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Effects of Variation in Egg Size on Maternal Fitness in a Population of House Sparrows (*Passer domesticus*)

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Abstract

According to life history theory individuals will optimize investment into growth, reproduction and self-maintenance. Egg size is an important life history trait predicted to have an optimum that maximizes maternal individual fitness. Bet-hedging theory suggests that natural selection in addition to act on the mean of egg size also will act on the variance of egg size. Studies in several taxa have demonstrated a great variation where some studies have found evidence for an optimum egg size but others not. In a metapopulation of house sparrows (*Passer domesticus*) in northern Norway this study aimed to investigate the effects of variation in egg size on maternal individual fitness. Maternal individual fitness was defines as the sum of annual survival and half the number of recruits produced.

The most central findings revealed i) no effect of mean egg size on short- and long term production of offspring, maternal survival and maternal individual fitness. ii) There was a positive effect of temperature during nestling period and a positive effect of within brood variation in egg size on fledgling production, but not on long-term recruit production. Finally, iii) an effect of maternal mass on recruit production, maternal survival and maternal individual fitness, depending on the number of broods laid.

This study highlight the importance of taking maternal ecology in to account, and calls for further investigation of the effect of maternal quality including body mass and the investment in the number of broods laid and how this affects maternal fitness.

Sammendrag

I følge livshistorieteori vil individer optimalisere investeringen i vekst, reproduksjon og selvvedlikehold. Eggstørrelse er et viktig livshistorietrekk som er predikert å ha et optimum som maksimerer mors individuelle fitness. Bet-hedgingteori foreslår at naturlig seleksjon i tillegg til å virke på gjennomsnittet av eggstørrelse også vil virke på variansen av eggstørrelse. Studier på flere arter har vist en stor variasjon der noen studier har funnet bevis for optimal eggstørrelse, mens andre ikke. I en metapopulasjon av gråspurv (*Passer domesticus*) i Nord-Norge tok denne studien sikte på å undersøke effekten av variasjon i eggstørrelse på mors individuelle fitness. Mors individuelle fitness ble definert som summen av årlig overlevelse og halvparten av antall rekrutter produsert.

De mest sentrale funnene viste i) ingen effekt av gjennomsnittlig eggstørrelse på kort- og langsiktig produksjon av avkom, mors overlevelse og mors individuell fitness. ii) Det var en positiv effekt av temperaturen under reirperioden og en positiv effekt av innenkullvariasjon i eggstørrelse på produksjon av flygeferdige unger, men ikke på langsiktig produksjon av rekrutter. Til slutt, iii) en effekt av mors kroppsmasse på både rekruttproduksjon, mors overlevelse og mors individuelle fitness, som var avhengig av antall kull mor la.

Denne studien understreker viktigheten av å ta høyde for mors økologi, og viser behovet for videre undersøkelse av effekten av mors kvalitet, inkludert kroppsmasse og investeringen i antall kull som legges og hvordan dette påvirker mors fitness.

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Introduction

In nature, individuals have finite quantities of resources available which must be allocated between growth, reproduction and maintenance, and such compromises may lead to trade-offs between closely related life history traits (Roff, 2002; Smith & Fretwell, 1974; Stearns & Stearns, 1989; van Noordwijk & de Jong, 1986). One widely studied trade-off is the one between number and size of offspring (Fox & Czesak, 2000). Life history theory suggests that there exist an intermediate optimum for the size and number of offspring which maximizes parental fitness (Lack, 1947; McGinley, Temme, & Geber, 1987; Smith & Fretwell, 1974). In empirical studies, there are evidence for optimal size of offspring and clutches with respect to maternal fitness from studies of fish (Rollinson & Hutchings, 2013), snakes (Ji, Du, Qu, & Lin, 2009), arthropods (Fox & Czesak, 2000), birds (Kontiainen, Brommer, Karell, & Pietiäinen, 2008; Pettifor, Perrins, & McCleery, 2001), and turtles (Janzen & Warner, 2009). Also, studies have shown that the optimal offspring size might change with environmental conditions (Kontiainen et al., 2008; Rollinson & Hutchings, 2013; Wilson, Pemberton, Pilkington, Clutton-Brock, & Kruuk, 2009). For instance, Rollinson and Hutchings (2013) found that in poor environments the optimal investment per offspring increased in atlantic salmon (*Salmo salar*), while Wilson et al. (2009) found that increased birth weight was selected for when soay sheep (*Ovis aries*) faced harsh environmental conditions. Furthermore, ural owls (*Strix uralensis*) adjust their egg sizes according to the fluctuating food availability created by the vole cycle (Kontiainen et al., 2008).

Nonetheless, many studies have failed to find evidence for a trade-off between offspring size and number (Bernardo, 1996; van Noordwijk & de Jong, 1986). One possibility is that the trade-off is masked by a large variation in quality between individuals and thus large variation in their total investment (van Noordwijk & de Jong, 1986). Then, despite an underlying trade-off, positive covariance between life-history traits is possible if the variation in allocation

between life-history traits is low (van Noordwijk & de Jong, 1986). Bernardo (1996) argues that since offspring size can be seen as a joint phenotype of the offspring and its mother, the ecology of mothers should be taken in to account in studies of offspring size. The females' body mass might for instance reflect the amount of resources carried by the female (Gosler, Greenwood, Baker, & Davidson, 1998), which may relate to her quality. Hendry, Day, and Cooper (2001) incorporated effects of maternal size into the quality of the incubation environment for sockeye salmon (*Oncorhynchus nerka*) eggs in their optimality model and showed that both the optimal egg size and egg number with respect to maternal fitness may change with differences in maternal size. Lifjeld, Johnsen, and Petitguyot (2005) found that there was an increase in egg size with laying order for first clutches in the bluethroat (*Luscinia s. svecica*), but also significantly larger egg sizes for females in good condition as opposed to those in poor condition. Pettifor et al. (2001) conducted a brood manipulation experiment in great tits where they found that the optimal clutch size of a female (in terms of number of recruits produced) was her originally chosen clutch size, which they suggested was influenced by the condition of the female.

Support for a trade-off between size and number of offspring, and the existence of optimal sizes and numbers of offspring that maximizes parental fitness, has in particular been found in birds (Kontiainen et al., 2008; Lack, 1947; Lifjeld et al., 2005; Pettifor et al., 2001). For instance, Lack (1947) early showed that more offspring were produced by intermediate clutch sizes than by the largest clutch sizes, and suggested an optimum clutch size from a maternal perspective. More recently, Kvalnes, Ringsby, Jensen, and Sæther (2013) found a curvilinear concave relationship between size and number of eggs in house sparrows. This relationship included smaller egg sizes for clutch sizes both below and above the average, where they suggest that the latter reflected a trade-off between size and number of eggs above the median clutch size (Kvalnes et al., 2013). Since the number of surviving offspring is essential for

maternal fitness, factors affecting offspring survival is also likely to affect maternal fitness. A meta-study by Krist (2011) on the relationship between egg size and offspring quality found that there is generally a positive relationship between egg size and hatching success, chick survival and growth rate in empirical studies on birds. However, Kvalnes et al. (in press) showed that long term offspring mortality was affected by egg size, and that the optimal egg size regarding offspring fitness was a function of the environmental conditions (i.e. temperature and precipitation) during the nestling period. Thus, egg size might be affecting maternal fitness through fecundity in birds and other oviparous animals.

In variable and unpredictable environments, natural selection may act on both the mean and the variance of offspring size, and thus, uniformly sized offspring might not be the optimal strategy (Marshall, Bonduriansky, & Bussière, 2008; Olofsson, Ripa, & Jonzn, 2009; Sæther & Engen, 2015). Bet-hedging theory suggests that individuals should lower their variance in fitness among years in order to maximize fitness through lifetime (Marshall et al., 2008; Olofsson et al., 2009; Sæther & Engen, 2015). In such cases, arithmetic mean fitness could be reduced to gain less variation in maternal fitness between years, i.e. to reduce the impact of extreme events or unfavorable years (Marshall et al., 2008; Olofsson et al., 2009; Sæther & Engen, 2015). Three bet-hedging strategies involving production of variable sized offspring may be identified: conservative and diversified bet-hedging, and adaptive coin-flipping (Marshall et al., 2008; Olofsson et al., 2009; Sæther & Engen, 2015). The first involves always using the same, low-risk strategy with constant sized offspring, while the second is a "don't put all eggs in one basket- strategy" where several offspring sizes are included in the same brood, resulting in low variation in fitness over time (Marshall et al., 2008; Olofsson et al., 2009; Sæther & Engen, 2015). The third strategy will involve "flipping a coin" each breeding season and the probability of a given offspring size evolves to match the probability of the corresponding environmental conditions where the given size is optimal (Olofsson et

al., 2009). Olofsson et al. (2009) suggested that the optimal strategy for offspring size is a combination of all these three.

In an insular population of house sparrows *Passer domesticus* at the coast of Helgeland in northern Norway high-quality data on individual life history has been collected over several years by monitoring of nests, nestlings and parents (Jensen et al., 2004; Kvalnes et al., 2013; Pärn, Jensen, Ringsby, & Sæther, 2009; Ringsby, Sæther, & Solberg, 1998). Data on clutch sizes and egg sizes has also been collected (Kvalnes et al., 2013). This offers a unique opportunity to study viability and fecundity in this population.

In this study, I will investigate how variation in egg size affects individual fitness of mothers. First, I will investigate the relationship between number of offspring (i.e. fledglings and recruits) in each brood and the mean and coefficient of variation in egg size. Second, I will investigate whether the mother's survival and her production of recruits can be explained by the mean or coefficient of variation in egg size. Based on life history theory, I expect that there will be an optimum egg size with respect to maternal individual fitness, since egg size is likely to affect offspring quality and survival (Krist, 2011). This optimum might not be the same as the optimum egg size in terms of offspring fitness (e.g. Janzen and Warner (2009)). I also expect the optimum egg size to interact with clutch size (Kvalnes et al., 2013; Lack, 1947; Smith & Fretwell, 1974) and depend on variation in climatic conditions during the breeding season (e.g. Kvalnes et al. (in press)) and between breeding seasons due to environmental stochasticity (Bernardo, 1996; Kontiainen et al., 2008; Sæther & Engen, 2015).

Material and methods

Study system

This study is part of a long term study system at Helgeland in northern Norway, where 18

insular populations of house sparrows (*Passer domesticus*) have been studied since 1993 (for

a map of the study system, see Pärn, Ringsby, Jensen, and Sæther (2012)). The data in the

present study were collected in the population on the island Hestmannøy (66.537°N,

12.840°E) from 2003 to 2009. An island with scattered human settlements and several dairy

farms. The breeding season in this population last from May until mid-August and the nests

are typically located in cracks and cavities inside barns and cowsheds (Ringsby et al., 1998).

A few nest boxes have also been made available around the settlements and inside barns.

During the breeding season, house sparrows in this population lay 1-3 broods with 3-8 eggs in

each brood (Kvalnes et al., 2013; in press). The house sparrow is a non-migratory passerine

bird, widespread in both agricultural and urban communities (Anderson, 2006). It has a highly

social behaviour including flock foraging, semicolonial breeding and social monogamy, and

has high site fidelity and high nest site fidelity within years (Anderson, 2006; Kvalnes et al.,

2013; Pärn et al., 2009; Ringsby et al., 1998).

Data collection

Active nests with eggs or nestlings were found by thoroughly searching the breeding sites on

the island at least once a week during the breeding season. Follow-up visits were then made

two or three times during egg laying and incubation and one to three times during the nestling

period. A custom designed software were used to estimate egg sizes from standardized

photographs made during the incubation period from completed clutches (for details, see

Kvalnes et al. (2013) and Kvalnes et al. (in press)). The same camera, focal length and picture

quality was used for all photos and egg size was estimated as egg volume to the nearest 0.01

mm^3. Within each clutch, the mean egg size and coefficient of variation in egg size (CV egg

size) was calculated. The CV was calculated by dividing the variance in egg size by the mean. Clutch sizes were estimated as the maximum number of eggs recorded in a clutch, while clutch number was assigned based on a combination of both nest history and information about the mothers' identity and her reproductive performance during the season. Nevertheless, 24 and 10 broods were laid outside the expected intervals for lay date for first and second broods, which were set to respectively 35 and 70 (35 + 35) days after five percent of the first broods were laid (Kvalnes et al., 2013). These mothers very likely had an earlier unknown brood. In the first case, 1 was added to all broods of the current mothers, while for the second case only the second (and eventual third) brood was added 1 given that the first registered brood was within the expected time span. Number of broods laid by a mother each year was estimated as the number of recorded broods. Nestling age was estimated based on the size of the nestling, emergence of the remiges (flying feathers) and development of body-feathers, or observed directly during a nest visit. Number of fledglings (i.e. surviving nestlings until the fledgling stage) was estimated as the number of nestlings recorded in the nests at age 8-13 days.

Throughout the breeding season and for one-two weeks during the autumn (around September-October) adults and juveniles were caught using mist nets close to feeding stations or breeding sites. Captured birds were handled with caution and kept in hanging cloth bags for only a short amount of time before they were sampled for 25 μL blood, and body mass carefully measured. Maternal body mass was measured to the nearest 0.1 g using a Pesola spring balance, and can according to Gosler, Greenwood, and Perrins (1995) and Gosler et al. (1998) be used as an indicator for the fat reserves stored by the female. However, since most birds on average was measured once a year and twice during their life span average values of body mass were calculated to reduce variation due to measurement error (Kvalnes et al., 2013). To reduce the variation due to seasonal fluctuations in maternal body mass, only

values from the summer (May – August) were included in the calculations. Thus, mass is an estimate for individual "long-term" mass, but still includes some variance due to variation in time of measurement both on a seasonal and a daily basis (Kvalnes et al., 2013). The blood sample drawn from the brachial vein of all captured individuals enabled us to determine mother identity for all hatched clutches by genetic parenthood analyses of the nestlings in hatched broods. Genetic parenthood analyses and construction of a genetic pedigree of the population were based on genotyping of all sampled individuals on 14 polymorphic microsatellite loci (Billing et al., 2012; Jensen, Steinsland, Ringsby, & Sæther, 2008). Further details on procedures are given in Billing et al. (2012). Because of the high nest fidelity of house sparrows in this population, unhatched broods were assigned to the same mother as hatched broods within a nest site and breeding season (for details see, Kvalnes et al. (2013); Kvalnes et al. (in press)).

Before carefully released, all fledglings and unmarked captured individuals were given a numbered aluminum ring from Stavanger Museum (Norway) and three plastic colour rings in a unique combination. Thus, the identity of marked individuals could be determined by re-captures or sighting using binoculars. An individual had survived or recruited if recorded in the breeding season the following year. Maternal individual fitness was estimated as the sum of annual survival (S) and half the number of recruits (B) produced ($W_i = S_i + B_i/2$, for an individual i, Sæther and Engen (2015)). The division by two accounts for the paternal contribution with sexual reproduction. Age determination of individuals was based on plumage, but after the post-juvenile and post-breeding moult adults and juveniles have identical plumages. However, a large proportion (>90%) of the adults in the study population are marked (Kvalnes et al., 2013). Thus, unmarked individuals with adult-like plumage captured in the autumn were assumed to be juveniles, while those caught in the breeding season were assumed to be adults hatched in the previous year.

Data on average daily temperature and precipitation was available from a weather station ran by the Norwegian Meterological Institute at the island of Myken located approximately 30 km north-west of Hestmannøy. However, for shorter periods some values at Myken were missing, in which data from the weather station at the island Sleneset, approximately 20 km south of the study island, was included. The temporal variation in temperature and precipitation at the two weather stations has been found to be highly correlated (Ringsby, Sæther, Tufto, Jensen, & Solberg, 2002). The first five days after hatching are considered a critical period for nestlings as they lack thermoregulatory abilities and suffer high risk of mortality (Anderson, 2006). Accordingly, mean temperature and precipitation experienced at daytime for each brood during this period were estimated and used as indicators of weather conditions. These variables are henceforth named temperature and precipitation. Precipitation may especially be important to nestlings as it is likely to affect the feeding frequency of their parents (Öberg et al., 2015).

Statistical analyses

Models in all statistical analyses were fitted using the Statistical Software R, version 3.4.3 (R Development Core Team, 2011) with the packages lm4 (Bates, Mächler, Bolker, & Walker, 2015) and glmmTMB (Brooks et al., 2017). In total, data on egg size from 128 broods and data on number of recruits and survival from 81 female sparrows were available for analysis. Based on the study objectives I carried out four series of analyses with the following response variables: (1) number of fledglings from each brood, (2) number of recruits produced by mothers per year, (3) annual maternal survival and (4) maternal individual fitness. To avoid problems with multicollinearity (Graham, 2003), the relationships between explanatory variables were investigated both visually through pairwise scatterplots and by calculation of Pearson correlation coefficients (r). This ensured low ($r < 0.5$) correlations between all explanatory variables in each analysis. For all analyses maternal age was a categorical

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variable separating between one year olds (age 1) and older birds (age 2 or older). These to age classes were used since I expected a difference in fecundity between first year breeders and those older (Anderson, 2006; Geslin, Questiau, & Eybert, 2004; Kvalnes et al., 2017).

Factors affecting number of fledglings produced

In the analyses of the number of fledglings produced I fitted generalized linear mixed models with Poisson distribution and a log-link function. In addition to mean egg size, CV egg size and clutch size the following explanative variables were included: clutch number (categorical), temperature, precipitation, and body mass of the mother. Age of the mother was included as a categorical fixed effect in all models to account for age related variation in number of fledglings produced (Anderson, 2006; Engen, Lande, & Sæther, 2011; Kvalnes et al., 2017). A random intercept for mother identity was included to account for any dependency between broods by the same mother. For temperature, maternal mass, egg size and clutch size I hypothesized that there could be an optimum in accordance with optimality theory (e.g. Kontiainen et al. (2008); Kvalnes et al. (2017); (in press); Lack (1947)), hence second degree polynomials were included for these explanatory variables. To test the hypothesis that the effect of mean egg size and CV egg size on number of fledglings produced by the mother might depend on weather conditions, I included the interactions between CV egg size and temperature, CV egg size and precipitation, mean egg size and temperature and mean egg size and precipitation. The interaction between clutch size and precipitation was fitted to test the hypothesis that the effect of clutch size on number of fledglings produced might be dependent on the amount of precipitation during early nestling stage. To test the hypothesis that maternal quality (measured as body mass) combined with mean egg size and clutch size might influence the number of fledglings produced, I included both the interaction between body mass and mean egg size and body mass and clutch size, respectively.

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Factors affecting number of recruits produced, maternal survival and individual fitness

The mothers' annual survival was fitted using generalized linear mixed models with a binomial distribution and a logit-link function, while number of recruits per mother per year and maternal individual fitness were fitted using a Poisson distribution with a log-link function. To get a response which included only integers and allow the use of Poisson distribution, individual fitness was doubled (Wx2) in the analysis. I included an offset of ln 2 and weights of ½ to account for the doubling and get the correct estimates and standard errors for maternal individual fitness (W). The following explanatory variables were included in the analyses: CV egg size, mean egg size, body mass of the mother, number of broods and clutch size. Age of the mother was included as a categorical fixed effect in all models of recruits and individual fitness to account for age related variation in fecundity (Anderson, 2006; Engen et al., 2011; Kvalnes et al., 2017). For maternal mass, mean egg size and clutch size I hypothesized that there could be an optimum in accordance with optimality theory, hence second degree polynomials were included for these explanatory variables. To account for the non-independency of samples within the same mothers and years random intercepts for mother identity and year were included in the analyses of number of recruits produced. In the analysis of survival and maternal fitness, random intercepts for year were included to account for any dependency of samples within years. Interactions between mean egg size and body mass, clutch size and body mass, and number of broods and body mass were fitted to test the hypothesis that the effects of mean egg size, clutch size and number of broods on number of recruits produced and maternal fitness might depend on maternal quality through body mass. In addition, the interaction between mean egg size and clutch size was fitted to test the hypothesis that the effect of egg size on the survival of the mother might depend on clutch size.

Model comparisons

The analyses were based on an information theoretic approach using Akaike Information Criteria adjusted for small sample sizes, where candidate models considered to be biologically relevant to theory and current knowledge in the research field were ranked according to AICc (Akaike, 2011; Burnham, 2002). I also calculated delta AICc, Aikake weights (*w*), and evidence ratios (*ER*) relative to the highest ranked model to evaluate the support of each model. Models with delta AICc < 2 were considered to have substantial support in the data. The principle of parsimony and an assessment of the uncertainty of parameters were used to evaluate the support for effects included in the highly supported models. To minimize convergence problems all continuous explanation variables were centered by their grand mean, maternal mass was scaled by dividing by 10, and egg size was scaled by dividing by 1000 to get the measures in cm^3. In order to moderate the number and complexity of considered models in relation to the sample size in the study, I restricted the fitted models to only contain one interaction at a time, and only constructed models with a maximum of seven parameters. Interactions and second degree polynomials were not present in models without the first degree parameters present. Estimated parameters are given with 95% confidence intervals (CI = [lower, upper]) and ± 1 standard error, and mean values are given with ± 1 standard error.

Results

For the data set with number of recruits and survival on maternal level, the population mean egg size across mothers was 2.834 ± 0.021 cm^3 (n = 81) with a range of $2.240 - 3.265$ cm^3, and the population mean CV egg size within mothers was 0.041 ± 0.002 with a range of $0.010 - 0.087$ (n = 81).

Number of fledglings produced

The number of fledglings produced from each brood decreased with increased CV egg size and was positively related to temperature (Tables 1 and 2, and Fig.1a and 1b, respectively). However, there was no support for a linear or quadratic effect of mean egg size on the production of fledglings (model ranked 11: $b_E = -0.136 \pm 0.265$, CI$_E$ = [-0.655 , 0.384], ΔAICc = 2.15, $w = 0.010$, $ER = 3.00$, model ranked 34: $b_E^2 = -0.940 \pm 0.899$, CI$_E^2$ =[-2.702 , 0.822], ΔAICc = 3.36, $w = 0.006$, $ER = 5.00$). The negative effect of CV egg size was present in all the 10 highly ranked models (Table 1), while the positive effect of temperature was present in six out of 10 models (Table 1). The most parsimonious model was ranked 3 (Table 1), whereas the two higher-ranked models both included an uncertain negative effect of precipitation (Table 1, model 1: $b_P = -0.066 \pm 0.059$, CI$_P$ = [-0.181 , 0.050], model 2: $b_P = -0.083 \pm 0.057$, CI$_P$ = [-0.195 , 0.029]). Additionally, the highest-ranked model indicated an uncertain negative interaction between precipitation and clutch size ($b_{P \times CS} = -0.145 \pm 0.074$, CI$_{CS \times P}$ = [-0.290 , 0.001]). This interaction suggests that the negative effect of precipitation tended to be more pronounced for large clutch sizes. A positive effect of clutch size on fledgling production was present in six of the highly ranked models, but the effect was uncertain (e.g. model rank 1: $b_{CS} = 0.034 \pm 0.076$, CI$_{CS}$ = [-0.115 , 0.183]).

Number of recruits produced

The number of recruits produced by mothers per year increased in a non-linear way with increased maternal mass (Tables 3 and 4). The results suggested an optimum in maternal mass shifting from heavy to light mothers with increased number of broods laid (Fig.2a). There was low support for a linear or quadratic effect of mean egg size on the production of recruits (model ranked 4: $b_E = 0.011\pm0.653$, $CI_E = [-1.268 , 1.290]$, $\Delta AICc = 2.39$, $w = 0.078$, $ER = 3.31$, model ranked 10: $b_E^2 = 1.030\pm2.366$, $CI_E^2 = [-3.608 , 5.668]$, $\Delta AICc = 4.65$, $w = 0.025$, $ER = 10.32$), nor for a linear effect of CV egg size (model ranked 3: $b_{CV} = -1.848\pm9.713$, $CI_{CV} = [-20.884 , 17.188]$, $\Delta AICc = 2.35$, $w = 0.080$, $ER = 3.23$). The most parsimonious model was ranked 1 (Table 3), whereas the other highly ranked model additionally included an uncertain positive effect of clutch size (Table 3, model 2: $b_{CS} = 0.274\pm0.235$, $CI_{CS} = [-0.186 , 0.735]$). This effect suggests increased number of recruits produced with increased clutch size.

Maternal survival

The probability that the mother survived to next year increased with increased body mass for mothers that only had one brood, increased slightly with increased body mass for mothers with two broods and decreased with increased body mass for mothers with three broods (Tables 5 and 6, and Fig.2b). There was low support for a linear effect of clutch size on maternal survival (model ranked 4: $b_{CS} = 0.113\pm0.306$, $CI_{CS} = [-0.487 , 0.712]$, $\Delta AICc = 2.11$, $w = 0.033$, $ER = 2.85$). The interaction effect of body mass and number of broods were present in the all the three highly ranked models (Table 5). The most parsimonious model was ranked 1 (Table 5), whereas one of the other highly ranked model additionally included an uncertain trend for a decrease in survival for increased mean egg size (Table 5, model 2: $b_E = -1.158\pm0.961$, $CI_E = [-3.040 , 0.725]$), and one included an uncertain quadratic effect of mean egg size on survival (Table 5, model 3: $b_E^2 = 4.348\pm3.717$, $CI_E^2 = [-2.937 , 11.633]$).

Maternal fitness

Maternal individual fitness increased with increased body mass for mothers that only had one brood, was almost independent of body mass for mothers with two broods, and decreased with increased body mass for mothers with three broods (Tables 7 and 8, and Fig.2c). There was no support for a linear or quadratic effect of mean egg size (model ranked 5: b_E = -0.210±0.502, CI_E^2 = [-1.194 , 0.774], ΔAICc = 2.12, weight = 0.037, ER = 2.86, model ranked 12: b_E^2 = 1.661±1.575, CI_E^2 = [-1.426 , 4.749], ΔAICc = 3.41, w = 0.019, ER = 5.58), and a linear effect of CV egg size (model ranked 6: b_{CV} = -1.252±6.494, CI_{CV} = [-13.981 , 11.476], ΔAICc = 2.25, weight = 0.034, ER = 3.12). The interaction effect between body mass and number of broods were present in all three highly ranked models (Table 7). The most parsimonious model was ranked 1 (Table 7), whereas one of the other highly ranked models included an uncertain positive effect of clutch size (Table 7, model 3: b_{CS} = 0.106±0.165, CI_{CS} = [-0.217 , 0.429]). This suggests increased individual fitness with increased clutch size. Additionally, a third highly ranked model included an uncertain quadratic effect of body mass on individual fitness (Table 7, model 2: b_M^2 = -1.554±1.304, CI_M^2 = [-4.110 , 1.003]), suggesting an optimum in maternal body mass shifting from heavy to light mothers with increased number of broods laid.

Discussion

The present study on a wild oviparous vertebrate did not find evidence for an effect of egg size (mean or CV) on maternal individual fitness. However, annual survival, annual production of recruits, and the maternal fitness seemed to be affected by a combination of the mothers' body mass and the number of broods laid (Tables 3, 5 and 7). Heavy mothers performed better than lighter mothers with equal number of broods when laying only one brood, while the opposite held for mothers laying three broods (Fig. 2). With respect to the number of fledglings produced, there was a decrease with increased within brood variation in egg size (CV) and an increase with increased temperatures (Tables 1 and 2, Fig. 1).

In this study I found no evidence for a linear or quadratic effect of egg size and clutch size on short or long term offspring production, maternal survival and maternal individual fitness. However, uncertain negative effects of egg size were present in two of the highly ranked models in the analysis of maternal survival (Table 5), both consistent with a potential cost of increased investment in average egg size (Bowers, Sakaluk, & Thompson, 2012; Nager, Monaghan, & Houston, 2001; Williams, 2005). The lack of an optimal egg size and an optimal clutch size maximizing maternal individual fitness are congruent with several other similar results from other studies on different taxa (Bernardo, 1996; van Noordwijk & de Jong, 1986). As optimality theory predicts that maternal fitness most likely is the unit maximized by selection (Lack, 1947; McGinley et al., 1987; Smith & Fretwell, 1974), a natural prediction would be the existence of an optimal egg size and clutch size in terms of maternal fitness. The result in the present study is contrary to this prediction. Two explanations might be: 1) that a possible trade-off between size and number of offspring is masked by differences in individual quality or allocation between mothers (Fox & Czesak, 2000; van Noordwijk & de Jong, 1986), or 3) that selection on egg size is low due to a high quality environment (Fox & Czesak, 2000; Rollinson & Hutchings, 2013). In the present

study I controlled for the effect of quality differences between mothers by including maternal mass as an explanatory variable without discovering any significant effect. However, it may be that other maternal traits or a combination of traits would better reflect maternal quality than maternal body mass, such as food provision rate or bill depth as Ringsby, Berge, Saether, and Jensen (2009) found a positive effect of these phenotypic traits on fledglings success. The results in the present study also revealed a positive, but non-significant effect of clutch size on which was present in six of the highly ranked models in the fledgling analysis (Table 1), in addition to some of the highly ranked models in the analysis of recruit production and maternal survival (Table 3, Table 7). Accordingly, mothers laying larger broods were possibly in better condition than birds laying small broods (Pettifor et al., 2001), as their clutch sizes may indicate individual optima which reflects their level of resource acquirement. Low selection on egg size is unlikely in the present study considered the findings of Ringsby et al. (1998) where juvenile survival is highly dependent on size and condition of the fledglings, and the findings of a general positive relationship between egg size and growth-rate in birds (Krist, 2011). In addition, for this population of house sparrows in particular, a previous study have found that egg size was curvilinear related to the temperature two weeks prior to start of egg laying, indicating adaption to environmental conditions (Kvalnes et al., 2013). Besides, a previous study has shown that survival of the offspring in this population was a function of egg size and environmental conditions (Kvalnes et al., in press), but the present study shows no such effect on maternal fitness.

Environmental effect, such as temperature and precipitation, on both short- and long term offspring production were expected to be present from previously studies (Kvalnes et al., in press; Öberg et al., 2015). However, the present study only found such environmental effects on short term production of fledglings, but not on the long term production of recruits. This is consistent with findings from Ringsby et al. (2002) where survival of nestlings until

fledglings stage were highly dependent on weather conditions, while survival until recruitment were more affected by seasonal effects, measured as the seasonal day-number. Increased number of fledglings produced with increased temperatures (Fig. 1b) might indicate that offspring spend less energy on thermoregulation at higher temperatures (Seel, 1969). This is also supported by the earlier findings where offspring mortality until fledgling was reduced with increased temperatures and reduced precipitation (Kvalnes et al., in press; Ringsby et al., 2002). Low temperatures at early nestling age when thermoregulation is poorly developed increase the brooding requirements of the nestlings (Radford, McCleery, Woodburn, & Morecroft, 2001). Hence, this may force the mother to increase the time spent in the nest warming the brood at the expense of reduced feeding rates. It is also known that increased temperatures cause increased arthropod abundance (Hollander, Titeux, Walsdorff, Martinage, & Dyck, 2015), which may increase the number of fledglings produced through food availability. Thus, the increase in fledgling production as temperature increases is likely to be due to the combined effect of both increased food availability and the decrease in energy required for thermoregulation with increased temperatures. The present study found no significant relationship between precipitation and the number of fledglings produced. However, a considerable number of the highly ranked models included an uncertain negative effect of precipitation on fledgling production both as a main effect *per* se, and in interaction with clutch size (Table 1). Such relationship may be due to a reduction in food provisioning rates at higher levels of precipitation (Öberg et al., 2015). This is also supported by (Radford et al., 2001) which showed that nest visitation rates in the great tit decreased significantly for females, but not males, during periods of rainfall. Öberg et al. (2015) also found that rain during nestling period had long-term effects on both recruitment and parental survival in great tits. However, no such long-term effect of precipitation on recruit production was found in the present study. This might be because short-term offspring production is dependent on factors

related to food-availability and feeding frequencies as discussed here, while the long-term offspring production is more related to the offspring's prerequisites in terms of size and time of hatching (Ringsby et al., 1998; 2002). The non-significant negative interaction effect between clutch size and precipitation that is present in several of the highest ranked candidate models explaining fledglings production can potentially be caused if decreased provision rates have greater negative effects in large clutches than in small ones. Ringsby et al. (2009) showed how feeding frequencies increased with increased clutch size in house sparrows, but also how the average feeding rate per nestling decreased with increased clutch size. Consequently, a decrease in food availability and the following need for increased parental effort to find food will be more severe in terms of number of fledglings produced in large clutches than in smaller ones.

The number of fledglings produced decreased with increased within brood variation (CV) in egg size (Fig.1a). Possible explanations for this effect are: 1) a bet-hedging strategy, or 2) resource limitations in mothers. The effect of CV egg size complies with a central prediction from the theory on a diversified bet-hedging strategy (Marshall et al., 2008). Specifically, a mother may decrease her variation in fitness over time by reducing her arithmetic mean individual fitness and increasing her geometric mean fitness (Marshall et al., 2008; Sæther & Engen, 2015). A previous study have shown that variation in egg size due to plasticity within mothers are high in this population of house sparrows (Kvalnes et al., 2013). In order to investigate whether mothers in this population exhibit a diversified bet-hedging strategy it would be necessarily to calculate both each mothers' geometric mean fitness and each mothers' within brood variation in egg size. If a diversified bet-hedging strategy is present, there should exist a positive relationship between the geometric mean fitness and the within brood variation in egg size (Marshall et al., 2008; Olofsson et al., 2009; Sæther & Engen, 2015). In other words, it should be possible to observe lower variation in maternal individual

fitness between years among mothers with high within brood variation in egg size than among mothers with low within brood variation (Marshall et al., 2008; Olofsson et al., 2009). This prediction was not tested in this study due to the limited data material. However, a previous study found that the offspring mortality until fledglings was reduced with increased egg size during heavy precipitations, and that offspring mortality until recruitment depended on the combination of egg size and temperature (Kvalnes et al., in press). This suggests that it may be adaptive for mothers to lay a variation of egg sizes adapted to different environmental conditions (Marshall et al., 2008; Olofsson et al., 2009) and thus increase the probability that at least some of the chicks will survive. However, no such interaction effects between egg size and environmental conditions on the number of fledglings produced were found in this study. Together with the fact that no support was found for an effect of within brood variation in egg size on the number of produced recruits and the individual fitness, this gives no further support to a diversified bet-hedging strategy in mothers in this population. An alternative adaptive explanation for the effect of the within brood variation in egg size might be a brood reduction strategy or a brood survival strategy, were an egg size-hierarchy within the clutch is determining the fate of early versus late laid eggs (Bosman, 2014; Haftorn, 1986; Lowther, 1990; Slagsvold, Sandvik, Rofstad, Lorentsen, & Husby, 1984). However, the present study did not include data on size and laying order for each individual egg, thus, a brood reduction or brood survival hypothesis could not be tested.

Fox and Czesak (2000) suggest that most intra-clutch variation in offspring size could be due to environmental variation. For instance Jover, Ruiz, and González-Martín (1993) study on Purple Heron (*Ardea purpurea*) showed that among the parameters investigated only variation among years affected the variation in patterns of intra-clutch egg size variation. They (Jover et al., 1993) suggested that patterns in intra-clutch egg size variation were outcomes of the interaction between physiological and environmental factors, caused by for instance variation

in food supply during the egg formation period (Arnold, 1991; Murphy, 1994). The within brood variation observed might therefore reflect energetic or physiological limitations in mothers (Fox & Czesak, 2000; Nager & van Noordwijk, 1992; Slagsvold et al., 1984). Energy limitation and physiological constraints are also supported by Bernardo (1996), who highlights the importance of an explicit consideration of the ecological context in which the mother produces the eggs.

The present study suggests that heavier mothers perform better in terms of survival, recruit production and individual fitness than lighter mothers with equal number of broods when laying only one brood, while the opposite holds for mothers laying three broods (Fig.2). Two possible explanations are: 1) a potential "cost of being fat" (Gentle & Gosler, 2001; Gosler et al., 1995; Witter & Cuthill, 1993) or 2) that the timing of the broods are correlated with a seasonal pattern with effects depending on maternal body mass. Previously, evidence for an intermediate optimum in body mass has been found in house sparrows (Kvalnes et al., 2017). A cost of being fat might for instance be reflected in increased predation risk related to both take-off ability and flight performance, increased risk for injuries, decreased foraging ability, mass dependent foraging behaviour, and increased reproductive costs (Witter & Cuthill, 1993). For instance, if breeding involves higher exposure due to foraging one could imagine a combination of mass-dependent predation (Gosler et al., 1995; Macleod, Barnett, Clark, & Cresswell, 2005; Macleod, Gosler, & Cresswell, 2005) and an increasing risk of predation with increased number of broods produced or increased time spent nesting, which could potentially explain why heavier mothers with higher number of broods had higher mortality compared to lighter mothers. Third broods are laid later in the season. An alternative explanation for the observed effect might be the greater energy amount acquired to maintain metabolism in heavy mothers contra light ones (Witter & Cuthill, 1993). Hence, if the food availability is scarce later in season when third broods are laid, heavy mothers could be suffer

greater costs. The disadvantage of being light when laying only one brood may be explained by mortality patterns connected to precipitation and temperature. First broods are likely to be laid early in the season when the weather is colder and wetter. Larger females lay larger eggs (Kvalnes et al., 2013), which in turn have higher probability of survival at high precipitation and low temperatures than smaller eggs (Kvalnes et al., in press). On the other hand one could argue that the higher quality of large mothers should reduce the inequalities late in season because large mothers for instance might be better at providing parental care (Ringsby et al., 2009). However, the dataset did not allow for testing these hypotheses and it follows that one should be careful to draw biological conclusion from the observed pattern.

Conclusion

By investigating a oviparous vertebrate using a definition of maternal individual fitness adapted to analyse fitness in fluctuating environments (*sensu* Sæther and Engen (2015)) which included both the mothers' own survival and her number of recruits, the present study did not find evidence for an effect of egg size (mean or CV) on maternal individual fitness. However, the observed interaction effect of maternal body mass and number of broods indicates that quality differences between mothers may potentially mask the trade-off between clutch size and egg size predicted by life history theory. Accordingly, the study reveals that adaptive significance of the maternal quality in the reproductive outcome is highly important in a small passerine bird species which calls for further investigations.

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In this thesis I have been using the template of Oecologica concerning the layout of the manuscript, but deviated from the instructions for line numbering for the sake of readability.

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Tables

Table 1: The highest ranked models (ΔAICc < 2) explaining variation in number of fledglings produced per brood in a population of house sparrows in northern Norway. The most parsimonious model is shown in bold. The intercept model was ranked 209 (ΔAICc = 6.67, weight = 0.001, *ER* = 30.00) among the 915 compared candidate models. Generalized mixed effect models were fitted with a Poisson distribution, a log link function and a random intercept for female identity. In the table, the explanative variables are denoted as follows; maternal age (A), CV egg size (CV), clutch size (CS), precipitation (P), and temperature (T). Maternal age was included as a categorical fixed effect in all models. ΔAICc gives the difference in AICc value relative to the highest-ranked model, *w* is the Akaike weight and *ER* is the evidence ratio for each model compared to the highest-ranked model.

Rank	Model	ΔAICc	*w*	*ER*
1	A + CS + CV + P + T + CS$\times$P	0	0.030	1
2	A + CV + P + T	0.05	0.030	1
3	**A + CV + T**	**0.10**	**0.029**	**1.04**
4	A + CS + CV + P + CS$\times$P	0.13	0.028	1.07
5	A + CV + P	0.64	0.022	1.36
6	A + CS + CS^2 + CV + P + T + CS$\times$P	0.87	0.020	1.50
7	A + CS + CS^2 + CV + P + CS$\times$P	1.18	0.017	1.77
8	A + CS + CV + P + T	1.83	0.012	2.50
9	A + CV	1.94	0.012	2.50
10	A + CS + CV + T	1.98	0.011	2.73

Table 2: Parameter estimates and 95% confidence intervals for the most parsimonious model explaining the variation in number of fledglings produced in a population of house sparrows in northern Norway (see Table 1). The intercept for the older birds (age 2+ years) are given relative to the intercept for the first year birds (age 1 year, Intercept). The generalized mixed effects model was fitted with a Poisson distribution, a log link function and a random intercept for female identity.

		Confidence interval	
	Estimate	Lower	Upper
Intercept	0.758	0.587	0.929
Age class 2	0.187	-0.039	0.413
CV egg size	-7.705	-13.444	-1.965
Temperature	0.038	0.001	0.074

Table 3: The highest ranked models (ΔAICc < 2) explaining variation in annual number of recruits produced per mother in a population of house sparrows in northern Norway. The most parsimonious model is shown in bold. The intercept model was ranked 107 (ΔAICc $= 19.13$, weight < 0.0001, *ER* $= 14341.89$) among the 187 compared candidate models. Generalized mixed effect models were fitted with a Poisson distribution, a log link function and random intercepts for year and female identity. In the table, the explanative variables are denoted as follows; maternal mass (M), maternal age (A), number of broods (NB), and clutch size (CS). Maternal age was included as a categorical fixed effect in all models. ΔAICc gives the difference in AICc value relative to the highest-ranked model, *w* is the Akaike weight and *ER* is the evidence ratio for each model compared to the highest-ranked model.

Rank	Model	ΔAICc	*w*	*ER*
1	**A + M + M^2 + NB + NB×M**	**0**	**0.258**	**1**
2	A + M + M^2 + CS + NB + NB×M	1.08	0.150	1.72

Table 4: Parameter estimates and 95% confidence intervals for the most parsimonious model explaining number of recruits produced in a population of house sparrows in northern Norway (see Table 3). The intercept for the older birds (age 2+ years) are given relative to the intercept for the first year birds (age 1 year, Intercept). The generalized mixed effects model was fitted with a Poisson distribution, a log link function and random intercepts for year and female identity.

	Estimate	Confidence interval	
		Lower	Upper
Intercept	-0.925	-1.831	-0.018
Age class 2	0.103	-0.477	0.683
Mass	2.856	0.901	4.812
Mass^2	-6.059	-11.372	-0.746
Number of broods	0.947	0.483	1.411
Number of broods $\times$ Mass	-2.408	-4.304	-0.513

Table 5: The highest ranked models (ΔAICc < 2) explaining variation in annual survival of mothers in a population of house sparrows in northern Norway. The most parsimonious model is shown in bold. The intercept model was ranked 17 (ΔAICc = 3.93, weight = 0.013, *ER* = 7.23) among the 482 compared candidate models. Generalized mixed effect models were fitted with a Binomial distribution, a logit link function and a random intercept for year. In the table, the explanative variables are denoted as follows; maternal mass (M), number of broods (NB), and mean egg size (E). ΔAICc gives the difference in AICc value relative to the highest-ranked model, *w* is the Akaike weight and *ER* is the evidence ratio for each model compared to the highest-ranked model.

Rank	Model	ΔAICc	*w*	*ER*
1	**M + NB + NB×M**	**0**	**0.094**	**1**
2	M + E + NB + NB×M	0.77	0.064	1.47
3	M + E + E^2 + NB + NB×M	1.58	0.043	2.19

Table 6: Parameter estimates and 95% confidence intervals for the most parsimonious model explaining survival of mothers in a population of house sparrows in northern Norway (see Table 5). The generalized mixed effects model was fitted with a Binomial distribution, a logit link function and a random intercept for year.

	Estimate	Confidence interval	
		Lower	Upper
Intercept	0.448	0.034	0.862
Mass	0.432	-1.229	2.093
Number of broods	0.316	-0.275	0.907
Number of broods × Mass	-3.376	-5.818	-0.934

Table 7: The highest ranked models (ΔAICc < 2) explaining variation in maternal individual fitness in a population of house sparrows in northern Norway. The most parsimonious model is shown in bold. The intercept model was ranked 11 (ΔAICc = 3.38, weight = 0.019, *ER* = 5.58) among the 218 compared candidate models. Generalized mixed effect models were fitted with a Poisson distribution, a log link function, an offset of ln 2 and weights ½, and a random intercept for year. In the table, the explanative variables are denoted as follows; maternal mass (M), maternal age (A), number of broods (NB), and clutch size (CS). Maternal age was included as a categorical fixed effect in all models. ΔAICc gives the difference in AICc value relative to the highest-ranked model, *w* is the Akaike weight and *ER* is the evidence ratio for each model compared to the highest-ranked model.

Rank	Model	ΔAICc	*w*	*ER*
1	**A + M + NB + NB×M**	**0**	**0.106**	**1**
2	A + M + M^2 + NB + NB×M	0.63	0.077	1.38
3	A + M + CS + NB + NB×M	1.88	0.041	2.59

Table 8: Parameter estimates and 95% confidence intervals for the most parsimonious model explaining maternal individual fitness in a population of house sparrows in northern Norway (see Table 7). The intercept for the older birds (age 2+ years) are given relative to the intercept for the first year birds (age 1 year, Intercept). Generalized mixed effects models were fitted with a Poisson distribution, a log link function, an offset of ln 2 and weights ½, and a random intercept for year.

		Confidence interval	
	Estimate	Lower	Upper
Intercept	-0.226	-0.533	0.081
Age class 2	0.025	-0.414	0.463
Mass	0.317	-0.474	1.108
Number of broods	0.305	0.003	0.608
Number of broods × Mass	-1.414	-2.521	-0.307

Figure legends

Fig.1: The predicted effects of a) CV egg size and b) temperature (in degrees of Celsius) on the number of fledglings produced by the mother. Predictions were made by predicting 95% confidence intervals (CI) and estimates based on the observed values of CV egg size and temperature. Age was set to level 1, while other explanatory variables were kept at their mean.

Fig.2: The predicted effects of maternal body mass on a) number of recruits, b) maternal survival, and c) maternal individual fitness for mothers laying one, two and three broods respectively. The consequences of maternal body mass depend on the number of broods laid by the mother. Predictions were made by predicting the 95% confidence intervals (CI) and estimates based on the observed values of maternal body mass. Age was set to level 1, while other explanatory variables were kept at their mean.
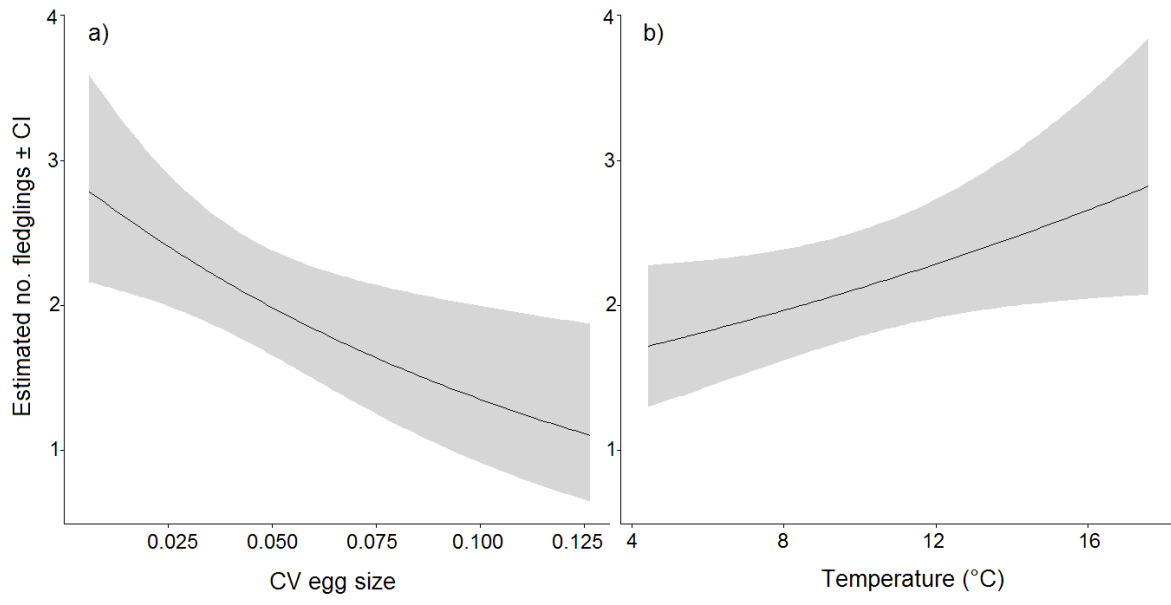
Figures

Figure 1

Figure 2