizes their individual fitness (Lack 1968; Verboven and Visser 1998). This optimal timing of breeding depends on the seasonality in the environment, and comprises a trade-off between adult condition and the prospects for offspring survival (Rowe *et al.* 1994; Verhulst and Nilsson 2008). For instance, early breeding may be constrained by energetic demands necessary for egg production compared to the resources currently available to females (Perrins 1970). There are also survival costs for parents and/or nestlings if breeding starts too early, when food is still scarce (Nilsson 1994; Verhulst and Nilsson 2008). Later breeding, however, may cause the nestlings to hatch outside the period of the most favourable environmental conditions (Visser *et al.* 2006; Verhulst and Nilsson 2008; Öberg *et al.* 2014). Seasonal patterns in reproductive success may arise through variation in individual or environmental quality (Brinkhof *et al.* 1993; Verhulst and Nilsson 2008; Harriman *et al.* 2017). The former suggests that individuals who breed early are of better quality or possess territories of higher quality, resulting in higher reproductive success (Price *et al.* 1988; Christians *et al.* 2001; Harriman *et al.* 2017). The latter suggests that variation in reproductive success arises from the timing of breeding in relation to seasonal variation in environmental quality, and should affect all individuals in a population similarly (Verhulst and Tinbergen 1991; Brinkhof *et al.* 1993; Siikamäki 1998; Harriman *et al.* 2017). However, these two hypotheses are not mutually exclusive (Brinkhof *et al.* 1993; Verhulst *et al.* 1995; Verhulst and Nilsson 2008).

Reproductive phenology and its consequences for reproductive performance may also vary between species with different reproductive strategies. Some species show declining reproductive success with later laying dates, as is commonly found in single-brooded species (Perrins 1965; Verhulst and Tinbergen 1991; Verhulst and Nilsson 2008). In contrast, others show a mid-season peak, which is the most common pattern observed in multi-brooded species (Brinkhof *et al.* 1993; Crick *et al.* 1993; Verhulst and Nilsson 2008). The reproductive success during a year in single-brooded species relies on the success of one brood (Perrins 1970; Crick *et al.* 1993; Svensson 1995). Thus, such species are assumed to have evolved to start breeding at a time so that the nestling feeding period matches optimal conditions (Lack 1968; Crick *et al.* 1993; Svensson 1995). On the other hand, the annual reproductive output in multi-brooded species relies on the number of broods as well as the success of each brood (Soler *et al.* 1995; Weggler 2006). Hence, such species have presumably evolved to raise the highest number of successful clutches within a season (Crick *et al.* 1993). Since one brood represents only a fraction of the annual reproductive output, individuals in multi-brooded species are predicted to be less prudent about the timing of breeding and start breeding as early as possible to increase the length of the breeding season and thus the possibility of more broods (Crick *et al.* 1993; Svensson 1995; Weggler 2006).

Breeding phenology in birds has been shown to be influenced by spring temperatures (McCleery and Perrins 1998; Crick and Sparks 1999; Both *et al.* 2004; Dunn 2004; Visser *et al.* 2009; Pärn *et al.* 2012; Chevin *et al.* 2015; Hinsley *et al.* 2016; Phillimore *et al.* 2016;

Simmonds *et al.* 2017; Drake and Martin 2018), in addition to winter temperatures and variation in the North Atlantic Oscillation (NAO), with earlier breeding following warm winters (Forchhammer *et al.* 1998; Przybylo *et al.* 2000; Sanz 2002; Williams *et al.* 2015). Temperature may affect the timing of breeding in birds through both reduced energetic costs at warmer temperatures for females during egg production and influences on the food availability (Dunn 2004; Dunn and Winkler 2010). The temporal fluctuations in arthropod production are assumed to be the driver of the timing of breeding in several passerine bird species, because protein rich food is crucial for fast growing nestlings (Lack 1968; Van Noordwijk *et al.* 1995; Naef-Daenzer *et al.* 2000; Cresswell and McCleery 2003; Visser *et al.* 2004; Visser *et al.* 2006; Charmantier *et al.* 2008). Individuals breeding outside the window of peak resource supply often have lower reproductive success (Thomas *et al.* 2001; Verboven *et al.* 2001; Visser *et al.* 2006; Verhulst and Nilsson 2008; Reed *et al.* 2013; Samplonius *et al.* 2016). However, in order for the nestling feeding period to coincide with peaks in arthropod biomass, parents have to initiate reproduction before the abundance of arthropods gets high. Hence, they have to react to cues affecting arthropod phenology (Visser *et al.* 2004). The phenology of both plants and arthropods are influenced by temperature, and phenological synchrony between herbivorous arthropod insects and plants is crucial for the developmental and reproductive success of several arthropod species (van Asch and Visser 2007). Thus, temperature and spring foliation may serve as indicators for the timing of arthropod development (Visser and Holleman 2001; Dunn 2004; Visser *et al.* 2004; van Asch and Visser 2007; Tobin *et al.* 2008; Saino *et al.* 2011; Hinks *et al.* 2015; Uelmen *et al.* 2016). For example, Cole *et al.* (2015) quantified the emergence of vegetation in spring using satellite-derived data, and found that this measure was positively related to the timing of breeding in both great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*), and to the peak availability of their caterpillar food source.

The effect of timing of breeding on reproductive success may differ due to heterogeneity in habitat quality. Resource availability may vary spatially because the seasonality and abundance of a specific resource as well as the composition of different resources may differ between contrasting habitat types (Eeva *et al.* 2000; Tremblay *et al.* 2003; Glądalski *et al.* 2017). For instance, caterpillars often form a distinct peak in oak forests while displaying lower abundances and later peaks in pine forests (Veen *et al.* 2010; Burger *et al.* 2012). Spatial variation in habitat quality has in many bird species been shown to influence both the timing of breeding and reproductive success (Svensson and Nilsson 1995; Tremblay *et al.* 2003; Burger *et al.* 2012; Seress *et al.* 2012; Goodenough 2014; Wawrzyniak *et al.* 2015). For instance, blue tits bred earlier and produced more offspring in a deciduous habitat with high abundances of food, compared to a poorer coniferous habitat (Lambrechts *et al.* 2004). Furthermore, the presence of livestock has been shown to positively influence the prevalence and reproductive success of several farmland bird species through higher abundance of invertebrates and availability of suitable nest sites in sheds and stables (Møller 2001; Robillard *et al.* 2013; Musitelli *et al.* 2016).

The density of conspecifics is another important factor that may affect the availability of resources such as food and nest sites (Gustafsson 1987; Ahola *et al.* 2012), and should therefore be seen in relation to habitat quality. High densities may result in positive density dependent effects on reproduction through increased efficiency to detect predators or new food sources, which has been found in several colonial bird species (Findlay and Cooke 1982; Westneat 1992). However, intraspecific competition for resources has been found to result in negative density dependent effects on reproductive success (Minot 1981; Arcese and Smith 1988; Rodenhouse *et al.* 2003). For instance, Both (1998) found experimental support for a causal relationship between breeding density and reproduction in great tits. Nest boxes were provided at different densities, and great tit reproductive output was higher at lower densities compared to higher densities (Both 1998). Accordingly, it may be beneficial for individuals to breed nonsynchronous relative to the rest of the population to reduce competition (Gustafsson 1987; Pakanen *et al.* 2016). Timing of reproduction relative to conspecifics may be especially important for birds with social dominance hierarchies (Johansson *et al.* 2014). In such species, offspring hatched early in the season are assumed to benefit from higher dominance positions in winter flocks and earlier settlement in territories compared to offspring that hatch late (Johansson *et al.* 2014; Pakanen *et al.* 2016). Also, in species without a stable flock hierarchy in the winter, early offspring may have higher survival rates relative to late offspring because they gain more experience prior to the onset of harsh conditions (Arcese and Smith 1985). In both cases, it may be beneficial for parents to breed earlier than conspecifics because early broods may have higher recruitment success compared to late broods (Arcese and Smith 1985; Johansson *et al.* 2014; Pakanen *et al.* 2016).

In relation to the recent and ongoing climate warming, a large number of studies have investigated the impact of environmental changes on phenological events, such as advancement of flowering and spring foliation in plants (Lieth 1974; Myneni *et al.* 1997), the timing of the annual peak abundance for some arthropod populations (Ellis *et al.* 1997; Buse *et al.* 1999; Visser *et al.* 2006), and the timing of breeding in birds (Crick *et al.* 1997; Visser and Both 2005; Dunn and Winkler 2010; Gienapp *et al.* 2013; Charmantier and Gienapp 2014; Dunn and Møller 2014). Several species of birds have advanced their egg-laying dates in accordance with increases in spring temperatures (Crick *et al.* 1997; McCleery and Perrins 1998; Both *et al.* 2004; Charmantier *et al.* 2008; Husby *et al.* 2010). This advancement is generally found to be greater in multi-brooded species, and results in an increased duration of the breeding season allowing increased productivity (Dunn and Møller 2014; Halupka and Halupka 2017). However, some species and populations fail to adapt (through evolution or plasticity) fast enough to a changing climate. The reason for this may be that a species' response differs from the response of organisms at a lower trophic level on which they depend (Stenseth and Mysterud 2002; Walther *et al.* 2002; Visser *et al.* 2004; Visser and Both 2005; Both *et al.* 2006; Parmesan 2006; Durant *et al.* 2007). Such temporal mismatches between birds and their prey have been found to vary across different habitats, both between and within species, and have in some cases lead to reduced fitness and population declines (Visser *et al.* 1998; Both *et al.* 2006; Burger *et al.* 2012). Climate models predict that the warming trends in the northern hemisphere will continue and that the overall weather in the future will be more variable (Stenseth and Mysterud 2002; Walther *et al.* 2002). Hence, understanding the demographic and environmental factors acting on important life history events, such as timing of breeding and reproduction, are necessary to predict how populations may respond to future changes in the environment (Post *et al.* 2009). There is generally a shortage of studies investigating these processes in multi-brooded species in different habitat types (but see Crick *et al.* 1993; Ringsby *et al.* 2002; Pärn *et al.* 2012; Dunn and Møller 2014).

The aim of this study was to investigate the temporal variation in timing of breeding in differing habitats and its consequences for reproductive success in a multi-brooded species. In order to accomplish this, I used data from a study system of house sparrows (*Passer domesticus*) including 9 islands with 11 populations during the period 2003 until 2012 in northern Norway (Ringsby *et al.* 1998; Ringsby *et al.* 1999; Sæther *et al.* 1999; Ringsby *et al.* 2002; Jensen *et al.* 2004; Pärn *et al.* 2012). Because of the long-term sampling of data on individual fitness components and life history traits in several populations, this study system provides a unique opportunity to study the eco-evolutionary dynamics of timing of reproduction. All populations were closely associated with human settlements, but on some islands the populations had access to dairy farms with shelter and concentrated grain foods. Hence, I classified the study populations into two habitat categories, farm and no-farm populations.

The following three objectives were addressed: first, I investigated whether variation was present in the onset of breeding (i.e. laying date of the first clutch) within and among the populations during the study period. Second, I investigated if the variation in laying date was influenced by environmental and demographic factors prior to the breeding season, which might be used by sparrows as cues for predicting the environmental conditions during the nestling period, such as measures of spring temperature, the NAO index, vegetation phenology (i.e. onset of spring) and population density. Finally, I investigated factors that may affect the variation in reproductive success, including population density, laying date and the deviance between laying date and onset of spring. The general expectation is that birds living in the no-farm populations are more exposed to temporal fluctuations in food availability and weather conditions (Pärn *et al.* 2012). Hence, I examined the differences between habitat categories in all analyses.

MATERIALS AND METHODS

Study species

The house sparrow is highly social and breeds and forages in loose colonies and flocks (Anderson 2006). Adult house sparrows are specialized as granivores and feed primarily on seeds and grains (Kalmbach 1940; Hammer 1948; Keil 1973; MacMillan 1981). However, this species is often described as an adaptive, innovative and opportunistic forager, and has been found to show a variety of dietary choices, for instance concentrated grain foods (Anderson 2006). The nestlings are fed with animal material the first few days, predominantly arthropods. The proportion of animal material in the diet is then gradually reduced with increased nestling age (Kalmbach 1940; MacMillan and Pollock 1985; Klvaňová *et al.* 2012).

House sparrows are stationary, socially monogamous and show a high degree of nest site fidelity (Anderson 2006; Kvalnes *et al.* 2013). In northern Norway, the breeding season lasts from early May until mid-August (Ringsby *et al.* 1998; Ringsby *et al.* 1999; Sæther *et al.* 1999; Ringsby *et al.* 2002; Jensen *et al.* 2004; Pärn *et al.* 2012; Kvalnes *et al.* 2013). House sparrows are hole-nesters and mainly breed near human settlements (Anderson 2006). They lay 1 – 3 clutches per season in our study area, with a mean clutch size of 4.6 eggs (Ringsby *et al.* 1998; Husby *et al.* 2006; Kvalnes *et al.* 2013; Westneat *et al.* 2014).

Study area

The study area is part of a larger study system of house sparrows including a total of 18 islands located in an archipelago off the coast of Helgeland in northern Norway (Fig. 1). Here, a high proportion of individuals have been monitored using capture-mark-recapture methods since 1993 until present (Ringsby *et al.* 1998; Ringsby *et al.* 1999; Sæther *et al.* 1999; Ringsby *et al.* 2002; Jensen *et al.* 2003; Jensen *et al.* 2004; Jensen *et al.* 2008; Pärn *et al.* 2009; Pärn *et al.* 2012; Kvalnes *et al.* 2013). Nine islands were included in the present study (Fig. 1). Five of these islands are located close to the mainland, where the house sparrows live in close association with dairy farms and have access to shelter and cattle food all year round (Ringsby *et al.* 2002; Pärn *et al.* 2012). The populations living on these islands are referred to as “farm populations”, and include Hestmannøy, Indre Kvarøy, Gjærøy, Nesøy and Aldra

(Fig. 1). The remaining four islands include Lovund, Husøy, Selvær and Myken, and are located further away from the mainland and have no dairy farms (Fig. 1). The populations living on these islands are referred to as "no-farm populations", and they live near human residents and their gardens and are more exposed to seasonal variation in weather conditions and food availability (Pärn *et al.* 2012). There is a single population on each of the study islands, except from Hestmannøy and Gjerøy where there are two populations (located in the northern and southern part of each island). Hence, there were 11 study populations in total (Fig. 1).

The landscape in the study area consists of a combination of moors, mountains and agricultural land. The climate is oceanic and the ground is regularly covered with snow during the winter, which reduces access to natural food sources such as grass seeds (Pärn *et al.* 2012). The house sparrows in the no-farm populations mainly breed in nest boxes or in ventilation shafts on the resident's houses, while the individuals in the farm populations mostly breed inside barns and cow sheds in cavities on beams, along walls and under the roof tops.

Data collection

Data were collected during the breeding seasons in the period 2003 – 2012. Each population was searched thoroughly for new and active nests at least once a week during this period. For each nest site, the brood number, the laying date of the first egg in a clutch, the day of hatching, and the number of eggs and fledglings were recorded. Nestlings were marked in the nests with a unique combination of a numbered aluminum ring and three plastic colour rings. The number of fledglings was estimated as the number of nestlings present at the last visit before fledging, at age 8 – 13 days (Ringsby *et al.* 1998; Sæther *et al.* 1999). Due to few visits during some breeding seasons, data were not available from Myken in 2003, Indre Kvarøy in 2009 and 2011, and Nesøy in 2012.

It was assumed that all clutches at a specific nest site belonged to the same female within a season (Kvalnes *et al.* 2013). Laying date was determined based on the increase in number of eggs between visits when nests were found during egg-laying, as house sparrows lay one egg per day. For clutches that were detected during or after the incubation period, the date of egg-laying was determined by subtracting the median incubation period of 11 days and the clutch size - 1 (incubation starts with the penultimate egg) from the hatching day (see Kvalnes *et al.* 2013). The hatching day was either observed directly or estimated based on an evaluation of the age of the nestlings on the first visit after hatching. The clutch size was defined as the maximum number of eggs in a clutch, or was estimated as the sum of unhatched eggs, alive and dead offspring if the clutch was found after hatching (Ringsby *et al.* 1998; Ringsby *et al.* 2002).

Laying date

Laying date was defined as the day number of the first egg laid in the first clutch for each nest site each year, where day 1 was January 1st. For some nest sites the true first clutch might have been missed. Thus, to avoid including any of the second clutches or clutches that were re-laid after a failed first attempt, I defined a criterion where clutches were categorized as first clutches only if they were laid within 35 days after the date at which 10 % of the recorded clutches in each study population had been laid. The 35 days criterion was chosen because this is the average time it takes for parents to raise a brood (i.e. from the first egg is laid until the fledglings have left the nest). In addition, no clutches were assigned as first clutches after the 15th of June. Subsequent analyses were performed with data from first, second and third clutches in nest sites where the above criteria for first clutches were fulfilled (except for a reduced dataset used in the analyses of nestling mortality, see below in the Statistical analyses section). When investigating factors that influence the variation in laying date, the absolute value of laying date was used. However, when applying laying date as one of the explanatory variables in analyses of reproductive success, laying date was mean centered within populations and years. In other words, in these analyses I used the relative laying date within each island and year to account for populations that bred consistently either early or late and varying environmental conditions from year to year.

Reproductive success

Three measures of reproductive success were used: (1) the number of fledglings in the first clutch and (2) the sum of fledglings in all broods within a nest site during the breeding season. Additionally, (3) the probability that nestlings in the first clutch died during the nestling period (i.e. nestling mortality) was analyzed. This was calculated using the proportion of eggs that did not result in a fledgling.

Environmental factors

Vegetation phenology during the breeding season

The normalized difference vegetation index (NDVI), provided by the Northern Research Institute (NORUT), was used as a measure of vegetation phenology. NDVI provides an estimate of the amount of vegetation primary productivity in a given area (Goward *et al.* 1985). Data on NDVI was derived from a Moderate Resolution Imaging Spectroradiometer (MODIS) satellite product, which has a spatial resolution of 250x250 m, from the period 2000 until 2012 (Tucker *et al.* 2005; Karlsen *et al.* 2014). Photosynthetic activity in the vegetation can be measured through optical satellite sensors, because chlorophyll in plants absorbs radiation in the red spectrum, while the near infrared radiation is reflected back to the satellite (Høgda *et al.* 2013; Cole *et al.* 2015). The onset of spring (OS) at each pixel was defined as the time when the NDVI value each year exceeded 70% of the 13 year (2000-2012) mean July NDVI value. The end of the season (ES) was defined as the time when the NDVI value was reduced below 92% of the annual maximum NDVI value. The method for mapping the onset and end of the season are adjusted thresholds from Karlsen *et al.* (2008). These two variables were recorded as a day number where day 1 was January 1st. The length of the growing season (SL) was calculated as the number of days between the onset and the end of the season.

The measures of vegetation phenology were calculated separately for each of the nine study islands. However, due to heterogeneity among islands in the types of vegetation cover and the size of the area with measurable vegetation cover, I used annual means across islands as estimates for onset of spring, end of the season and season length in the subsequent analyses. The mean pairwise Pearson's correlation (r) across years between the island specific values of onset of spring and the annual means of onset of spring was 0.78 (n = 9, SD = 0.12).

In order to investigate how the variation in reproductive success was influenced by the laying date relative to the onset of spring, I calculated the difference (as the number of days) between the laying date for each nest site and the onset of spring. This variable will be referred to as the deviance from spring (DFS).

Daily temperature

Data on daily mean temperatures (°C) were available from the weather station at the island Myken (66°45’ N, 12°29’ E), retrieved through the Norwegian Meteorological Institute’s climatic database (eKlima 2016). Because temperature data from 2011 was not available from this station, data from the weather station at the island Sleneset (66°21’ N, 12°36’ E) were used for this year in the dataset. Weather data from the meteorological station at Sleneset were only available after 2008. Even though Myken and Sleneset are located in the northern and southern part of the study area, respectively (Fig. 1), the variation in temperature between these two stations is highly correlated ($r = 0.83$, $P < 0.05$) (Ringsby *et al.* 2002; Pärn *et al.* 2012; Kvalnes *et al.* 2013). Thus, the temperatures recorded at these two islands are assumed to reflect temperature variation in the whole study area.

I included annual mean temperature in April (AT) as an explanatory variable in models explaining the variation in laying date, as previous studies suggest that house sparrows may adjust their breeding according to spring temperatures (Seel 1968; Ringsby *et al.* 2002; Pärn *et al.* 2009; Pärn *et al.* 2012; Kvalnes *et al.* 2013). Because the majority of females initiate egg-laying in May, it is plausible that the temperature during April may act as a cue that females use to decide when to initiate breeding. Across all study years, the earliest females started to lay their eggs at April 13th, and the mean laying date was at May 14th.

Cumulative degree days

Temperature is the main driver of arthropod development (Briere *et al.* 1999; Logan *et al.* 2006; Tobin *et al.* 2008). Accumulation of degree days is a common method used to estimate temperature increases relevant to arthropod phenology (van Asch and Visser 2007; Tobin *et al.* 2008; Naves and de Sousa 2009). Degree days measure temperatures accumulating above a predefined base temperature during a certain period, below which it is assumed no arthropod development can take place (Herms 2004; van Asch and Visser 2007). I used the “average method” for calculating degree days (Herms 2004) where the sum of the maximum and minimum temperatures during a day divided by two is used as the average daily temperature.

The number of degrees by which the average daily temperature remained above the predefined base temperature gave the number of degree days contributed by a specific day (Herms 2004). The temperature at which arthropods start to develop is in several species found to be close to 10 degrees (Briere *et al.* 1999; Tobin *et al.* 2001; Kontodimas *et al.* 2004; Nietschke *et al.* 2007; Ranjbar Aghdam *et al.* 2009). However, in the present study there were almost no days before the 1st of May with daily mean temperatures above 10 degrees. Hence, I used a base temperature of 5 degrees and assumed that there were microclimates on the islands and periods during the day that allowed arthropods to develop. Development in plants or arthropods may occur in periods with temperatures above the base temperature, even though the temperatures are cold during rest of the day (Herms 2004). Cumulative degree days (CDD) accumulating from 1st of January until 1st of May were used in the analyses.

The North Atlantic Oscillation Index

Regional North Atlantic Oscillation indices were obtained from the National Weather Service Climate Prediction Center, USA (NOAA 2016). The mean values of the North Atlantic Oscillation index (estimated based on the difference in normalized sea pressures between the Azores and Iceland) from December to March (NAO) was used in this study as a measure of regional winter climate (Hurrell 1995; Hurrell *et al.* 2001). Positive NAO index values indicate warmer winter and spring temperatures in north-western Europe (Hurrell 1995; Post *et al.* 1997; Ottersen *et al.* 2001; Pearce-Higgins and Green 2014).

Demographic factors

Population density

Population size was defined as the total number of adult individuals present in each population during the breeding season each year. In the no-farm populations, this was estimated by counting the number of adult individuals present at the beginning of the breeding season. In the farm populations, both the proportion of ringed birds and the recapture and resighting rates were usually greater than 90 %. Therefore, the breeding population size in these populations was estimated as the number of adult individuals observed or captured during the breeding season in a given year in addition to individuals observed or captured in both a previous and a subsequent year (Ringsby *et al.* 1999; Pärn *et al.* 2012; Jensen *et al.*

2013; Baalsrud *et al.* 2014). These two methods have been found to be highly correlated (Jensen *et al.* 2013). Before the post-juvenile moult late in the breeding season, all individuals outside nests could be identified as juveniles or adults (Jensen *et al.* 2004). Unmarked birds caught during the autumn were assumed to be juveniles due to the high proportion of marked birds in the populations (Kvalnes *et al.* 2013). Population size was mean centered within populations across years and used as a relative measure of population density (PD).

Statistical analyses

The statistical analyses were performed using linear and generalized linear mixed effects models that were fitted using the packages lme4 (Bates *et al.* 2014) and glmmADMB (Skaug *et al.* 2015) in the statistical software R, version 3.2.5 (R Core Team 2016).

In total, reproductive data from 1365 nests in 11 different populations over 10 years were included in the analyses. These data had a nested hierarchical structure, with reproductive data nested within populations and years. Hence, population and year were included with random intercepts in all analyses.

An important assumption when performing multiple regression analyses is that the explanatory variables are uncorrelated (Graham 2003). Hence, the explanatory variables that were included in the analyses were thoroughly evaluated using pairwise Pearson's correlations (r), graphical visualization and variance inflation factors (VIF). Estimates of r above 0.5 and VIF's above 3 indicate potentially problematic levels of collinearity between the explanatory variables (Graham 2003).

The analyses were performed in three sections. First, the variation in laying date was decomposed into its temporal and spatial components using a linear mixed effects model. The model contained no fixed effects except the intercept, but had random intercepts for population, year and the interaction between population and year in order to decompose the variance (Table A1).

Second, when investigating factors influencing the variation in laying date, a linear mixed effects model was fitted. To test which environmental cues in the spring that affected the initiation of breeding, I included mean temperature in April (AT), NAO and cumulative degree days (CDD) as explanatory variables (Table A1). We expected the birds to breed earlier with increasing values of these variables. Onset of spring (OS) was also included, with an expected positive association with laying date. Additionally, population density (PD) was included as an explanatory variable, which was hypothesized to affect the variation in laying date through altering the availability of resources. To investigate the difference in laying date between farm and no-farm populations, habitat category (HC) was included as a categorical factor. In addition, the interaction between habitat category and each of the other explanatory variables were included to investigate whether the explanatory variables influenced the response variable differently in farm versus no-farm populations. In all analyses, the first-order effects of each variable were always kept in models where their interaction was included. The variables AT, OS and CDD contain information that partly describe the same biological processes in the local environment of the birds. As expected, these variables were highly correlated and were not included in the same models (Table A2). NAO, which represents large scale regional climatic processes, did not show any correlation with the local climatic variables (Table A2).

Finally, when investigating factors which influence the variation in different components of reproductive success, generalized linear mixed effects models were fitted. A Poisson distribution with a log link was used in models where the response variable was the number of fledglings in the first clutch or the total number of fledglings per nest site. One assumption underlying Poisson models is that the variance of the response variable is equal to the mean. However, a common problem associated with such models is overdispersion (i.e. the variance of the response variable is greater than the mean). In order to account for possible overdispersion due to additional variation specific to each observation, I included an observation-level random factor, nest site ID (Harrison 2014).

When analyzing the probability of nestling mortality until the fledgling stage in the first clutch, a Binomial distribution with a complementary log-log link function was used (Ringsby *et al.* 2002). Nestling mortality was modeled as a response vector calculated from the number of dead offspring and the total clutch size in the first clutch. The dataset used in these analyses was restricted to clutch sizes between three and seven to reduce the number of first clutches with possibly false clutch sizes (n = 1235) (Husby *et al.* 2006; Kvalnes *et al.* 2013). This may arise due to factors such as detection of a clutch after unhatched eggs and/or dead offspring have been removed, or relaying of a female on an old/existing clutch. All nestlings should have the same probability of dying according to the assumptions of the Binomial model. However, each individual’s fate is often not independent from that of its siblings within a clutch. Such dependencies may increase the variance of the mortality rate. Hence, the observation-level random factor, nest site ID, were also included in these analyses to account for possible overdispersion (Ringsby *et al.* 1998; Harrison 2014).

The explanatory variables included in these models were: laying date (LD), population density (PD), deviance from spring (DFS), habitat category (HC) and the interaction between habitat category and each of the other explanatory variables (Table A1). PD is expected to act on the variation in the number and mortality rate of fledglings through density dependent effects such as competition for resources. We expect LD to reflect resource availability and thus affect the different components of reproductive success. As LD was centered within populations and year, a value equal to zero represents the mean laying date of first clutches for a given population in a given year. Onset of spring is expected to be a proxy for the emergence of arthropods, and we predict reproductive success to be affected by changes in the deviance between laying date and onset of spring. For the analyses of the number of fledglings per nest, the length of the growing season (SL) was also included as an explanatory variable. A longer growing season is expected to increase the number of fledglings, as this may provide an opportunity to raise more broods. We also predict the production of fledglings per nest to be larger with earlier laying dates, as this may result in an extended length of the breeding season. In order to investigate if there was a non-linear relationship between LD or DFS with any of the response variables, second-degree polynomials of these two explanatory variables were included. The variables LD and DFS both contain information about laying date. Accordingly, these variables were highly correlated and were not included in the same models (Table A3). First-degree polynomials were always kept in models where their second-degree polynomials were present.

Model comparisons were performed using the Akaike Information Criterion corrected for small sample sizes (AIC_c). This involved ranking all candidate models fitted with maximum likelihood (ML) for each response variable according to AIC_c, in order to identify models with high support in the data (Burnham and Anderson 2002). The candidate model with the lowest AIC_c value was considered to have the highest support in the data. This model was used for relative comparison with the remaining set of candidate models, and has a ΔAIC_c value equal to zero. However, candidate models which had AIC_c values less than two units larger than the best model (i.e. $\Delta AIC_c \leq 2$) were considered to have equal support in the data (Burnham and Anderson 2002). In such cases, all relevant models with associated parameter estimates were evaluated. AIC_c weights ($wAIC_c$) and evidence ratios (ER) were also calculated. $wAIC_c$ for a given model is the probability that the model is the best, given the data and the set of candidate models (Burnham and Anderson 2002). ER is here defined as the relative probability that the highest ranked model is the best compared to the model under consideration, and was calculated as the ratio between the $w\mathrm{AIC}_c$ of the highest ranked model and the $w\mathrm{AIC}_c$ of the given model (Burnham and Anderson 2002). In order to easily perform the model comparisons, I applied the dredge function from the R package MuMIn (Barton 2014) which automatically fitted the models specified above. Additionally, to avoid over-parameterization, I specified only models containing a maximum of four explanatory variables and three interactions. All fitted models were considered biologically relevant according to current theory and empirical knowledge. Means and standard deviations (SD) are given. Estimated effect sizes (β) were reported with 95 % confidence intervals (CI), and were considered significantly different from zero when their CI did not overlap zero. In the figures for the fitted relationships of the variables affecting laying date, the shaded areas that indicate CI were obtained by parametric bootstrapping using the bootMer function in the R package lme4 (Bates *et al.* 2014). The shaded areas indicating CI in the figures showing the variables with effects on reproductive success were obtained based on parameter estimates and the variance-covariance matrix for the parameter estimates of fixed effects from the R package glmmTMB (Magnusson *et al.* 2016).

RESULTS

Laying date varied considerably between populations and years (Fig. 2). The mean laying date across all populations and years was May 14th (*n* = 1365, SD = 12.92), and ranged from April 28th on northern Hestmannøy in 2010 to June 9th on Nesøy in 2010 (Fig. 2). In the no-farm populations, the mean laying date across the study period was May 9th (*n* = 487, SD = 11.77), whereas it was May 17th (*n* = 878, SD = 12.56) in the farm populations.

Across all populations and years, the mean number of fledglings in the first clutch was 1.61 (*n* = 1365, SD = 1.80) and the mean total number of fledglings per nest site through a season was 2.85 (*n* = 1365, SD = 2.81). The mean production of fledglings in the first clutch and per nest site in the no-farm populations were 2.36 (*n* = 487, SD = 1.97) and 3.74 (*n* = 487, SD = 3.12), respectively. In the farm populations, the mean number of fledglings in the first clutch was 1.20 (*n* = 878, SD = 1.56), and the mean number of fledglings per nest site was 2.36 (*n* = 878, SD = 2.49). See Table A4 for information about the number of nest sites with 1, 2 and 3 clutches across all years in the farm populations, the no-farm populations and in total. The mean probability of nestling mortality across all populations and years was 64% (*n* = 1235, SD = 37%). In the farm populations, the mean probability of nestling mortality was 73% (*n* = 784, SD = 34%), while it was 50% (*n* = 451, SD = 39%) in the no-farm populations.

Decomposing variation in laying date

Most of the variation in laying date was due to differences between nest sites (62.8 %). Further, 15.6 % of the variation in laying date was due to mean differences between populations, and 1.3 % of the variation was due to differences between years. Finally, the interaction between population and year accounted for 20.4 % of the variation in laying date, which indicates that laying date was asynchronous between populations (Fig. 2 and 3).

Factors affecting laying date

The highest ranked model explaining variation in laying date included population density, onset of spring and the two-way interactions of these variables with habitat category (Table 1). The effect of population density on laying date differed among habitats (Table 2).

Population density was negatively related to laying date in the no-farm populations (β = -0.114, CI = [-0.190, -0.039]), while there was an uncertain positive relationship in the farm populations (Table 2). Thus, sparrows generally started to breed earlier with higher population densities in the no-farm populations, but not in the farm populations (Table 2, Fig. 4a).

Onset of spring also influenced laying date differently in farm and no-farm populations (Table 2). In the farm populations, there was a negative effect (Table 2), while there was no effect in the no-farm populations (β = 0.002, CI = [-0.272, 0.277]). Hence, the model suggested that breeding started later with earlier onset of spring in the farm populations, but not in the no-farm populations (Table 2, Fig. 4b). Birds in no-farm populations generally started to breed earlier than those in farm populations (Table 2). This can also be seen from the structure of the observed data (Fig. 5).

The second highest ranked model explaining variation in laying date had $\Delta AIC_c = 1.38$ and about half the AIC_c weight compared to the highest ranked model (AIC_c weight model 1 = 0.287, AIC_c weight model 2 = 0.144, Table 1). Both the highest ranked models in Table 1 included the same explanatory variables, except for a weak uncertain positive effect of NAO in the second highest ranked model (β = 0.48, CI = [-0.85, 1.82]) (Table 1).

Factors affecting reproductive success

The number of fledglings in the first clutch

Variation in the number of fledglings in the first clutch was best explained by a model including population density, laying date, the second-degree polynomial of laying date, habitat category, the interaction between population density and habitat category, and the interaction between laying date and habitat category (Table 3). The number of fledglings in the first clutch decreased with higher population densities in the farm populations, indicating a negative density dependent effect (Table 4). However, this relationship differed to the no-farm populations (Table 4), where there was an uncertain positive trend (β = 0.005, CI = [-0.002, 0.012]). In general, there were more fledglings in the first clutches in the no-farm populations than in the farm populations at high population densities (Fig. 6a).

The number of fledglings in the first clutch was curvilinearly related to laying date, with both early and late clutches having more fledglings than clutches initiated around the mean laying date (Table 4, Fig. 7a). The production of fledglings in the first clutch was generally higher in the no-farm populations when compared to the farm populations (Table 4). This general pattern was also present in the observed data (Fig. 8a).

Among the tested candidate models, both the two highest ranked models had substantial support in the data (ΔAIC_c model 2 = 0.51, Table 3). These two models included the same explanatory variables, but the highest ranked model contained one more interaction term with an uncertain effect between habitat category and the second-degree polynomial of laying date (β = -0.001, CI = [-0.002, 0.000]). Considering the uncertainty of the interaction term in model 1 and following the principle of parsimony (i.e. including the fewest number of parameters in a model that satisfactory represent the data (Burnham and Anderson 2002)), I present model 2 only (Table 3 and 4).

The number of fledglings per nest

The best model explaining variation in the number of fledglings per nest included population density, season length, laying date, the second-degree polynomial of laying date, habitat category, the interaction between population density and habitat category, and the interaction between season length and habitat category (Table 5). The relationship between population density and the production of fledglings per nest differed between habitats (Table 6). There was a negative relationship in the farm populations (Table 6), while there was an uncertain positive relationship in the no-farm populations (β = 0.006, CI = [-0.001, 0.013]) (Fig. 6b).

The length of the season influenced fledgling production differently in the two habitat types (Table 6), as there was an uncertain negative relationship between season length and the number of fledglings per nest in the farm populations (Table 6), and an uncertain positive trend in the no-farm populations (β = 0.011, CI = [-0.004, 0.027]) (Fig. 9). There were generally more fledglings per nest in the no-farm compared to the farm populations, especially in long seasons and at higher population densities (Fig. 6b and 9). This general pattern of a higher production of fledglings per nest in the no-farm populations was also indicated by the observed data (Fig 8b).

There was a convex relationship between laying date and the total number of fledglings per nest site (Table 6). The production of fledglings was higher when the laying date of the first clutch was earlier than the mean laying date in the population, and lower in nests where first clutches were initiated later (Table 6, Fig. 7b).

The two highest ranked models both had high support from the data (ΔAIC_c model 2 = 0.94, Table 5). Both models included the same explanatory variables, but the highest ranked model included an additional interaction term between habitat category and laying date with an uncertain effect ($\beta = -0.010$, CI = [-0.022, 0.001]) (Table 5). According to the principle of parsimony and given the uncertainty of the interaction term in model 1, only the results from model 2 are presented (Table 5 and 6).

Nestling mortality in the first clutch

The highest ranked model explaining variation in nestling mortality in the first clutch included population density, laying date, the second-degree polynomial of laying date, habitat category, the interaction between population density and habitat category, and the interaction between laying date and habitat category (Table 7). Higher population densities increased the probability of nestlings dying in the first clutch in the farm populations (Table 8). This relationship differed in the no-farm populations, where there was an uncertain negative effect ($\beta = -0.006$, CI = [-0.017, 0.005]) (Table 8, Fig 6c). The mortality was generally higher in the farm populations at higher population densities, when compared to the no-farm populations (Fig. 6c).

The mortality rate in the first clutch was curvilinearly related to laying date, with the highest probability of mortality in clutches initiated around the mean laying date (Table 8, Fig. 7c). The nestling mortality was generally higher in farm-populations than in no-farm populations (Table 8, Fig. 6c and 7c). This pattern can also be seen in the observed data (Fig. 8c).

The highest ranked model had a weight of 0.631 and was over two times more likely to be the best model among the candidate models compared to the second best model (ER= 2.01, $\Delta AIC_c = 1.40$, Table 7). Both the highest ranked models contained the same explanatory variables, but the second best model included one more interaction term with an uncertain effect between the second-degree polynomial of laying date and habitat category ($\beta = 0.001$, CI = [-0.001, 0.002]) (Table 7).

DISCUSSION

The extensive knowledge of the breeding ecology of single-brooded species (e.g. Both *et al.* 2006; Visser *et al.* 2006; Phillimore *et al.* 2016) does not necessarily extend into multi-brooded species. However, understanding the factors affecting breeding in multi-brooded species are particularly relevant since climate change has been found to lengthen the breeding seasons in many regions, and thus facilitate species with multiple breeding attempts in a year (Dunn and Møller 2014; Halupka and Halupka 2017). The present study demonstrates the influence of local phenology and local demography on important life history traits in populations of a multi-brooded species, the house sparrow, living in two different habitats. Therefore, this study represents an important contribution to the knowledge on how a multi-brooded species may adjust its reproductive strategies compared to well documented strategies typical for single-brooded species (e.g. Van Noordwijk *et al.* 1995; Cresswell and McCleery 2003; Cole *et al.* 2015). Interestingly, the effects of environmental and demographic factors on laying date and reproductive success differed between populations, depending on their habitat type. In the no-farm populations, individuals advanced their laying dates with higher population densities (Table 2, Fig. 4a), and produced more fledglings than the farm populations, especially during longer season lengths (Table 4 and 6, Fig. 9). Sparrows in the farm populations started breeding slightly later when onset of spring was early (Table 2, Fig. 4b), and their reproductive success decreased with higher population densities (Table 4, 6 and 8, Fig. 6). These results suggest that habitat type is an important factor determining reproductive decisions and consequences in these populations. Furthermore, house sparrows had higher reproductive success in first clutches and produced more fledglings throughout the entire season when initiating their first clutches before the mean laying date of the population (Table 4, 6 and 8, Fig. 7).

The no-farm populations generally started to lay their eggs earlier than farm populations (Fig. 5). There were multiple factors that influenced these differences in laying date between habitat categories. For instance, the results suggested that sparrows started to breed earlier with higher population densities in the no-farm populations (Table 2, Fig. 4a). At least three alternative hypotheses could explain this pattern. First, larger population densities may reflect favourable environmental conditions the previous year, potentially resulting in a larger production of offspring, higher body condition of individuals and higher over-wintering survival rates (Yalden and Pearce-Higgins 1997; Ringsby *et al.* 1998; Sæther *et al.* 2004;

Robb *et al.* 2008). Based on the general assumption that initiation of egg-laying is proximately limited by the physiological state of the females (Perrins 1970; Johansson *et al.* 2014), this suggests that individuals of higher quality (measured by e.g. age and/or body condition) may be able to start breeding earlier and achieve higher reproductive success (i.e. the quality hypothesis, Price *et al.* 1988; Hasselquist *et al.* 2001; Bêty *et al.* 2003; Devries *et al.* 2008; Verhulst and Nilsson 2008).

A second hypothesis for why individuals started to breed earlier with higher population densities in the no-farm populations is that larger population densities may lead to earlier breeding through increased social stimulation (Darling 1938; Waas *et al.* 2005). Darling (1938) hypothesized that social stimulation such as the presence or sound from conspecifics would accelerate physiological changes in reproductive organs in females. As a result, birds living in populations or colonies with higher densities will lay earlier and be more synchronous due to higher levels of social stimulation compared to birds in less dense populations (Darling 1938; Gochfeld 1980). Experimental support of Darling’s hypothesis was provided by Waas *et al.* (2005) using zebra finches (*Taeniopygia guttata*) and a playback system of their sound under laboratory conditions.

Finally, as house sparrows are highly social and live and forage in flocks, larger population densities may result in higher levels of competition for nest sites and food to feed nestlings (Gustafsson 1988; Newton 1998; Krist 2004). Thus, at high population densities, it may be advantageous for individuals to breed earlier than the majority of pairs in the spring in order to reduce competition with conspecifics for resources. This hypothesis may be underpinned by our findings of higher reproductive success at early laying dates and lower reproductive success around the mean laying date (Table 4, 6 and 8, Fig. 7), which may indicate that resource competition may play an important role for reproductive decisions in these house sparrow populations. Further support was provided by Ahola *et al.* (2012) in a study on pied flycatchers (*Ficedula hypoleuca*) in Finland, who found that selection for earlier egg-laying dates was stronger at higher breeding population densities. This suggests that being early can be more important when high population densities increase the level of intraspecific competition (Ahola *et al.* 2012).

Curiously, the present study showed that a relationship between laying date and population density was only found in the no-farm populations, but not in the farm populations (Table 2, Fig. 4a). This suggests that house sparrow's decision for when to initiate breeding is based on the combined effects of both population density and habitat type. For instance, it is possible that the variation in nest site quality differ among habitats. In the farm populations, sparrows utilize nest sites within the barns that may be more or less exposed to the same conditions, while in the no-farm populations, individuals mostly breed in nest boxes that are scattered over a larger area with varying exposure to weather conditions. If nest site quality is more variable in the no-farm populations, there might be a lack of high quality nest boxes for all breeding pairs at high densities, forcing some pairs to settle in nest boxes of lower quality (Ahola *et al.* 2012). Such a mechanism may favor early breeders in the no-farm populations that occupy the best nest boxes.

The results suggested that onset of spring did not influence laying date in the no-farm populations (Table 2, Fig. 4b). This was unexpected as onset of spring is often found to be correlated with the emergence of arthropods (Cole *et al.* 2015; Hinks *et al.* 2015), which is a crucial determinant for timing of breeding in several passerine bird species (Blancher and Robertson 1987; Van Noordwijk *et al.* 1995; Dias and Blondel 1996; Visser *et al.* 1998; Both *et al.* 2006; Visser *et al.* 2006; Charmantier *et al.* 2008; Dunn *et al.* 2011; Reed *et al.* 2013; Cole *et al.* 2015). However, the majority of these studies are conducted on generally single-brooded species such as great and blue tits and pied flycatchers. Such species are assumed to time their breeding to optimal conditions in order to maximize their annual reproductive output, which is determined by the success of a single brood (Husby *et al.* 2010; Chevin *et al.* 2015; Phillimore *et al.* 2016). On the contrary, the annual reproductive output in multi-brooded species is largely determined by the number of breeding attempts, and they are assumed to time their breeding in order to maximize the number of successful broods (Crick *et al.* 1993; Soler *et al.* 1995; Svensson 1995; Weggler 2006). Thus, the importance of matching breeding with the period of highest food abundance may differ between single and multi-brooded species. For instance, Verboven *et al.* (2001) compared different great tit populations that were single-brooded or facultatively double-brooded. The single-brooded populations displayed a positive relationship between breeding date and peak food date, while timing of breeding was not related to the time of the food peak in the double-brooded populations (Verboven *et al.* 2001). Other studies from multi-brooded species have also found no relationship between timing of breeding and the peak availability of food (Weggler 2006).

Instead, breeding time in such species may be determined by other factors. For instance, it is suggested that reproductive success in multiple breeders may be more constrained by season length than by optimal timing of the first clutch, and that they start to breed as soon as environmental conditions are above a certain threshold in order to extend the breeding season (Svensson 1995; Weggler 2006).

The phenology of different prey species and the foraging strategy of house sparrows may also explain why onset of spring did not influence laying date in the no-farm populations. Matching breeding with peaks in arthropod biomass may be less important for generalist bird species living in habitats with broad food peaks compared to specialist species in habitats with marked food peaks (Visser *et al.* 2006; Halupka *et al.* 2008; Both *et al.* 2010; Samplonius *et al.* 2016). House sparrows are generalists, and the composition of arthropods in the diet of their nestlings has been shown to vary seasonally (Anderson 1984; MacMillan and Pollock 1985). However, generalist bird species may still be adapted to time their breeding to the outbreak of food resources in the spring (Dyrcz and Halupka 2009). The measure of onset of spring used in the present study is based on NDVI values, i.e. chlorophyll in leaves. While the phenology of several herbivorous caterpillar species depend on leaves (van Asch and Visser 2007), other components of the house sparrow's diet, such as spiders who are predatory, do not (Logan *et al.* 2006). Thus, the NDVI values may not necessarily be the optimal proxy reflecting the phenology of house sparrows' prey species, possibly resulting in the lack of relationship between initiation of breeding and onset of spring found in this study.

House sparrows in the farm populations started to breed later with earlier onset of spring (Table 2, Fig. 4b). This result contrasts with the expected positive relationship between timing of breeding and spring phenological events, such as the emergence of leaves and arthropods (Cole *et al.* 2015; Hinks *et al.* 2015). A possible reason for the opposite effect found in the present study is that an early onset of spring may reflect favourable winter conditions with resulting higher survival rates (Yalden and Pearce-Higgins 1997; Altwegg *et al.* 2003). Since juvenile survival is found to be more influenced by weather during winter compared to adult survival (Balen 1980; Altwegg *et al.* 2003), there might be a higher proportion of young individuals in a population after a mild winter than after a harsh one. Juveniles often breed later and achieve lower reproductive success than older individuals, since older individuals generally are of higher quality due to factors such as longer experience, increased foraging ability and settlement in territories/acquisition of nest sites of high quality (Anderson 1990; Wheelwright and Schultz 1994; Forslund and Pärt 1995; Martin 1995; Weggler 2001;

Weggler 2006; Hatch and Westneat 2007; Verhulst and Nilsson 2008; Stubberud *et al.* 2017). For instance, Robertson and Rendell (2001) found that laying dates advanced and reproductive success increased from first-time breeders to middle-aged individuals of tree swallows (*Tachycineta bicolor*). This age-effect might be prevalent in the no-farm populations as well, but it may be cancelled by other effects. For instance, the no-farm populations are more exposed to fluctuating weather conditions and may start breeding earlier than the farm populations when spring arrival is early. However, note that the range of the effect of onset of spring on laying date is about 5 days difference in laying date in the farm populations, across the whole range of onset of spring of about 20 days, ranging from April 28th until May 16th (Fig. 4b).

Temperature affects the development of both arthropods and vegetation (Logan *et al.* 2006; van Asch and Visser 2007). As expected, both measures of temperature included in this study, mean temperature in April (AT) and cumulative degree days (CDD), showed high levels of correlation with onset of spring (OS) (AT: $r = -0.67$, $P < 0.001$, CDD: $r = -0.83$, $P < 0.001$). Thus, it is likely that our measure of onset of spring should have some predictive abilities regarding resource availability. In particular, degree days is a common method used to estimate the emergence of arthropods in the spring (van Asch and Visser 2007; Tobin *et al.* 2008). A model including CDD was ranked as the 4th highest in the AIC_c ranking of candidate models explaining variation in laying date ($\Delta AIC_c = 2.89$, AIC_c weight = 0.068, Table 1). This model included the same explanatory variables as model 1, except that OS was replaced by CDD. In the farm populations, there was a positive, although uncertain, relationship between CDD and laying date ($\beta = 0.090$, CI = [-0.028, 0.212]), which is compatible with the negative effect of OS found in model 1 (Table 2, Fig. 4b). Accordingly, the seasonal distribution and abundance of arthropods in relation to laying date and fledgling production within the different broods can be fruitful to pursuit in order to obtain further insights into these processes.

During the study period of ten years, reproductive success was generally higher in the no-farm populations compared to the farm populations (Fig. 8). Several factors contributed to these differences between habitat categories. For example, population density influenced components of reproductive success differently among the two types of habitat. As population density increased in the farm populations, the mortality rate in the first clutch increased, and the number of fledglings in the first clutch and in sum per nest decreased (Table 4, 6 and 8, Fig. 6). House sparrows live and forage in flocks, and the negative effects of population density in the farm populations may be explained by possibly higher rates of competition and limited access to resources such as food for nestlings and high quality nest sites when many birds breed at the same time. Such negative density dependent effects on reproductive success have been reported in several bird species (Perrins 1965; Both 1998; Rodenhouse *et al.* 2003; Sillett and Holmes 2005; Holmes 2007). For instance, Arcese and Smith (1988) found that reproductive success of song sparrows (*Melospiza melodia*) declined with increasing population densities. To test if this pattern in reproductive success was related to a shortage of food when population densities were high, they conducted a food supplement experiment in a year of peak density. In support of their hypothesis, supplemental food resulted in a higher number of breeding attempts, clutch sizes, nestling weights, number of fledglings and advanced egg-laying dates (Arcese and Smith 1988).

Interestingly, an uncertain positive relationship between population density and reproductive success was present in the no-farm populations (Table 4, 6 and 8, Fig. 6), indicating that the effect of population density varies depending on properties of the habitat. One reason for this may be that sparrows in the no-farm populations spread more out and utilize nest sites and resources from a larger area when population density is high. Sparrows in the farm populations, however, breed in a more confined area inside barns. Consequently, higher population densities in the farm populations may generate higher levels of intraspecific competition for resources compared to the no-farm populations.

The results further suggested that reproductive success from first clutches was influenced by a curvilinear effect of laying date, in both the farm and the no-farm populations, with fewer fledglings and higher nestling mortality in first clutches that were initiated around the mean laying date (Table 4 and 8, Fig. 7a and c). As laying dates were centered within populations and years, these results provide information about the density of breeding pairs experienced by individual birds within a given year. Thus, the convex shape of the relationships in both habitats may reflect the decreasing food availability as a consequence of more adults searching for food for their chicks at the same time around the mean laying date. This result may thus be explained by negative density dependent effects such as competition for arthropod prey. In other study systems, the density of breeders has been found to be negatively related to the production of fledglings (Dhondt *et al.* 1992; Rodenhouse *et al.* 2003; Ahola *et al.* 2009; Ahola *et al.* 2012). Accordingly, individuals may reduce competition by breeding earlier or later than the mean breeding time in the population, and thereby achieve higher reproductive success than when breeding in synchrony with conspecifics (Gustafsson 1987; Pakanen *et al.* 2016).

The findings of lower reproductive success around the mean laying date contrast with many studies on both single-brooded and colonial bird species. Single-brooded species are often found to time their breeding so that nestlings are in the nest at peaks in food availability, with reduced breeding success for pairs breeding at a time that deviate from the majority of pairs (Verhulst and Nilsson 2008; Chevin *et al.* 2015). One classical example of this is the great tit system in Wytham Wood, Oxford, UK (Perrins and McCleery 1989; Van Noordwijk *et al.* 1995; Buse *et al.* 1999; Cresswell and McCleery 2003; Charmantier *et al.* 2008; Simmonds *et al.* 2017). Colonial species have been found to attain higher reproductive success when breeding in synchrony due to advantages such as dilution of predation pressure and enhanced efficiency in detecting new food patches (Findlay and Cooke 1982; Westneat 1992). However, if matching breeding with the peak abundance of food items is not very essential, which may be the case for many multi-brooded species, or if the food peak is not very marked, other factors such as competition and breeding nonsynchronous relative to conspecifics may be more important (Gustafsson 1987; Weggler 2006; Pakanen *et al.* 2016).

The house sparrows who initiated their first clutches earlier than the majority of breeding pairs in the population produced a higher number of fledglings through the whole breeding season (Table 6, Fig. 7b). Breeding earlier than conspecifics has previously been found to result in a higher annual reproductive output in multi-brooded species, since this may extend the breeding season and increase the possibility of more broods (Svensson 1995; Weggler 2006). For instance, the earlier female black redstarts (*Phoenicurus ochruros*) laid their first clutches compared to other female conspecifics, the more subsequent broods were initiated and fledglings produced (Weggler 2006). There are also other reasons for why breeding earlier than conspecifics may be beneficial. For instance, offspring hatched early in the season may benefit from higher survival rates due to higher dominance positions in winter flocks, earlier settlement in territories and longer experience compared to late hatched offspring (Arcese and Smith 1985; Johansson *et al.* 2014; Pakanen *et al.* 2016). Breeding early relative to the majority of conspecifics may also increase reproductive output due to reduced predation pressure if predators synchronize their breeding with the peak in fledgling production of their prey (Götmark 2002; Verhulst and Nilsson 2008; Both *et al.* 2009). Additionally, as mentioned above, older individuals are often of higher phenotypic quality and able to breed earlier and achieve higher reproductive success compared to younger individuals.

The length of the season influenced the total production of fledglings per nest site differently among habitats, suggesting that the effect of season length must be understood in relation to properties of the habitat. There was an uncertain negative trend in the farm populations and an uncertain positive trend in the no-farm populations (Table 6, Fig. 9). The tendency of a lower production of fledglings in the farm populations during longer breeding seasons may be explained by the finding in the present study that the sparrows in these populations started to breed later with earlier onset of spring (Table 2, Fig. 4b). However, individuals in the no-farm populations appeared to produce a higher annual number of fledglings compared to the farm populations during longer seasons (Fig. 9). Although the positive effect in the no-farm populations was uncertain, the positive trend is consistent with findings from previous studies from multi-brooded species (Svensson 1995; Weggler 2006). A longer duration of the breeding season may allow more time between broods, a higher number of broods, and possibly result in higher reproductive success in species laying several broods per season (Svensson 1995; Halupka *et al.* 2008; Dunn and Møller 2014; Halupka and Halupka 2017). For instance, Weggler (2006) conducted a study on black redstarts and found that the annual reproductive success of individuals increased linearly with the number of broods, and that the number of breeding attempts was mainly determined by the length of the breeding season.

Conclusion

In conclusion, this study suggests that spatial heterogeneity among habitats leads to spatial variation in environmental and density dependent effects on reproductive traits in house sparrow populations in northern Norway. The study revealed how onset of spring, population density and season length influenced laying date and reproductive success differently in the two habitat types. Further, this study indicates that the reproductive traits and strategies found in these house sparrow populations correspond to previous findings from other multi-brooded species, and differ from several of the strategies found in single-brooded species. As climate change might lead to longer breeding seasons, the fitness-benefits of breeding early may be enhanced and the annual reproductive success may increase for multi-brooded species, depending on the type of habitat. This study underlines the importance of considering habitat characteristics and the reproductive strategy of a species in order to understand how populations may respond to future changes in the climate. To better understand how climate change may affect life history strategies in this species, it would be interesting to investigate other aspects of the house sparrow’s multi-brooded strategy (e.g. number of broods and the seasonal distribution of reproductive success), how properties of the two habitats differ, and if the factors affecting nestling mortality and fledgling production also affect the number of recruits.

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TABLES

Table 1: Ranking of candidate linear mixed effects models according to AIC_c criteria explaining variation in laying date in a house sparrow metapopulation in Helgeland in northern Norway. Models with $\Delta AIC_c < 5$ relative to the highest ranked model are listed. A total of 58 candidate models were compared, of which a model only containing the intercept was ranked 36. The variables "population" and "year" were included with random intercepts in all models. All parameters in the various models are: population density (PD), onset of spring (OS), mean temperature in April (AT), North Atlantic Oscillation index (NAO), cumulative degree days (CDD) and habitat category (HC), where the study populations were assigned to live on either farm or no-farm islands (see the Materials and Methods section for further explanation). Interactions between variables are indicated by a colon. For each model, the ΔAIC_c (difference in AIC_c value of the focal model compared to the highest ranked model), $wAIC_c$ (Akaike weight) and ER (evidence ratio for each model compared to the highest ranked model) are presented.

Rank	**Model parameters**	**ΔAIC_c**	**$wAIC_c$**	**ER**
1	PD + OS + HC + PD:HC + OS:HC	0	0.287	1
2	PD + OS + NAO + HC + PD:HC + OS:HC	1.38	0.144	1.99
3	PD + AT + HC + PD:HC + AT:HC	2.89	0.068	4.22
4	PD + CDD + HC + PD:HC + CDD:HC	2.89	0.068	4.22
5	PD + OS + HC + PD:HC	3.06	0.062	4.63
6	PD + HC + PD:HC	3.13	0.06	4.78
7	PD + CDD + HC + PD:HC	4.05	0.038	7.55
8	PD + CDD + NAO + HC + PD:HC + CDD:HC	4.41	0.032	8.97
9	PD + OS + NAO + HC + PD:HC	4.47	0.031	9.26
10	PD + AT + NAO + HC + PD:HC + AT:HC	4.53	0.03	9.57
11	PD + NAO + HC + PD:HC	4.59	0.029	9.9
12	PD + AT + HC + PD:HC	4.84	0.025	11.48

Table 2: The explanatory variables included in the highest ranked model explaining laying date in a house sparrow metapopulation in northern Norway (see Table 1). Parameter estimates (β) and 95% confidence intervals are from a linear mixed effects model. The variables "population" and "year" were included with random intercepts in the model. Interactions between variables are indicated by a colon.

Variable	**β**	**95% Confidence interval**	
		Lower limit	Upper limit
Intercept	176.947	138.559	215.334
Population density	0.016	-0.014	0.046
Onset of spring	-0.315	-0.613	-0.017
No-farm populations	-47.771	-83.426	-12.116
Population density : no-farm populations	-0.130	-0.206	-0.055
Onset of spring : no-farm populations	0.317	0.043	0.591

Table 3: Ranking of candidate generalized linear mixed effects models according to AIC_c criteria explaining variation in the number of fledglings in the first clutch in a house sparrow metapopulation in Helgeland in northern Norway. Models with $\Delta AIC_c < 5$ relative to the highest ranked model are listed. A total of 49 candidate models were compared, of which a model only containing the intercept was ranked 49. The variables "population", "year" and "nest site ID" were included with random intercepts in all models. All parameters in the various models are: population density (PD), laying date (LD), laying date^2 (LD^2), deviance from spring (DFS), deviance from spring^2 (DFS^2) and habitat category (HC), where the study populations were assigned to live on either farm or no-farm islands (see the Materials and Methods section for further explanation). Interactions between variables are indicated by a colon. For each model, the ΔAIC_c (difference in AIC_c value of the focal model compared to the highest ranked model), $wAIC_c$ (Akaike weights) and ER (evidence ratio for each model compared to the highest ranked model) are presented.

Rank	**Model parameters**	**ΔAIC_c**	**$wAIC_c$**	**ER**
1	PD + LD + LD^2 + HC + PD:HC + LD:HC + LD^2:HC	0	0.537	1
2	PD + LD + LD^2 + HC + PD:HC + LD:HC	0.51	0.417	1.29
3	PD + LD + LD^2 + HC + PD:HC + LD^2:HC	4.91	0.046	11.67

Table 4: The explanatory variables included in the second highest ranked model explaining the number of fledglings in the first clutch in a house sparrow metapopulation in northern Norway (see Table 3). Parameter estimates (β) and 95% confidence intervals are from a generalized linear mixed effects model. The variables "population", "year" and "nest site ID" were included with random intercepts in the model. Interactions between variables are indicated by a colon.

Variable	**β**	**95% Confidence interval**	
		Lower limit	Upper limit
Intercept	-0.303	-0.604	-0.001
Population density	-0.006	-0.009	-0.003
Laying date	0.009	0.001	0.017
Laying date^2	0.001	0.001	0.002
No-farm populations	0.780	0.372	1.187
Population density : no-farm populations	0.011	0.005	0.018
Laying date : no-farm populations	-0.024	-0.036	-0.012

Table 5: Ranking of candidate generalized linear mixed effects models according to AIC_c criteria explaining variation in the number of fledglings per nest in a house sparrow metapopulation in Helgeland in northern Norway. Models with $\Delta AIC_c < 5$ relative to the highest ranked model are listed. A total of 137 candidate models were compared, of which a model only containing the intercept was ranked 135. The variables "population", "year" and "nest site ID" were included with random intercepts in all models. All parameters in the various models are: population density (PD), laying date (LD), laying date^2 (LD^2), deviance from spring (DFS), deviance from spring^2 (DFS^2), season length (SL) and habitat category (HC), where the study populations were assigned to live on either farm or no-farm islands (see the Materials and Methods section for further explanation). Interactions between variables are indicated by a colon. For each model, the ΔAIC_c (difference in AIC_c value of the focal model compared to the highest ranked model), $wAIC_c$ (Akaike weight) and ER (evidence ratio for each model compared to the highest ranked model) are presented.

Rank	**Model parameters**	**ΔAIC_c**	**$wAIC_c$**	**ER**
1	PD + LD + LD^2 + SL + HC + PD:HC + SL:HC + LD:HC	0	0.473	1
2	PD + LD + LD^2 + SL + HC + PD:HC + SL:HC	0.94	0.281	1.68
3	PD + LD + LD^2 + SL + HC + PD:HC + SL:HC + LD^2:HC	2.83	0.122	3.88
4	PD + LD + LD^2 + HC + PD:HC + LD:HC	4.86	0.045	10.51
5	PD + LD + LD^2 + HC + PD:HC	4.91	0.031	15.26

Table 6: The explanatory variables included in the second highest ranked model explaining the number of fledglings per nest in a house sparrow metapopulation in northern Norway (see Table 5). Parameter estimates (β) and 95% confidence intervals are from a generalized linear mixed effects model. The variables "population", "year" and "nest site ID" were included with random intercepts in the model. Interactions between variables are indicated by a colon.

Variable	**β**	**95% Confidence interval**	
		Lower limit	Upper limit
Intercept	1.904	0.080	3.729
Population density	-0.005	-0.008	-0.002
Laying date	-0.011	-0.017	-0.005
Laying date^2	0.001	0.000	0.001
Season length	-0.011	-0.024	0.003
No-farm populations	-2.501	-4.578	-0.423
Population density : no-farm populations	0.011	0.004	0.018
Season length : no-farm populations	0.022	0.007	0.037

Table 7: Ranking of candidate generalized linear mixed effects models according to AIC_c criteria explaining variation in the mortality of nestlings in the first clutch in a house sparrow metapopulation in Helgeland in northern Norway. Models with $\Delta AIC_c < 5$ relative to the highest ranked model are listed. A total of 49 candidate models were compared, of which a model only containing the intercept was ranked 49. The variables "population", "year" and "nest site ID" were included with random intercepts in all models. All parameters in the various models are: population density (PD), laying date (LD), laying date^2 (LD^2), deviance from spring (DFS), deviance from spring^2 (DFS^2) and habitat category (HC), where the study populations were assigned to live on either farm or no-farm islands (see the Materials and Methods section for further explanation). Interactions between variables are indicated by a colon. For each model, the ΔAIC_c (difference in AIC_c value of the focal model compared to the highest ranked model), $wAIC_c$ (Akaike weight) and ER (evidence ratio for each model compared to the highest ranked model) are presented.

Rank	**Model parameters**	**ΔAIC_c**	**$wAIC_c$**	**ER**
1	PD + LD + LD^2 + HC + PD:HC + LD:HC	0	0.631	1
2	PD + LD + LD^2 + HC + PD:HC + LD:HC + LD^2:HC	1.40	0.314	2.01
3	PD + LD + LD^2 + HC + LD:HC	4.89	0.055	11.47

Table 8: The explanatory variables included in the highest ranked model explaining the mortality of nestlings in the first clutch in a house sparrow metapopulation in northern Norway (see Table 7). Parameter estimates (β) and 95% confidence intervals are from a generalized linear mixed effects model. The variables "population", "year" and "nest site ID" were included with random intercepts in the model. Interactions between variables are indicated by a colon.

Variable	**β**	**95% Confidence interval**	
		Lower limit	Upper limit
Intercept	0.922	0.492	1.353
Population density	0.006	0.002	0.011
Laying date	-0.014	-0.026	-0.002
Laying date^2	-0.002	-0.003	-0.002
No-farm populations	-1.194	-1.775	-0.614
Population density : no-farm populations	-0.015	-0.026	-0.004
Laying date : no-farm populations	0.047	0.027	0.067

FIGURES

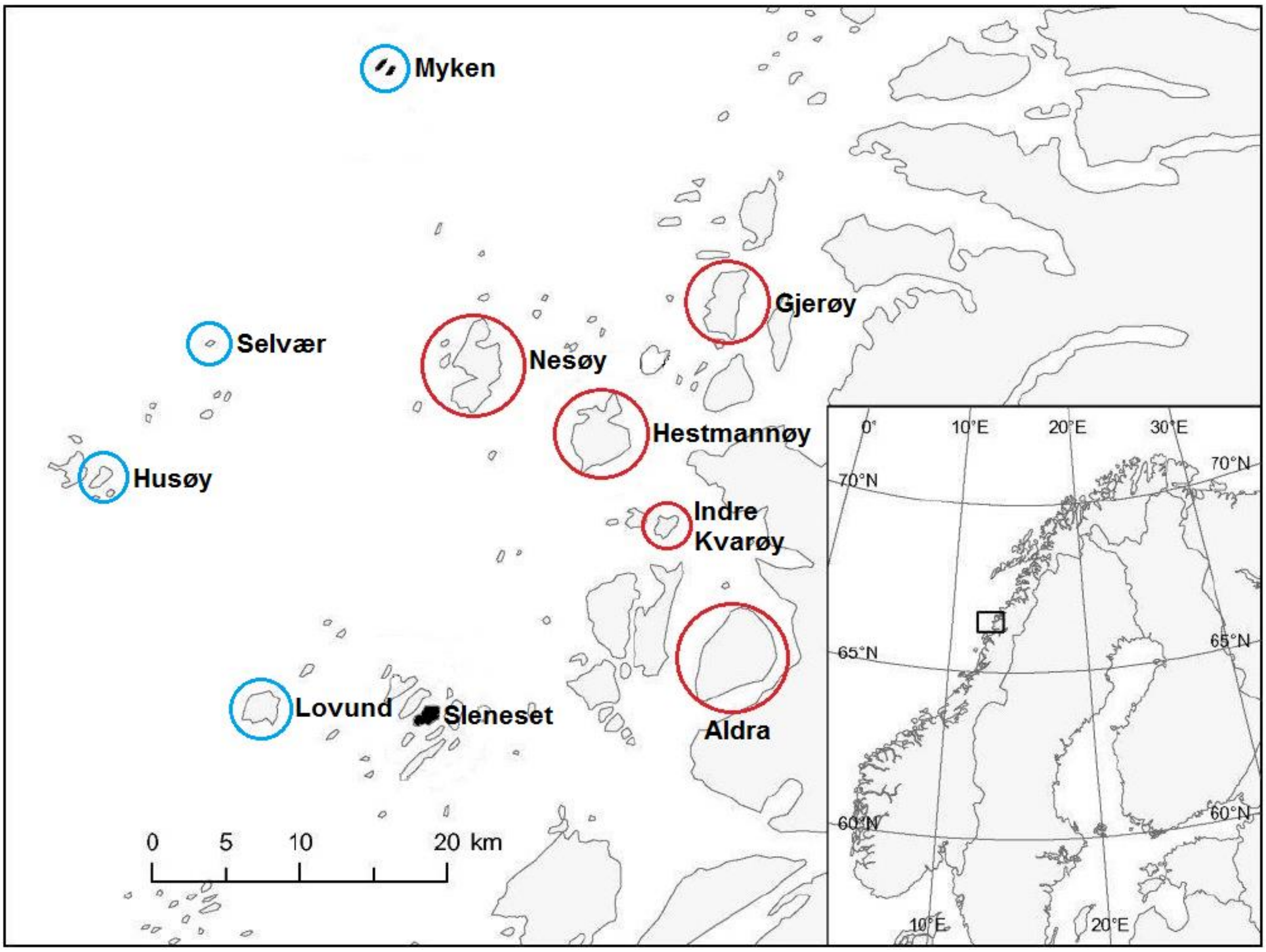

Fig. 1: Map of the study area, situated off the coast of Helgeland in northern Norway. The farm populations living on the islands Gjerøy, Nesøy, Hestmannøy, Indre Kvarøy and Aldra, which are encircled in red. The no-farm populations living on the islands Myken, Selvær, Husøy and Lovund, which are encircled in blue. Weather stations are located on Myken and Sleneset.

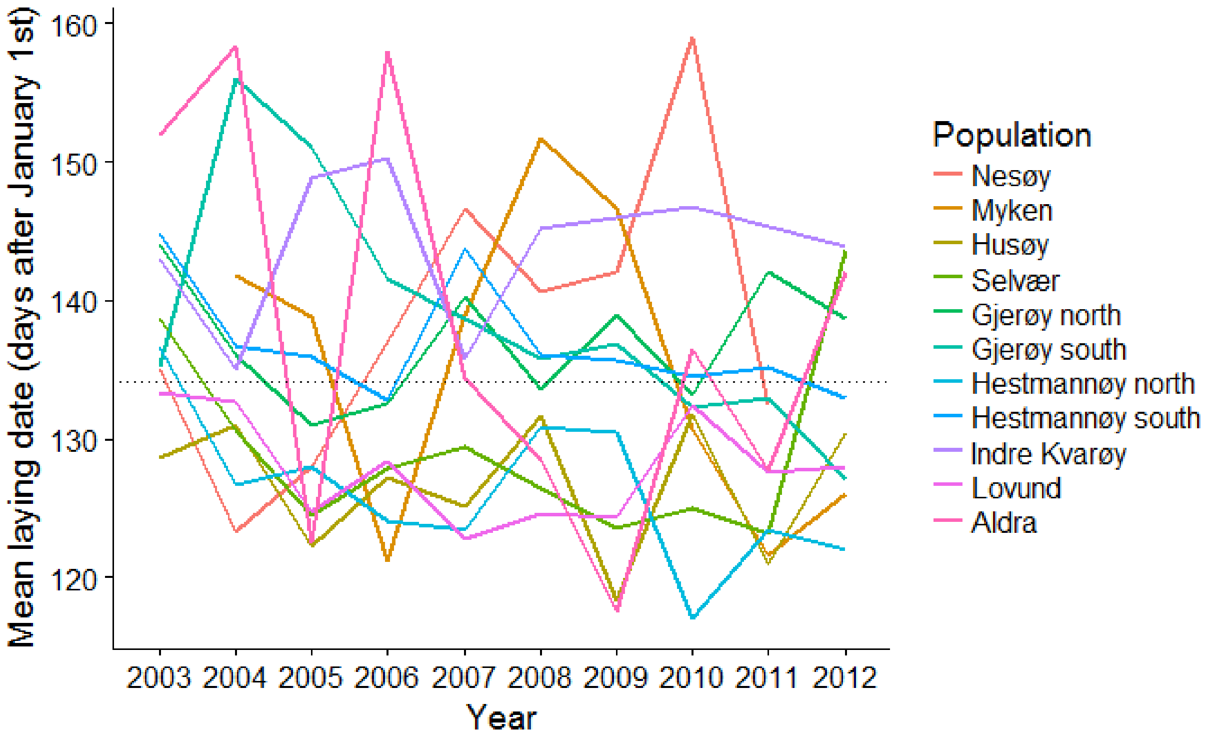

Fig. 2: The mean laying date of the first clutch in each study population each year, based on data from 11 insular populations of house sparrows situated in northern Norway, in the period from 2003 until 2012. The dotted line indicates the mean laying date of the first clutch across populations and years.

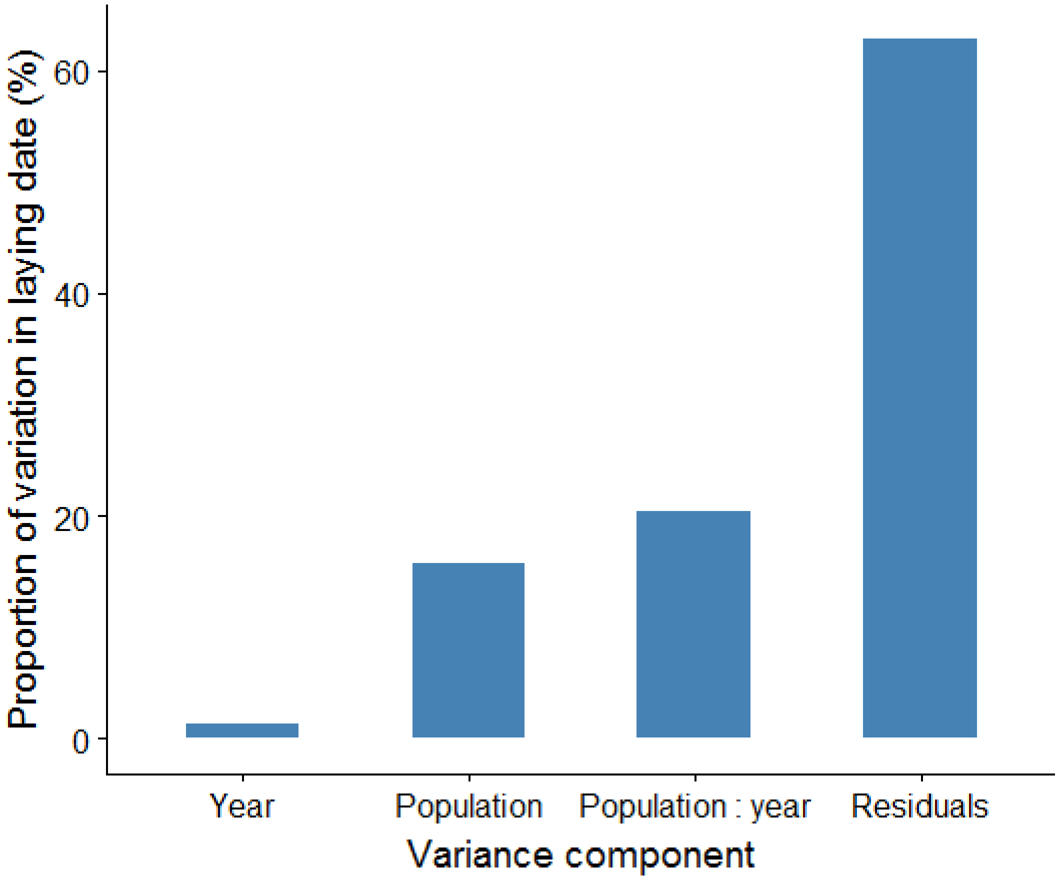

Fig. 3: The proportion (%) of variation in laying dates of the first clutch that is due to differences within the four variance components year, population, population:year interaction, and residuals (i.e. differences between nest sites). Data on laying dates are from 11 populations of house sparrows situated in northern Norway, from the year 2003 until 2012.

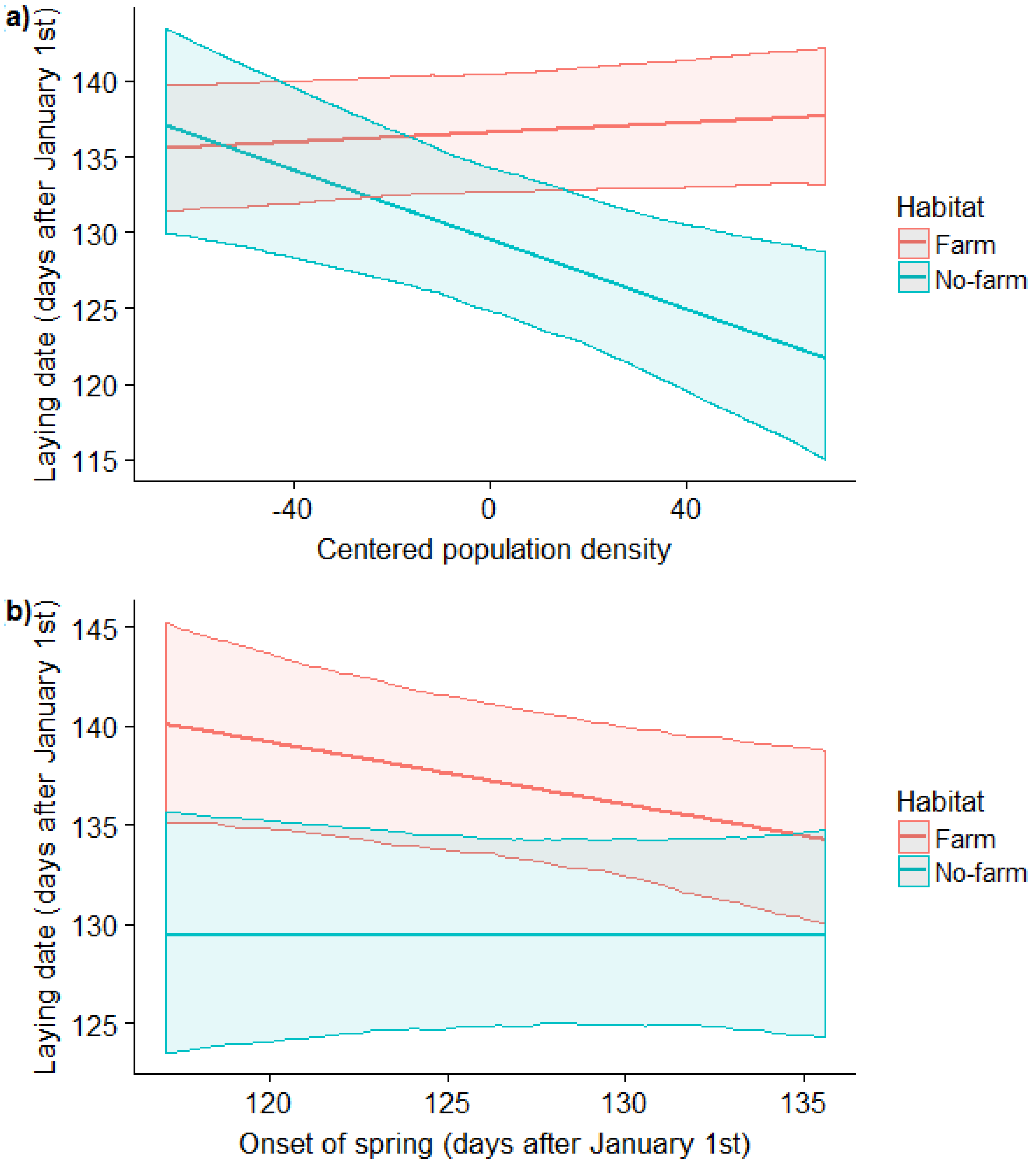

Fig. 4: a) The fitted relationship between laying date of the first clutch and population density (centered within study population) in the farm and the no-farm populations. **b)** The fitted relationship between laying date and onset of spring in the farm and the no-farm populations. Data on laying dates and population densities are from 11 populations of house sparrows situated in northern Norway, from the year 2003 until 2012. The regression lines in each figure (a – b) are the partial effects of the explanatory variables from the linear mixed effects model. Shaded areas indicate the 95% confidence intervals (CI). Details of the model are provided in Table 2.

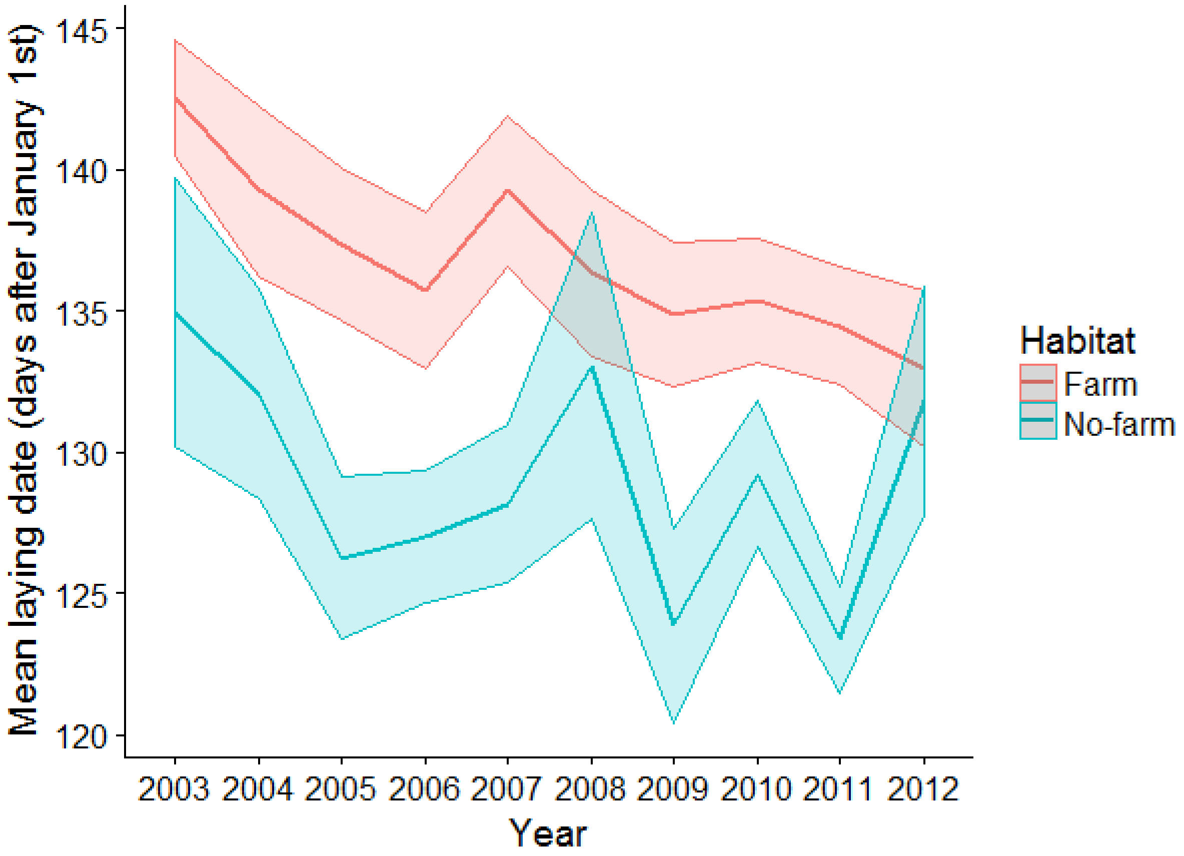

Fig. 5: The mean laying date of the first clutch in the farm and the no-farm populations each year, based on data from 11 insular populations of house sparrows situated in northern Norway, in the period from 2003 until 2012. Shaded areas indicate the 95% confidence intervals (CI) of the mean.

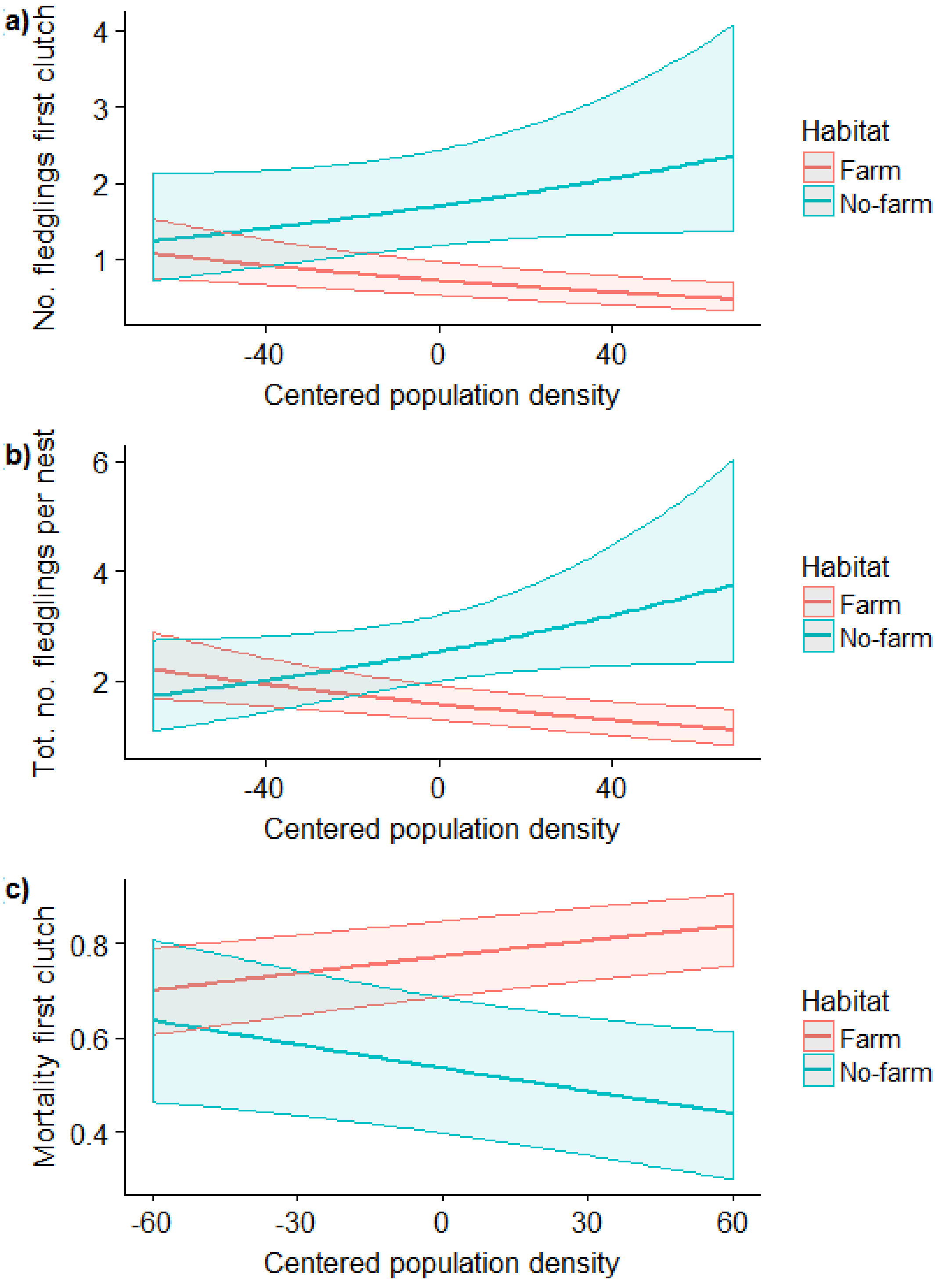

Fig. 6: The fitted relationships between population density (centered within study population) and **(a)** the number of fledglings in the first clutch, **(b)** the total number of fledglings per nest and **(c)** the probability of nestling mortality in the first clutch, in the farm and the no-farm populations. Data on reproductive success and population densities are collected from an insular house sparrow metapopulation in northern Norway, in the period from 2003 until 2012. The regression lines in each figure (a – c) are the partial effects of the explanatory variable from the generalized linear mixed effects models specified in Table 4, 6 and 8, respectively. Shaded areas indicate the 95% confidence interval (CI).

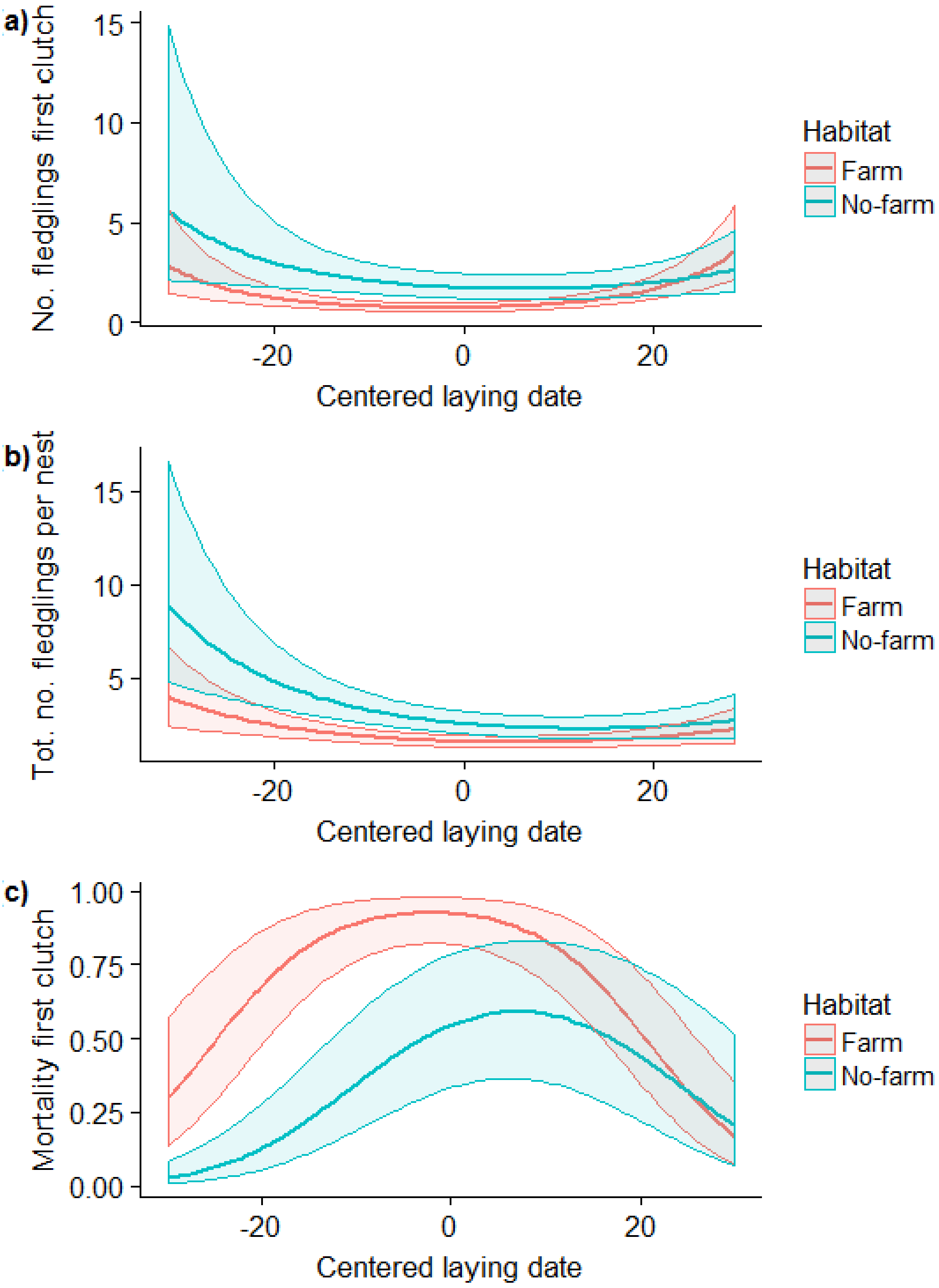

Fig. 7: The fitted relationships between laying date of the first clutch (centered within study population) and **(a)** the number of fledglings in the first clutch, **(b)** the total number of fledglings per nest and **(c)** the probability of nestling mortality in the first clutch, in the farm and the no-farm populations. Data on reproductive success and laying dates are collected from an insular house sparrow metapopulation in northern Norway, in the period from 2003 until 2012. The regression lines in each figure (a – c) are the partial effects of the explanatory variable from the generalized linear mixed effects models specified in Table 4, 6 and 8, respectively. Shaded areas indicate the 95% confidence interval (CI).

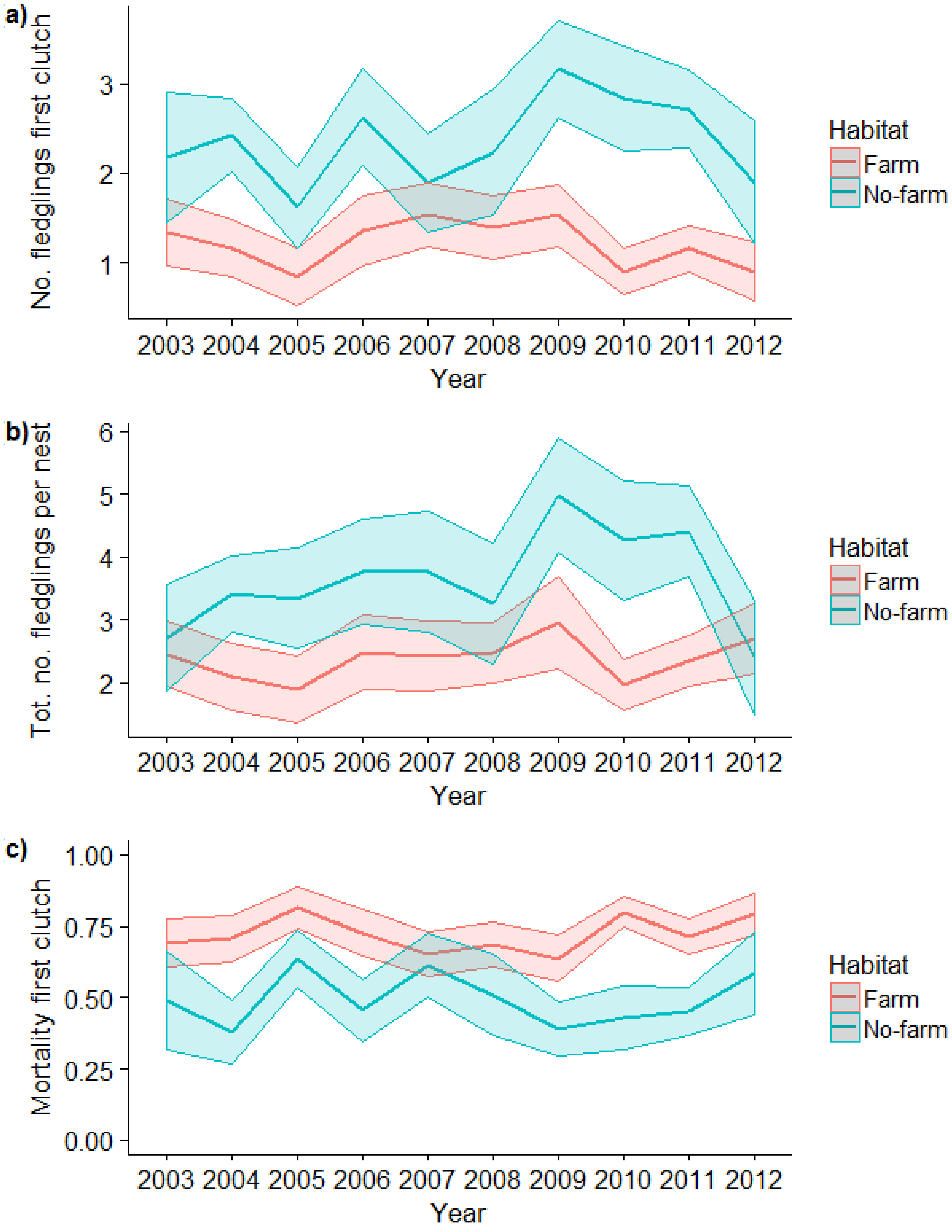

Fig. 8: The mean **(a)** number of fledglings produced in the first clutch, **(b)** number of fledglings produced per nest, and **(c)** probability of nestling mortality in the first clutch. The means are shown for the farm and the no-farm populations each year, based on data from 11 insular populations of house sparrows situated in northern Norway, in the period from 2003 until 2012. Shaded areas indicate the 95% confidence intervals (CI) of the mean.

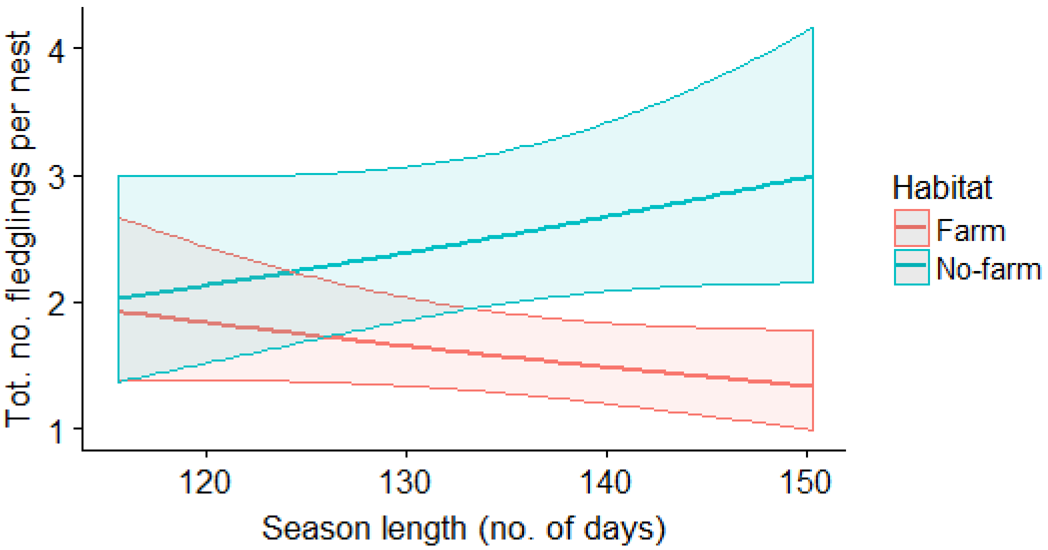

Fig. 9: The fitted relationship between season length and the total number of fledglings produced per nest in the farm and the no-farm populations. Data on the number of fledglings are collected from an insular house sparrow metapopulation in northern Norway, in the period from 2003 until 2012. The regression lines are the partial effects of the explanatory variable from the generalized linear mixed effects model specified in Table 6. Shaded areas indicate the 95% confidence interval (CI).

APPENDIX

Table A1: The variables included in the model to decompose the variation in laying date, and the variables included in the global models to explain the variation in each response variable. The response variables were laying date, the number of fledglings in the first clutch, the total number of fledglings per nest and the probability of nestling mortality in the first clutch. The explanatory variables were population density (PD), mean temperature in April (AT), onset of spring (OS), the North Atlantic Oscillation index (NAO), cumulative degree days (CDD), laying date (LD), laying date^2 (LD^2), deviance from spring (DFS), deviance from spring^2 (DFS^2), season length (SL) and habitat category (HC). Random factors were population, year, the interaction between population and year, and nest site ID. LMM refers to linear mixed effects models. GLMM refers to generalized linear mixed effects models. “x” indicate that the respective variable was included in the model. “x” (in red) indicate that the interaction between the respective explanatory variable and HC was included in the model in addition to the main effect.

	LMM	LMM	GLMM	GLMM	GLMM
	Laying date	Laying date	No. fledglings 1st clutch	Tot. no. fledglings per nest	Mortality 1st clutch
Explanatory variables:					
PD		x	x	x	x
AT		x			
OS		x			
NAO		x			
CDD		x			
LD			x	x	x
LD^2			x	x	x
DFS			x	x	x
DFS^2			x	x	x
SL				x	
HC		x	x	x	x
Random factors:					
Population	x	x	x	x	x
Year	x	x	x	x	x
Population : year	x				
Nest site ID			x	x	x

Table A2: Pearson correlations between explanatory continuous variables used to explain the variation in laying date. Variables included were the North Atlantic Oscillation index (NAO, *n* = 10), cumulative degree days (CDD, *n* = 10), mean temperature in April (AT, *n* = 10), onset of spring (OS, *n* = 10) and population density (mean centered within populations) (PD, *n* = 110). Statistically significant correlations are indicated in bold.

	NAO	CDD	AT	OS	PD
NAO	**1.00**				
CDD	**0.15**	**1.00**			
AT	**-0.29**	**0.65**	**1.00**		
OS	**-0.10**	**-0.83**	**-0.67**	**1.00**	
PD	**-0.18**	**-0.36**	0.01	**0.41**	**1.00**

Table A3: Pearson correlations between explanatory continuous variables used to explain the variation in the number of fledglings in the first clutch, the total number of fledglings per nest and the probability of nestling mortality in the first clutch. Variables included were population density (mean centered within populations) (PD, *n* = 110), laying date (mean centered within populations and years) (LD, *n* = 1365) and deviance from spring (DFS, *n* = 1365) and season length (SL, *n* = 10). Statistically significant correlations are indicated in bold.

	PD	LD	DFS	SL
PD	**1.00**			
LD	0.00	**1.00**		
DFS	**-0.24**	**0.71**	**1.00**	
SL	**-0.34**	0.00	**0.36**	**1.00**

Table A4: The number of nest sites with 1, 2 or 3 clutches in a breeding season across all years in total, in the farm populations and in the no-farm populations.

	1 clutch	2 clutches	3 clutches
Total	1365	547	179
Farm populations	878	315	130
No-farm populations	487	232	49