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Effects of Variation in Egg Size on Offspring Fitness in Populations of House Sparrow (*Passer domesticus*)

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SUMMARY

1. Egg size represents an important life-history trait, which may have effects on the fitness of offspring. The effect of variation in egg size on offspring fitness has been studied within many taxa, but there is still a lack of knowledge about both the adaptive significance of variation in egg size under fluctuating environmental conditions and the long-term effects of egg size on offspring fitness in wild species.

2. By studying an island population of house sparrows in northern Norway, I investigated the effects of among-brood variation in mean egg size, within-brood variation in egg size and climatic conditions on offspring fitness. Offspring fitness was measured as mortality from hatching until fledging stage and until recruitment stage, and as fledgling body mass and tarsus length.

3. The study revealed that large mean egg sizes reduced nestling mortality and had marginally positive effect on fledgling body mass, whereas large within-brood variation in egg size increased nestling mortality. There was also carry-over effects of mean egg size to the recruitment stage. Fledgling tarsus was little influenced by egg size. However, the fitness consequences of a given egg size was dependent on the weather conditions that the brood was exposed to during the early nestling stage. The difference in performance between individuals from small and large eggs was most pronounced under harsh climatic conditions. Overall, large egg sizes had a positive effect on offspring performance, but the results also indicated that offspring from large eggs suffered a higher probability of mortality until recruitment stage if they experienced high temperatures during the nestling stage.

4. The findings in this correlational study may suggest that the observed variation in egg size among and within broods may be adaptations towards temporal fluctuations in environmental conditions, and that the optimal egg size for maximizing fitness may differ in relation to environmental conditions.

SAMMENDRAG

1. Eggstørrelse representerer et viktig livshistorietrekk som kan ha effekter på fitnessen til avkom. Effekten av variasjonen i eggstørrelse på avkoms fitness har blitt studert innenfor mange taxa, men det er fortsatt mangel på kunnskap vedrørende den adaptive betydningen av eggstørrelsevariasjon i fluktuerende miljøer og langtidseffektene av eggstørrelse på avkoms fitness hos ville arter.

2. Ved å bruke gråspurv fra en øypopulasjon i Nord-Norge som studiesystem, undersøkte jeg effektene av mellomkullsvariasjon i gjennomsnittseggstørrelse, innenkullsvariasjon i eggstørrelse og klimatiske forhold på fitnessen til avkom. Avkommenes fitness var målt som mortalitet fra klekking til utflyvningsstadiet og til rekrutteringsstadiet, og som kroppsmasse og tarslengde hos flyveferdige avkom.

3. Jeg fant at store gjennomsnittseggstørrelser reduserte mortaliteten til utflyvningsstadiet og hadde en marginal positiv effekt på kroppsmassen til flyveferdige unger, mens stor innenkullsvariasjon i eggstørrelse økte mortaliteten til utflyvningsstadiet. Jeg fant også en overføringseffekt av gjennomsnittseggstørrelse til rekrutteringsstadiet. Tarslengde hos flyveferdige unger var lite påvirket av eggstørrelse. Fitnesskonsekvensene av en gitt eggstørrelse var imidlertid avhengig av de klimatiske forholdene kullene opplevde i løpet av de første dagene etter klekking. Forskjellen i fitness mellom individer fra små og store egg kom mest til uttrykk under tøffe klimatiske forhold. Alt i alt hadde store gjennomsnittseggstørrelser en positiv effekt på fitnessen til avkom, men resultatene indikerte også at avkom fra store egg hadde lav

sannsynlighet for å overleve til rekrutteringsstadiet hvis de opplevde høye temperaturer under reirstadiet.

4. Funnene fra dette korrelasjonsstudiet kan indikere at den observerte variasjonen i eggstørrelse blant og innenfor kull var tilpasninger til fluktuerende klimatiske forhold, og at den optimale eggstørrelsen for maksimering av fitness endrer seg under forskjellige klimatiske forhold.

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INTRODUCTION

Egg size is an important life-history trait, by which parents may affect the fitness of their offspring (Stearns 1992; Roff 2002). A positive effect of egg size on offspring fitness has been found in many species (Krist 2011), but the effect on offspring performance will often depend on environmental conditions, and may primarily be of importance in harsh environments (Kaplan 1992; Einum & Fleming 1999; Fox 2000). Even though the effects of variation in egg size on offspring fitness has been studied within many taxa, there is still a lack of knowledge about both the adaptive significance of variation in egg size under fluctuating environmental conditions and the long-term effects of egg size on offspring fitness in wild species (Krist 2011). The present study will shed light on both short-term and long-term consequences of variation in egg size on offspring fitness in a small passerine bird species.

There is often large variation in egg size between individuals in species of oviparous vertebrates, in which the largest eggs within a population might be 50 % larger or more than the smallest eggs (Christians 2002). Most of this variation in egg size is due to variation between broods rather than within broods (Christians 2002). The amount of egg yolk in an egg is positively related to the size of the egg (Goulden, Henry & Berrigan 1987; Williams 1994; Ahn, Kim & Shu 1997). Thus, egg size reflects the amount of resources available for an offspring during embryonic development and is commonly held to be an important index of egg quality (Bolton 1991). Due to the extra amount of resources available for offspring that hatch from large eggs, one should expect egg size to be an important parameter in determining offspring survival (Fleming 1996; Krist 2011). Indeed, a positive correlation between egg size and nestling survival during the period after hatching has been found in several bird species (Williams 1994; Krist 2011). Egg size has also been found to have a generally positive influence on other fitness related traits, such as hatching success (Amundsen, Lorentsen & Tveraa 1996; Krist 2011) and body mass of nestlings (Bolton 1991; Amundsen *et al.* 1996; Blomqvist, Johansson & Götmark 1997; Pelayo & Clark 2003; Skrade & Dinsmore 2013). In birds, most studies on egg size have focused on the first week after hatching, however, the available evidence indicates that the effect of egg size tends to decrease with the age of nestlings (Amundsen *et al.* 1996; Styrsky, Eckerle & Thompson 1999; Christians 2002). This finding may be caused by increased parental care during the nestling period as a compensation for the “tough start” of being hatched from a small egg; the effect of post-hatching parental care masks the effect of egg size on offspring fitness (Ricklefs 1984; Monteith, Andrews & Smiseth 2012). Few studies on egg size have followed the offspring during the post-fledging stages (Christians 2002; Krist 2011), and therefore, the evidences for long-lasting carry-over effects of egg size are scarce.

Variation in egg size is caused by several factors. Studies have documented that egg size in birds has an additive genetic component, typically reported within the range 0.50-0.70 (Larsson & Forslund 1992; Christians 2002; Kontiainen *et al.* 2008; Kvalnes *et al.* 2013). Egg size may co-vary with maternal traits, such as age (Hipfner, Gaston & Forest 1997) and body mass (Kvalnes *et al.* 2013). Also, environmental conditions, such as temperature (Nager & Noordwijk 1992) and resource availability (Wiebe & Bortolotti 1995) might be important factors in determining egg size. For instance, in a study of house sparrows in northern Norway, Kvalnes *et al.* (2013) found that egg size was positively correlated with both maternal body mass and spring temperature. Females could be expected to adaptively adjust the egg size in response to the current environmental conditions; if large eggs are of advantage under harsh environmental conditions, females may be expected to increase the egg sizes under poor conditions and reduce egg sizes under good conditions (Yampolsky & Scheiner 1996; Kontiainen *et al.* 2008). Studies on diverse taxa have demonstrated that the effects of variation in egg size on offspring performance depend on environmental conditions (Kaplan 1992; Einum & Fleming 1999; Fox & Csezak 2000), where the fitness difference between offspring hatching from large and small eggs is most pronounced in harsh, low-quality environments (Fox & Csezak 2000). Under such conditions, the extra nutrient reserves from an increased egg size may potentially prevent starvation, whereas under good conditions, good parental care may compensate for small eggs and equalize the fitness differences of offspring from different sized eggs (Christians 2002).

Accordingly, a female may adjust the amount of nutrients and energy invested in each offspring by varying egg sizes (Kontiainen *et al.* 2008; Rollinson & Hutchings 2013), but allocating resources to produce an extra offspring is likely to be costly (Perrins 1996; Sinervo & DeNardo 1996; Nager 2006). Hence, reproductive investment may either be divided into a few, large, or many, small offspring (Smith & Fretwell 1974; Einum & Fleming 2000; Krist 2011). The possible trade-off between size and number of offspring may represent a parent-offspring conflict, as the offspring size that maximizes offspring fitness may not be equivalent to that which maximizes parental fitness (Janzen & Warner 2009). In temporally unpredictable environments, females may vary the egg sizes within broods as a bet-hedging strategy (Slagsvold *et al.* 1984; Marshall, Bonduriansky & Bussière 2008; Olofsson, Ripa & Jonzén 2009);

producing offspring of different sizes in a brood ensures that at least some of the offspring will approach the optimum size for the environment (Marshall *et al.* 2008). In altricial birds, hatching asynchrony has been suggested to enable a brood reduction strategy in birds that lay relatively many eggs in relation to the number of nestlings they can feed. Thus, by investing most in the first-laid eggs and less in the last-laid eggs, females may adjust the number of offspring they rear in relation to the environmental conditions experienced during the nestling stage, as the nestlings from the last-laid eggs may only survive under good conditions (Slagsvold *et al.* 1984; Amundsen & Slagsvold 1998; Hillström 1999). For instance, Hargitai *et al.* (2011) found that collared flycatcher females, *Ficedula albicollis*, invested less in the last-laid eggs in years were the weather was cold during the early breeding season than in years with more favorable weather conditions. However, within-brood variation in egg size may also reflect physiological constraints and the condition of the egg-laying female; females may be limited in the amount of substances they can allocate to their eggs or be unable to produce eggs of identical size (Slagsvold *et al.* 1984; Fox & Csezak 2000; Ferrari, Martinelli & Saino 2006; Crean & Marshall 2009). Therefore, it may be problematic to determine whether variation in egg size is adaptive or not (Crean & Marshall 2009). Regardless of whether large within-brood variation in egg size is the result of an adaptation to temporally unpredictable environments or simply a reflection of female quality or physiological constraints, we could expect that large within-brood variation in egg size would particularly increase the nestling mortality under poor conditions, whereas under good conditions, all nestlings in a brood may have a higher chance of survival. This is due to the constraint of parental care in harsh environments, for instance when feeding rates are decreased during rainy periods (e.g. Öberg *et al.* 2015). Poor environmental conditions may result in lesser food allocation to small or weak nestlings, for instance when parents favor to allocate food to large nestlings or nestlings with special color shades signaling nestling health (Wiebe & Slagsvold 2012).

In this study, I investigated the consequences of variation in egg size, measured as egg volume, on individual survival and on two morphological traits; body mass and tarsus length, by using a correlational (non-experimental) approach. Data material was obtained from a long-term study of house sparrows, *Passer domesticus* (Sæther *et al.* 1999; Ringsby *et al.* 2002; Jensen *et al.* 2004; Pärn *et al.* 2009; Kvalnes *et al.* 2013)*,* where individual survival had been recorded with high accuracy (Ringsby, Sæther & Solberg 1998; Ringsby *et al.* 1999). Focusing on the fitness consequences of egg size on offspring, I addressed two issues; first, I investigated whether variation in mean egg size among broods and within-brood variation in egg size affected mortality until two important life stages; the fledging stage (when the individuals leave the nest) and the recruitment stage (when individuals enter the next years breeding population). Second, I investigated how mean egg size among broods and within-brood variation in egg size affected the body mass and tarsus length (structural size) of the fledglings. Based on current life history theory and current empirical knowledge (outlined above), I hypothesized that mean egg size would positively affect both survival until fledging and fledgling morphology, which led to the predictions that individuals that hatched from broods with large mean egg sizes would experience a reduced mortality probability, have higher fledgling body mass and have a longer fledgling tarsus compared to individuals from broods with smaller mean egg sizes. I also predicted that the effects of egg size would be most pronounced in periods of cold and rainy weather, i.e. when food resources were scarce and cooling of individuals in the nest high. Also, if the maternal distribution of food among nestlings was influenced by the number and size of siblings, I predicted that a large within-brood variation in egg sizes would particularly increase the mortality in periods of cold and rainy weather, as small and weak individuals may receive less parental care under such conditions.

MATERIAL AND METHODS

Study system

The house sparrow is a small passerine bird, with a length of 14-16 cm and a weight of 25-35 g. Individuals start breeding at the age of one year (Anderson 2006), and the breeding season in Norway lasts from early May until the middle of August. Each bird can lay 1-3 broods per season, with 4-8 eggs per brood (Husby et al. 2006; Ringsby et al. 1998). Eggs are incubated for approximately 11 days, and after hatching the nestlings stay in the nest for about 14 days before they fledge (Anderson 2006; Kvalnes *et al.* 2013). House sparrows are socially monogamous, but for ca. 25 % of the offspring, the genetic father does not resemble the social father (Larsen *et al.* unpublished results). The birds are non-migratory and have high site fidelity (Altwegg et al. 2000; Kvalnes *et al.* 2013; Pärn *et al*. 2009; Pärn et al. 2012; Ringsby *et al.* 1998), these characteristics enables the collection of high-quality data on survival and fecundity.

The data used in this study were collected on the island Hestmannøy (Fig. 1), which is located in an archipelago in northern Norway (66°N, 13°E). The island is part of a long-term study system of 18 islands where populations of house sparrows have been studied since 1993 until present (Jensen *et al*. 2003; Jensen *et al.* 2004; Jensen *et al.* 2006; Jensen *et al.* 2008; Kvalnes *et al.* 2013; Ringsby *et al.* 1998; Ringsby *et al.* 2002; Sæther *et al*. 1999). Individuals in these populations live in close association with human settlements around dairy farms, and typically breed underneath roofing tiles, in cracks and holes inside buildings, or in the few available nest boxes.

Data collection

Data collection for this study was performed annually during the breeding season and for a shorter period in September/October. Juvenile and adult house sparrows were captured with a mist net and marked with a unique set of three plastic color rings and a numbered aluminium ring. In addition, a small blood sample (25 µl) was taken from the birds' brachial vein for parental analyses. During the breeding season, active nests were systematically searched for weekly, and all active nests were visited several times during egg laying, incubation and the nestling period. In the period 2003-2009, egg photos were taken of all eggs in complete clutches. The egg photos were taken in a standardized way, where the eggs were placed in a tube with a flat surface and a holder for a digital camera at the other end. The flat surface was equipped with six dents where the eggs were placed. When taking the pictures, the same type of digital camera, built-in-flash, focal length and picture quality was used. (for more details, see Kvalnes *et al.* 2013, supplementary material). See description of egg size estimation below.

Active nests were monitored to determine the hatch date, and nestlings were handled when 5 days old, to take a blood sample and ring them with an aluminium ring. At the age of 8-13 days (defined as the fledging stage), the nestlings were ringed with unique plastic color rings, and measured for body mass and tarsus length

To account for consistent differences in measurement technique of tarsus length among fieldworkers, each fieldworkers' measure was tested against the corresponding T.H.R. measure. Any significant (*P<0.05)* mean differences found by paired t-tests were then added to all measurements of the fieldworker to remove any deviations from T.H.R. measurements. In addition, all morphological measurements collected between 8-13 days of age were adjusted to the age of 11 days by fitting a Gompertz growth curve to the change in each morphological trait with age, using an extended data set with nestlings at Hestmannøy from 1993 to 2013 (Kvalnes, unpublished results). Residuals for each bird from this curve were calculated and added to the fitted value at 11 days of age. However, to account for a trend of higher variance among lower ages, all residuals were adjusted according to the standard deviation at 11 days of age.

Clutch size was estimated as the maximum number of eggs present during the period of egg laying and incubation. The number of nestlings that survived to the fledging stage was estimated as the maximum number of chicks recorded from nests in where chicks were 8-13 days old. The brood number for the female (the first, second or third brood laid by a female per year) could be determined based on mother identity achieved from genetic parenthood analyses combined with information about the nest history. Due to the high nest site fidelity (Kvalnes *et al.* 2013) it was assumed that a female was responsible for all broods within a year at a given nest site.

Survival of individuals until recruitment stage was determined on basis of recaptures and/or resightings. Individuals, marked as chicks, were determined to have survived to the recruitment stage if they were recaptured and/or observed during the years following their hatch year.

Data on average daily temperature and precipitation was obtained from a weather station at the island Myken (about 30 km north-west of Hestmannøy; Fig.1), which was available from the Norwegian Meteorological Institute (The Norwegian Meteorological Institute 2014). While this weather station had the most complete data set available for the area, for a few dates, the climate data was missing. Hence, I supplied with data from another weather station located at the island

Sleneset (about 20 km south of Hestmannøy; Fig. 1). The temporal variation in climate at these two weather stations were highly correlated (Ringsby *et al.* 2002). The mean temperature and precipitation at daytime experienced for each brood during the five first days after hatching was estimated. This interval corresponds to a critical period for nestlings as they have not yet developed thermoregulatory abilities at this age (Anderson 2006).

Estimation of egg volumes

The egg photos were analyzed by using the Sparrow egg software (Sæther & Almås, unpublished) which calculates the volume of the egg to the nearest 0.01 mm^3 after the scale (numbers of pixels in a millimeter) and the edges of each egg in a photo has been defined (see Kvalnes *et al.* 2013, supplementary material, for further descriptions). The digital measurements were slightly larger than the actual measurements and were therefore adjusted to avoid inflation of mean and variance in egg size. To correct egg volumes, egg length and widths of 29 eggs from randomly selected house sparrow nests were photographed and measured by slide calipers three times, and their means were calculated. Thereafter, egg volumes was estimated both digitally and according to $V = K_v * LW^2$ (Hoyt 1979), where V is egg volume, K_v is a correction coefficient (0.51), L is egg length and W is egg width. The relationship between digitally measured egg volumes and egg volumes calculated by linear dimensions was estimated (major axis regression: manual egg volume = 96.483 + 0.909 * digital egg volume), and used for correcting the volume of all eggs.

Individual nestlings could not be traced back to a specific egg; hence, I computed the average egg volume within each brood. Also, I estimated the associated coefficient of variation for each brood as a measure of within-brood variation in egg size (CV = σ /μ, where σ is the within-brood variance in egg size and μ is the mean egg size in the brood). Throughout the rest of the text, I will denote egg volume as “egg size”.

Statistical analyses

In total, a sample of estimated mean egg sizes from 179 broods and data on fledgling morphology of 472 individuals was used in the analyses. Multi-model comparisons were based on an information theoretic approach using the Akaike Information Criteria adjusted for small sample sizes (AICc) (Burnham & Anderson 2002). This involved ranking models representing alternative hypotheses, according to AICc values, to identify models with high support in the data. One important assumption when performing multiple regression analyses is that the explanative variables are uncorrelated (Graham 2003). Hence, I calculated Pearson’s product-moment correlations between all pairs of variables to ensure none of the variables were highly correlated ($r > 0.5$). The statistical analyses were performed in three sections, as described below.

I constructed models with the following explanatory variables, which all may potentially influence offspring fitness according to current theory and literature; mean and CV of egg size of each brood, brood number, clutch size, precipitation and temperature. The combinations of explanatory variables that were included in each model have been found to affect mortality and morphology in the literature, and all combinations of variables made therefore biologically sense. As I suspected that some interactions between variables could be of particular importance, I entered the interactions between the CV of egg size and temperature, and CV of egg size and precipitation, in addition to the interactions between mean egg size and temperature and mean egg size and precipitation, into some of my candidate models. The respective main effect was always present in models with interactions. To reduce the complexity of the candidate models, I restricted the candidate models to include only one interaction at a time. To avoid convergence failures when running the models, all variables were mean centered.

The first section of the analyses focused on investigating whether variation in mean egg size and within-brood variation in egg size influenced the mortality of nestlings from hatching until the fledging stage at 11 days of age. In the second part of my analyses, I looked at whether the explanatory variables affected the mortality of individuals from hatching until recruitment stage. In both the analysis of nestling mortality and mortality until recruitment, I used generalized mixed-effects models fitted with binomial error structure and a complementary log-log link function (Ringsby *et al.* 2002). The hatch year of the nestlings was entered as a random factor in the models to account for the correlation in nestling mortality within years. Theoretically, I could also have used the nest site identity as a random factor in the analyses. However, only few of the nest sites had more than one brood, which led to convergence problems when trying to enter nest site as a random factor in the models. I therefore performed a random selection of broods, and selected only one brood for each nest site, which was used in the further analysis. I excluded the broods where none of the eggs had hatched from the analyses. The response variable for the nestling mortality analysis was modeled a response vector consisting of the number of nestlings that did not survive until fledging stage and the number of nestlings that did survive until this stage within each brood (Bates *et al.* 2014). Likewise, the response variable for the analysis of mortality until recruitment was modeled a response vector consisting of the total number of nestlings that did not survive until recruitment stage and the number of nestlings that did survive until this stage within each brood.

In the third section of the analyses, I investigated whether the morphology of the fledglings was influenced by mean egg size and other explanatory variables, by applying linear mixed-effects models. I performed separate analyses with fledgling body mass and fledgling tarsus length as response variables, respectively, and ran the same set of candidate models as for the mortality analyses. In the fledgling morphology analyses, birth year of the fledglings, mother identity and brood identity were entered as random factors, to account for the dependency of the data.

All statistical analyses were performed using package lme4 (Bates *et al.* 2014) in the statistical software R, version 3.1.2 (R Core Team 2014). Means are given with ±1 standard error. The uncertainty of regression coefficients are given as the lower and upper 95 % confidence estimates respectively (CI = [lower, upper]).

RESULTS

The population mean egg size across broods was 2.85 ± 0.017 cm^3 (n = 179), with a range of 2.17-3.42 cm^3, and the population mean CV of egg size within broods was 0.04 ± 0.001, with a range of 0.006-0.12 (n = 179). Mean fledgling body mass in the population was 25.47 ± 0.11 g (n = 472), with a range of 8.2-35.7 g, and the mean fledgling tarsus length was 18.50 ± 0.04 mm (n = 472), with a range of 12.0-21.6 mm (see Appendix, Fig. 1).

Nestling mortality

In the analysis of factors that influenced nestling mortality until fledging, there were six models with Δ AICc < 2, in which all included a negative effect of temperature and a positive effect of precipitation on mortality (Table 1). The highest ranked model included a negative effect of temperature, a positive effect of CV of egg size and a negative interaction between mean egg size and precipitation (Table 1 and 2; AICc weight = 0.12). While increasing CV of egg size increased the mortality until fledging stage, the confidence intervals of the parameter estimates included zero (Table 2). On the other hand, there was a clear reduction of nestling mortality with increasing temperatures. The interaction found in the highest ranked model indicated that the positive effect of increased egg sizes was most pronounced in periods with high precipitation (Fig. 2a). This interaction was present in four of the highest ranked models, whereas two models instead included the interaction between CV of egg size and precipitation. The interaction between precipitation and CV egg size that was present in model 3 and 4 (Table 1) provided some support to the hypothesis that large within-brood variation in egg size was mainly a disadvantage under high levels of precipitation (Fig. 2b; estimate = 4.23, CI = [0.60, 7.83] for the interaction in model 3).

Morphology

In the analysis of factors that influenced fledgling body mass, there were three models with

Δ AICc < 2, which all included brood number and temperature (Table 3). The highest ranked model also included a positive interaction between mean egg size and temperature (Table 4) and the AICc weight indicated that there were 11 % probability that the highest ranked model was the best, given the data and the candidate models. The parameter estimates of the highest ranked model revealed that the fledglings with highest body mass hatched in the first and second brood, while fledglings in the third brood were lightest. The positive interaction effect between mean egg size and temperature (Table 4) indicated that large mean egg sizes increased fledgling body mass for fledglings that experienced high temperatures during the first five days of the nestling stage. However, note the uncertainty as the confidence interval included zero marginally.

In the corresponding analysis of factors that influenced fledgling tarsus length, there were three models with Δ AICc < 2, which all included brood number, temperature and precipitation (Table 5). The highest ranked model received relatively high support in the data (AICc weight = 0.16) compared to the second ranked model (AICc weight = 0.08, ER = 1.80). The parameter estimates for this model revealed that the fledglings with the longest tarsus were hatched in the first and second brood, while the fledglings from the third brood had the shortest tarsus. High temperatures during the nestling stage increased the tarsus length, whereas high precipitation reduced tarsus length (Table 6). However, note that the parameter estimates for the precipitation effect included zero. The second-best model also included egg size and an interaction between mean egg size and temperature, indicating that egg size increased fledgling tarsus length for nestlings that had experienced high temperatures during the nestling stage (Table 5). However, the confidence interval included zero (estimate = 0.19, CI = [-0.07, 0.46]).

Mortality until recruitment

In the analysis of factors that influenced mortality rate from egg to recruitment, there were 12 models with Δ AICc < 2 (Table 7), indicating that many candidate models explained the variation in mortality equally well. The highest ranked model indicated that the second brood had a slightly lower mortality rate compared to the first and third broods. Also, the mortality until recruitment was lowered by high mean temperatures during the nestling stage and by large clutch sizes. Furthermore, the highest ranked model included a positive interaction between mean egg size and temperature (Table 8). This interaction indicated that large mean egg sizes at low temperatures reduced the mortality until recruitment somewhat, but that small egg sizes at high temperatures reduced the mortality most (Fig.3).

DISCUSSION

The present correlational study suggested that mean egg size and the variation in egg sizes within broods (CV of egg size) influenced the fitness of offspring, measured as nestling mortality (Table 1 and 2, Fig. 2). The results also indicated that there were carry-over effects of egg size on mortality rate from egg stage until recruitment stage (Table 8, Fig. 3). Additionally, the results indicated an effect of mean egg size on fledgling body mass (Table 4). However, due to the correlative nature of the present study, one should be cautious with indicating causal relationships (Rossman & Brosius 2004).

The fitness consequences of being hatched from a given egg size was suggested to depend on the weather conditions (temperature and/or precipitation) that the brood was exposed to during the early nestling stage. Accordingly, this may suggest that the observed variation in mean egg size among broods and the CV within broods may be adaptations towards temporal fluctuations in environmental conditions. For instance, large mean egg sizes in broods reduced nestling mortality in periods of cold and rainy weather, whereas the effect of egg size was small under mild climatic conditions. This finding is consistent with the theory that egg size is primarily of importance for offspring fitness under harsh conditions (Fox & Csezak 2000; Krist 2011). Under cold and rainy conditions, house sparrow nestlings may experience reduced foraging opportunities due to a decrease in prey availability, as the insect activity in general is reduced during periods with rainfall or low temperatures (Mellanby 1939; Taylor 1963). Consequently, provisioning rates may be reduced during rainy or cold periods (e.g. Öberg *et al.* 2015), and high provisioning rates have been found to have a positive effect on offspring fitness in some bird species (Ringsby *et al.* 2009; Öberg *et al.* 2015). The low thermoregulatory ability of the young house sparrow nestlings

(Anderson 2006) could also make them vulnerable to difficult climatic conditions. Under unfavorable climatic conditions, nestlings that hatched from large eggs might be better prepared for periods of starvation than nestlings from small eggs due high nutrient reserves, and it has also been suggested that nestlings hatched from large eggs might be able to utilize their energy stores more efficiently than small-egg nestlings (Ankney 1980; Dawson & Clark 1996). However, under good conditions, small egg sizes may be compensated for by good parental care (Christians 2002).

Also, other studies on different species have found that increased egg size is primarily important for offspring survival under unfavorable climatic conditions. For instance, Einum & Fleming (1999) found that juveniles of brown trout, *Salmo trutta,* from large eggs experienced growth and survival advantages over siblings from small eggs, and that the difference in performance between juveniles from small and large eggs was most pronounced in the poorer growth environments. That large egg sizes are mainly important for survival under unfavorable conditions has also been found for some species of birds, for instance, Smith & Bruun (1998) investigated the effect of egg size and habitat on nestling survival in the European starling, *Sturnus vulgaris*. They found that offspring survival during the early part of the nestling period, but not later, was related to egg size when the availability of invertebrates was low, but not when it was high. Likewise, it has been found that the selection for larger egg sizes in a species of seed beetle, *Stator limbatus*, increased as the environmental quality decreased (Fox 2000). Fox & Csezak (2000) reviewed studies on progeny size in arthropods, and also found that the effect of egg size on offspring fitness was mostly pronounced in harsh environments. They suggested that studies that have failed to detect fitness advantages of hatching from large eggs have raised progeny in high-quality environments and that this indicates that selection on egg size is generally weak in high quality environments, but favors larger eggs in lower-quality environments.

The finding that large-within brood variation in egg size increased the nestling mortality in rainy periods, could potentially be interpreted in terms of bet-hedging strategy. The study revealed that the females with the smallest variation in within-brood egg size experienced least offspring mortality, and under rainy conditions, the females with high variation in within-brood variation in egg size experienced high nestling mortality in their broods. However, to increase the within-brood variation in egg size as a bet-hedging strategy is a strategy used for handling unpredictable environments (Crean & Marshall 2009). In my study, I have no measure for how unpredictable the environment is, and hence, I have no evidence for concluding that the finding was the result of a bet-hedging strategy. Within-brood variation in egg size may as well be a result of physiological constraints (Fox & Csezak 2000), thus the females with smallest within-brood variation in egg size could for instance be high-quality females, potentially providing better parental care, resulting in higher probability of nestling survival. For instance, Amat, Fraga & Arroyo (2001a) found that females of better body condition were more able than females in lower body condition of laying eggs of more similar size in the Kentish plover, *Charadrius alexandrinus.*

My study further suggested that the interaction effect between environmental conditions at hatching and mean egg size also had long-term carry-over effects to mortality until recruitment. The results revealed that the effect of mean egg size on morality after fledging was different from the effect of mean egg size on mortality until fledging. One might predict the existence of an optimum level of resource investment in each offspring, but such a possible optimum may differ between clutches within a season in fluctuating environments (Fox & Csezak 2000; Rollinson &

Hutchings 2013). Hence, a female may adaptively adjust the egg size in correspondence with the expected temperatures during the season, but it may not always be possible to lay eggs of the "right" size since temperatures may fluctuate unpredictable. My study suggests that if a female laid small eggs, the temperatures should be high during the nestling stage for ensuring that the fledglings survived to the recruitment stage, whereas average-sized eggs in combination with high temperatures resulted in some, but fewer fledglings that survived until recruitment. The combination of large eggs and high temperatures during nestling stage increased the mortality until recruitment. However, large mean egg sizes decreased the mortality until recruitment when temperatures were low during nestling stage (Fig. 3). I have found no obvious adaptive explanation for the observed pattern that after the fledgling stage, it was disadvantageous to have been hatched from a large egg at high temperatures. However, egg size was negatively correlated with hatch date for broods ($r = -0.17$, $p = 0.01$) and temperature ($r = -0.14$, $p = 0.05$), which means that small eggs were laid more frequently under high temperatures later in the season. Hence, the observed result indicated that it probably existed underlying unmeasured factors that were correlated with egg sizes late in the season, which may explain the observed pattern.

Few studies have investigated the effect of egg size on mortality until recruitment (Krist 2011), and to my knowledge there are none that also take environmental conditions into account. However, if focusing only on the main effect of egg size, for example Amat, Fraga & Arroyo (2001b) studied the effect of intra-clutch variation of egg size on offspring survival in the Kentish plover, *Charadrius alexandrinus*, and found that large eggs produced heavy chicks that were recruited as adults more often than their siblings from smaller eggs in the same clutches. Dawson

& Clark (2000) found that recruitment probability increased with natal egg size in the lesser scaup, *Aythya affinis*. In accordance with my study, Both *et al*. (1998) found that offspring from large clutches of great tit, *Parus major,* recruited better than offspring from smaller clutches. That offspring from large clutches survive better than offspring from small clutches could be due to high-quality parents, managing to breed large clutches with offspring of high quality. Pettifor *et al.* (2001) tested the "individual optimization hypothesis" and found that the size of a clutch laid by a female great tit indicated the condition of the parents; birds that laid large clutches were "fitter" than birds laying small clutches.

The results also indicated that mean egg size influenced fledgling body mass. The interaction between mean egg size and temperature found in the highest ranked model regarding fledgling body mass suggested that large egg sizes contributed to higher body mass of fledglings that experienced high temperatures during the nestling stage (but there were uncertainties in the estimates) (Table 4). Thus, as high temperatures may increase the foraging opportunities, this may also enable chicks to allocate more resources to growth instead of to metabolic maintenance, which may demand more energy under cold conditions (Kovatch 2008). Tarsus length of fledglings was, however, primarily influenced by climatic conditions during the nestling stage. Other studies on the influence of egg size on fledgling body mass and tarsus length have provided varying results. For instance, Ferrari, Martinelli & Saino (2006) found a positive correlation between egg size and both body mass and tarsus length in barn swallow, *Hirundo rustica,* at day 12 after hatching, when the growth of these morphological traits is complete. Amundsen *et al*. (1996) found a positive effect of egg size on nestling tarsus length until the age of 12 days in the Antarctic petrel, *Thalassoica antarctica.* They also found a positive effect of egg size on nestling body mass at the age of three days, but not at later ages. Several studies have indeed found that egg size is most correlated with morphological traits during the early part of the nestling period, but not always until fledging stage (Williams 1994). For instance, in the European starling, *Sturnus vulgaris*, it was found that nestling body mass was positively related to mean egg mass until 7 days of age, but not later (Smith & Bruun 1998). In house wrens, *Troglodytes aedon,* Styrsky *et al.* (1999) found that in early-season broods, nestling body mass was correlated with egg size the first six days, but not later. The authors suggested the early disappearing correlation to be due to high food availability early in the season; due to high food provisioning, the initial effect of egg mass on nestling mass was lost as the nestlings aged. However, in late-season broods, nestling body mass was correlated with egg mass until nestlings achieved asymptotic mass, suggesting that decreased food resources late in the breeding season constrained the parent's ability to provision nestlings. Dawson & Clark (1996) found that body mass at any ages in ducklings of lesser scaup, *Aythya affinis,* was unrelated to egg size. In an experimental study, Killpack & Karasov (2012) investigated the growth and development in house sparrow nestlings in response to food restrictions, and found that chicks that had been fed with a 25 % reduced amount of food during the nestling period obtained a reduced body mass and body temperature. However, the skeletal growth was maintained, suggesting that the nestlings that had experienced food restrictions prioritized to allocate resources to structural growth by the energy-saving act of reducing the body mass and body temperature. This is in accordance with the results found in the present study, where I found stronger effects of mean egg size on fledgling body mass compared to fledgling tarsus length.

As mentioned previously, egg size has been found to affect several fitness-related traits. However, many of the conducted studies have been of an observational approach (Williams 1994, 2001). In an experimental study, Bolton (1991) found that parental quality was more important than egg size in determining offspring survival in the lesser black-backed gull, *Larus fuscus,* and he stressed the importance of conducting experimentally manipulations (in contrast to observational studies) in studies that investigate the effect of egg size, due to the possible confounding effect of female characteristics and parental care. Such a manipulation could be conducted by exchanging eggs between nests (cross-fostering), by manipulating egg size or by investigating within-brood effects of egg size (Williams 2001; Krist 2009). Several experimental studies have also found that egg size affects fitness related traits (e.g. Amat, Fraga & Arroyo 2001b; Ferrari, Martinelli & Saino 2006; Krist 2009). But; for instance, Magrath (1992) conducted a cross-fostering experiment in blackbirds, *Turdus merula,* and found that large egg sizes produced both heavier and larger nestlings, but had no effect on survival probability. He found no correlations of nestling body mass or size between nestlings and their foster parent's hatchlings early in the nestling period, but correlations were found later in the nestling period. Thus, he suggested that pre-hatching attributes of the egg affected nestling size early in the nestling period, but that environmental effects, such as parental quality and habitat quality, had an effect late in the nestling period. I suggest that future research on effects of egg size should, whenever possible, include an experimental design, as such studies are considered more valid than observational studies since they to a greater extent indicates causal mechanisms (Krist 2009).

In the present study, I have focused on the consequences of egg size and environmental conditions on offspring fitness. A potential parent-offspring conflict may reveal that the optimal egg size differs between mothers and offspring (Janzen & Warner 2009). As egg size has been found to be an inheritable trait in general (Christians 2002) as well as in the present population (Kvalnes *et al.* 2013), my results suggest that egg size should be adaptively adjusted in correspondence to the prevailing environmental conditions to maximize maternal fitness. In order to fully understand the adaptive significance of variation in egg sizes, one should look further into the fitness consequences seen from a maternal perspective of allocating resources into variation in egg size between broods, variation in egg size within broods and to clutch size, preferentially by using an experimental approach.

Conclusion

The present study found that mean variation in egg size among broods and variation in egg size within broods influenced fitness of offspring, measured as fledgling body mass and mortality until fledging and recruitment. Egg size had little influence on fledgling tarsus length, suggesting that allocation to structural growth may be prioritized over body mass. However, the fitness consequences of a given egg size and of the within- brood variation in egg size was dependent upon climatic conditions the individual had experienced during the nestling stage. The difference in performance between individuals from small and large eggs was most pronounced under poor climatic conditions, but my results also indicated that offspring from large eggs suffered a higher probability of mortality until recruitment stage if they experienced high temperatures during nestling stage. This suggests that there was no existence of a given optimum egg size applicable for all conditions, but that the optimum egg size differed in relation to environmental conditions.

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TABLES

Table 1. The highest ranked candidate models according to AICc criteria explaining variation in nestling mortality from hatching until the fledging stage in a house sparrow population in northern Norway. The highest ranked models with Δ AICc <2 relative to the highest ranked model are shown. The AICc value for the highest ranked model was 658.22. A model with only the intercept was ranked 121 among a total of 128 compared models, and the evidence ratio for the intercept model indicated that the highest ranked model was > 4.0 x 10^8 times more likely to be the best model compared to the model with only the intercept. All models were fitted with year as a random factor. ΔAICc is the difference in AICc value from the highest ranked model, *w* is the Akaike weight, while ER equals the evidence ratio for each model compared to the highest ranked model. Variables in the models are mean egg size (ES), temperature (T), precipitation (P), clutch size (CS) and coefficient of variation in egg size (CV). Interactions between variables are indicated by a colon.

Rank	**Model parameters**	**Δ AICc**	***w***	**ER**
1	ES + CV + T + P + ES:P	0	0.12	1.0
2	ES + T + P + ES:P	0.10	0.11	1.05
3	ES + CV + T + P + CV:P	0.42	0.10	1.23
4	CV + T + P + CV:P	1.35	0.06	1.97
5	ES + CV + T + P + CS + ES:P	1.87	0.04	2.55
6	ES + T + P + CS + ES:P	1.91	0.04	2.60

Table 2. The highest ranked model explaining fledgling mortality (see table 1) in a house sparrow population in northern Norway. Parameter estimates and confidence intervals are presented for each of the explanative variables. See Methods for further description.

Variable	**Estimate**	**95 % Confidence interval**	
		Lower limit	Upper limit
Intercept	-0.25	-0.35	-0.16
Mean egg size	-0.31	-0.72	0.09
CV egg size	3.40	-1.03	7.71
Temperature	-10.00	-0.14	-0.07
Precipitation	0.05	-0.03	0.12
Mean egg size:precipitation	- 0.39	-0.72	-0.06

Table 3. The highest ranked candidate models according to AICc criteria explaining variation in fledgling body mass in a house sparrow population in northern Norway. The highest ranked models with Δ AICc <2 relative to the highest ranked model are shown. The AICc value for the highest ranked model was 2168.20. A model with only the intercept was ranked 43 among a total of 128 compared models, and the evidence ratio for the intercept model indicated that the highest ranked model was 27 times more likely to be the best model compared to the model with only the intercept. All models were fitted with year, brood identity and mother identity as random factors. ΔAICc is the difference in AICc value from the highest ranked model, *w* is the Akaike weight, while ER equals the evidence ratio for each model compared to the highest ranked model. Variables in the models are brood number (BN), mean egg size (ES), temperature (T) and precipitation (P). Interactions between variables are indicated by a colon.

Rank	**Model parameters**	**Δ AICc**	***w***	**ER**
1	BN + ES + T + ES:T	0	0.11	1.0
2	BN + ES + T	0.51	0.08	1.29
3	BN + T	1.08	0.06	1.71

Table 4. The highest ranked model explaining fledgling body mass (see table 3) in a house sparrow population in northern Norway. Parameter estimates and confidence intervals are presented for each of the explanative variables. See Methods for further description.

Variable	**Estimate**	**95 % Confidence interval**	
		Lower limit	Upper limit
Intercept	25.82	25.07	26.56
Brood number 2	0.71	-0.47	1.92
Brood number 3	-2.86	-5.26	-0.56
Mean egg size	1.47	-0.88	3.87
Temperature	0.26	0.06	0.46
Mean egg size:temperature	0.69	-0.10	1.49

Table 5. The highest ranked candidate models according to AICc criteria explaining variation in fledgling tarsus in a house sparrow population in northern Norway. The highest ranked models with Δ AICc <2 relative to the highest ranked model are shown. The AICc value for the highest ranked model was 1284.54. A model with only the intercept was ranked 112 among a total of 128 compared models, and the evidence ratio for the intercept model indicated that the highest ranked model was 5 x 10^5 times more likely to be the best model compared to the model with only the intercept. All models were fitted with year, brood identity and mother identity as random factors. ΔAICc is the difference in AICc value from the highest ranked model, *w* is the Akaike weight, while ER equals the evidence ratio for each model compared to the highest ranked model. Variables in the models are brood number (BN), mean egg size (ES), temperature (T) and precipitation (P). Interactions between variables are indicated by a colon.

Rank	**Model parameters**	**Δ AICc**	***w***	**ER**
1	BN + T + P	0	0.16	1.0
2	BN + ES + T + P + ES:T	1.18	0.08	1.80
3	BN + ES + T + P	1.26	0.08	1.88

Table 6. The highest ranked model explaining fledgling tarsus (see table 5) in a house sparrow population in northern Norway. Parameter estimates and confidence intervals are presented for each of the explanative variables. See Methods for further description.

Variable	**Estimate**	**95 % Confidence interval**	
		Lower limit	Upper limit
Intercept	18.65	18.39	18.90
Brood number 2	0.04	- 0.36	0.46
Brood number 3	-1.14	- 1.94	- 0.37
Temperature	0.17	0.09	0.24
Precipitation	-0.16	- 0.34	0.00

Table 7. The highest ranked candidate models according to AICc criteria explaining variation in mortality from hatching until recruitment in a house sparrow population in northern Norway. The highest ranked models with Δ AICc <2 relative to the highest ranked model are shown. The AICc value for the highest ranked model was 247.89. A model with only the intercept was ranked 82 among a total of 128 compared models, and the evidence ratio for the intercept model indicated that the highest ranked model was 28 times more likely to be the best model compared to the model with only the intercept. All models were fitted with year as a random factor. ΔAICc is the difference in AICc value from the highest ranked model, *w* is the Akaike weight, while ER equals the evidence ratio for each model compared to the highest ranked model. Variables in the models are brood number (BN), mean egg size (ES), temperature (T), precipitation (P), clutch size (CS) and coefficient of variation in egg size (CV). Interactions between variables are indicated by a colon.

Rank	**Model parameters**	**Δ AICc**	***w***	**ER**
1	BN + CS + ES + T + ES:T	0	0.05	1.00
2	BN + CS + T	0.05	0.05	1.02
3	CS + ES + T + ES:T	0.24	0.05	1.13
4	CS + T	0.52	0.04	1.30
5	BN + CS	0.89	0.03	1.56
6	BN + CS + P	1.52	0.02	2.14
7	BN + CS + ES + T + P + ES:T	1.56	0.02	2.18
8	BN + CS + CV + T	1.58	0.02	2.20
9	BN + CS + T + P	1.63	0.02	2.26
10	CS + CV + ES + T + ES:T	1.69	0.02	2.33
11	BN + CS + CV + ES + T + ES:T	1.72	0.02	2.37
12	CS + CV + T	1.78	0.02	2.43

Table 8. The highest ranked model explaining mortality from hatching until recruitment (see Table 7) in a house sparrow population in northern Norway. Parameter estimates and confidence intervals are presented for each of the explanative variables. See Methods for further description.

Variable	**Estimate**	**95 % Confidence interval**	
		Lower limit	Upper limit
Intercept	1.16	1.01	1.31
Brood number 2	-0.21	-0.45	0.02
Brood number 3	0.22	-0.34	0.86
Clutch size	-0.14	-0.27	-0.01
Mean egg size	-0.11	-0.55	0.31
Temperature	-0.03	-0.07	0.10
Mean egg size:temperature	0.16	0.00	0.32

FIGURES

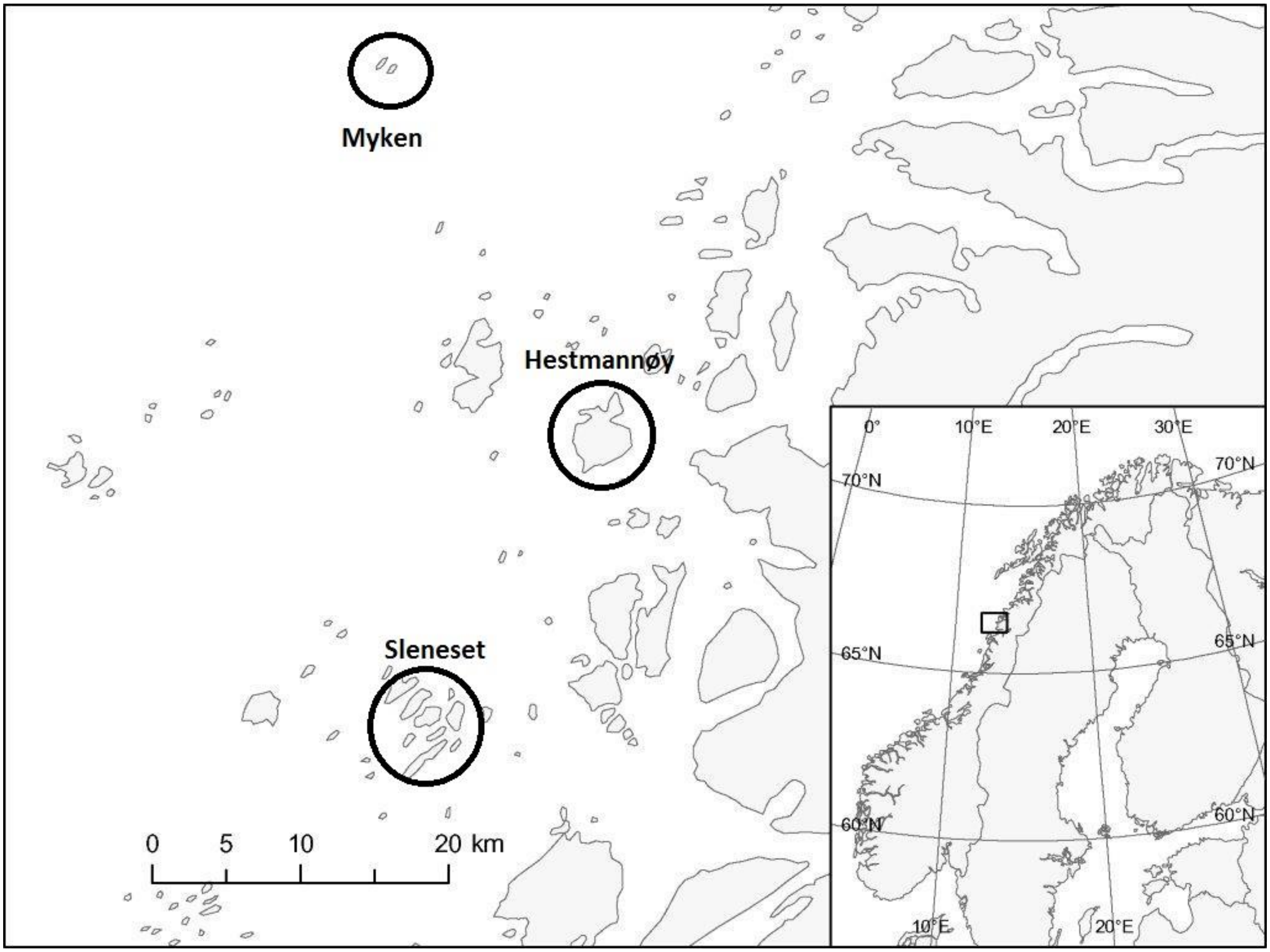

Fig. 1. The study area, located in an archipelago off the coast of northern Norway. The study island Hestmannøy, and Myken and Sleneset, in where the weather stations are located, are encircled.

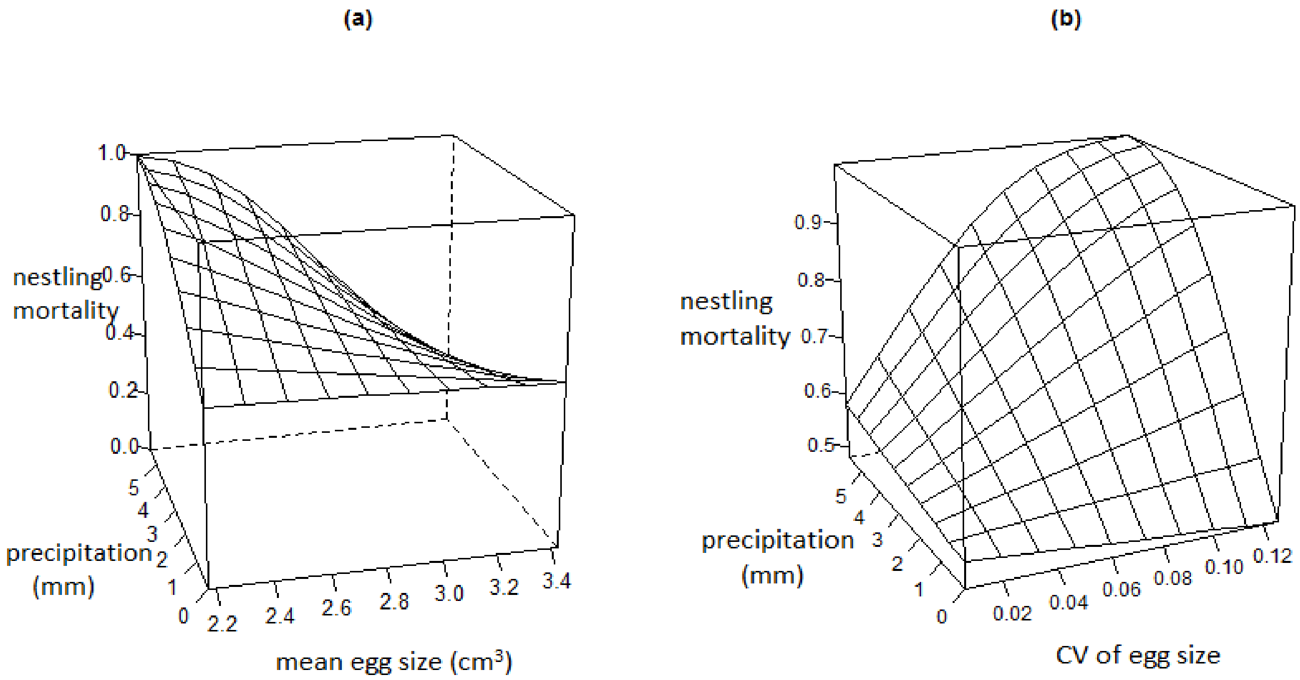

Fig. 2. The effect of the interaction between precipitation and (a) mean egg size (cm^3) (as found in model 1; Table 1) and (b) CV of egg size (as found in model 3; Table 1) on nestling mortality in a house sparrow population (*Passer domesticus)* in northern Norway.

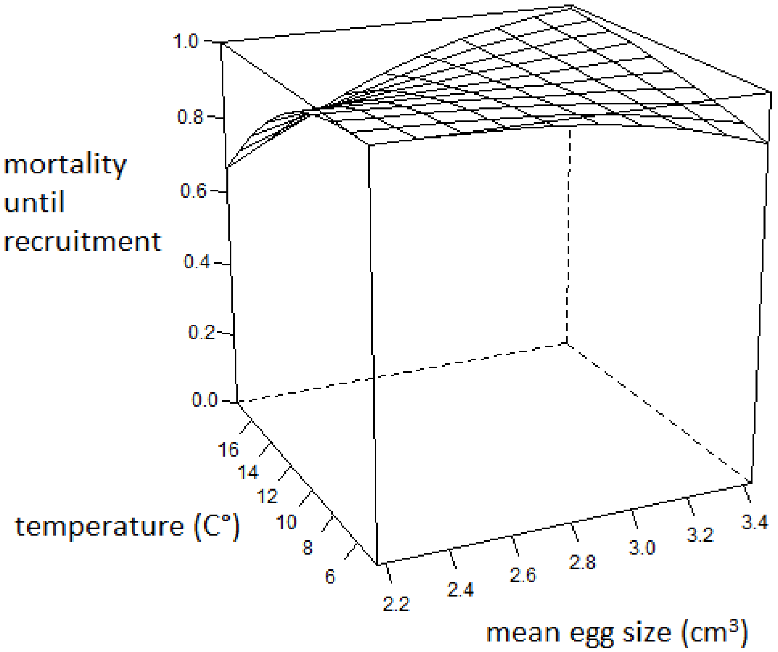

Fig. 3. The effect of the interaction between temperature (C°) and mean egg size (cm^3) on mortality until recruitment in a house sparrow *(Passer domesticus)* population in northern Norway (as found in model 1; Table 8).

APPENDIX

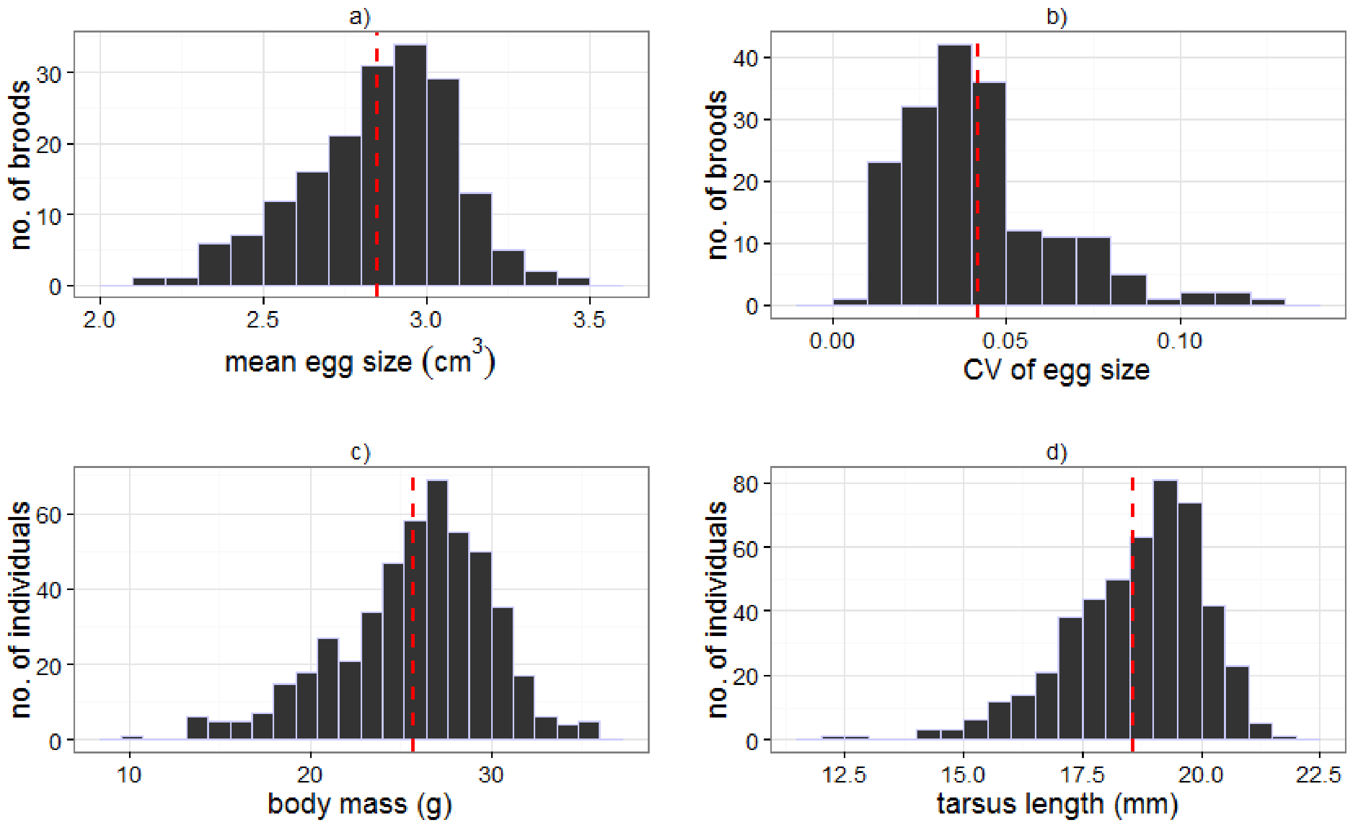

Fig. 1. The distribution of a**)** mean egg size among broods (cm^3), b) CV of egg size within broods, c) fledgling body mass (g) and d) fledgling tarsus (mm) in a house sparrow (*Passer domesticus*) population at Hestmannøy, Norway between the years 2003 and 2009. The population mean is indicated by the dashed line.