Nest Microclimate in Relation to Maternal Phenotypic Quality and Reproductive Success in a Wild Population of House Sparrows (*Passer domesticus*)

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Abstract

A better understanding of the factors affecting fledgling and recruit production is important in order to understand ecological and evolutionary processes. The early stages of life are crucial for survival, which in avian species is highly dependent on the experience in the nest. An important characteristic of avian nests is the microclimate as both eggs and nestlings have physiological criteria for the climatic conditions in order to hatch and survive. This microclimate is especially crucial in cold and humid areas where the optimal climate can differ substantially from the ambient climate. The objective of this study was to investigate the microclimate and its relationship with both maternal phenotypic quality and reproductive success in a wild house sparrow (*Passer domesticus*) population in northern Norway by measuring the temperature and humidity close to the nest cup during the last seven days before hatching.

Nest microclimate was repeatable within mothers, suggesting that nest microclimate is a stable individual characteristic of female house sparrows and the study found support for the extended phenotype hypothesis of avian nests. Mean temperature, coefficient of variance of temperature and mean humidity in nests were all affected by the age of the mothers. The results also indicated that mean temperature within nests was influenced by the bill shape of the mother, but the effect was uncertain. An effect of the nest microclimate on the reproductive success was found as fewer fledglings were produced in nests with higher humidity and larger temperature variability, measured as the coefficient of variance of nest temperature, providing further evidence of the importance of the microclimatic conditions in the nests during incubation on avian reproductive success.

Sammendrag

En bedre forståelse av faktorene som påvirker produksjonen av flyvedyktige unger og rekrutterende fugler er viktig for å forstå økologiske og evolusjonære prosesser. De tidligste livsstadiene er kritiske for overlevelse, som hos fugler er svært avhengig av erfaringer i reiret. Et viktig karaktertrekk for fuglereir er mikroklimaet siden både egg og fugleunger har fysiologiske klimakriterier for å klekke og overleve. Dette mikroklimaet er spesielt kritisk i kalde og fuktige områder hvor det optimale klimaet kan avvike betydelig fra de klimatiske forholdene i omgivelsene. Objektivet i dette studiet var å undersøke mikroklimaet og dets forhold til både mors fenotypiske kvalitet og reproduktiv suksess i en vill gråspurvpopulasjon (*Passer domesticus*) i Nord-Norge ved å måle temperatur og fuktighet nær reirskålen i løpet av de siste syv dagene før klekking.

Reirmikroklimaet var repeterbart innen mødre, noe som tyder på at reirmikroklimaet er et stabilt individualistisk trekk for gråspurvhunner og studien fant støtte for hypotesen om den utvidede fenotypen for fuglereir. Gjennomsnittstemperatur, variasjonskoeffisienten for temperatur og gjennomsnittsfuktighet i reir var alle påvirket av mors alder. Resultatene indikerte også at gjennomsnittstemperatur i reirene var påvirket av nebbformen til mødrene, men effekten var usikker. En effekt av reirmikroklima på reproduktiv suksess ble funnet da færre fugleunger nådde flyvedyktig alder i reir med høyere fuktighet og større temperaturvariasjon, som gir ytterliggere bevis for viktigheten av de mikroklimatiske forholdene i reiret i løpet av rugeperioden for fuglers reproduktive suksess.

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1. Introduction

Understanding the factors influencing reproductive success is of fundamental importance in ecology. By building nests, avian species can extend their control of the environment by and shaping a microclimate within it, which plays a crucial role in the early life stages and successful incubation (Hansell, 2000; Ar and Sidis, 2002; Hérbert, 2002).

Avian nests serve to protect the eggs from predation and to create an environment suitable for embryonic development (Collias, 1964; Ligon, 1999). This microenvironment is shaped both by the nest and the bird itself, where the nest becomes increasingly important for smaller birds such as passerines (Deeming, 2002; Deeming and Reynolds, 2015). During incubation, the eggs become sensitive to temperatures outside the optimal range for development (White and Kinney, 1974; Webb, 1987). Webb (1987) found that optimal incubation temperature and the range of temperatures favourable for hatching differs among avian species, but most species seem to have an optimal egg temperature range of 35-39 °C and are able to tolerate up to 10 hours of temperatures ranging from 16 to 41 °C. However, Webb (1987) noted that the temperature actually experienced by eggs during incubation in natural conditions are lower, around 32 to 35 °C. Incubation temperatures lower than optimal can lead to reduced hatching success (Webb, 1987; Nord and Nilsson, 2011), longer incubation period (Eiby and Booth, 2008; Nord and Nilsson, 2011; Auera and Martin, 2017; Ospina et al., 2018), reduced fledgling success (Ardia, 2013; Ospina et al., 2018), reduced growth (Nilsson et al., 2008; Larson et al., 2015; Auera and Martin, 2017), lower-quality fledgling phenotype (Ardia et al., 2010; Nord and Nilsson, 2011; Ospina et al., 2018) and reduced long-term survival (Berntsen and Bech, 2015). High variability in nest temperature have also been found to have a negative effect on reproductive success (Nord and Nilsson, 2011; Larson et al., 2015).

Life history theory posits that individuals have limited amounts of resources which promotes trade-offs in energy allocation between life history traits such as survival and reproduction (Stearns, 1989; 2000). This suggest a negative correlation between different life history traits among individuals. However, empirical studies often find a positive correlation (e.g. De Steven, 1980; Smith, 1981; Allan, 1984). van Noordwijk and de Jong (1986) demonstrated that this positive correlation is due to an individual difference in the total resource budget, i.e. some individuals can invest more in both survival and reproduction because they have more resources available (high quality individuals) than others (low quality individuals).

Incubation is energetically costly for the incubating bird and in 1996, Williams (cited in Deeming, 2002; Nord and Williams, 2015) argued that incubation is especially costly in cold environments, with larger clutches and when eggs needs reheating after a period of abandonment, e.g. due to foraging. The cost of incubation can also be influenced by the design of the nest. For instance, Calder (1973) showed that incubating females of the broad-tailed hummingbird (*Selasphorus platycercus*), breeding in open-cup nests, experienced more heat loss when exposing more of her body above the nest cup.

In temperate regions, reproduction can be initiated even when ambient temperatures are below a threshold stopping egg development, sometimes referred to as "the physiological zero", resulting in a heightened demand on the parents to transfer heat to the eggs and to ensure that the nest temperature does not drop severely in periods of absence from the incubating bird (Hérbert, 2002). Thus, the microclimate of the nests in cold regions serve a crucial role in sustaining optimal temperatures for reproduction, thereby reducing energetic demands of the parents during incubation. The nest microclimate continues to be of importance after the egg period, especially for nestlings of altricial bird species, which depend on parental care and are slower in developing thermoregulatory functions compared to precocial nestlings (Nice, 1962).

The design of the nest can strongly influence the microclimate that the eggs and nestlings will experience (Hansell, 2000). Characteristics associated with thermal properties of the nest that has been recognized in the literature include the thickness and density of the nest wall (Smith et al., 1974; Whittow and Berger, 1977; Skowron and Kern, 1980; Kern and Van Riper, 1984; Heenan, 2013; Akresh et al., 2017), nest size and mass (Skowron and Kern, 1980; Windsor et al., 2013; Akresh et al., 2017; Botero-Delgadillo et al., 2017; Gray and Deeming, 2017), cup depth (Calder, 1973; Windsor et al., 2013), entrance size (Skowron and Kern, 1980; Michielsen et al., 2019), entrance orientation (Ricklefs and Hainsworth, 1969; Inouye et al., 1981; Wiebe, 2001; Ardia et al., 2006) and materials including those cavity-nest are built in (Wiebe, 2001) and those used for lining such as feathers (Møller, 1984; Lombardo et al., 1995; Windsor et al., 2013) and other types of lining (Hansell, 2000). However, avian nests show interspecific variation in the design and composition that can cause differences in the insulation properties (Hansell, 2000; Britt and Deeming, 2011; Biddle et al., 2018). For instance, the wall thickness might not affect the insulation in open-cup nests, as reported by Kern and Van Riper (1984) who found no effect in the nests of Hawaiian Amakihi (*Chlorodrepanis virens*) and Gray and Deeming (2017) who found no effect of wall thickness in six species of common European passerines, which all breed in open cups.

Avian eggs loose about 15-20 % of their initial weight during incubation due to water vapour diffusion through the porous eggshell, which is crucial for the accumulation of the right amount of air in the egg (Wangensteen and Rahn, 1970; Rahn and Ar, 1974; Ar and Rahn, 1980; Deeming and Jarrett, 2015). Low humidity will cause further weight loss and dehydration and high humidity will not cause enough air to accumulate in the egg and difficulties for breaking through the egg, resulting in an intermediate nest humidity as the optimal, which is recorded in several species (Lomholt, 1976; Rahn et al., 1977; Morgan et al., 1978; Grant, 1982; Ar and Sidis, 2002). Determining the optimum humidity levels for all avian species if difficult, but a recommended level of humidity for artificial incubation of domesticated chickens (*Gallus gallus*) is 40-70 % relative humidity (RH), with the optimum found at around 50 %RH (Barott, 1937; Robertson, cited in Bruzual et al., 2000). In the wild, nest humidity is largely determined by nest site selection and nest characteristics, although some cases of manipulation of nest humidity by parental behaviour have been observed (Grant, 1982; Ar and Sidis, 2002).

Nest humidity have also been associated with the prevalence of ectoparasites (Heeb et al., 2000; Moyer et al., 2002) and the thermal conditions inside the nests, as wet nesting materials will lead to higher cooling rates (Hilton et al., 2004). The relationship between humidity and temperature can vary between nests of different sizes and nesting materials (Slagsvold, 1989a; b). Hilton et al. (2004) showed that down is a more effective insulator compared to plant materials when dry, but worse when wet, while plant materials do not show big changes in thermal properties when saturated compared to dry. This results in a potential trade-off for birds to choose materials that are effective insulators, but prone to a variation in insulative effect depending on the weather, or materials with poorer, but more stable insulative properties. Botero-Delgadillo et al. (2017) discovered such a potential trade-off for the thorn-tailed rayaditos (*Aphrastura spinicauda*) between nest insulation and humidity where birds adapted to this trade-off in relation to the ambient climate. The study found that birds from a temperate rainforest built larger nests with more plant materials that absorbed less water, while birds from a colder and less humid area built smaller nests lined with animal materials that were better insulated. This also demonstrate the spatial intraspecific variation in nest building as birds adapt the construction and composition of the nest according to the local ambient climate (Rohwer and Law, 2010; Mainwaring et al., 2012; Heenan et al., 2015; Botero-Delgadillo et al., 2017).

The importance of the microclimate within nests changes as the ambient temperature fluctuates seasonally (Ricklefs and Hainsworth, 1969; O'Connor, 1978; Inouye et al., 1981; Franklin, 1995). Accordingly, it has been shown in several species that birds adjust the construction of the nest according to the current ambient temperature (McGowan et al., 2004; Mainwaring and Hartley, 2008; Britt and Deeming, 2011; Deeming et al., 2012; McClintock et al., 2014). For instance, Schleicher et al. (1996) found that females of Eurasian penduline-tits (*Remiz pendulinus*) selected nests with better insulatory properties early in the breeding season when ambient temperatures were low, while this selection was not present later in the breeding season when ambient temperatures were higher and more stable.

Nest building can be an individual trait as studies have found intraspecific variation in nest characteristics and repeatability of nest characteristics for builders both within and among years (Møller, 2006; Walsh et al., 2010; Järvinen et al., 2017; Patrick et al., 2017; O'Neill et al., 2018). Nest construction has also been found to be an energetically costly and a condition-dependent behaviour (Withers, 1977). In support of this, Mainwaring and Hartley (2009) and Smith et al. (2013) found that female blue tits (*Cyanistes caeruleus*) who received supplementary food either built bigger nests within the same time frame as control females or built similar nests faster than control females.

Because variation in nest characteristics are associated with fitness, show intraspecific variation, but also individual repeatability, and there is a cost of nest building, nests have been proposed as an extended phenotypic trait, where higher quality individuals would be able to build higher quality nests (Dawkins, 1982; Mainwaring et al., 2014). Individuals of higher body condition have also been found to increase nest building effort, suggesting it to be a reliable signal of quality (Zahavi, 1975; Soler et al., 2007). The concept of extended phenotypes was formulated by Dawkins (1982) who argued that genes are expressed not only as phenotypes typically measured on an organism, such as body mass and length, but also as behaviours and artefacts, such as avian nests. Because a gene is not selected for directly, but rather through the organism and its phenotype, behaviour and artefacts could therefore be viewed as an extension of the effects of the gene. Choosing a nest-site and constructing a nest with optimal microclimate is associated with benefits and costs and the climatic characteristics of nests could therefore represent an extended phenotype for birds.

Lifetime reproductive success varies substantially among individuals in natural populations and individuals carrying phenotypic traits linked to high reproductive performance are typically recognized as “high quality individuals” (van Noordwijk and de Jong, 1986). Honest signals of phenotypic quality have been found in several bird species, for instance the badge of male house sparrows (Rohwer, 1975; Møller, 1987; 1988; Veiga, 1993; Solberg and Ringsby, 1997), but see Sánchez-Tójar et al. (2018). Other phenotypic traits have been linked to lifetime reproductive success, for instance Darwin (1874) proposed that larger females are able to produce more offspring and this fecundity advantage hypothesis has received empirical support in a wide range of taxa (Tilley, 1968; Allainé et al., 1987; Kozłowski, 1992; Preziosi et al., 1996; Berger et al., 2008), but see Shine (1988). Reproductive success in birds has also been related to age, likely due to age-related experience and improvement of competence in for instance breeding, foraging and resource acquisition (Nol and Smith, 1987; Forslund and Pärt, 1995; Hatch and Westneat, 2007). However, the relationship between reproductive success and age is not necessarily linearly due to reproductive senescence, a decline in reproductive success at older ages (Holmes et al., 2003; Jones et al., 2008; Reed et al., 2008; Crombie and Arcese, 2018).

Nest microclimate is strongly linked to the climate outside of the nest and several studies have reported a correlation between reproductive success and climate variables, such as temperature (Järvinen, 1993; Sheaffer and Malecki, 1996; Skinner et al., 1998; Ringsby et al., 2002; Smith et al., 2018), precipitation (Sheaffer and Malecki, 1996; Bradley et al., 1997; Skinner et al., 1998; Smith et al., 2018), wind (McGillivray, 1981), storms (Bradley et al., 1997) and extreme weather events (Pipoly et al., 2013). However, climate can influence many factors important for breeding indirectly, such as food availability, egg development, nestling morphology and survival. Reid et al. (2000) designed an experimental study on European starlings (*Sturnus vulgaris*) where they placed a heat pad under the nests, allowing them to investigate the effects of nest temperature independent of ambient temperature. The result was higher fitness to females in heated nests because she could allocate resources into other reproductive stages in both current and future broods due to a reduction of incubation demand caused by a better thermal condition in the nest.

Even though nest microclimate depends strongly on the ambient climate, there may be components of the variation in nest microclimate that are not being explained solely by the ambient climate. Since variation in individual quality can alter the amount of resources available, and hence their ability to acquire high quality nests, it is interesting to investigate if the quality of the mother can explain the variation in nest microclimate. Few studies have taken this phenotypic quality into account when studying the effects of thermal conditions in avian nests.

This study includes data from a long-term capture-mark-recapture study system of a house sparrow metapopulation in the Helgeland archipelago, Norway. Helgeland is a temperate rainy area, with mild winters where temperatures are well below the physiological zero during the breeding season, suggesting that the microclimate in the nest could serve a crucial role in egg development and nestling survival. Individual life histories have been thoroughly recorded from egg stage and all throughout the life of the sparrows and data loggers recording temperature and humidity have been placed inside nests since 2006. This study system offers a unique possibility to investigate how nest microclimate relates to individual variation in life history traits and to measures of reproductive success.

Quality proxies of adult females used here are age, tarsus length (which is a commonly used measure of skeletal size), body mass (which represent the amount of resources acquired) and bill length (which in the study population was found by Ringsby et al. (2009) to have a positive relationship with female feeding rates). Although male house sparrows acquire the nest-site, the study focus will be limited to maternal quality because of extra-pair paternity, female-limited incubation and because nest building is performed mainly by the female (Summers-Smith, 1958; Wetton and Parkin, 1991; Anderson, 2006; Griffith et al., 2008).

Two separate questions will be addressed in the study. First, is there a relationship between maternal quality, measured as morphological traits, and nest quality, measured as temperature and humidity during incubation? Hypothesizing that nest microclimate serve as an extended phenotypic trait, this predicts that high quality females will have warmer, drier and more climatically stable nests. Morphological traits are assumed to correlate linearly with higher phenotypic quality, while age is assumed to have a non-linear relationship with mother quality with a peak in reproductive performance at intermediate ages due to experience-related increase in quality and senescence at older ages. Secondly, does nest quality affect reproductive success, measured as the number of fledglings and recruits produced? More fledglings and recruits are hypothesized to be produced in warmer, drier and more climatically stable nests due to temperatures being closer to the optimal for embryonic development, less humidity stress to the embryos and lower energetic costs of thermoregulation.

2. Methods

2.1. Study species

The house sparrow is a non-migratory passerine species with a global distribution (Anderson, 2006; BirdLife International, 2018). It is secondary cavity nester with a socially monogamous mating system, thought to be upheld by female-female aggression (Veiga, 1992; Anderson, 2006). They live in close proximity to people commonly nesting in human-made structures while forming loose breeding colonies (Anderson, 2006). Nest temperature during the nestling stage is very important for survival as house sparrow nestlings are not able to maintain a regular body temperature above the ambient temperature before they are 10-11 days old because of feather production that are effectively complete after 9-10 days (Seel, 1969). However, temperatures should not exceed 35°C as panting and water loss are documented above this temperature (O'Connor, 1975; Anderson, 2006).

The house sparrow population at Hestmannøy averaged around 160 adult individuals (estimated pre-breeding) during 2006-2013 and is part of a metapopulation on several islands in Helgeland, Norway. The study population contains five breeding colonies centred around cattle farms and has a breeding period lasting from early May until mid-August (Ringsby et al., 1998; Ringsby et al., 2002). Breeding sites are also used by European starlings which normally produces one clutch early in the breeding season and seems to be a big nest-site competitor for the house sparrow (B. Rønning, pers. comm.). Nest site fidelity is high within years and one to three clutches are produced each breeding season (Summers-Smith, 1958; Ringsby et al., 1998; Ringsby et al., 2002). Female house sparrows lay one egg per day in the early morning hours and produce an average clutch size of 5.14 ± 0.06 at Hestmannøy (Kvalnes et al., 2013). Incubation starts after laying of the penultimate egg and is performed by the female without feeding from the male (Seel, 1968; Anderson, 2006). Hatching is synchronized for all but the last laid egg and both sexes contribute in feeding the altricial nestlings with a diet mainly consisting of insects (Seel, 1968; 1969; Anderson, 2006; Julseth, 2019). The incubation period is 11 days and nestlings fledge after about 14 days (Ringsby et al., 1998; Ringsby et al., 2002; Pärn et al., 2009; Pärn et al., 2012).

2.2. Study area

Hestmannøy (66°33'N, 12°50'E, Fig. 1) is located in an archipelago off the coast of Nordland county, Norway. The arctic circle crosses the northern part of the island, which means that the sun does not set in mid-summer, neither rises during mid-winter. Hestmannøy covers 12.8 km^2 and is located 4 km off the mainland. The landscape constitutes fields, cattle farms, sparse forest and rocky mountains separating the north and the south side.

At Hestmannøy, the sparrows find food and shelter all year round in barns, and nest in nest-boxes and crevices in the roof and walls of the barns (Ringsby et al., 2002). The dataset includes clutches nested on five different farms. One of the farms was located on the south side of the island while the other four farms were located on the north side (Fig. 1), separated approximately 3 km apart by the mountains (Table A1 in appendix).

2.3. Data collection

2.3.1. Field procedures

Nests were visited regularly, at least once a week, during the breeding season to check for activity in known nests and to search for new nests (Ringsby et al., 1998; Ringsby et al., 2002; Pärn et al., 2009). Once a clutch was located, the number of eggs present was recorded and clutch size was determined as the maximum number of eggs or nestlings found. The lay date (the date the first egg was laid) was determined exactly by nest visit during egg laying period or calculated by estimation (Kvalnes et al., 2013). Hatch date was either directly observed when visiting the nest or calculated by age-determining nestlings when nests were visited after hatching. The offspring were categorized as fledglings at the age of 8-13 days. Fledglings were ringed with a numbered metal ring and a unique combination of coloured bands, and body mass, tarsus length and wing length were measured (Altwegg et al., 2000; Ringsby et al., 2002). 25 µL of blood was taken from the brachial vein for parental determination using 14 microsatellite markers with 90 % confidence (Jensen et al., 2003; Jensen et al., 2008; Kvalnes et al., 2013; Rønning et al., 2016). Recruits were defined as the number of fledglings observed alive after April 1st the next year and an individual was assumed to be dead if not observed within five years since last recorded alive (Ringsby et al., 2002).

Adult and juvenile birds were identified through observations or caught in mist nets during summer and fall. The proportion of marked individuals in the population on Hestmannøy was above 90 % and the recapture rate was high (Billing et al., 2012; Kvalnes et al., 2017). Unmarked individuals were marked and blood sampled. Body mass was measured with a Pesola spring balance to the nearest 0.1 g, tarsus length, bill depth and culmen (the upper ridge of the bill) length were measured with a Vernier slide calliper to the nearest 0.01 mm and wing length was measured with a ruler to the nearest 1 mm (Ringsby et al., 2009; Kvalnes, 2016). Bill depth was measured on a 90° angle relative to the beak opening from the front of the nostrils and culmen length was measured from a notch in the forehead to the beak tip (Fig. A1 in appendix). Measurements taken only during the summer were averaged and used in the analyses because of seasonal variation in morphological measures, and due to diurnal variation in adult female body mass during egg laying (Anderson, 2006; Kvalnes et al., 2017). To account for sampling error caused by consistent measuring differences between fieldworkers, measurements were standardized to T. H. Ringsby by adjusting the mean values when differences were significant (see Kvalnes et al., 2018).

2.3.2. Climate data

At first visit of an active nest a data logger (Hygrochron iButton DS1923, Dallas Semiconductor, Dallas, TX, USA) was placed ca. 10 cm from the edge of the nest in order to avoid strong influence of the heat produced by parents and nestlings. The iButton have an accuracy of 0.5 °C and was set to record temperature (°C) and humidity in percent relative humidity (%RH) once every hour.

Ambient temperature and precipitation data was retrieved from a weather station on the island Myken (66°46’N, 12°29’E) run by the Norwegian Meteorological Institute (MET) (Meteorologisk institutt, 2019). Some data on Myken were missing and supplemented by data from a MET weather station on a nearby island, Solvær (66°21’N, 12°38’E). Myken lies 30 km northwest from Hestmannøy while Solvær lies 25 km southwest from Hestmannøy (see map in Ringsby et al., 2002). The weather stations was highly correlated in temporal climate variation (Ringsby et al., 2002). Ambient temperature data was available on an hourly basis.

Because iButtons were put in nests at first visit of an active nests, the number of days with nest climate data varied between clutches. To be able to compare clutches, ambient climate data from the weather stations and microclimate inside the nests recorded by iButtons was compiled for a seven-day period before hatch day. Clutches with less than four days of climate data were excluded. Mean and coefficient of variance (CV) were then calculated for the ambient temperature and the nest temperature during the seven-day period. Additionally, mean and CV was calculated for nest humidity in the seven-day period. Temperature was converted to Kelvin scale in order to correctly estimate the CV, as CV should only be measured on ratio scale. The difference between nest and ambient temperature was calculated by subtracting the ambient temperature from the mean temperature per hour.

2.4. Statistical analysis

Nine sets of candidate models based on generalized linear mixed model were composed to investigate the role of nest microclimate. Candidate model sets 1A-E examined whether the nest microclimate could be explained by the quality of the mother (question 1), whereas candidate model sets 2A-B explored the effect of nest microclimate on the survival of fledglings and production of recruits (question 2). An overview of the model sets and their variables is given in Table 1. Sections 2.4.1 and 2.4.2 provide further explanations of the different model sets. Sample sizes vary in the different model sets due to some missing data of mother identity and morphological measures in addition to some missing data on ambient climate. A detailed description of the different sample sizes used are given in appendix I.

All statistical analyses were done using the statistical software R, version 3.4.2 (R Core Team, 2019). Generalized linear mixed models were implemented for all models using the *glmmTMB* package (Brooks et al., 2017). Out of the total of 85 unique mothers, 39 was represented with more than one brood in the data set (Table A1 in appendix). Mother identity (ID) was therefore included as a random intercept in all models to account for the non-independence within-females. When the model sets allowed for it (i.e. no convergence problem), year was also included as a random effect to account for temporal variation in factors that were not parameterised in the models, but could still influence annual variation in nest climate and fitness (model 1A-C did not include year as a random variable because of lack of convergence). Such factors could include wind condition, which has been shown to affect incubation effort (Hilde et al., 2016).

Multicollinearity among explanatory variables in general linear regression models can cause spurious relationships between the explanatory variables and the response (Graham, 2003). Pearson's product moment correlation (r_p) was therefore performed on all pairs of explanatory variables (Fig. A2 for maternal phenotypic traits, and Fig. A3 for nest microclimate variables) table and variables with high correlations ($r_p > 0.5$) were not included in the same candidate models to avoid multicollinearity. Some variables were also scaled and cantered to facilitate convergence of models.

All models in each model sets were fitted with maximum likelihood methods and compared by Akaike's Information Criterion corrected for small sample sizes, AIC_c, (Akaike, 1974; Sugiura, 1978; Burnham and Anderson, 2002). The *aictab* function from the R-package *AICcmodavg* (Mazerolle, 2019) created a table with all candidate models ranked according to their AIC_c value. According to the AIC_c criteria, the top-ranked model is the one with the lowest AIC_c value, however, substantial support is also given to models with $\Delta AIC_c < 2$ relative to the top-ranked model (Burnham and Anderson, 2002). The *aictab* function also computed weighted AIC_c values, $wAIC_c$, which provides the probability of each candidate model in the set being the theoretically best model in a Kullback-Leibler information sense, given the models and the data (Burnham and Anderson, 2002; Burnham et al., 2011). Evidence ratios (ER), the ratio of the $wAIC_c$ relative to the top model, was also calculated. ER can be interpreted as the empirical support of a specific model relative to the top model (Burnham et al., 2011). The top ranked model was then refitted with restricted maximum likelihood to obtain parameter estimates. Model diagnostics was performed with the R-package *DHARMa* (Hartig, 2019).

Repeatability within mothers was estimated for mean nest temperature, CV of nest temperature and mean nest humidity to investigate how much of the variation in the different microclimate variables could be explained by individual differences. Ambient climate was accounted for and mother ID and year were included as random factors. Point estimates (R) was calculated with the *rpt* function in the R-package *rptR* by using the linear mixed effect model (LMM) based method (Nakagawa and Schielzeth, 2010; Stoffel et al., 2017). The same function was used to calculate confidence intervals and statistical significance (p-values) by using 1000 parametric bootstraps and 1000 permutations (Nakagawa and Schielzeth, 2010).

2.4.1. *Analysing the effects of phenotypic quality on nest microclimate*

To investigate whether a mother's quality influence the microclimate in the nest she breeds in, five sets of general linear mixed effect candidate models were composed. Response variables were mean nest temperature (1A), CV of nest temperature (1B), mean humidity (1C), the difference between nest and ambient temperature (1D) and the CV of the difference between nest and ambient temperature (1E). Since the climate in the nest is highly correlated with ambient temperature, the corresponding ambient climate variable(s) was included as a fixed effect in the models sets investigating the nest microclimate directly. An overview of the response variables and fixed explanatory variables used in each candidate model set is given in Table 1. The CV of nest humidity was evaluated as a candidate response variable, however it was highly correlated with the CV for nest temperature ($r_p = 0.91$, $n = 154$, $P < 0.001$, Fig. A3 in appendix) and thus excluded from further analyses.

Tarsus length is often used as a measure of avian body size because it can be measured precisely and is a skeletal measure which show higher repeatability than external measures prone to wear and tear (Rising and Somers, 1989; Freeman and Jackson, 1990; Senar and Pascual, 1997). Body mass is commonly used as a measure of condition and resource availability (Gosler et al., 1998; Kvalnes et al., 2013). Wing length was correlated with body mass ($r_p = 0.52$, $n = 135$, $P < 0.001$, Fig. A2 in appendix), and the measure has also been shown to change with age (Rising and Somers, 1989). Wing length was therefore excluded for further analyses. Bill length can exhibit a measure of parental investment as it was found by Ringsby et al. (2009) to have a positive relationship with female feeding rates in the study population. Culmen length and bill depth did not correlate with any other morphological measures or age (Fig. A2 in appendix). The culmen length and bill depth was combined to a single value for bill size by assuming that the cross section of the house sparrow bill is composed of two right-angled triangles where the hypotenuse is the culmen length measured in the field (as shown in Fig. A1 in appendix). This enables calculations of both the angle of the bill tip and the anterior length of the bill, hereafter referred to as bill length (Fig. A1 in appendix). Bill length was negatively correlated with the angle of the bill tip ($r_p = -0.70$, $n = 133$, $P < 0.001$, Fig. A4 in appendix), indicating that longer beak also had a sharper angle. Accordingly, bill length could be interpreted as a measure of both length and shape of the beak. Mother age was also included in the analyses as a proxy for mother quality along with a quadratic term as age was hypothesized to have a non-linear effect due to experience and senescence (Forslund and Pärt, 1995; Holmes et al., 2003; Jones et al., 2008).

2.4.2. Nest microclimate and reproductive success

Question 2 investigates whether variation in the nest microclimate can explain the observed variation in reproductive success. Two sets of candidate models were composed, where one used the number of fledglings as response variable ($2A_1$, Table 1) and the other used number of recruits as response variable ($2B_1$, Table 1). Both response variables are count data and follow a Poisson distribution. However, the variables included more zero-values than expected in a Poisson distribution. This zero-inflation can be produced by a separate process (i.e. sampling error) and can cause over-dispersion (Zuur et al., 2009). In a Poisson distribution, the variance in the response variable should be equal to the mean and over-dispersion is present when the variance is larger than the mean. The models were therefore fitted with a Poisson error distribution including zero-inflation (Zuur et al., 2009).

Because the objective in this analysis was to investigate how nest microclimate influenced the number of fledglings and recruits, respectively, nest microclimate (mean temperature, CV of temperature and mean humidity) variables were supposed to be included as fixed effects. However, this imposes a problem as they were all intercorrelated (Fig. A3 in appendix). Therefore, a principle component analysis (PCA) of the three nest microclimate variables (mean temperature, CV of temperature and mean humidity) was performed in order to account for the intercorrelation and avoid multicollinearity in the analyses (Table 2). PC1 explained the majority of the variance in the nest climate variables (75 %), while PC2 explained 18 % of the variance and PC3 explained 7 % of the variance (see Table 2 for loadings of each PC variable, their eigenvalue and the proportion of variation each explained). Accordingly, the analyses of how microclimate (measured as principle components) affected the number of fledglings and recruits were performed in model sets $2A_1$ and $2B_1$, respectively (Table 1).

A second set of analyses for both fledglings ($2A_2$, Table 1) and recruits ($2B_2$, Table 1) were conducted to examine whether reproductive success was affected by nest temperature after accounting for ambient temperature. The difference between nest and ambient temperature and the mean ambient temperature was used to avoid collinearity. Clutch number was included in these sets of candidate models ($2A_2$ and $2B_2$, Table 1) to account for variation between clutches during the season caused by physiological and behavioural effects acting on the mothers. Three alternative models were composed for each model set ($2A_1$ and $2B_2$, Table 1); the first investigated the mean difference between nest and ambient temperature as well as mean ambient temperature, the second investigated the difference between the CV of nest and ambient temperature as well as the CV of ambient temperature, and the third included only the clutch number.

3. Results

Across all years, the mean temperature measured in the nest during the last week of incubation was 16.03 °C ($n = 154$, SD = 3.73 °C) with the lowest measured temperature of 0.06 °C and the highest measured temperature of 57.56 °C. The corresponding mean ambient temperature was 10.34 °C ($n = 148$, SD = 2.62 °C) with the lowest measured temperature of 1.10 °C and the highest measured temperature of 23.50 °C. There were considerable differences in the mean nest temperature between years (ANOVA: $F_{7,\,146} = 3.602$, $P = 0.001$), where 2007 and 2009 were significantly warmer ($P = 0.001$ and $P = 0.028$, respectively) (Fig. 2). The mean temperatures inside and outside the nests were highly correlated ($r_p = 0.82$, $n = 148$, $P < 0.001$), but there was a significant difference between the two temperatures (paired t-test: mean difference = 5.62 °C, $t = 30.95$, $df = 147$, $P < 0.001$), with the nest temperature being on average 5.62 °C ($n = 148$, SD = 2.21 °C) higher than the ambient temperature. The temperature variation experienced in the nests before hatching differed substantially among clutches. In the extreme cases, one clutch experienced a temperature range of 50.93 °C (Fig. A5a in appendix), while another clutch experienced a range of temperature of only 3.51 °C (Fig. A5b in appendix). Mean nest temperature and mean nest humidity were negatively correlated ($r_\mathrm{p} = -0.54$, $n = 154$, $P < 0.001$, Fig. A3 in appendix), indicating that warmer nests were drier compared to colder nests.

The mean CV of nest temperature across years was 1.72 ($n = 154$, SD = 0.74), while the corresponding mean CV of ambient temperature was lower, 0.52 ($n = 148$ SD = 0.18). CV of nest temperature and CV of ambient temperature were positively correlated ($r_p = 0.42$, $n = 148$, $P < 0.001$) in a fan shaped pattern with a weaker correlation with higher values of CV (Fig. A6 in appendix). They were also significantly different from each other (paired t-test: mean difference = 1.17, $t = 20.69$, $df = 147$, $P < 0.001$). The CV of the nest temperature showed a range of 0.27 to 4.09, which was much larger than the CV of the ambient temperature that ranged from 0.20 to 1.18 (Fig. A6 in appendix).

The mean precipitation per year during the breeding season was 205.84 mm ($n = 5$ years, SD = 58.45 mm). For clutches with a full 7-day interval of climate date, the mean precipitation during the week before hatching ranged from 0.00 to 37.40 mm with an average of 7.36 mm ($n = 112$, SD = 8.41 mm). The mean daily precipitation was 1.33 mm ($n = 148$, SD = 1.63 mm). The mean humidity measured in nests across all years was 69.59 %RH ($n = 154$, SD = 10.90 %RH), ranging from 44.10 to 96.11 %RH.

Female house sparrows showed significant repeatability in mean nest temperatures when accounting for mean ambient temperature (*R* = 0.279, CI = [0.050, 0.496], *P* = 0.008), CV of nest temperature when accounting for ambient temperature variation (*R* = 0.415, CI = [0.178, 0.590], *P* = 0.001) and mean nest humidity when accounting for ambient temperature and precipitation (*R* = 0.324, CI = [0.120, 0.528], *P* = 0.005).

Mean lay date was May 14th for first clutches (*n* = 59, SD = 11.3 days), June 17th for second clutches (*n* = 62, SD = 14.8 days) and July 9th for third clutches (*n* = 30, SD = 15.9 days). No pattern of different lay dates was observed for mothers of different ages. Mean mother body mass was 32.65 g (*n* = 135, SD = 3.29 g), mean mother tarsus length was 19.41 mm (*n* = 135, SD = 0.83 mm) and mean mother bill length 13.45 mm (*n* = 135, SD = 0.37 mm). The mean clutch size was 5.02 (*n* = 154, SD = 1.08) with an average of 2.01 (*n* = 147, SD = 1.71) fledglings produced and 0.28 (*n* = 154, SD = 0.60) recruits produced per clutch.

3.1. The effect of maternal phenotypic traits on nest microclimate

3.1.1. Mean temperature

The top ranked model according to the AIC_c criteria in the model set explaining the effect of maternal phenotypic quality on the variation in mean nest temperature (model set 1A, Table 1) included mean ambient temperature, mother bill length, mother age and a quadratic term of mother age (Table A2 in appendix). There was a strong positive relationship between mean ambient temperature and mean nest temperature (Table 3). Bill length had a marginal positive effect on mean nest temperature as the confidence interval was close to not overlapping zero (β = 1.131, CI = [-0.040, 2.301], Table 3, Fig. 3a). The relationship between mean nest temperature and mother age had a convex function where temperature decreased from 1-year olds to 3-year olds and thereafter increased with older mothers (Table 3, Fig. 3b).

The top ranked model explaining the variation in mean nest temperature had a 21 % chance of being the best model given the candidate models and the data ($wAIC_c$ = 0.21). There were also three other models that had a $\Delta AIC_c < 2$ compared to the top model, however, the highest ranked model was 1.62, 2.10 and 2.15 times more likely to be the best model compared to the second, third and fourth model, respectively (Table A2 in appendix).

All lower ranked models showed a strong positive relationship between mean nest temperature and mean ambient temperature (second ranked; β = 1.201, CI = [1.067, 1.335], third ranked; β = 1.188, CI = [1.054, 1.323], fourth ranked; β = 1.181, CI = [1.045, 1.316]). The second ranked model included body mass, bill length and a nonlinear effect of age in addition to mean ambient temperature. Here, bill length had a significantly positive effect and age showed a significantly convex function (body mass; $\beta = 0.078$, CI = [-0.063, 0.220], bill length; $\beta = 1.172$, CI = [0.001, 2.342], age; $\beta = -1.589$, CI = [-2.816, -0.361], age^2; $\beta = 0.253$, CI = [0.039, 0.467]). The third ranked model included in addition to mean ambient temperature, a non-linear effect of age which showed a significantly convex relationship with mean nest temperature (age; $\beta = -1.416$, CI = [-2.649, -0.182], age^2; $\beta = 0.231$, CI = [0.015, 0.446]). The forth ranked model included mean ambient temperature in addition to bill length as explanatory factors, with bill length having an uncertain positive linear relationship with mean nest temperature (bill length; $\beta = 0.929$, CI = [-0.209, 2.067]). The model including only mean ambient temperature ranked number sixth and had a $\Delta AIC_c > 2$ compared to the top ranked model (Table A2 in appendix).

3.1.2. CV of temperature

The top ranked model explaining the variation in the CV of nest temperature (model set 1B, Table 1) included maternal age, in addition to CV of ambient temperature (table A3 in appendix). Maternal age showed a convex non-linear effect on the CV of nest temperature where the variability decreased from 1-year olds to 2-year olds and thereafter increased with older mothers (Table 4, Fig. 3c). As expected, there was a positive relationship between CV of nest temperature and CV of ambient temperature (Table 4).

Only one candidate model had a ΔAIC_c value that deviated less than two units from the top ranked model (Table A3 in appendix). The alternative model suggested a strong positive effect of the ambient CV of temperature on the CV of nest and ambient temperature ($\beta = 1.596$, CI = [1.054, 2.137]), as well as a convex function of mother age and an uncertain positive correlation of mother body mass on the CV of nest temperature (body mass; $\beta = 0.023$, CI = [-0.024, 0.070], age; $\beta = -0.326$, CI = [-0.679, 0.027], age^2; $\beta = 0.073$, CI = [0.012, 0.135]).

The highest ranked model had 27 % chance of being the best model given the candidate models and the data, whereas the second ranked model had half the weight and was almost two times less likely to be the best model according to the evidence ratio (Table A3 in appendix). Accordingly, the evaluation of candidate models based on AIC_c suggests that the CV of nest temperature was best explained by a non-linear convex effect of maternal age, in addition to the CV of the ambient temperature. The model including only CV of ambient temperature ranked number fifth and was almost four times less likely to be the best model compared to the top ranked model according to the evidence ratio (ER = 3.86, Table A3 in appendix).

3.1.3. Mean humidity

The top ranked model explaining the effect of maternal phenotypic quality on the variation in mean humidity in the nest (model set 1C, Table 1) included maternal age, in addition to both mean ambient temperature and total precipitation (Table A4 in appendix). As expected, mean ambient temperature influenced negatively mean nest humidity while total precipitation had a positive effect on mean nest humidity (Table 5). Maternal age showed a concave non-linear effect on mean nest humidity with an increase in nest humidity for 2-year olds compared to 1-year olds, thereafter decreasing for mothers older than 2-3 years (Table 5, Fig. 3d).

Three candidate models had a ΔAIC_c value within two units from the top ranked model (Table A4 in appendix). A significant concave effect of maternal age on the mean nest humidity was present in the second ranked (age; β = 6.013, CI = [0.555, 11.472], age^2; β = -1.263, CI = [-2.218, -0.308]), third ranked (age; β = 5.780, CI = [0.346, 11.215], age^2; β = -1.238, CI = [-2.190, -0.286]) and fourth ranked (age; β = 5.912, CI = [0.436, 11.387], age^2; β = -1.255, CI = [-2.211, -0.298]) models. Additionally the second ranked model included a negative effect of bill length (β = -3.037, CI = [-8.631, 2.557]). The third ranked model additionally included a negative effect of body mass (β = -0.241, CI = [-0.944, 0.462]), while the fourth model included a negative effect of tarsus length (β = -0.859, CI = [-3.495, 1.777]), although all of these effects were uncertain.

In all four highest ranked models, mean nest humidity was negatively influenced by mean ambient temperature (second ranked; β = -0.740, CI = [-1.303, -0.178], third ranked; β = -0.700, CI = [-1.260, -0.140], fourth ranked; β = -0.670, CI = [-1.258, -0.138]) and positively with precipitation (second ranked; β = 0.547, CI = [0.384, 0.711], third ranked; β = 0.551, CI = [0.387, 0.715], fourth ranked; β = 0.551, CI = [0.387, 0.715]).

The top ranked model had a 27 % chance of being the best model given the candidate models and the data, while the second ranked model had a 16 % chance of being the best model, additionally, the third and fourth ranked model were both 2.45 times less likely than the top model of being the best model (Table A4 in appendix). Accordingly, the AIC_c criteria favoured the model including maternal age in addition to mean ambient temperature and precipitation as the best model explaining the variation in mean nest humidity. The model including only mean ambient temperature and precipitation ranked number seventh and was more than five times less likely of being the best model compared to the top ranked model (ER = 5.40, Table A4 in appendix)

3.1.4. Mean difference between nest and ambient temperature

When investigating whether maternal characteristics influenced the variation in the deviance between nest and ambient temperature (model set 1D, Table 1), the intercept model received the highest support from the data among the candidate models with a 14 % chance of being the best model given the candidate models and the data (Table A5 in appendix). However, seven candidate models deviated less than 2 ΔAIC_c from the highest ranked model and could thus be considered relevant, with the second ranked model receiving a 12 % chance, the second ranked an 11 % chance and the fourth ranked a 10 % chance of being the best model given the candidate models and the data (Table A5 in appendix). The fifth, sixth, seventh and eight ranked models, however, were two times (or more) less likely of being the best model compared to the top model (Table A5 in appendix). Although several candidate models were close to the top model when investigating the AIC_c criteria, the fact that the top ranked model was the intercept model gives support to the null hypothesizes stating no effect of maternal characteristics on the difference between nest and ambient temperature.

Among the lower ranked models, a non-significant effect of body mass was present in the fifth, sixth, seventh and eight ranked models, while a positive, but non-significant effect of bill length was present in the second, third, sixth and seventh ranked model (Table A6 in appendix). In addition, a convex relationship between maternal age and the mean difference between nest and ambient temperatures were present in the third, fourth, sixth and eight ranked model with the relationship being significant when bill length and body mass was included (sixth ranked model) (Table A6 in appendix).

3.1.5. CV of the difference between nest and ambient temperature

When investigating whether maternal characteristics influenced the variation in the CV of the difference between nest and ambient temperature (model set 1E, Table 1), the intercept model received the highest support from the data among the candidate models (Table A7 in appendix). Two models had a ΔAIC_c value less than two units compared to the intercept model, but with substantially lower support in the data with a 12 and 10 % chance of being the best model given the candidate models and the data, compared to a 27 % chance for the top model (Table A7 in appendix). The top model was also the intercept model, which did not support any effect of maternal characteristics on the CV of the difference in the mean and ambient temperature.

The second ranked model included an approximately linear, but non-significant, positive effect of age (age; $\beta = 1.009$, CI = [-13.402, 15.421], age^2; $\beta = 0.430$, CI = [-2.077, 2.937]), while the third ranked model included a non-significant positive effect of body mass ($\beta = 0.406$, CI = [-1.337, 2.148]).

3.2. The effect of nest microclimate on reproductive success

3.2.1. Fledglings

When investigating whether nest microclimate influenced the number of fledglings produced ($2A_1$, Table 1) the top model included PC3 (Table A8 in appendix). PC3 was positively correlated with CV temperature and mean humidity (but note that PC3 only explained 7 % of the variation in nest microclimate, Table 2) and had a negative effect on the number of fledglings produced ($\beta = -0.285$, CI = [-0.539, -0.030], Table 6, Fig. 4).

Two models had a ΔAIC_c value less than two units compared to the top ranked model, which both included PC3 (Table A8 in appendix). The second ranked model included a positive, but non-significant effect of PC1 ($\beta = 0.054$, CI = [-0.031, 0.139]) and a negative effect of PC3 ($\beta = -0.282$, CI = [-0.534, -0.030]) on the number of fledglings produces. PC1 was positively correlated with mean and CV of temperature, and negatively correlated with mean humidity in the nest (Table 2).

The third ranked model included a negative, but non-significant effect of PC2 ($\beta = -0.047$, CI = [-0.221, 0.126]) and a negative effect of PC3 ($\beta = -0.277$, CI = [-0.532, -0.022]) on the number of fledglings produced. PC2 was strongly negatively correlated with mean temperature, positively correlated with CV of temperature, and negatively correlated with mean humidity in the nest (Table 2).

The top ranked model had a 32 % chance of being the best model explaining the effect of nest microclimate on the production of fledglings, given the candidate models and the data (Table A8 in appendix). In comparison, the second and third ranked model had a 23 % and 12 % chance, respectively (Table A8 in appendix). The intercept model ranked number forth and had a $\Delta AIC_c > 2$ compared to the top ranked model and was more than three times less likely to be the best model compared to the top ranked model (Table A8 in appendix).

The second analysis on fledglings ($2A_2$, Table 1) tested whether the number of fledglings were best explained by the mean difference between nest and ambient temperature or the CV of the difference between nest and ambient temperature when accounting for ambient temperature and seasonal effects between the clutches of a mother. The top ranked model included only the effect of clutch number (Table A9 in appendix), where second clutches had a significantly higher fitness compared to the first and third clutches (Table 7, Fig. 5a). The top ranked model had significantly higher support in the data with a 68 % chance of being the best model given the candidate models and the data (Table A9 in appendix). In comparison, the second ranked model (including the CV of temperature) had a 23 % chance of being the best model, and the third ranked model (including the mean temperature) had only a 9 % chance of being the best model (Table A9 in appendix). Thus, further examination of the lower ranked model was not relevant.

3.2.2. Recruits

When investigating whether nest microclimate influenced the number of recruits produced ($2B_1$, Table 1), the top model included only the intercept (Table A10 in appendix). The top ranked model had a 26 % chance of being the best model given the candidate models and the data (Table A10 in appendix). One model were slightly less likely of being the best model with a 22 % chance of being the best model, while the third ranked model and the fourth ranked model was 1.73 and 2.36 less likely, respectively, to be the best model compared to the top ranked model (Table A10 in appendix). However, the top ranked model included only the intercept, supporting less effect of nest microclimate PCA components on the number of fledglings produced.

The second ranked model included a positive effect of PC1 (β = 0.141, CI = [-0.099, 3.902]), the third ranked model included a positive effect of PC3 (β = 0.544, CI = [-0.393, 1.480]) and the fourth ranked model included a positive effect of PC1 and a positive effect of PC3 (PC1; β = 0.117, CI = [-0.133, 0.368], PC3; β = 0.456, CI = [-0.467, 1.410]). However, the effects of all variables in these candidate models were non-significant.

The second analysis on recruits ($2B_2$, Table 1) tested whether the number of recruits were best explained by the mean difference between nest and ambient temperature or the CV of the difference between nest and ambient temperature when accounting for ambient temperature and seasonal effects between the clutches of a mother. The analyses revealed that the CV of the difference between nest and ambient temperature explained the number of recruits produced better than the model including mean temperature or the model including only clutch number (Table A11 in appendix). The top ranked model had strong support in the data as is had an 81 % chance of being the best model given the candidate models and the data and was more than five times more likely than the second ranked model (Table A11 in appendix). The highest ranked model showed that second clutches produced significantly more recruits than both first and third clutches (Table 8, Fig. 5b). Additionally, the CV of the difference between nest and ambient temperature had an uncertain positive effect on number of recruits produced whereas the CV of the ambient temperature had a significant positive effect on number of recruits (Table 8, Fig. 5c and 5d).

4. Discussion

The natal environment can be crucial for survival when ambient climate is not optimal for embryonic and nestling development. Understanding the fitness consequences of the microclimate in nests and the factors affecting the nest microclimate is essential for a better understanding of the ecology and the evolution of avian reproduction. The present study indicated that nest microclimate in a population of house sparrows on the coast of northern Norway was influenced by maternal phenotypic traits and that microclimate in the nest affected the number of fledglings produced. This supports to the hypothesis that nests could be interpreted as extended phenotypic traits.

The temperature experienced in the nest was significantly higher than the ambient temperature (Fig. 2) which indicates that the house sparrows build nests with insulator properties that resulted in incubation temperatures closer to the optimum. However, nest temperatures averaged at 16.03 °C, which is still far below the hypothesized optimum of 32.2 °C and on the lower limit of the temperature range which eggs can tolerate for short periods of time (Webb, 1987). Consequently, female house sparrows are adapted to allocate considerable time and energy on incubation to avoid hypothermia in the eggs.

This study did not find evidence of a trade-off between humidity and temperature in nest microclimate as humidity and temperature were negatively correlated ($r_p = -0.54$, $n = 154$, $P < 0.001$, Fig. A3 in appendix). This contradicts the hypothesis of Hilton et al. (2004) and Botero-Delgadillo et al. (2017), but the composition of nesting materials was not investigated.

Parental care includes every behaviour that increases the fitness of the offspring, and high quality individuals are hypothesized to be able to increase parental care because of higher resource availability (van Noordwijk and de Jong, 1986; Clutton-Brock and Godfray, 1991; Hanssen et al., 2003). Providing an environment suitable for offspring development can therefore be expected to correlate positively with other aspects of reproductive investment, for instance food provisioning to nestlings. With increasing age, the experience and reproductive performance is expected to increase, and higher quality individuals with superior phenotypes are expected to represent a larger proportion of old age classes due to selection (Clutton-Brock, 1988; Forslund and Pärt, 1995). Several studies have found that reproductive success increases with age in many avian species (Nol and Smith, 1987; Forslund and Larsson, 1992; Hatch and Westneat, 2007; Pigeault et al., 2019). For instance, adult Tree swallows (*Tachycineta bicolor*) were found to insulate their nests better than sub-adults (Lombardo, 1994). However, studies often compare 1-year olds to a pooled group of all the older individuals, and reproductive senescence can cause a decline in reproductive success in later life stages (Holmes et al., 2003; Jones et al., 2008; Reed et al., 2008). Accordingly, reproductive success has often been found to be highest for birds of intermediate age in studies accounting for senescence (Møller and De Lope, 1999; Bouwhuis et al., 2010; Balbontín et al., 2012; Crombie and Arcese, 2018). A decline in fitness contributions for house sparrows in this study system has previously been found after 4 years of age (Jones et al., 2008). One could therefore hypothesize that the most optimal nest microclimate would be observed at intermediate ages in house sparrows at Hestmannøy. The present result indicated that maternal age predicted the microenvironment (mean temperature, CV of temperature and mean humidity), in the nest non-linearly when controlling for the ambient climate (Fig. 3). However, the observed pattern was not in alignment with the expectations assuming that intermediate aged mothers would be associated to the warmer and drier nests. We expected the relationship between mother age and both mean temperature and CV of temperature to have a concave function, while the relationship between mother age and mean humidity would have a convex function. However, the present study suggested that intermediate aged mothers inhabited nests that were colder (Fig. 3b) and had higher humidity (Fig. 3d). Only the relationship between mother age and the CV of temperature showed the expected pattern (Fig. 3c), as mothers of intermediate age were expected to have nests with more stable temperatures.

An alternative explanation for why intermediate aged females had colder and more humid nests could be that they initiated egg laying earlier in the season when ambient climate was harsher. However, a generalized linear mixed effect model showed no non-linear effect of mother age on the lay day for first and second clutches, while third clutches showed a weak negative quadratic effect of mother age on lay day (age; β = 14.347, CI = [-1.745, 30.438], age^2; β = -2.389, CI = [-5.009, 0.231]), excluding the possible explanation of intermediate-aged mothers having colder nests by starting to lay eggs earlier in the season.

Because mean nest temperature was positively correlated with CV of nest temperature and CV temperature also correlated negatively with mean humidity (Fig. A3 in appendix), this suggest a trade-off between CV of temperature and both mean temperature and humidity. The analyses investigating the effect of nest microclimate on the number of fledglings produced revealed that CV of temperature was important for reproductive success (Table 6). This supports the observed trend of females of intermediate age having nests with lower CV of temperature (Table 4, Fig. 3c) and explains the significant, but opposite age effect than expected for mean nest temperature

(Table 3, Fig. 3b) and humidity (Table 5, Fig. 3d). However, the interpretation of the results for maternal age should be interpreted with caution as the relationship between age and nest microclimate might be affected by the presence of two clutches with a 6-year old mother. The two clutches stemmed from the same mother in the same year and discharging them removed all significant relationships of age.

Bill morphology is important for mechanical handling of food items and the feeding ecology of bird species and have been the subject of adaptive radiations causing large variations of avian bill shapes and sizes (Storer, 1971). A classic example of this is the natural selection of *Geospiza* finches on Galapagos, where finches evolved different bill shapes and sizes due to adaptations of different feeding niches (Grant, 1986). Riyahi et al. (2013) demonstrated a similar adaptation in bill morphology for the house sparrow where populations settled around human populations became larger and more “pointy” (measured from digital images of dorsal-viewed skull) compared to a population settled in a natural habitat, and suggested that this difference was caused by processing of cultivated crops in the human associated population. Adult house sparrows are granivorous, and the population at Hestmannøy have large and easily accessible sources of cattle feed and cultivated crops, a diet matching their bill shape (Hespenheide, 1966; Willson, 1971; 1972; Anderson, 2006). Nestling house sparrows, however, feed mainly on insects, a diet associated with smaller, more elongated and narrower bill shapes (Lederer, 1975).

A previous study of the house sparrows in the Helgeland archipelago concluded that a significant component of the variation in feeding rate of the mothers could be explained by bill morphology (Ringsby et al., 2009). However, the effect was only present for bill depth, not for bill culmen length (a measure that, in this study, was highly correlated with bill length, Fig. A2 in appendix). Larger bill depth corresponds to longer, but broader bills, a shape associated with a more granivorous diet (Hespenheide, 1966; Willson, 1971; 1972). However, Ringsby et al. (2009) used number of foraging trips as a proxy of parental provisioning rate, but was not able to measure the amount of food brought by each visit. Hypothetically, the positive relationship between bill depth and feeding rate of females observed might therefore have been a result of compensation for a lower efficiency by females with more granivorous adapted bill shape.

In this study, females with longer and narrower beaks, a trait associated with higher insect catch rate (Lederer, 1975), inhabited nests with temperatures closer to the optimum for egg development (Table 3, Fig. 3a). This supports the hypothesis that individuals that presumably were effective in insect catching acquire higher quality nests. Bill length was not correlated with age (table A2 in appendix), meaning that the effect of bill length on nest microclimate was not caused by an indirect effect of age.

Bill morphology also plays a role in thermoregulation according to Allen's rule which states that endotherms should have smaller peripherals in colder climates due to a reduced heat loss over smaller peripherals (Allen, 1877). Avian bills have been shown to have such a thermoregulatory function, explaining geographical variations in bill morphology (Symonds and Tattersall, 2010; Tattersall et al., 2017). Bill morphology is determined by both genetics and phenotypic plasticity, and the heritability (h^2) in bill depth and bill culmen length for female house sparrows on Hestmannøy have previously been estimated to a significant level of 0.542 and 0.539, respectively (Jensen et al., 2003). A plastic response to temperature according to Allen's rule is hypothesized to determine some of the intraspecific variation in bill morphology (Tattersall et al., 2017). Such variation in bill morphology as a response to nest temperature have been found in Japanese quails (*Coturnix japonica*) and Adelaide rosella (*Platycercus elegans adelaidae*) where warm-reared chicks developed larger bills (Burness et al., 2013; Larson et al., 2018). Accordingly, female house sparrows reared in warmer nests could have developed larger bill sizes. A certain level of heritability in nest microclimate could be expected if nest microclimate function as an extended phenotype. Females might therefore acquire a nest site with similar microclimatic characteristics as she was reared in, and offspring bill sizes could be determined as a plastic response to the temperature in the nest.

The mean difference between nest and ambient temperature did not show any relationship with maternal characteristics. Neither did the variation in the difference between nest and ambient temperature. To be able to account for ambient temperature, the difference was appropriate to use in order to avoid multicollinearity, as nest and ambient temperature were highly correlated ($r_p = 0.82$). The ambient temperature data was obtained from islands 25 and 30 km away from Hestmannøy, which most likely caused some deviations from the actual local temperature at Hestmannøy. Recording ambient temperature locally would have provided data that were more accurate, and possibly altered the lack of relationship between mother characteristics and mean difference between nest and ambient temperature, and likewise for CV of the difference between nest and ambient temperature, model set 1D (Table A5 in appendix) and 1E (Table A7 in appendix), respectively. However, it is noteworthy that age, bill length and body mass were included in several models within 2 ΔAIC_c compared to the top model. In these candidate models, bill length and body mass were positively, but not significantly related with the difference between nest and ambient temperature, and age showed the same relationship with mean and CV of temperature as in the analyses investigating nest microclimate directly. The results investigating the mean and CV of the difference between nest and ambient temperature were therefore in alignment with the results from the analyses investigating mean and CV of nest temperature directly (model sets 1A and 1B, Table 1). However, these models were less likely to explain the difference in nest and ambient temperature than the mean (the intercept model) based on AIC_c criteria (Table A5 and A7 in appendix).

The number of fledglings produced was found to increase with decreasing values of PC3 (Table 6, Fig. 4), which was positively correlated with CV of temperature and mean humidity in the nest (Table 2). Notably, PC3 only explained 7 % of the variation in nest microclimate, which could promote exclusion of the variable from further analyses. Still, PC3 was the only PCA component where both CV of temperature and humidity correlated in the same direction (Table 2), and a PCA analyses was run to avoid collinearity, not to reduce the number of parameters. Thus, increasing PC3, interpreted as higher variability in temperature and higher humidity experienced in the nest during the last week of incubation, had a negative effect on the reproductive success, supporting the hypothesis that avian eggs become sensitive to variation in temperatures during incubation (White and Kinney, 1974; Webb, 1987). Larson et al. (2015) found a similar result for a cavity-nesting bird species, the Crimson Rosella (*Platycercus elegans*), which had lower fledgling success in nests with higher temperature variability.

The range of humidity measured in the nest ranged from 44.10 to 96.11 %RH with a mean of 69.59 %RH, which is at the upper limit of the optimal humidity levels for domesticated chickens (Barott, 1937; Robertson, cited in Bruzual et al., 2000). A decrease in humidity, relative to the mean, in this study was therefore approaching optimum humidity levels of 50 % found for chickens and observed in wild avian nests (Lomholt, 1976; Rahn et al., 1977; Morgan et al., 1978; Grant, 1982; Ar and Sidis, 2002). The high humidity values found in this study suggests that the eggs are prone to slower cooling rates or reduced hatching due to restricted weight loss (Ar and Rahn, 1980; Hilton et al., 2004; Deeming and Jarrett, 2015). A negative effect on fledgling production with higher humidity supports this hypothesis, but the underlying factor remains uncertain (Table 6, Fig. 4).

Nest humidity can also affect the development and physiological state of nestlings through parasite prevalence (Heeb et al., 2000; Moyer et al., 2002). At Hestmannøy, the frequent reuse of nests exposes the house sparrows to horizontal transmission and nest parasites have been shown to reduce the fitness in house sparrows (Møller and Erritzøe, 1996; Weddle, 2000; Szabó et al., 2002; Anderson, 2006). Heeb et al. (2000) found a higher prevalence of both hen fleas

(*Ceratophyllus gallinae*) and blow flies (*Protocalliphora spp.*), two ectoparasites also found in house sparrow nests (Anderson, 2006), in drier nests compared to wetter nests of great tit (*Parus major*). Reproductive success for house sparrows at Hestmannøy was found to increase with decreasing humidity, which provides stronger support for nest-site selection against humidity stress rather than selection against nest parasites.

Studies have also found a relationship between parasite abundance and nest temperature (Martínez-de la Puente et al., 2010; Castaño-Vázquez et al., 2018). Dawson et al. (2005) found the relationship to be non-linear with a decrease in parasite prevalence for nests warmer than 25 °C, however, this is the upper limit of mean nest temperatures measured in the present study. Selection for low nest temperatures reducing the abundance of nest parasites could therefore explain why this study did not find the expected positive relationship between nest temperature and reproductive success.

The CV of nest temperature showed a disproportionally high range compared to the CV of ambient temperatures (Fig. A6 in appendix, note the differences on the axis scales), and extreme variability in nest temperatures was observed with multiple nests showing a temperature range over 40 °C. Temperatures in the nest were higher than ambient temperatures and large variation was caused by heating rather than cooling. This was probably due to some nests being located under metal roofs inside the barns, which could cause very high temperatures when the sun was shining while still falling to low temperatures when ambient temperatures were low on an overcast day. Imlay et al. (2019) found that cliff swallows (*Petrochelidon pyrrhonota*) nesting under metal roofs experienced larger variation than those nesting under wood roofs, probably due to the smaller heat capacity of metal compared to wood, which resulted in decreased breeding success. Studies have found hyperthermia to cause higher mortality in avian species than hypothermia and even species in cold climates can experience lethal hyperthermia (Mertens, 1977; Webb, 1987; Carey, 2002). A higher risk of hyperthermia could therefore explain why the CV in nest temperature seemed to be more important in explaining reproductive success than the mean temperature (Table A8 in appendix).

No effects of nest microclimate during incubation on the number of recruits produced were found (Table A10). This is not surprising as there are numerous factors influencing the variance in recruitment during the period between incubation and recruitment the following year, such as food availability, predation etc., which may conceal the hypothesized relationship between nest microclimate and recruitment success. However, individuals that are able to recruit to the next breeding season have obviously survived the fledgling stage, which was shown here to be affected by nest microclimate (Table 6, Fig. 4), and fledgling phenotypes have been found to affect recruitment on Hestmannøy (Ringsby et al., 1998). A long-term effect of nest microclimate was therefore hypothesised, but not supported by the data.

Interestingly, a significant positive effect of the CV of ambient temperature on the number of recruits produced was detected (Table A11 in appendix). This contradicts the earlier findings of the negative effect of CV of nest temperature on reproductive success, measured as the number of fledglings (Tabell 6, Fig. 4). However, this positive relationship between CV of nest temperature and recruitment could be explained by a positive correlation between the CV of ambient temperature and maximum ambient temperature ($r_p = 0.56$, $n = 148$, $P < 0.001$, Fig. A3 in appendix), which could have a positive effect on reproductive success. Additionally, CV of ambient temperature was negatively correlated with nest humidity ($r_p = -0.29$, $n = 148$, $P < 0.001$, Fig. A3 in appendix), which was shown to have a negative effect on fledgling production (Tabell 6, Fig. 4).

A significantly higher production of fledglings and recruits was found for second clutches (Table 7 and 8, Fig. 5a and b). This pattern could arise due to several ecological mechanisms, partly due to increased insect abundance through the season at Hestmannøy (Julseth, 2019) and competition with the larger European starlings for nest sites early in the season, and also reduced parental investment due to deprivation of energy resources later in the season.

The second part of the analyses of reproductive success ($2A_2$ and $2B_2$, Table 1) was not able include humidity (which was found to be of importance in the production of fledglings, Table 6), which could explain why the expected effect of mean temperature and CV of temperature was not detected. Additionally, the study was not able to include incubation behaviour, which has a major impact on the temperature actually experienced by the eggs (Deeming, 2002). The amount of investment females have to put into incubation is however affected by the nest temperature. Studies have found females to adapt her incubation effort to not let the eggs experience hypothermia or in a response to the temperature by increasing the time spent incubating in colder temperatures (Haftorn, 1988; Hepp et al., 2006; McClintock et al., 2014). Females can therefore save energy in warmer temperatures by reducing the incubation effort, and consequently reallocate resources to self or to future broods (Reid et al., 2000; Álvarez and Barba, 2014). Females can also adjust to warmer nests by increasing the incubation period to increase reproductive success according to the energetic-bottleneck hypothesis (Yom-Tov and Hilborn, 1981). The hypothesis proposes an opportunity to increase the time spent incubating, which is costly, because the cost is reduced in warmer nests and has been supported for great tits (Bryan and Bryant, 1999). Consequently, the temperature in the nest can affect the offspring as well as the incubating bird, and although this study only found a relationship between reproductive success, measured as the number of fledglings produced, and the CV of nest temperature, not mean nest temperature (Table A8 in appendix), the temperature variability was caused by increased daytime temperatures.

This study used the number of fledglings or recruits as proxies of reproductive success and did not consider the phenotypic quality of the offspring. Parental care can have important carry-over effect later in life and several studies have found nest temperature to influence both morphological and physiological quality of the fledglings (Mousseau, 1998; Lindström, 1999; Hepp et al., 2006; Ardia et al., 2010; Pipoly et al., 2013; Rodríguez and Barba, 2016; Auera and Martin, 2017; Andreasson et al., 2018; Griebel et al., 2019). Such effects could appear after the natal period, and a previous study on the house sparrow population at Hestmannøy revealed that fledgling size and condition were significantly affecting survival during the first year (Ringsby et al., 1998). Consequently, an effect of nest microclimate on recruits was hypothesized, but could not be confirmed (Table A10). Future studies should include nestling quality when investigating effects of nest microclimate on reproductive success.

Albeit a negative relationship between the number of fledglings produced and the combined effect of humidity and variability in temperature was found (i.e. the effect of PC3, Table 6), it is not clear if this correlation was caused by the nest microclimate itself or by the quality of the parent as mother age was found to affect the CV of temperature and humidity in the nest (Table 4 and 5). An experimental study design is needed to address this issue.

This study suggests that nest microclimate is an extended phenotypic trait for house sparrows based on how nest microclimate was repeatable within mothers, the observed variation in relation to mother characteristics and the fitness consequences of nest microclimate observed. However, the repeatability within mothers might partly be a result of nest reuse as female house sparrows show high nest site fidelity (Summers-Smith, 1958; Ringsby et al., 1998; Anderson, 2006). Extended phenotypic traits should be costly to be a reliable signal of individual quality and the cost of nest construction in the house sparrow should therefore be further studied in order to test whether nest microclimate can be considered as an extended phenotypic trait.

Several studies investigating the role of avian nests as extended phenotypic trait have studied a potential signalling function of the nests where nest quality signal individual quality of their builder (Moreno et al., 1994; Soler et al., 1996; Soler et al., 1998a; Soler et al., 1998b; De Neve, 2004; Polo and Veiga, 2006; Mainwaring et al., 2008; Moreno, 2012; Jelínek et al., 2016). Some species, such as bowerbirds (*Ptilonorhynchidae*) and weaverbirds (*Ploceidae*), build elaborate nests that are important in mate pairing according to the handicap hypothesis, allowing males to attract females, and females to assess the quality of potential mates before mating (Zahavi, 1975; Schaedelin and Taborsky, 2009; Moreno, 2012). Recent studies have also hypothesized that nests can function as a post-mating signal according to the differential allocation hypothesis where mates continuously assess the quality of their mates to adjust their own parental effort accordingly, a strategy that can be used by both sexes in both monogamous and non-monogamous species (Burley, 1986; Soler et al., 1998b; Moreno, 2012). To be able to assess a potential signalling function of the nest microclimate as described by Moreno (2012) and Schaedelin and Taborsky (2009), the provisioning rates of the parents should also be investigated.

In conclusion, nest microclimate was shown to relate to maternal phenotypic traits and mothers showed repeatability in microclimate characteristics, suggesting that the nest microclimate can potentially be considered as extended phenotypic traits for house sparrows. This study also showed that nest microclimate during incubation influenced the number of fledglings produced, which provides further evidence for the importance of early-life environment on avian reproductive success.

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References

Akaike, H. 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, 19(6), pp. 716-723.

Akresh, M. E., Ardia, D. R. & King, D. I. 2017. Effect of nest characteristics on thermal properties, clutch size, and reproductive performance for an open-cup nesting songbird. *Avian Biology Research*, 10(2), pp. 107-118.

Allainé, D., Pontier, D., Gaillard, J. M., Lebreton, J. D., Trouvilliez, J. & Clobert, J. 1987. The relationship between fecundity and adult body weight in Homeotherms. *Oecologia*, 73(3), pp. 478-480.

Allan, J. D. 1984. Life history variation in a freshwater copepod: evidence from population crosses. *Evolution*, 38(2), pp. 280.

Allen, J. A. 1877. The influence of physical conditions in the genesis of species. *Radical Review*, 1, pp. 108–140.

Altwegg, R., Ringsby, T. H. & Sæther, B. E. 2000. Phenotypic correlates and consequences of dispersal in a metapopulation of house sparrows *Passer domesticus*. *Journal of Animal Ecology*, 69(5), pp. 762-770.

Álvarez, E. & Barba, E. 2014. Behavioural responses of great tits to experimental manipulation of nest temperature during incubation. *Ornis Fennica*, 91(4), pp. 220-230.

Anderson, T. R. 2006. *Biology of the ubiquitous house sparrow: from genes to populations*, Oxford, Oxford University Press.

Andreasson, F., Nord, A. & Nilsson, J.-Å. 2018. Experimentally increased nest temperature affects body temperature, growth and apparent survival in blue tit nestlings. *Journal of Avian Biology*, 49(2), pp. jav-01620.

Ar, A. & Rahn, H. 1980. Water in the avian egg: overall budget of incubation. *American Zoologist*, 20, pp. 373-384.

Ar, A. & Sidis, Y. 2002. Nest microclimate during incubation. *In:* Deeming, D. C. (ed.) *Avian incubation: behaviour, environment, and evolution.* Oxford: Oxford University Press.

Ardia, D. R. 2013. The effects of nestbox thermal environment on fledging success and haematocrit in tree swallows. *Avian Biology Research*, 6(2), pp. 99-103.

Ardia, D. R., Pérez, J. H. & Clotfelter, E. D. 2006. Nest box orientation affects internal temperature and nest site selection by tree swallows. *Journal of Field Ornithology*, 77(3), pp. 339-344.

Ardia, D. R., Pérez, J. H. & Clotfelter, E. D. 2010. Experimental cooling during incubation leads to reduced innate immunity and body condition in nestling tree swallows. *Proceedings of the Royal Society B: Biological Sciences*, pp.

Auera, S. K. & Martin, T. E. 2017. Parental care mitigates carry-over effects of poor early conditions on offspring growth. *Behavioral Ecology*, 28(4), pp. 1176-1182.

Balbontín, J., Møller, A. P., Hermosell, I. G., Marzal, A., Reviriego, M. & de Lope, F. 2012. Geographical variation in reproductive ageing patterns and life-history strategy of a short-lived passerine bird. *Journal of Evolutionary Biology*, 25(11), pp. 2298-2309.

Barott, H. G. 1937. Effect of temperature, humidity and other factors on hatch of hen's eggs and on energy metabolism of chick embryos. *United States Department of Agriculture Technical Bulletin* 553, pp.

Berger, D., Walters, R. & Gotthard, K. 2008. What limits insect fecundity? Body size- and temperature-dependent egg maturation and oviposition in a butterfly. *Functional Ecology*, 22(3), pp. 523-529.

Berntsen, H. H. & Bech, C. 2015. Incubation temperature influences survival in a small passerine bird. *Journal of Avian Biology*, 47, pp. 141-145.

Biddle, L. E., Broughton, R. E., Goodman, A. M. & Deeming, D. C. 2018. Composition of bird nests is a species-specific characteristic. *Avian Biology Research*, 11(2), pp. 132-153.

Billing, A. M., Lee, A. M., Skjelseth, S., Borg, Å. A., Hale, M. C., Slate, J., Pärn, H., Ringsby, T. H., Sæther, B.-E. & Jensen, H. 2012. Evidence of inbreeding depression but not inbreeding avoidance in a natural house sparrow population. *Molecular Ecology*, 21(6), pp. 1487-1499.

BirdLife International. 2018. *Passer domesticus (amended version of 2017 assessment).* [Online]. The IUCN Red List of Threatened Species 2018: e.T103818789A129643357. Available: http://dx.doi.org/10.2305/IUCN.UK.2017-1.RLTS.T103818789A129643357.en [Accessed July 7th 2019.].

Botero-Delgadillo, E., Orellana, N., Serrano, D., Poblete, Y. & Vásquez, R. A. 2017. Interpopulation variation in nest architecture in a secondary cavity-nesting bird suggests site-specific strategies to cope with heat loss and humidity. *The Auk*, 134(2), pp. 281-294.

Bouwhuis, S., Van Noordwijk, A. J., Sheldon, B. C., Verhulst, S. & Visser, M. E. 2010. Similar patterns of age-specific reproduction in an island and mainland population of great tits *Parus major*. *Journal of Avian Biology*, 41(6), pp. 615-620.

Bradley, M., Johnstone, R., Court, G. & Duncan, T. 1997. Influence of weather on breeding success of peregrine falcons in the arctic. *The Auk,* 114(4), pp. 786-791.

Britt, J. & Deeming, D. C. 2011. First-egg date and air temperature affect nest construction in blue tits *Cyanistes caeruleus* , but not in great tits *Parus major*. *Bird Study,* 58(1), pp. 78-89.

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M. & Bolker, B. M. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R journal*, 9(2), pp. 378-400.

Bruzual, J. J., Peak, S. D., Brake, J. & Peebles, E. D. 2000. Effects of relative humidity during the last five days of incubation and brooding temperature on performance of broiler chicks from young broiler breeders. 79(10), pp. 1385-1391.

Bryan, S. M. & Bryant, D. M. 1999. Heating nest–boxes reveals an energetic contraint on incubation behaviour in great tits, *Parus major*. *Proceedings of the Royal Society B: Biological Sciences,* 266(1415), pp. 157-162.

Burley, N. 1986. Sexual selection for aesthetic traits in species with biparental care. *The American Naturalist,* 127(4), pp. 415-445.

Burness, G., Huard, J. R., Malcolm, E. & Tattersall, G. J. 2013. Post-hatch heat warms adult beaks: irreversible physiological plasticity in Japanese quail. *Proceedings of the Royal Society B: Biological Sciences,* 280(1767), pp. 20131436-2013143.

Burnham, K. P. & Anderson, D. R. 2002. *Model selection and multimodel inference: a practical information-theoretical approach,* New-York, Springer-Verlag.

Burnham, K. P., Anderson, D. R. & Huyvaert, K. P. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology,* 65, pp. 23-35.

Calder, W. A. 1973. An estimate of the heat balance of a nesting hummingbird in a chilling climate. *Comparative Biochemistry and Physiology Part A: Physiology,* 46(2), pp. 291-300.

Carey, C. 2002. Incubation in extreme environments. *In:* Deeming, D. C. (ed.) *Avian incubation: behaviour, environment, and evolution.* Oxford: Oxford University Press.

Castaño-Vázquez, F., Martínez, J., Merino, S. & Lozano, M. 2018. Experimental manipulation of temperature reduce ectoparasites in nests of blue tits (*Cyanistes caeruleus*). *Journal of Avian Biology,* pp.

Clutton-Brock, T. & Godfray, C. 1991. Parental investment. *In:* Krebs, J. R. & Davies, N. B. (eds.) *Behavioural ecology.* 3. ed. Oxford: Blackwell Scientific Publications.

Clutton-Brock, T. H. 1988. *Reproductive success: studies of individual variation in contrasting breeding systems,* Chicago, University of Chicago Press.

Collias, N., E. 1964. The evolution of nests and nest-building in birds. *American Zoologist,* 4, pp. 175-190.

Crombie, M. D. & Arcese, P. 2018. Temporal variation in the effects of individual and environmental factors on nest success. *The Auk,* 135(2), pp. 326-341.

Darwin, C. R. 1874. *The descent of man, and selection in relation to sex,* Appleton, New York.

Dawkins, R. 1982. *The extended phenotype: the gene as the unit of selection,* Oxford, Oxford University Press.

Dawson, R. D., Hillen, K. K. & Whitworth, T. L. 2005. Effects of experimental variation in temperature on larval densities of parasitic *Protocalliphora* (Diptera: Calliphoridae) in nests of tree swallows (Passeriformes: Hirundinidae). *Physiological Ecology,* 34(3), pp. 563-568.

De Neve, L. 2004. Nest size predicts the effect of food supplementation to magpie nestlings on their immunocompetence: an experimental test of nest size indicating parental ability. *Behavioral Ecology,* 15(6), pp. 1031-1036.

De Steven, D. 1980. Clutch size, breeding success, and parental survival in the tree swallow (*lridoprocne bicolor*). *Evolution,* 34(2), pp. 278-291.

Deeming, D. C. (ed.) 2002. *Avian incubation: behaviour, environment, and evolution,* Oxford: Oxford University Press.

Deeming, D. C. & Jarrett, N. S. 2015. Applications of incubation science to aviculture and conservation. *In:* Deeming, D. C. & Reynolds, S. J. (eds.) *Nests, eggs, & incubation.* Oxford: Oxford University Press.

Deeming, D. C., Mainwaring, M. C., Hartley, I. R. & Reynolds, S. J. 2012. Local temperature and not latitude determines the design of blue tit and great tit nests. *Avian Biology Research,* 5(4), pp. 203-208.

Deeming, D. C. & Reynolds, S. J. 2015. Perspectives on avian nests and eggs. *In:* Deeming, D. C. & Reynolds, S. J. (eds.) *Nests, eggs, & incubation.* Oxford: Oxford University Press.

Eiby, Y. & Booth, D. 2008. Embryonic thermal tolerance and temperature variation in mounds of the Australian brush-turkey (*Alectura lathami*). *The Auk,* 125(3), pp. 594-599.

Forslund, P. & Larsson, K. 1992. Age-related reproductive success in the barnacle goose. *Journal of Animal Ecology,* 61, pp. 195.

Forslund, P. & Pärt, T. 1995. Age and reproduction in birds — hypotheses and tests. *Trends in Ecology & Evolution,* 10(9), pp. 374-378.

Franklin, D. C. 1995. Helmeted honeyeaters build bulkier nests in cold weather. *The Auk,* 112(1), pp. 247-248.

Freeman, S. & Jackson, W. M. 1990. Univariate matrics are not adequate to measure avian body size. *The Auk,* 107, pp. 69-74.

Gosler, A. G., Greenwood, J. J. D., Baker, J. K. & Davidson, N. C. 1998. The field determination of body size and condition in passerines: a report to the British Ringing Committee. *Bird Study,* 45(1), pp. 92-103.

Graham, M. H. 2003. Confronting multicollinearity in ecological multiple regression. *Ecology,* 84(11), pp. 2809-2815.

Grant, G. S. 1982. Avian incubation: egg temperature, nest humidity, and behavioral thermoregulation in a hot environment. *Ornithological Monographs,* (30), pp. iii-ix, 1-75.

Grant, P. R. 1986. *Ecology and evolution of Darwin's finches,* Princeton, Princeton University Press.

Gray, L. A. & Deeming, D. C. 2017. Effect of air movement on the thermal insulation of avian nests. *Bird Study,* 64(4), pp. 492-501.

Griebel, I. A., Fairhurst, G. D., Marchant, T. A. & Clark, R. G. 2019. Effects of parental and nest-site characteristics on nestling quality in the tree swallow (*Tachycineta bicolor*). *Canadian Journal of Zoology,* 97(1), pp. 63-71.

Griffith, S. C., Stewart, I. R. K., Dawson, D. A., Owens, I. P. F. & Burke, T. 2008. Contrasting levels of extra-pair paternity in mainland and island populations of the house sparrow (*Passer domesticus*): is there an 'island effect'? *Biological Journal of the Linnean Society,* 68(1-2), pp. 303-316.

Haftorn, S. 1988. Incubating female passerines do not let the egg temperature fall below the 'physiological zero temperature' during their absences from the nest. *Ornis Scandinavica,* 19(2), pp. 97-110.

Hansell, M. 2000. *Bird nests and construction behaviour,* Cambridge, Cambridge University Press.

Hanssen, S. A., Erikstad, K. E., Johnsen, V. & Bustnes, J. O. 2003. Differential investment and costs during avian incubation determined by individual quality: an experimental study of the common eider (Somateria mollissima). *Proceedings of the Royal Society B: Biological Sciences,* 270, pp. 531-537.

Hartig, F. 2019. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.2.4.

Hatch, M. I. & Westneat, D. F. 2007. Age-related patterns of reproductive success in house sparrows *Passer domesticus*. *Journal of Avian Biology,* 38(5), pp. 603-611.

Heeb, P., Kölliker, M. & Richner, H. 2000. Bird-ectoparasite interactions, nest humidity, and ectoparasite community structure. *Ecology,* 81(4), pp. 958-968.

Heenan, C., B. 2013. An overview of the factors influencing the morphology and thermal properties of avian nests. *Avian Biology Research,* 6(2), pp. 104-118.

Heenan, C. B., Goodman, B. A. & White, C. R. 2015. The influence of climate on avian nest construction across large geographical gradients. *Global Ecology and Biogeography,* 24(11), pp. 1203-1211.

Hepp, G. R., Kennamer, R. A. & Johnson, M. H. 2006. Maternal effects in wood ducks: incubation temperature influences incubation period and neonate phenotype. *Functional Ecology,* 20(2), pp. 308-314.

Hérbert, P. N. 2002. Ecological factors affecting initiation of incubation behaviour. *In:* Deeming, D. C. (ed.) *Avian incubation: behaviour, environment, and evolution.* Oxford: Oxford University Press.

Hespenheide, H. A. 1966. The selection of seed size by finches. *The Wilson Bulletin,* 78(2), pp. 191-197.

Hilde, C. H., Pélabon, C., Guéry, L., Gabrielsen, G. W. & Descamps, S. 2016. Mind the wind: microclimate effects on incubation effort of an arctic seabird. *Ecology and Evolution,* 6(7), pp. 1914-1921.

Hilton, G. M., Hansell, M. H., Ruxton, G. D., Reid, J. M. & Monaghan, P. 2004. Using artificial nests to test importance of nesting material and nest shelter for incubation energetics. *The Auk,* 121(3), pp. 777.

Holmes, D. J., Thomson, S. L., Wu, J. & Ottinger, M. A. 2003. Reproductive aging in female birds. *Experimental Gerontology,* 38, pp. 751-756.

Imlay, T. L., Nickerson, D. & G. Horn, A. 2019. Temperature and breeding success for cliff swallows (*Petrochelidon pyrrhonota*) nesting on man-made structures ecological traps? *Canadian Journal of Zoology,* 97, pp. 429-435.

Inouye, R. S., Huntly, N. J. & Inouye, D. W. 1981. Non-random orientation of cila woodpecker nest entrances in saguara cacti. *Condor,* 83, pp. 88-89.

Jelínek, V., Požgayová, M., Honza, M. & Procházka, P. 2016. Nest as an extended phenotype signal of female quality in the great reed warbler. *Journal of Avian Biology,* 47(3), pp. 428-437.

Jensen, H., Steinsland, I., Ringsby, T. H. & Sæther, B. E. 2008. Evolutionary dynamics of a sexual ornament in the house sparrow (*Passer domesticus*): the role of indirect selection within and between sexes. *Evolution,* 62(6), pp. 1275-1293.

Jensen, H., Sæther, B. E., Ringsby, T. H., Tufto, J., Griffith, S. C. & Ellegren, H. 2003. Sexual variation in heritability and genetic correlations of morphological traits in house sparrow (*Passer domesticus*). *Journal of Evolutionary Biology,* 16(6), pp. 1296-1307.

Jones, O. R., Gaillard, J.-M., Tuljapurkar, S., Alho, J. S., Armitage, K. B., Becker, P. H., Bize, P., Brommer, J., Charmantier, A., Charpentier, M., Clutton-Brock, T., Dobson, F. S., Festa-Bianchet, M., Gustafsson, L., Jensen, H., Jones, C. G., Lillandt, B.-G., McCleery, R., Merilä, J., Neuhaus, P., Nicoll, M. A. C., Norris, K., Oli, M. K., Pemberton, J., Pietiäinen, H., Ringsby, T. H., Roulin, A., Sæther, B.-E., Setchell, J. M., Sheldon, B. C., Thompson, P. M., Weimerskirch, H., Jean Wickings, E. & Coulson, T. 2008. Senescence rates are determined by ranking on the fast-slow life-history continuum. *Ecology Letters,* 11(7), pp. 664-673.

Julseth, M. G. 2019. *The effect of arthropod availability on reproductive phenology and success in a multi-brooded passerine Passer domesticus.* Master's thesis, Norwegian University of Science and Technology.

Järvinen, A. 1993. Spatial and temporal variation in reproductive traits of adjacent northern pied flycatcher *Ficedula hypoleuca* populations. *Ornis Scandinavica,* 24(1), pp. 33.

Järvinen, P., Kluen, E. & Brommer, J. E. 2017. Low heritability of nest construction in a wild bird. *Biology letters,* 13(10), pp. 20170246.

Kern, M. D. & Van Riper, C., III 1984. Altitudinal variations in nests of the Hawaiian honeycreeper *Hemignathus virens virens*. *The Condor,* 86(4), pp. 443-454.

Kozłowski, J. 1992. Optimal allocation of resources to growth and reproduction: Implications for age and size at maturity. *Trends in Ecology & Evolution,* 7(1), pp. 15-19.

Kvalnes, T. 2016. *Evolution by natural selection in age-structured populations in fluctuating environments.* Doctoral Thesis, Norwegian University of Science and Technology.

Kvalnes, T., Ringsby, T. H., Jensen, H., Hagen, I. J., Rønning, B., Pärn, H., Holand, H., Engen, S. & Sæther, B. E. 2017. Reversal of response to artificial selection on body size in a wild passerine. *Evolution,* 71(8), pp. 2062-2079.

Kvalnes, T., Ringsby, T. H., Jensen, H. & Sæther, B. E. 2013. Correlates of egg size variation in a population of house sparrow *Passer domesticus*. *Oecologia,* 171(2), pp. 391-402.

Kvalnes, T., Røberg, A. Å., Jensen, H., Holand, H., Pärn, H., Sæther, B.-E. & Ringsby, T. H. 2018. Offspring fitness and the optimal propagule size in a fluctuating environment. *Journal of Avian Biology,* pp.

Larson, E. R., Eastwood, J. R., Buchanan, K. L., Bennett, A. T. D. & Berg, M. L. 2015. How does nest-box temperature affect nestling growth rate and breeding success in a parrot? *Emu - Austral Ornithology,* 115(3), pp. 247-255.

Larson, E. R., Eastwood, J. R., Micallef, S., Wehbe, J., Bennett, A. T. D. & Berg, M. L. 2018. Nest microclimate predicts bill growth in the Adelaide rosella (Aves: Psittaculidae). *Biological Journal of the Linnean Society*, pp.

Lederer, R. J. 1975. Bill size, food size, and jaw forces of insectivorous birds. *The Auk,* 92(2), pp. 385-387.

Ligon, J. D. 1999. *The evolution of avian breeding systems,* Oxford, Oxford University Press.

Lindström, J. 1999. Early development and fitness in birds and mammals. *Trends in Ecology & Evolution,* 14(9), pp. 343-348.

Lombardo, M. P. 1994. Nest architecture and reproductive performance in tree swallows (*Tachycineta bicolor*). *The Auk,* 111(4), pp. 814-824.

Lombardo, M. P., Bosman, R. M., Faro, C. A., Houtteman, S. G. & Kluisza, T. S. 1995. Effect of feathers as nest insulation on incubation behavior and reproductive performance of tree swallows (*Tachycineta bicolor*). *The Auk,* 112(4), pp. 973-981.

Lomholt, J. P. 1976. Relationship of weight loss to ambient humidity of birds eggs during incubation. *Journal of Comparative Physiology,* 105(2), pp. 189-196.

Mainwaring, M. C., Benskin, C. M. H. & Hartley, I. R. 2008. The weight of female-built nests correlates with female but not male quality in the blue tit *Cyanistes caeruleus*. *Acta Ornithologica,* 43(1), pp. 43-48.

Mainwaring, M. C. & Hartley, I. R. 2008. Seasonal adjustments in nest cup lining in blue tits *Cyanistes caeruleus*. *Ardea,* 96(2), pp. 278-282.

Mainwaring, M. C. & Hartley, I. R. 2009. Experimental evidence for state-dependent nest weight in the blue tit, *Cyanistes caeruleus*. *Behavioural Processes,* 81(1), pp. 144-146.

Mainwaring, M. C., Hartley, I. R., Bearhop, S., Brulez, K., du Feu, C. R., Murphy, G., Plummer, K. E., Webber, S. L., James Reynolds, S. & Deeming, D. C. 2012. Latitudinal variation in blue tit and great tit nest characteristics indicates environmental adjustment. *Journal of Biogeography,* 39(9), pp. 1669-1677.

Mainwaring, M. C., Hartley, I. R., Lambrechts, M. M. & Deeming, D. C. 2014. The design and function of birds' nests. *Ecology and Evolution,* 4(20), pp. 3909-3928.

Martínez-de la Puente, J., Merino, S., Lobato, E., Rivero-de Aguilar, J., del Cerro, S., Ruiz-de-Castañeda, R. & Moreno, J. 2010. Nest-climatic factors affect the abundance of biting flies and their effects on nestling condition. *Acta Oecologica,* 36, pp. 543-547.

Mazerolle, M. J. 2019. AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 2.2-1.

McClintock, M. E., Hepp, G. R. & Kennamer, R. A. 2014. Plasticity of incubation behaviors helps wood ducks (*Aix sponsa*) maintain an optimal thermal environment for developing embryos. *The Auk,* 131(4), pp. 672-680.

McGillivray, B. W. 1981. Climatic influences on productivity in the house sparrow. *The Wilson Bulletin,* 93, pp. 196-206.

McGowan, A., Sharp, S. P. & Hatchwell, B. J. 2004. The structure and function of nests of long-tailed tits *Aegithalos caudatus*. *Functional Ecology,* 18(4), pp. 578-583.

Mertens, J. A. L. 1977. Thermal conditions for successful breeding in great tits (*Parus major* L.). *Oecologia,* 28(1), pp. 1-29.

Meteorologisk institutt. 2019. *eKlima* [Online]. Available: http://eklima.met.no [Accessed February 2nd 2019].

Michielsen, R. J., Ausems, A. N. M. A., Jakubas, D., Pętlicki, M., Plenzler, J., Shamoun-Baranes, J. & Wojczulanis-Jakubas, K. 2019. Nest characteristics determine nest microclimate and affect breeding output in an Antarctic seabird, the Wilson's storm-petrel. *PLOS ONE,* 14(6), pp. e0217708.

Moreno, J. 2012. Avian nests and nest-building as signals. *Avian Biology Research,* 5(4), pp. 238-251.

Moreno, J., Soler, M., Møller, A. P. & Linden, M. 1994. The function of stone carrying in the black wheatear, *Oenanthe leucura*. *Animal Behaviour,* 47(6), pp. 1297-1309.

Morgan, K. R., Paganelli, C. V. & Rahn, H. 1978. Egg weight loss and nest humidity during incubation in two Alaskan gulls. *The Condor,* 80(3), pp. 272-275.

Mousseau, T. 1998. The adaptive significance of maternal effects. *Trends in Ecology & Evolution,* 13(10), pp. 403-407.

Moyer, B. R., Drown, D. M. & Clayton, D. H. 2002. Low humidity reduces ectoparasite pressure: implications for host life history evolution. *Oikos,* 97(2), pp. 223-228.

Møller, A. P. 1984. On the use of feathers in birds' nests: predictions and tests. *Ornis Scandinavica,* 15(1), pp. 38-42.

Møller, A. P. 1987. Variation in badge size in male house sparrows *Passer domesticus*: evidence for status signalling. *Animal Behaviour,* 35(6), pp. 1637-1644.

Møller, A. P. 1988. Badge size in the house sparrow *Passer domesticus*. *Behavioral Ecology and Sociobiology,* 22(5), pp. 373-378.

Møller, A. P. 2006. Rapid change in nest size of a bird related to change in a secondary sexual character. *Behavioral Ecology,* 17(1), pp. 108-116.

Møller, A. P. & De Lope, F. 1999. Senescence in a short-lived migratory bird: age-dependent morphology, migration, reproduction and parasitism. *Journal of Animal Ecology,* 68(1), pp. 163-171.

Møller, A. P. & Erritzøe, J. 1996. Parasite virulence and host immune defense: host immune response is related to nest reuse in birds. *Evolution,* 50(5), pp. 2066-2072.

Nakagawa, S. & Schielzeth, H. 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biological Reviews,* 85, pp. 935-956.

Nice, M. M. 1962. Development of behaviour in precocial birds. *Transactions of the Linnaean Society of New York,* 8, pp. 1-211.

Nilsson, J. F., Stjernman, M. & Nilsson, J.-Å. 2008. Experimental reduction of incubation temperature affects both nestling and adult blue tits *Cyanistes caeruleus*. *Journal of Avian Biology,* 39(5), pp. 553-559.

Nol, E. & Smith, J. N. M. 1987. Effects of age and breeding experience on seasonal Reproductive success in the song sparrow. *The Journal of Animal Ecology,* 56(1), pp. 301.

Nord, A. & Nilsson, J.-Å. 2011. Incubation temperature affects growth and energy metabolism in blue tit nestlings. *The American Naturalist,* 178(5), pp. 639-651.

Nord, A. & Williams, J. B. 2015. The energetic costs of incubation. *In:* Deeming, D. C. & Reynolds, S. J. (eds.) *Nests, eggs, & incubation.* Oxford: Oxford University Press.

O'Connor, R. J. 1975. Nestling thermolysis and developmental change in body temperature. *Comparative Biochemistry and Physiology Part A: Physiology,* 52(3), pp. 419-422.

O'Connor, R. J. 1978. Nest-box insulation and the timing of laying in the Wytham Woods population of great tits *Parus major*. *Ibis,* 120(4), pp. 534-537.

O'Neill, L. G., Parker, T. H. & Griffith, S. C. 2018. Nest size is predicted by female identity and the local environment in the blue tit (*Cyanistes caeruleus*), but is not related to the nest size of the genetic or foster mother. *Royal Society Open Science,* 5(4), pp.

Ospina, E. A., Merrill, L. & Benson, T. J. 2018. Incubation temperature impacts nestling growth and survival in an open-cup nesting passerine. *Ecology and Evolution,* 8(6), pp. 3270-3279.

Patrick, A. M. K., Rohwer, V. G. & Martin, P. R. 2017. Evidence for individual consistency and location effects on nest morphology in a population of yellow warblers (*Setophaga petechia*). *The Wilson Journal of Ornithology,* 129(3), pp. 469-480.

Pigeault, R., Cozzarolo, C. S., Glaizot, O. & Christe, P. 2019. Effect of age, haemosporidian infection and body condition on pair composition and reproductive success in great tits *Parus major*. *Ibis*, pp.

Pipoly, I., Bókony, V., Seress, G., Szabó, K. & Liker, A. 2013. Effects of extreme weather on reproductive success in a temperate-breeding songbird. *PLoS ONE,* 8(11), pp. e80033.

Polo, V. & Veiga, J. P. 2006. Nest ornamentation by female spotless starlings in response to a male display: an experimental study. *Journal of Animal Ecology,* 75(4), pp. 942-947.

Preziosi, R. F., Fairbairn, D. J., Roff, D. A. & Brennan, J. M. 1996. Body size and fecundity in the waterstrider *Aquarius remigis*: a test of Darwin's fecundity advantage hypothesis. *Oecologia,* 108(3), pp. 424-431.

Pärn, H., Jensen, H., Ringsby, T. H. & Sæther, B.-E. 2009. Sex-specific fitness correlates of dispersal in a house sparrow metapopulation. *Journal of Animal Ecology,* 78(6), pp. 1216-1225.

Pärn, H., Ringsby, T. H., Jensen, H. & Sæther, B. E. 2012. Spatial heterogeneity in the effects of climate and density-dependence on dispersal in a house sparrow metapopulation. *Proceedings of the Royal Society B: Biological Sciences,* 279(1726), pp. 144-52.

R Core Team 2019. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Rahn, H., Ackerman, R. A. & Paganelli, C. V. 1977. Humidity in the avian nest and egg water loss during incubation. *Physiological Zoology,* 50(4), pp. 269-283.

Rahn, H. & Ar, A. 1974. The avian egg: incubation time and water loss. *The Condor*, 76(2), pp. 147-152.

Reed, T., E., Kruuk Loeske, E. B., Wanless, S., Frederiksen, M., Cunningham, E., J. A. & Harris Michael, P. 2008. Reproductive senescence in a long-lived seabird: rates of decline in late-life performance are associated with varying costs of early reproduction. *The American Naturalist,* 171(2), pp. E89-E101.

Reid, J. M., Monaghan, P. & Ruxton, G. D. 2000. Resource allocation between reproductive phases: the importance of thermal conditions in determining the cost of incubation.

Proceedings of the Royal Society of London. Series B: Biological Sciences, 267(1438), pp. 37-41.

Ricklefs, R. E. & Hainsworth, F. R. 1969. Temperature regulation in nestling cactus wrens: the nest environment. *The Condor,* 71(1), pp. 32-37.

Ringsby, T. H., Berge, T., Sæther, B. E. & Jensen, H. 2009. Reproductive success and individual variation in feeding frequency of house sparrows (*Passer domesticus*). *Journal of Ornithology,* 150(2), pp. 469-481.

Ringsby, T. H., Sæther, B. E. & Solberg, E. J. 1998. Factors affecting juvenile survival in house sparrow *Passer domesticus*. *Journal of Avian Biology,* 29(3), pp. 241-247.

Ringsby, T. H., Sæther, B. E., Tufto, J., Jensen, H. & Solberg, E. J. 2002. Asynchronous spatiotemporal demography of a house sparrow metapopulation in a correlated environment. *Ecology,* 83(2), pp. 561-569.

Rising, J. D. & Somers, K. M. 1989. The measurement of overall body size in birds. *The Auk,* 106(4), pp. 666-674.

Riyahi, S., Hammer, Ø., Arbabi, T., Sánchez, A., Roselaar, C. S., Aliabadian, M. & Sætre, G.-P. 2013. Beak and skull shapes of human commensal and non-commensal house sparrows *Passer domesticus*. *BMC Evolutionary Biology,* 13(200), pp.

Rodríguez, S. & Barba, E. 2016. Nestling growth is impaired by heat stress: an experimental study in a mediterranean great tit population. *Zoological Studies,* 55(40), pp. 1-13.

Rohwer, S. 1975. The social significance of avian winter plumage variability. *Evolution,* 29(4), pp. 593-610.

Rohwer, V. G. & Law, J. S. Y. 2010. Geographic variation in nests of yellow warblers breeding in Churchill, Manitoba, and Elgin, Ontario. *The Condor,* 112(3), pp. 596-604.

Rønning, B., Broggi, J., Bech, C., Moe, B., Ringsby, T. H., Pärn, H., Hagen, I. J., Sæther, B.-E. & Jensen, H. 2016. Is basal metabolic rate associated with recruit production and survival in free-living house sparrows? *Functional Ecology,* 30(7), pp. 1140-1148.

Sánchez-Tójar, A., Nakagawa, S., Sánchez-Fortún, M., Martin, D. A., Ramani, S., Girndt, A., Bókony, V., Kempenaers, B., Liker, A., Westneat, D., Burke, T. & Schroeder, J. 2018. Meta-analysis challenges a textbook example of status signalling: evidence for publication bias. *eLife,* 7, pp. e37385.

Schaedelin, F. C. & Taborsky, M. 2009. Extended phenotypes as signals. *Biological Reviews,* 84(2), pp. 293-313.

Schleicher, B., Hoi, H. & Valera, F. 1996. Seasonal change in female mate choice criteria in penduline tits (*Remiz pendulinus*). *Ardeola,* 43(1), pp. 19-29.

Seel, D. C. 1968. Clutch-size, incubation and hatching success in the house sparrow and tree sparrow *Passer spp.* at Oxford. *Ibis,* 110(3), pp. 270-282.

Seel, D. C. 1969. Food, feeding rates and body temperature in the nestling house sparrow *Passer domesticus* at Oxford. *Ibis,* 111(1), pp. 36-47.

Senar, J. C. & Pascual, J. 1997. Keel and tarsus length may provide a good predictor of avian body size. *Ardea,* 85, pp. 269-274.

Sheaffer, S. E. & Malecki, R. A. 1996. Predicting breeding success of Atlantic population Canada geese from meteorological variables. *The Journal of Wildlife Management,* 60(4), pp. 882.

Shine, R. 1988. The evolution of large body size in females: a critique of Darwin's "fecundity advantage" model. *The American Naturalist,* 131(1), pp. 124-131.

Skinner, W. R., Jefferies, R. L., Carleton, T. J., Abraham, R. F. R. & Dagger, K. F. 1998. Prediction of reproductive success and failure in lesser snow geese based on early season climatic variables. *Global Change Biology,* 4(1), pp. 3-16.

Skowron, C. & Kern, M. 1980. The Insulation in nests of selected North American songbirds. *The Auk,* 97(4), pp. 816-824.

Slagsvold, T. 1989a. Experiments on clutch size and nest size in passerine birds. *Oecologia,* 80(3), pp. 297-302.

Slagsvold, T. 1989b. On the evolution of clutch size and nest size in passerine birds. *Oecologia,* 79(3), pp. 300-305.

Smith, J. A., Harrison, T. J. E., Martin, G. R. & Reynolds, S. J. 2013. Feathering the nest: food supplementation influences nest construction by blue (*Cyanistes caeruleus*) and great tits (*Parus major*). *Avian Biology Research,* 6(1), pp. 18-25.

Smith, J. N. M. 1981. Does high fecundity reduce survival in song sparrows? *Evolution,* 35(6), pp. 1142-1148.

Smith, M. G., Kaiser, S. A., Sillett, T. S. & Webster, M. S. 2018. Variation in nest characteristics and brooding patterns of female black-throated blue warblers is associated with thermal cues. *The Auk,* 135(3), pp. 733-747.

Smith, W. K., Roberts, S. W. & Miller, P. C. 1974. Calculating the nocturnal energy expenditure of an incubating Anna's hummingbird. *The Condor,* 76(2), pp. 176-183.

Solberg, E. J. & Ringsby, T. H. 1997. Does male badge size signal status in small island populations of house sparrows, *Passer domesticus*? *Ethology,* 103(3), pp. 177-186.

Soler, J. J., Cuervo, J. J., Møller, A. P. & De Lope, F. 1998a. Nest building is a sexually selected behaviour in the barn swallow. *Animal Behaviour,* 56(6), pp. 1435-1442.

Soler, J. J., Martin-Vivaldi, M., Haussy, C. & Møller, A. P. 2007. Intra- and interspecific relationships between nest size and immunity. *Behavioral Ecology,* 18(4), pp. 781-791.

Soler, J. J., Møller, A. P. & Soler, M. 1998b. Nest building, sexual selection and parental investment. *Evolutionary Ecology,* 12(4), pp. 427-441.

Soler, M., Soler, J. J., Møller, A. P., Moreno, J. & Lindén, M. 1996. The functional significance of sexual display: stone carrying in the black wheatear. *Animal Behaviour,* 51(2), pp. 247-254.

Stearns, S. C. 1989. Trade-offs in life-history evolution. *Functional Ecology,* 3(3), pp. 259-268.

Stearns, S. C. 2000. Life history evolution: successes, limitations, and prospects. *Naturwissenschaften,* 87(11), pp. 476-486.

Stoffel, M. A., Nakagawa, S. & Schielzeth, H. 2017. rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution,* 8(11), pp. 1639-1644.

Storer, R. W. 1971. Adaptive radiation of birds. *In:* Marshall, A. J. (ed.) *Biology and Comparative Physiology of Birds.* New York: Academic Press.

Sugiura, N. 1978. Further analysis of the data by Akaike's information criterion and the finite corrections. *Communications in Statistics - Theory and Methods,* 7(1), pp. 13-26.

Summers-Smith, D. 1958. Nest-site selection, pair formation and territory in the house-sparrow *Passer domesticus*. *Ibis,* 100(2), pp. 190-203.

Symonds, M., R. E. & Tattersall, G. J. 2010. Geographical variation in bill size across bird species provides evidence for Allen’s rule. *The American Naturalist,* 176(2), pp. 188-197.

Szabó, K., Szalmás, A., Liker, A. & Barta, Z. 2002. Effects of haematophagous mites on nestling house sparrows (*Passer domesticus*). *Acta Parasitologica,* 47(5), pp. 318-322.

Tattersall, G. J., Arnaout, B. & Symonds, M. R. E. 2017. The evolution of the avian bill as a thermoregulatory organ. *biological Reviews*, 92, pp. 1630-1656.

Tilley, S. G. 1968. Size-fecundity relationships and their evolutionary implications in five *Desmognathine* salamanders. *Evolution,* 22(4), pp. 806-816.

van Noordwijk, A. J. & de Jong, G. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. *The American Naturalist*, 128(1), pp. 137-142.

Veiga, J. P. 1992. Why are house sparrows predominantly monogamous? a test of hypotheses. *Animal Behaviour,* 43(3), pp. 361-370.

Veiga, J. P. 1993. Badge size, phenotypic quality, and reproductive success in the house sparrow: a study on honest advertisement. *Evolution,* 47(4), pp. 1161-1170.

Walsh, P. T., Hansell, M., Borello, W. D. & Healy, S. D. 2010. Repeatability of nest morphology in African weaver birds. *Biology Letters,* 6, pp. 149-151.

Wangensteen, O. D. & Rahn, H. 1970. Respiratory gas exchange by the avian embryo. *Respiration Physiology,* 11, pp. 31-45.

Webb, D. R. 1987. Thermal tolerance of avian embryos: a review. *The Condor,* 89(4), pp. 874-898.

Weddle, C. B. 2000. Effects of ectoparasites on nestling body mass in the house sparrow. *The Condor,* 102(3), pp. 684–687.

Wetton, J. H. & Parkin, D. T. 1991. An association between fertility and cuckoldry in the house sparrow, *Passer domesticus*. *Proceedings of the Royal Society of London. Series B: Biological Sciences,* 245(1314), pp. 227-233.

White, F. N. & Kinney, J. L. 1974. Avian incubation. *Science,* 186(4159), pp. 107-115.

Whittow, G. C. & Berger, A. J. 1977. Heat loss from the nest of the Hawaiian honeycreeper, "amakihi". *The Wilson Bulletin,* 89(3), pp. 480-483.

Wiebe, K. L. 2001. Microclimate of tree cavity nests: is it important for reproductive success in Northern flickers? *The Auk,* 118(2), pp. 412-421.

Willson, M. F. 1971. Seed selection in some North American finches. *The Condor,* 73(4), pp. 415-429.

Willson, M. F. 1972. Seed size preference in finches. *The Wilson Bulletin,* 84(4), pp. 449-455.

Windsor, R. L., Fegely, J. L. & Ardia, D. R. 2013. The effects of nest size and insulation on thermal properties of tree swallow nests. *Journal of Avian Biology,* 44(4), pp. 305-310.

Withers, P. C. 1977. Energetic aspects of reproduction by the cliff swallow. *The Auk,* 94(4), pp. 718-725.

Yom-Tov, Y. & Hilborn, R. 1981. Energetic constraints on clutch size and time of breeding in temperate zone birds. *Oecologia,* 48, pp. 234-243.

Zahavi, A. 1975. Mate selection—A selection for a handicap. *Journal of Theoretical Biology,* 53(1), pp. 205-214.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. M. 2009. *Mixed effects models and extensions in ecology with R,* New York, USA., Springer.

Tables

Table 1: An overview of the nine model sets made in this thesis with their response variables, explanatory variables, fixed explanatory variables, random factors and sample sizes. Mother characteristics includes body mass, tarsus length, bill length and age. Nest microclimate variables included in the principle component analysis (PCA) includes mean temperature, coefficient of variance (CV) of temperature and mean humidity. See appendix I for a detailed description of the different sample sizes used.

Model set	**Response variable**	**Explanatory variables**	**Explanatory variables present in all candidate models**	**Random factors**	**Sample size, *N***
1A	Mean nest temperature	Mother characteristics	Mean ambient temperature	Mother ID	135
1B	CV nest temperature	Mother characteristics	CV ambient temperature	Mother ID	135
1C	Mean nest humidity	Mother characteristics	Mean ambient temperature + total precipitation	Mother ID	135
1D	Mean difference between nest and ambient temperature	Mother characteristics	None	Mother ID + year	135
1E	CV difference between nest and ambient temperature	Mother characteristics	None	Mother ID + year	135
$2A_1$	Fledglings	Nest microclimate (PCA)	None	Mother ID + year	147
$2A_2$	Fledglings	Difference between nest and ambient temperature + ambient temperature	Clutch number	Mother ID + year	138
$2B_1$	Recruits	Nest microclimate (PCA)	None	Mother ID + year	154
$2B_2$	Recruits	Difference between nest and ambient temperature + ambient temperature	Clutch number	Mother ID + year	145

Table 2: Loadings from the principle component analysis of the three intercorrelated nest microclimate variables; mean temperature, CV temperature and mean humidity. Nest climate data was measured in 154 house sparrow nests on Hestmannøy, Norway. Loadings were obtained by the function *prcomp* in the statistical software R (R Core Team, 2019).

	PC1	**PC2**	**PC3**
Mean temperature	0.52	-0.86	0.02
CV temperature	0.60	0.38	0.70
Mean humidity	-0.61	-0.35	0.71
Eigenvalue	2.25	0.55	0.20
% variation explained	0.75	0.18	0.07

Table 3: The most parsimonious model explaining the variation in mean nest temperature by the effect of mother characteristics (model set 1A, see Table A2) in 135 wild house sparrow clutches at Hestmannøy, Norway. The table includes parameter estimates (β) and their 95 % confidence intervals.

Variable	**β**	**95 % Confidence interval**	
		Lower limit	**Upper limit**
Intercept	-65.379	-107.948	-22.810
Mean ambient temperature	1.203	1.069	1.337
Bill length	1.131	-0.040	2.301
Age	-1.539	-2.769	-0.309
Age^2	0.244	0.030	0.459

Table 4: The most parsimonious model explaining the variation in the coefficient of variation (CV) of nest temperature by the effect of mother characteristics (model set 1B, see Table A3) in 135 wild house sparrow clutches at Hestmannøy, Norway. The table includes parameter estimates (β) and their 95 % confidence intervals.

Variable	**β**	**95 % Confidence interval**	
		Lower limit	**Upper limit**
Intercept	1.109	0.578	1.639
CV ambient temperature	1.609	1.060	2.159
Age	-0.317	-0.676	0.041
Age^2	0.072	0.009	0.135

Table 5: The most parsimonious model explaining the variation in mean nest humidity by the effect of mother characteristics (model set 1C, see Table A4) in 135 wild house sparrow clutches at Hestmannøy, Norway. The table includes parameter estimates (β) and their 95 % confidence intervals.

Variable	**β**	**95 % Confidence interval**	
		Lower limit	**Upper limit**
Intercept	260.723	102.654	418.793
Mean ambient temperature	-0.706	-1.265	-0.146
Total precipitation	0.558	0.396	0.721
Age	5.614	0.182	11.046
Age^2	-1.209	-2.161	-0.256

Table 6: The most parsimonious model explaining the variation in the number of fledglings by the effect of three principle components variables of the nest microclimate (composed by mean temperature, coefficient of variance of temperature and mean humidity) (model set $2A_1$, see Table A8) in 147 wild house sparrow clutches at Hestmannøy, Norway. The table includes parameter estimates (β) and their 95 % confidence intervals. PC3 was positively correlated with CV of nest temperature and mean nest humidity (Table 2).

Variable	**β**	**95 % Confidence interval**	
		Lower limit	**Upper limit**
Intercept	0.917	0.788	1.047
PC3	-0.285	-0.539	-0.030

Table 7: The most parsimonious model explaining the variation in the number of fledglings by the effect of nest microclimate when accounting for ambient climate and clutch number in 138 wild house sparrow clutches at Hestmannøy, Norway (model set $2A_2$, Table A9). The table includes parameter estimates (β) and their 95 % confidence intervals.

Variable	**β**	**95 % Confidence interval**	
		Lower limit	**Upper limit**
Intercept	0.736	0.495	0.978
Clutch nr. 2	0.376	0.097	0.655
Clutch nr. 3	-0.351	-0.827	0.126

Table 8: The most parsimonious model explaining the variation in the number of recruits by the effect of nest microclimate when accounting for ambient climate and clutch number in 145 wild house sparrow clutches at Hestmannøy, Norway (model set $2B_2$, Table A11). The model included clutch number and the coefficient of variance of the difference between nest and ambient temperature (CV difference) and the coefficient of variance of ambient temperature (CV ambient temperature). The table includes parameter estimates (β) and their 95 % confidence intervals.

Variable	**β**	**95 % Confidence interval**	
		Lower limit	**Upper limit**
Intercept	-3.662	-5.489	-1.835
Clutch nr. 2	0.826	0.097	1.554
Clutch nr. 3	-0.642	-1.948	0.664
CV difference	0.007	-0.007	0.020
CV ambient temperature	2.338	0.728	4.167

Figures

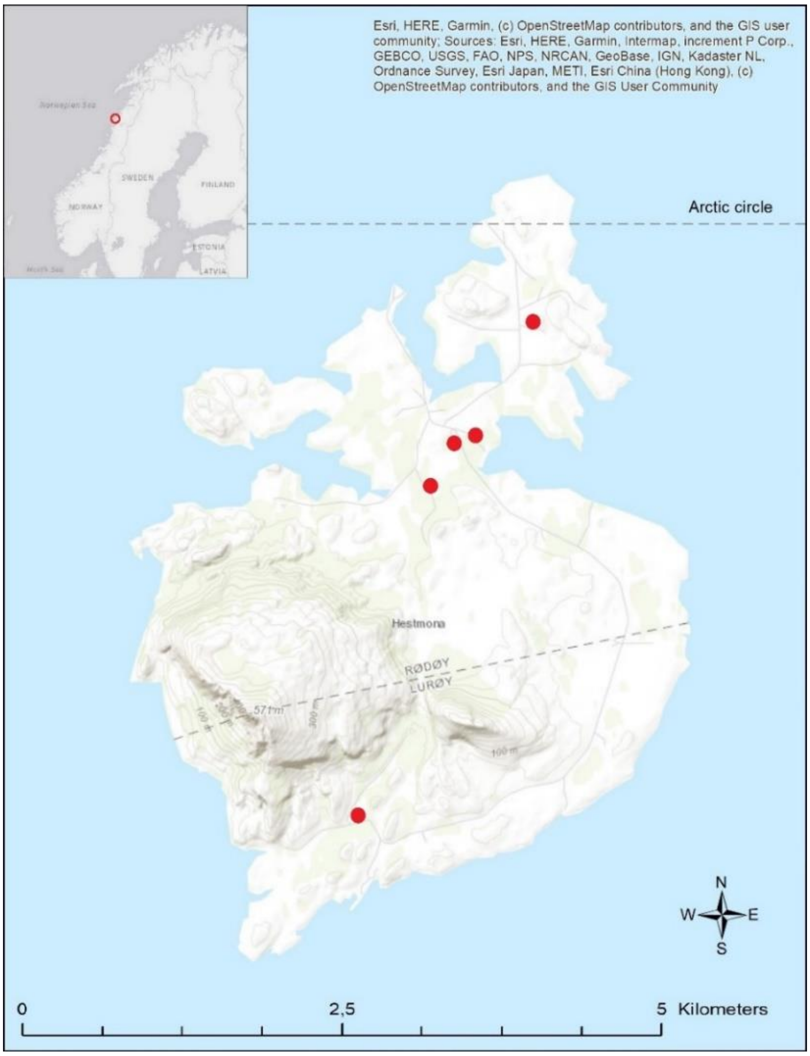

Figure 1: Topographic map of Hestmannøy (also called Hestmona) with location of breeding colonies on farms marked by red dots. The top left map show the islands location in Scandinavia. The upper line crossing the northernmost part of the island indicates the arctic circle, and the line crossing the middle of the island is the municipality border between Rødøy (north) and Lurøy (south) municipality.

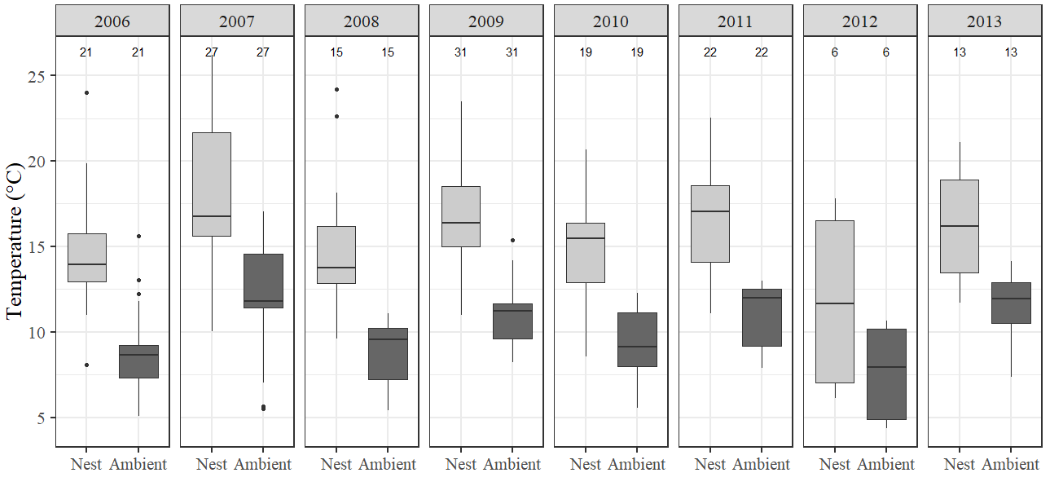

Figure 2: Boxplot of nest and ambient temperature for all years. The boxes visualizes the 25th and 75th percentile, with the horizontal centerline representing the median. The whiskers extend above to the largest values within 1.5 times the interquantile range above the 75th percentile, and below to the smallest values within 1.5 times the interquantile range below the 25th percentile. The dots indicates outliers. Light grey boxes represent the temperature in all nests in the given year while the dark grey boxes represent the corresponding ambient temperature. Sample sizes are presented above each box.

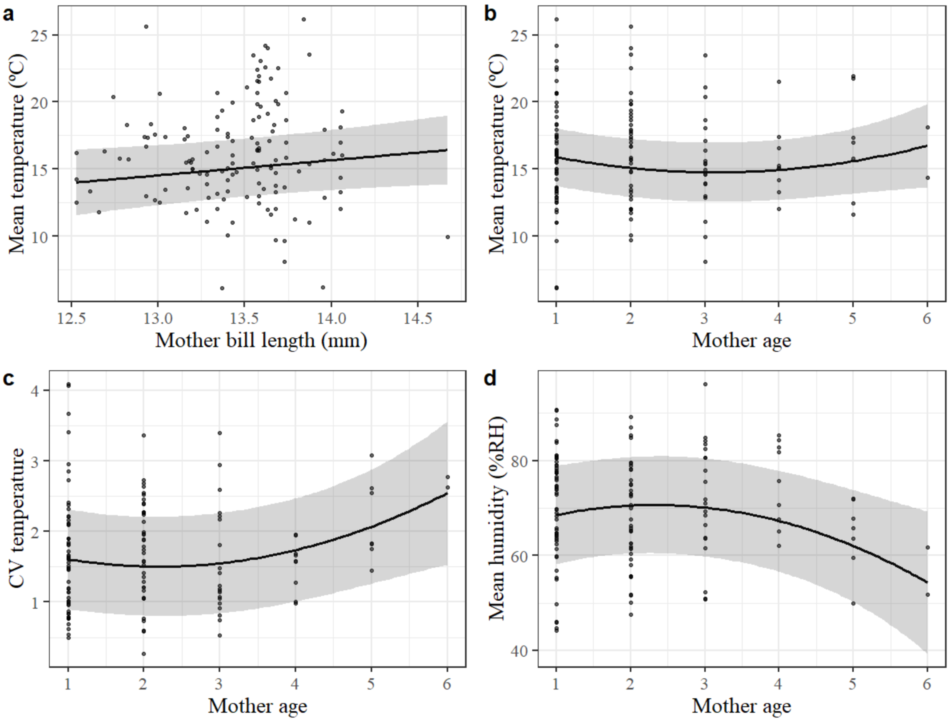

Figure 3: Panel (a) and (b) show the fitted relationship between mean nest temperature (°C) and (a) mother bill length and (b) mother age (model set 1A, Table 3). Panel (c) show the fitted relationship between the coefficient of variation (CV) of nest temperature and mother age (model set 1B, Table 4). Panel (d) show the fitted relationship between mean nest humidity (%RH) and mother age (model set 1C, Table 5).

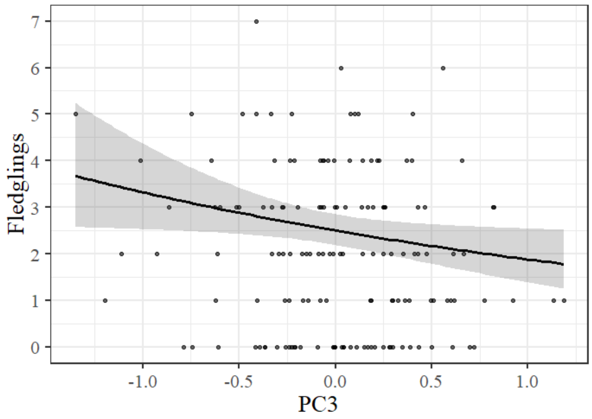

Figure 4: The fitted relationship between number of fledglings produced and PC3 (model set $2A_1$, Table 6). PC3 correlated with the coefficient of variance of temperature and mean humidity in the nest (Table 2) in 147 wild house sparrow clutches at Hestmannøy, Norway.

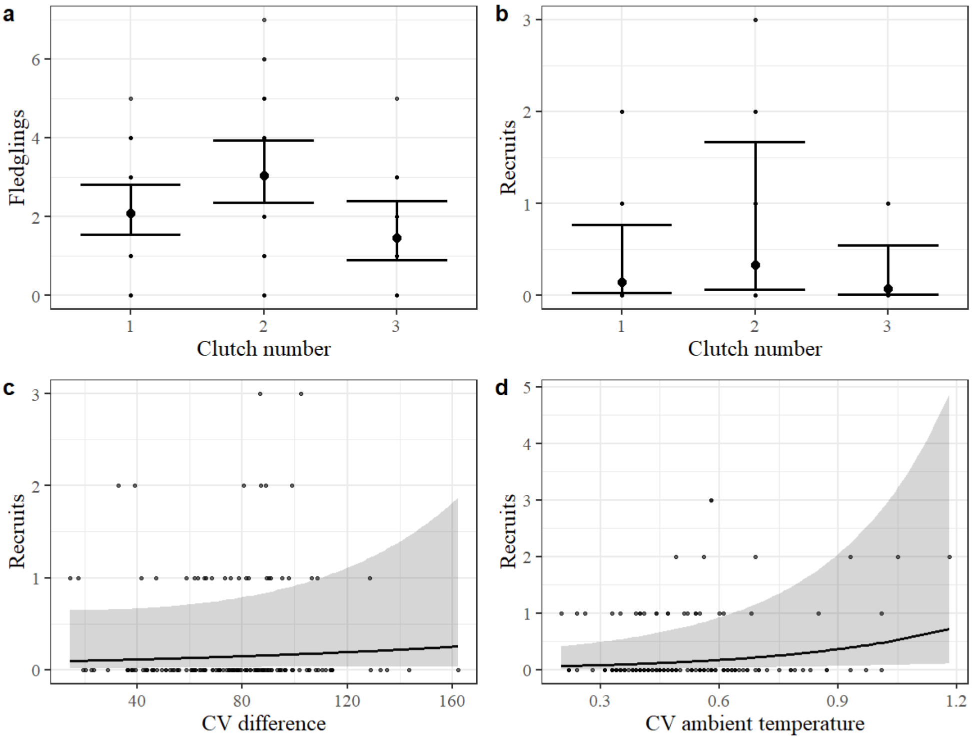

Figure 5: Panel (a) show the fitted relationship between the number of fledglings produced and clutch number. (model set $2A_2$, table 7). Panel (b), (c) and (d) show the fitted relationship between the number of recruits produced and (b) clutch number, (c) the coefficient of variance (CV) of the difference between nest and ambient temperature and (d) the CV of ambient temperature (model set $2B_2$, table 8).

Appendix

I: Sample sizes

There were 282 clutches that had data on nest microclimate during 2006-2013, of which 27 clutches had less than 4 days of climate data and were excluded. Additionally 101 clutches had an unknown mother and had to be excluded, bringing the total sample size to 154 clutches over the eight years of study (Table A1 in the appendix). Some data from both MET stations were missing in 2007, resulting in six clutches lacking data on ambient temperature and precipitation, as well as the difference between nest and ambient climate. The sample sizes for all model sets are shown in Table 1. As the sample sizes vary for many of the models sets, I will present a brief explanation for this.

Question 1 examines morphological variables and age in relation to nest microclimate and uses ambient climate as fixed explanatory variables. Nineteen clutches had mothers with no morphological measurements or lacked data on ambient climate. The sample size for all model sets in question 1 was therefore 135 clutches.

Question 2 examines reproductive variables in relation to nest microclimate and uses mother ID as random factor. All clutches had data on the number of recruits produced, however the number of fledglings were missing for seven clutches, making 154 clutches available for the analyses of nest microclimate on recruits and 147 clutches available for the analyses of nest microclimate on fledglings.

Part 2 of question 2 includes the difference between nest and ambient temperature and therefore uses data of ambient climate, which was missing for 6 clutches. Additionally, three clutches were the fourth clutch produced by the mothers, which had to be excluded for the analysis as it caused convergence problems. The mean laying date for these fourth clutches was the exact same as for all third clutches. The sample size for the models using recruits as response variable was then 145 clutches, while for the models using fledglings as response variable, the sample size was 138.

II: Tables

Table A1: Number of clutches available for nest climate analyses per year in an eight-year study of the house sparrow at Hestmannøy, Norway, and the partitioning in the north and south subpopulation. The north subpopulation consisted of breeding colonies around four farms, while the south subpopulation consisted of a breeding colony around a single farm. The number of unique mothers are also listed per year. The total number of clutches and mothers across all years are presented in the bottom line. Total number of unique mothers across all years does not equal to the sum of each year as 4 mothers occurred in three years and 13 mothers occurred in two years while the remaining 68 mothers occurred only in one year.

	Total number of clutches	**Clutches on the north side**	**Clutches on the south side**	**Number of unique mothers**
2006	21	16	5	15
2007	27	20	7	20
2008	15	10	5	11
2009	31	29	2	20
2010	19	17	2	11
2011	22	22	–	15
2012	6	–	6	5
2013	13	1	12	9
Total	154	115	39	85

Table A2: AIC_c ranking of generalized mixed effects models explaining the variation in mean nest temperature by mother characteristics in 135 wild house sparrow clutches at Hestmannøy, Norway (model set 1A, Table 1). Mother characteristics included tarsus length (tarsus), body mass (mass), bill length (bill) and age. Mother ID was included with random intercept in all models. Mean ambient temperature (MAT) was also included as an explanatory variable in all models and the intercept model included only this explanatory variable. The difference in AIC_c value to the top ranked model (ΔAIC_c), weighted AIC_c ($w\text{AIC}_c$) and evidence ratio compared to the top ranked model (ER) is presented for all candidate models. All models with $\Delta\text{AIC}_c < 2$ compared to the top ranked model are italicized.

Rank	**Model parameters**	**ΔAIC_c**	**$w\text{AIC}_c$**	**ER**
1	*MAT + Bill + Age + Age*^{2}	*0.00*	*0.21*	*1.00*
2	*MAT + Mass + Bill + Age + Age*^{2}	*0.99*	*0.13*	*1.62*
3	*MAT + Age + Age*^{2}	*1.48*	*0.10*	*2.10*
4	*MAT + Bill*	*1.73*	*0.09*	*2.33*
5	MAT + Tarsus + Bill + Age + Age^2	2.15	0.07	3.00
6	MAT	2.18	0.07	3.00
7	MAT + Tarsus + Mass + Bill + Age + Age^2	2.54	0.06	3.50
8	MAT + Mass + Age + Age^2	2.75	0.05	4.20
9	MAT + Mass + Bill	3.05	0.05	4.20
10	MAT + Tarsus + Bill	3.52	0.04	5.25
11	MAT + Mass	3.67	0.03	7.00
12	MAT + Tarsus + Age + Age^2	3.70	0.03	7.00
13	MAT + Tarsus + Mass + Bill	4.04	0.03	7.00
14	MAT + Tarsus	4.26	0.02	10.50
15	MAT + Tarsus + Mass + Age + Age^2	4.87	0.02	10.50
16	MAT + Tarsus + Mass	5.43	0.02	10.50

Table A3: AIC$_c$ ranking of generalized mixed effects models explaining the variation in the coefficient of variation (CV) of nest temperature by mother characteristics in 135 wild house sparrow clutches at Hestmannøy, Norway (model set 1B, Table 1). Mother characteristics included tarsus length (tarsus), body mass (mass), bill length (bill) and age Mother ID was included with random intercept in all models. CV of ambient temperature (CVAT) was also included as an explanatory variable in all models and the intercept model included only this explanatory variable. The difference in AIC$_c$ value to the top ranked model (ΔAIC$_c$), weighted AIC$_c$ (*w*AIC$_c$) and evidence ratio compared to the top ranked model (ER) is presented for all candidate models. All models with ΔAIC$_c$ < 2 compared to the top ranked model are italicized.

Rank	**Model parameters**	**ΔAIC$_c$**	***w*AIC$_c$**	**ER**
1	*CVAT + Age + Age*^{2}	*0.00*	*0.27*	*1.00*
2	*CVAT + Mass + Age + Age*^{2}	*1.31*	*0.14*	*1.93*
3	CVAT + Tarsus + Age + Age^2	2.04	0.10	2.70
4	CVAT + Bill + Age + Age^2	2.06	0.10	2.70
5	CVAT	2.62	0.07	3.86
6	CVAT + Tarsus + Mass + Age + Age^2	2.84	0.07	3.86
7	CVAT + Mass + Bill + Age + Age^2	3.35	0.05	5.40
8	CVAT + Tarsus + Bill + Age + Age^2	4.06	0.04	6.75
9	CVAT + Mass	4.07	0.04	6.75
10	CVAT + Tarsus	4.52	0.03	9.00
11	CVAT + Bill	4.58	0.03	9.00
12	CVAT + Tarsus + Mass + Bill + Age + Age^2	4.69	0.03	9.00
13	CVAT + Tarsus + Mass	5.47	0.02	13.50
14	CVAT + Mass + Bill	6.01	0.01	27.00
15	CVAT + Tarsus + Bill	6.42	0.01	27.00
16	CVAT + Tarsus + Mass + Bill	7.19	0.01	27.00

Table A4: AIC_c ranking of generalized mixed effects models explaining the variation in mean nest humidity by mother characteristic in 135 wild house sparrow clutches at Hestmannøy, Norway (model set 1C, Table 1). Mother characteristics included tarsus length (tarsus), body mass (mass), bill length (bill) and age. Mother ID was included with random intercept in all models. Mean ambient temperature (MAT) and total precipitation (TP) was also included as an explanatory variable in all models, the intercept model included these two explanatory variable. The difference in AIC_c value to the top ranked model (ΔAIC_c), weighted AIC_c ($wAIC_c$) and evidence ratio compared to the top ranked model (ER) is presented for all candidate models. All models with $\Delta AIC_c < 2$ compared to the top ranked model are italicized.

Rank	**Model parameters**	**ΔAIC_c**	**$wAIC_c$**	**ER**
1	*MAT + TP + Age + Age*^{2}	*0.00*	*0.27*	*1.00*
2	*MAT + TP + Bill + Age + Age*^{2}	*1.08*	*0.16*	*1.69*
3	*MAT + TP + Mass + Age + Age*^{2}	*1.79*	*0.11*	*2.45*
4	*MAT + TP + Tarsus + Age + Age*^{2}	*1.84*	*0.11*	*2.45*
5	MAT + TP + Mass + Bill + Age + Age^2	2.78	0.07	3.86
6	MAT + TP + Tarsus + Bill + Age + Age^2	3.13	0.06	4.50
7	MAT + TP	3.28	0.05	5.40
8	MAT + TP + Tarsus + Mass + Age + Age^2	3.90	0.04	6.75
9	MAT + TP + Bill	4.41	0.03	9.00
10	MAT + TP + Tarsus + Mass + Bill + Age + Age^2	5.06	0.02	13.50
11	MAT + TP + Mass	5.18	0.02	13.50
12	MAT + TP + Tarsus	5.25	0.02	13.50
13	MAT + TP + Mass + Bill	6.25	0.01	27.00
14	MAT + TP + Tarsus + Bill	6.55	0.01	27.00
15	MAT + TP + Tarsus + Mass	7.32	0.01	27.00
16	MAT + TP + Tarsus + Mass + Bill	8.51	0.00	∞

Table A5: AIC$_c$ ranking of generalized mixed effects models explaining the variation in the mean difference between nest and ambient temperature by mother characteristic in 135 wild house sparrow clutches at Hestmannøy, Norway (model set 1D, Table 1). Mother characteristics included tarsus length (tarsus), body mass (mass), bill length (bill) and age. Mother ID and year were included with random intercepts in all models. The difference in AIC$_c$ value to the top ranked model (ΔAIC$_c$), weighted AIC$_c$ (*w*AIC$_c$) and evidence ratio compared to the top ranked model (ER) is presented for all candidate models. All models with ΔAIC$_c$ < 2 compared to the top ranked model are italicized.

Rank	**Model parameters**	**ΔAIC$_c$**	***w*AIC$_c$**	**ER**
1	*Intercept*	*0.00*	*0.14*	*1.00*
2	*Bill*	*0.32*	*0.12*	*1.17*
3	*Bill + Age + Age^2*	*0.54*	*0.11*	*1.27*
4	*Age + Age^2*	*0.76*	*0.10*	*1.40*
5	*Mass*	*1.34*	*0.07*	*2.00*
6	*Mass + Bill + Age + Age^2*	*1.38*	*0.07*	*2.00*
7	*Mass + Bill*	*1.49*	*0.07*	*2.00*
8	*Mass + Age + Age^2*	*1.86*	*0.06*	*2.33*
9	Tarsus	2.14	0.05	2.80
10	Tarsus + Bill	2.34	0.04	3.50
11	Tarsus + Bill + Age + Age^2	2.77	0.04	3.50
12	Tarsus + Mass + Bill	2.91	0.03	4.67
13	Tarsus + Age + Age^{2}Mass	2.97	0.03	4.67
14	Tarsus + Mass + Bill + Age + Age^2	3.18	0.03	4.67
15	Tarsus + Mass	3.26	0.03	4.67
16	Tarsus + Mass + Age + Age^2	4.03	0.02	7.00

Table A6: Parameter estimates for the eight models within 2 ΔAIC_c when investigating whether maternal characteristics influenced the variation in the difference between nest and ambient temperature (model set 1D, see table A5). The parameter estimates (*β*) are given for each explanatory variable with their confidence intervals in brackets. Explanatory variable not included in each candidate models are marked with a greyed out cell. None of the candidate models within 2 ΔAIC_c included tarsus length.

Model rank	Explanatory variables			
	Body mass	Bill length	Age	Age^2
1				
2		0.783 [-0.358, 1.924]		
3		0.921 [-0.251, 2.092]	-1.308 [-2.561, -0.055]	0.212 [-0.008, 0.432]
4			-1.219 [-2.472, 0.033]	0.203 [-0.017, 0.423]
5	0.063 [-0.075, 0.202]			
6	0.083 [-0.058, 0.224]	0.968 [-0.204, 2.141]	-1.369 [-2.620, -0.118]	0.222 [0.003, 0.441]
7	0.069 [-0.068, 0.207]	0.820 [-0.325, 1.966]		
8	0.075 [-0.067, 0.218]		-1.272 [-2.523, -0.021]	0.212 [-0.007, 0.432]

Table A7: $\mathrm{AIC_c}$ ranking of generalized mixed effects models explaining the variation in the coefficient of variation (CV) of the difference between nest and ambient temperature by mother characteristic in 135 wild house sparrow clutches at Hestmannøy, Norway (model set 1E, Table 1). Mother characteristics included tarsus length (tarsus), body mass (mass), bill length (bill) and age. Mother ID and year were included with random intercepts in all models. The difference in $\mathrm{AIC_c}$ value to the top ranked model ($\Delta\mathrm{AIC_c}$), weighted $\mathrm{AIC_c}$ ($w\mathrm{AIC_c}$) and evidence ratio compared to the top ranked model (ER) is presented for all candidate models. All models with $\Delta\mathrm{AIC_c} < 2$ compared to the top ranked model are italicized.

Rank	**Model parameters**	**$\Delta\mathrm{AIC_c}$**	**$w\mathrm{AIC_c}$**	**ER**
1	*Intercept*	*0.00*	*0.27*	*1.00*
2	*Age + Age^2*	*1.62*	*0.12*	*2.25*
3	*Mass*	*1.94*	*0.10*	*2.70*
4	Bill	2.03	0.10	2.70
5	Tarsus	2.13	0.09	3.00
6	Bill + Age + Age^2	3.57	0.05	5.40
7	Mass + Age + Age^2	3.60	0.05	5.40
8	Tarsus + Age + Age^2	3.76	0.04	6.75
9	Tarsus + Mass	3.99	0.04	6.75
10	Mass + Bill	4.02	0.04	6.75
11	Tarsus + Bill	4.21	0.03	9.00
12	Tarsus + Mass + Age + Age^2	5.60	0.02	13.50
13	Mass + Bill + Age + Age^2	5.63	0.02	13.50
14	Tarsus + Bill + Age + Age^2	5.79	0.02	13.50
15	Tarsus + Mass + Bill	6.15	0.01	27.00
16	Tarsus + Mass + Bill + Age + Age^2	7.74	0.01	27.00

Table A8: AIC$_c$ ranking of generalized mixed effects models explaining the variation in the number of fledglings by three principle components variables of the nest microclimate (composed by mean temperature, coefficient of variance of temperature and mean humidity) in 147 wild house sparrow clutches at Hestmannøy, Norway (model set 2A$_1$, Table 1). Mother ID and year were included with random intercepts in all models. The difference in AIC$_c$ value to the top ranked model (ΔAIC$_c$), weighted AIC$_c$ (*w*AIC$_c$) and evidence ratio compared to the top ranked model (ER) is presented for all candidate models. All models with ΔAIC$_c$ < 2 compared to the top ranked model are italicized.

Rank	**Model parameters**	**ΔAIC$_c$**	***w*AIC$_c$**	**ER**
1	*PC3*	*0.00*	*0.32*	*1.00*
2	*PC1 + PC3*	*0.66*	*0.23*	*1.39*
3	*PC2 + PC3*	*1.89*	*0.12*	*2.67*
4	Intercept	2.41	0.10	3.20
5	PC1 + PC2 + PC3	2.49	0.09	3.56
6	PC1	3.18	0.06	5.33
7	PC2	3.92	0.04	8.00
8	PC1 + PC2	4.57	0.03	10.67

Table A9: AIC$_c$ ranking of generalized mixed effect models explaining the variation in the number of fledglings by effects of nest microclimate (the mean difference between nest and ambient temperature, mean difference, and the coefficient of variance of the difference between nest and ambient temperature, CV difference) when accounting for ambient temperature in 138 wild house sparrow clutches at Hestmannøy, Norway (model set 2A$_2$, Table 1). Mother ID and year were included with random intercepts in all models. Clutch number (CN) was included as an explanatory variable in all models and the intercept model included only this explanatory variable. The difference in AIC$_c$ value to the top ranked model (ΔAIC$_c$), weighted AIC$_c$ (*w*AIC$_c$) and evidence ratio compared to the top ranked model (ER) is presented for all candidate models. All models with ΔAIC$_c$ < 2 compared to the top ranked model are italicized.

Rank	**Model parameters**	**ΔAIC$_c$**	***w*AIC$_c$**	**ER**
1	*CN*	*0.00*	*0.68*	*1.00*
2	CN + CV difference + CV ambient temperature	2.20	0.23	2.96
3	CN + Mean difference + Mean ambient temperature	4.11	0.09	7.56

Table A10: AIC_c ranking of generalized mixed effects models explaining the variation in the number of recruits by effects of three principle components variables of the nest microclimate (composed of mean temperature, coefficient of variance of temperature and mean humidity) in 154 wild house sparrow clutches at Hestmannøy, Norway (model set $2B_1$, Table 1). Mother ID and year were included with random intercepts in all models. The difference in AIC_c value to the top ranked model (ΔAIC_c), weighted AIC_c ($wAIC_c$) and evidence ratio compared to the top ranked model (ER) is presented for all candidate models. All models with $\Delta AIC_c < 2$ compared to the top ranked model are italicized.

Rank	**Model parameters**	**ΔAIC_c**	**$wAIC_c$**	**ER**
1	*Intercept*	*0.00*	*0.26*	*1.00*
2	*PC1*	*0.38*	*0.22*	*1.18*
3	*PC3*	*1.05*	*0.15*	*1.73*
4	*PC1 + PC3*	*1.82*	*0.11*	*2.36*
5	PC2	2.06	0.09	2.89
6	PC1 + PC2	2.42	0.08	3.25
7	PC2 + PC3	3.17	0.05	5.20
8	PC1 + PC2 + PC3	3.93	0.04	6.50

Table A11: AIC_c ranking of generalized mixed effect candidate models explaining the variation in the number of recruits by effects of nest microclimate (the mean difference between nest and ambient temperature, mean difference, and the coefficient of variance of the difference between nest and ambient temperature, CV difference) when accounting for ambient climate in 145 wild house sparrow clutches at Hestmannøy, Norway (model set $2B_2$, Table 1). Mother ID and year were included with random intercepts in all models. Clutch number (CN) was included as an explanatory variable in all models, the intercept model included only this explanatory variable. The difference in AIC_c value to the top ranked model (ΔAIC_c), weighted AIC_c ($wAIC_c$) and evidence ratio compared to the top ranked model (ER) is presented for all candidate models. All models with $\Delta AIC_c < 2$ compared to the top ranked model are italicized.

Rank	**Model parameters**	**ΔAIC_c**	**$wAIC_c$**	**ER**
1	*CN + CV difference + CV ambient temperature*	*0.00*	*0.81*	*1.00*
2	CN	3.19	0.16	5.06
3	CN + Mean difference + Mean ambient temperature	6.58	0.03	27.00

III: Figures

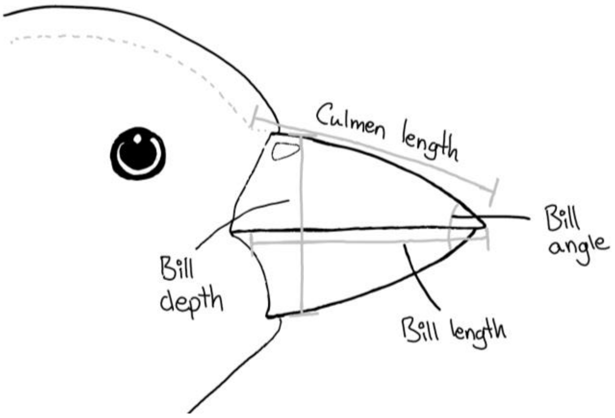

Figure A1: Diagram of the bill measurements of house sparrows used in this study. The dotted line indicates the skeletal contour. The culmen length measured the upper ridge of the beak from the base of the bill to the bill tip. The bill depth measured the height of the beak from the top in front of the nostrils and in a 90° angle down. Culmen length and bill depth were measured in the field with a calliper. The bill length and bill angle were calculated by assuming that a cross section of the bill is composed of two right-angled triangles where the one leg is half the bill depth and the hypotenuse is the culmen length.

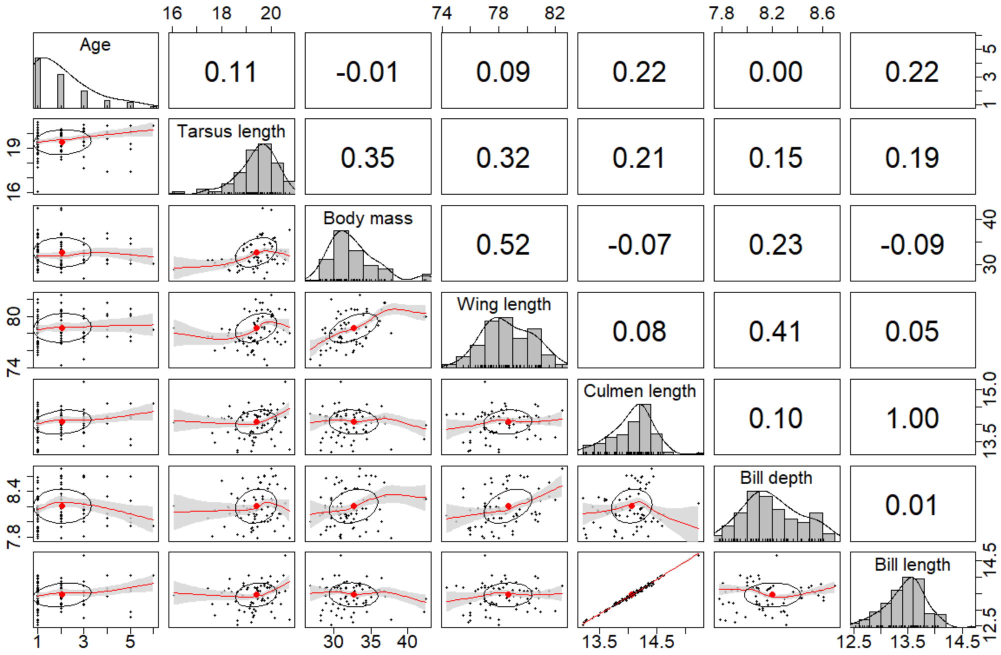

Figure A2: Correlation matrix of phenotypic traits for house sparrows at Hestmannøy, Norway. Pearson's product moment correlations (r_p) are given above the diagonal. The histograms on the diagonal line provides the frequency distribution of each variable. The plots below the diagonal shows the bivariate scatter plot between the variables with correlation ellipses and regression fitted with locally weighted scatterplot smoothing (LOWESS) in red including the confidence interval in grey. Age is in year, body mass is in grams and the rest of the measures are on millimetre scale.

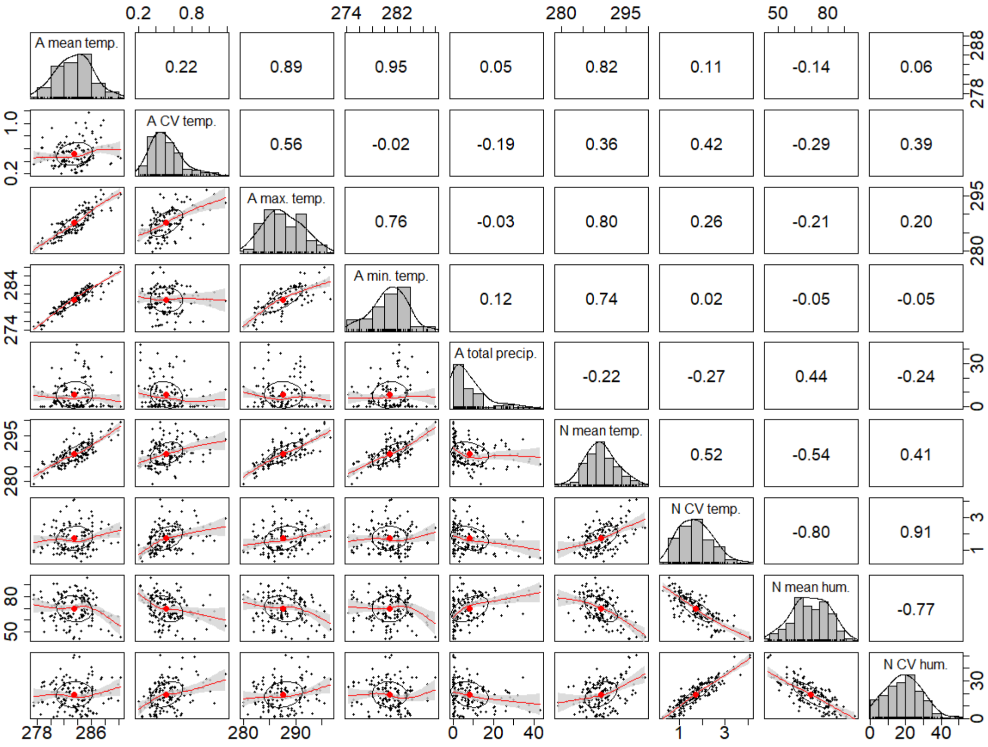

Figure A3: Correlation matrix of nest (marked with "N") and ambient (marked with "A") climate variables experienced during the last seven days of incubation in nests of house sparrows on Hestmannøy, Norway. Temperature is abbreviated as "temp", coefficient of variance as "CV", maximum as "max", minimum as "min", precipitation as "precip" and humidity as "hum". 154 clutches had data on nest microclimate and 148 clutches had data on ambient climate. Pearson's product moment correlations (r_p) are given above the diagonal. The histograms on the diagonal line provides the frequency distribution of each variable. The plots below the diagonal shows the bivariate scatter plot between the variables with correlation ellipses and regression fitted with locally weighted scatterplot smoothing (LOWESS) in red including the confidence interval in grey. Temperature is on Celsius scale, the unit of humidity is %RH and coefficient of variation (CV) is unitless.

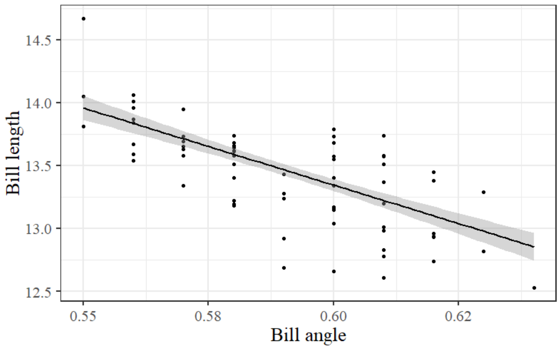

Figure A4: The relationship between bill length and bill angle in a house sparrow population on Hestmannøy, Norway. Bill length and bill angle were negatively correlated with each other ($r_p = -0.70$, $n = 133$, $P < 0.001$).

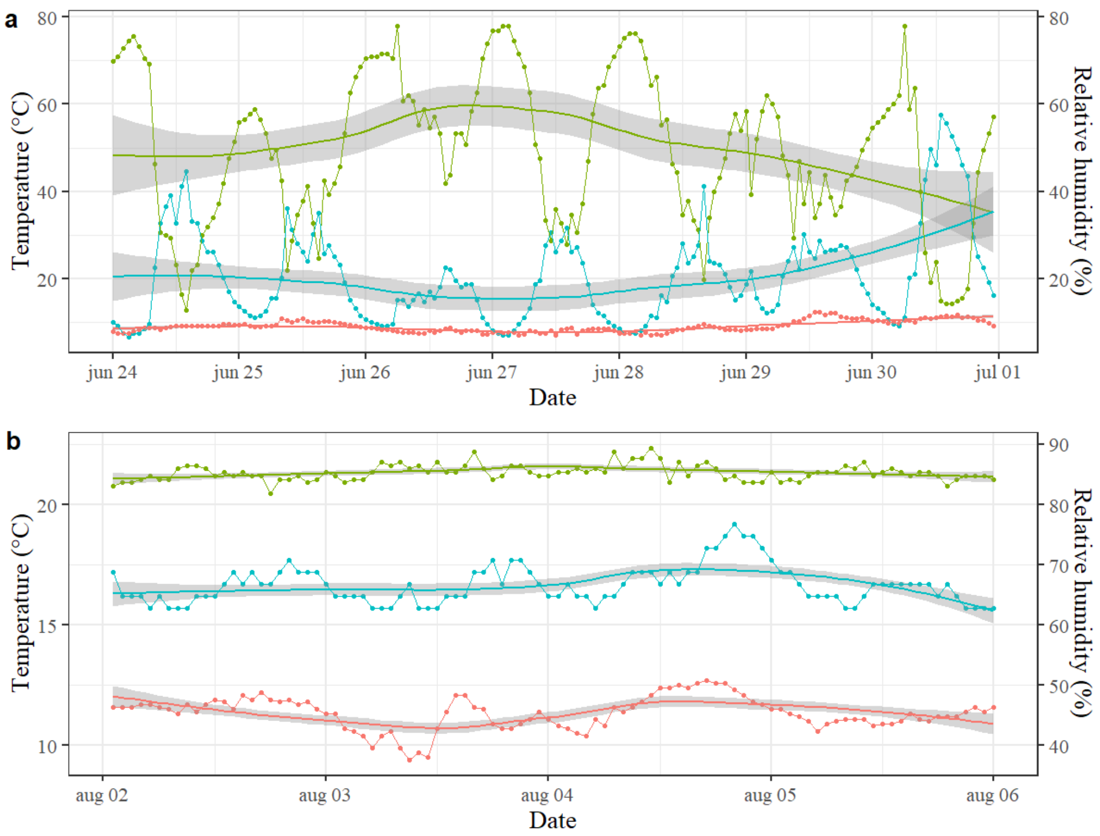

Figure A5: A visual representation of nest (blue dots) and ambient (red dots) temperature (°C) and relative humidity (green dots, %RH) in two house sparrow nest experiencing a nest temperature range of (a) 50.93 °C and (b) 3.50 °C at Hestmannøy, Norway. Lines are drawn between points in the corresponding colour along with locally weighted scatterplot smoothing (LOWESS).

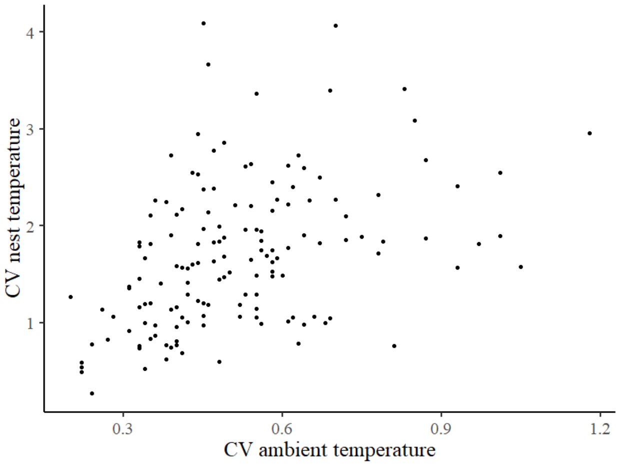

Figure A6: Coefficient of variance (CV) of ambient temperature plotted against CV of nest temperature in a wild house sparrow population at Hestmannøy, Norway. CV of nest temperature and CV of ambient temperature were 0.42 positively correlated with each other (n = 148, P < 0.001).