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Letter

Offspring fitness and the optimal propagule size in a fluctuating environment

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Propagule size is an important maternal effect on offspring fitness and phenotype in birds and other oviparous animals. The performance of propagules often increases with size, but a fluctuating environment may introduce temporal variation in the optimal phenotype. Understanding these mechanisms will provide novel insights into the eco-evolutionary dynamics of life history strategies in parental reproductive investment. We investigated the interaction between propagule size (measured as egg volume) and environmental conditions on offspring mortality and phenotype in a Norwegian house sparrow population. Increased propagule size reduced offspring mortality in early life, with more pronounced effects under heavy precipitation. However, the optimal propagule size for low offspring mortality until recruitment shifted from large to small as temperature increased. Propagule size had no significant effect on fledgling body mass and tarsus length. These results reveal a potential for eco-evolutionary dynamics in propagule size, as populations adapt to fluctuating environmental conditions. The ultimate outcome of this dynamic process will also depend on variation in parental fitness and tradeoffs with other life-history traits, particularly clutch size.

Keywords: Egg volume, individual fitness, *Passer domesticus*, plasticity, survival

Introduction

Parents may affect the fitness of their offspring through variation in propagule size (Mousseau and Fox 1998). Propagule size reflects the amount of resources in terms of energy and nutrients available for an offspring during embryonic development (reviewed by Williams 1994). For instance, Ojanen (1983) found a linear relationship between lipid content and egg mass in great tits *Parus major* and pied flycatchers *Ficedula hypoleuca*. Accordingly, propagule size is commonly held to be an important index of propagule quality (Krist 2011). A positive effect of propagule size on offspring fitness components has been found for hatching success (Amundsen et al. 1996, Fox and Czesak 2000, Krist 2011), early life body mass (Bolton 1991, Amundsen et al. 1996, Heath and Blouw 1998, Fox and Czesak 2000) and early life survival in several species of birds (Williams 1994, Krist 2011), arthropods (Fox and Czesak 2000) and



fish (Heath and Blouw 1998). The long-term effects of propagule size on offspring fitness, such as survival until recruitment, is not well established (Krist 2011). The functional form of the relationship between propagule size and offspring fitness is critical to optimality models of reproductive investment in life history theory (Hendry et al. 2001, Rollinson and Hutchings 2013b, Rollinson and Rowe 2016). For instance, when neglecting variation in parental care the traditional tradeoff between size and number of propagules assumes that offspring fitness increases monotonically with the size of propagules (Smith and Fretwell 1974, McGinley et al. 1987, Roff 2002, Rollinson and Hutchings 2013b, Koch and Meunier 2014).

Studies in several taxa have demonstrated that the effect of propagule size on offspring performance is most pronounced in low-quality environments (Kaplan 1992, Einum and Fleming 1999, Fox and Czesak 2000, Rollinson and Hutchings 2013a, but see Krist 2011). Under such conditions, the nutrient reserves in large propagules may prevent starvation. In contrast, high-quality environments may reduce any fitness difference among propagules of different size (Einum and Fleming 1999, Fox and Czesak 2000). However, the relationship between propagule size and offspring performance does not need to be monotonically increasing (Janzen and Warner 2009). For instance, an intermediate optimal propagule size may arise due to opposite effects of propagule size on offspring performance at different life stages (Hendry et al. 2001) or due to interactions with environmental conditions (Kaplan 1992). The degree to which fluctuating environments cause temporal variation in the optimal propagule size, and the long-term effects of propagule size on offspring fitness, is important in order to understand the eco-evolutionary dynamics of propagule size and parental investment in life history theory (McGinley et al. 1987, Fox and Czesak 2000, Chevin et al. 2010, 2017, Dias and Marshall 2010, Krist 2011).

In this study, we investigated the consequences of variation in propagule size, measured as egg volume, on individual offspring fitness. Data were obtained from a long-term study of house sparrows, where individual-based data have been recorded with high accuracy (Billing et al. 2012, Kvalnes et al. 2013). We investigated the effects of among-clutch differences in mean propagule size on: 1) mortality until fledging (when the individuals leave the nest), 2) mortality until recruitment (when individuals enter the breeding population) and 3) fledgling body mass and tarsus length (a proxy for body size). We were particularly interested in the fitness consequences of the interaction between propagule size and the prevailing environmental conditions (ambient temperature and precipitation) during the early life of nestlings.

Material and methods

Data

The data were collected in the insular population of farm-dwelling house sparrows on Hestmannøy in Norway

(66°33'N, 12°50'E), where individuals are sampled for blood (25 µl) and marked at first capture (Kvalnes et al. 2013). For seven breeding seasons (May until mid-August 2003–2009), active nests were monitored for brood number (annually 1–3 broods per female), clutch size, hatch date and number of fledglings (age 8–13 days). Standardised digital photographs of eggs were used to estimate mean within-brood propagule size ($\pm 0.005 \text{ mm}^3$, Supplementary material Appendix 1 text A1). Individual nestlings could not be traced from a specific egg. Fledgling body mass ($\pm 0.05 \text{ g}$) and tarsus length ($\pm 0.005 \text{ mm}$) were measured. Using paired t-tests on a test set of 25–30 birds, tarsus measurements were adjusted by removing any significant ($p < 0.05$) mean differences between each fieldworker and THR. Traits were separately adjusted to age 11 days using a Gompertz growth curve, estimated using an extended data set from 1993–2013 at Hestmannøy (Kvalnes et al. unpubl.). Fledglings recruited (survival = 1) if alive in a subsequent breeding season (otherwise 0). Individuals were genotyped on 14 polymorphic microsatellites for genetic parentage analyses (Billing et al. 2012). The same female was assigned to all broods in a nest within years (Kvalnes et al. 2013). A total of 179 broods and 388 fledglings from 107 females were available for analysis (descriptive statistics in Supplementary material Appendix 1 text A2).

Weather data were obtained from Myken national weather station (30 km northwest of Hestmannøy), with a few missing entries collected from Sleneset national weather station (21.5 km south of Hestmannøy). The temporal variation in weather at these two weather stations is highly correlated (Ringsby et al. 2002). Daytime (07:00–19:00) mean temperature (°C) and precipitation (mm) over five days after hatching were estimated for each brood. Henceforth referred to as temperature and precipitation. This interval corresponds to the period with the highest mortality rate in the nest, and a period when nestlings have not yet developed the ability to thermoregulate (Ivanov 1987, Anderson 2006, Andreasson et al. 2016).

Statistical analyses

First, we investigated mortality from hatching until fledging using generalized linear mixed-effects models (Bates et al. 2015) with brood number as a fixed factor, a random intercept for cohort, binomial distribution and a complementary log–log link function. We randomly selected one of the broods from each nest, as there were too few nests with multiple broods to fit a random intercept for nest. Second, we analysed mortality from hatching until recruitment, using the same approach as above. Finally, we explored fledgling body mass and tarsus length using linear mixed-effects models (Bates et al. 2015), with brood number as a fixed factor and random intercepts for cohort, mother and brood id. In all three analyses, model assumptions were thoroughly checked using diagnostic plots. Models for mortality until fledging appeared to be slightly overdispersed ($\sigma_{\text{fledging}}^2 = 2.2$, $\sigma_{\text{recruitment}}^2 = 0.92$) due to a small excess of zeros. Accordingly,

we repeated this analysis using a zero-inflated binomial mixed-effects model (Brooks et al. 2017). Results using models with and without zero-inflation were similar, with only minor differences in the estimated intercepts (Kvalnes et al. unpubl.). Thus, we only present the results from the binomial mixed-effects models.

In each analysis, mean propagule size, clutch size, temperature, temperature² and precipitation were included as covariates. To test the hypothesis that the effect of propagule size on offspring fitness depend on the environmental conditions, the interactions between mean propagule size and temperature or mean propagule size and precipitation were also included. Covariates were mean centred to ensure model convergence. We used AICc (Burnham and Anderson 2002) to rank candidate models (Supplementary material Appendix 1 Table A1–A2) and report Akaike weights (w_{rank}) for the highest ranked models. Estimated parameters are given with 95% confidence intervals (CI = [lower, upper]). All statistical analyses were performed in the statistical software R, ver. 3.5.0 (<www.r-project.org>).

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.m74c7m9>> (Kvalnes et al. 2018).

Results

The population mean propagule size across clutches was $2.853 \pm 0.018 \text{ cm}^3$ ($n=179$), with a range of 2.171–3.437 cm^3 . Mean fledgling body mass in the population was $25.6 \pm 0.2 \text{ g}$ ($n=388$), with a range of 9.6–35.7 g, and the mean fledgling tarsus length was $18.54 \pm 0.08 \text{ mm}$ ($n=386$), with a range of 12.0–21.6 mm. Temperature had a mean of $10.0 \pm 0.2^\circ\text{C}$ and a range of 4.4–17.6°C, while precipitation had a mean of $0.8 \pm 0.09 \text{ mm}$ and a range of 0.0–5.7 mm.

Mortality until fledging decreased with increased temperature, and decreased substantially with increased propagule size during periods of heavy precipitation (Fig. 1a, Table 1a, $w_1=0.525$).

The influence of propagule size on mortality until recruitment depended on temperature (Fig. 1b, Table 1b, $w_1=0.277$). The predicted fitness landscape had a ridge of low mortality along the diagonal, where small propagules were favoured at high temperatures and large propagules were favoured at low temperatures (Fig. 1b, Supplementary material Appendix 1 Fig. A3). In addition, mortality decreased with increased clutch size (Table 1b).

Fledgling body mass and tarsus length were both positively related to temperature, and tarsus length was negatively related to precipitation (Table 2a–b, $w_{1, \text{body mass}}=0.293$ and $w_{1, \text{tarsus length}}=0.218$). Furthermore, there was an uncertain trend for increased fledgling body mass with increased propagule size, which was more pronounced at high temperature (Table 2a).

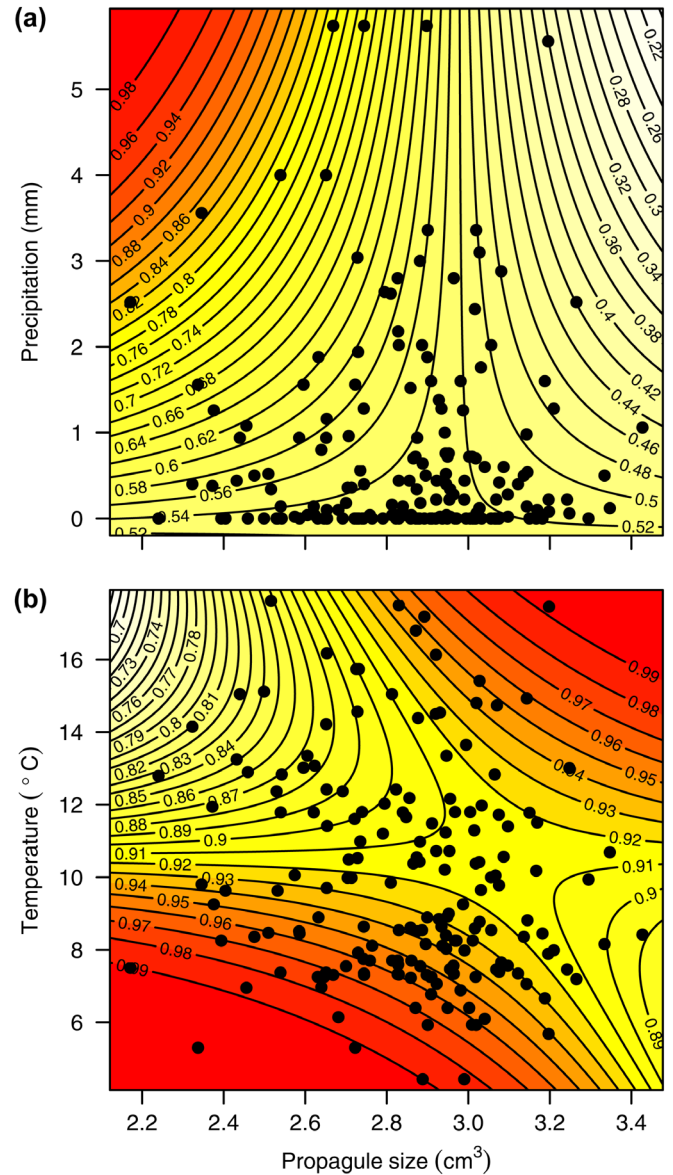


Figure 1. The predicted consequences of propagule size on offspring mortality from hatching until (a) fledging and (b) recruitment in a population of house sparrows in Norway. The effect of propagule size on mortality depends on the weather conditions during the early life of nestlings (age 0 to 5 days of age). Heat map with contour lines for mortality (red=high, white=low) as a result of the interaction between propagule size and temperature or precipitation; other explanatory variables in the models were kept at their mean value.

Discussion

Fluctuating and changing environments are known to play an important role in the evolution of life-histories (McGinley et al. 1987, Tuljapurkar et al. 2009, Chevin et al. 2010), e.g. by modifying the optimal parental investment in size and number of offspring (McGinley et al. 1987, Garant et al. 2007, Allen et al. 2008, Marshall et al. 2008).

Table 1. Parameter estimates and 95% confidence intervals for the highest-ranked model explaining variation in offspring mortality until (a) fledging and (b) recruitment in a population of house sparrows in Norway. Generalized linear mixed effects models were fitted with a random intercept for cohort, binomial distribution and a complementary log-log link function. Estimates for second and third broods are relative to the first brood (Intercept). Propagule size was measured in cm³, temperature in degrees Celsius and precipitation in mm.

		Confidence interval	
	Estimate	Lower	Upper
(a) Fledging			
Intercept	−0.263	−0.379	−0.147
Second brood	0.011	−0.244	0.266
Third brood	0.129	−0.423	0.681
Mean propagule size	−0.380	−0.782	0.021
Temperature	−0.106	−0.146	−0.065
Precipitation	0.051	−0.029	0.131
Mean propagule size × Precipitation	−0.400	−0.730	−0.070
(b) Recruitment			
Intercept	1.079	0.927	1.231
Second brood	−0.159	−0.402	0.083
Third brood	0.096	−0.482	0.675
Clutch size	−0.157	−0.281	−0.032
Mean propagule size	−0.099	−0.528	0.331
Temperature	−0.055	−0.104	−0.007
Temperature ²	0.011	−0.001	0.022
Mean propagule size × Temperature	0.194	0.028	0.360

This study demonstrates an environmentally induced fitness ridge for propagule size (Table 1b) in a wild vertebrate, where the optimal propagule size for low long-term offspring mortality decrease as temperature increases (Fig. 1b). However, for

Table 2. Parameter estimates and 95 % confidence intervals (restricted maximum likelihood) for the highest-ranked model explaining variation in fledgling (a) body mass (g) and (b) tarsus length (mm) in a population of house sparrows in Norway. Estimates for second and third broods are relative to the first brood (Intercept). Linear mixed effects models were fitted with random intercepts for cohort, mother and brood id. Propagule size was measured in cm³, temperature in degrees Celsius and precipitation in mm.

		Confidence interval	
	Estimate	Lower	Upper
(a) Body mass			
Intercept	26.456	25.403	27.509
Second brood	0.140	-1.250	1.531
Third brood	-3.481	-6.145	-0.818
Mean propagule size	1.941	-0.568	4.449
Temperature	0.348	0.117	0.579
Temperature ²	-0.066	-0.126	-0.006
Mean propagule size × Temperature	0.673	-0.188	1.533
(b) Tarsus length			
Intercept	18.830	18.457	19.203
Second brood	-0.102	-0.606	0.403
Third brood	-1.513	-2.457	-0.568
Temperature	0.206	0.121	0.291
Temperature ²	-0.017	-0.039	0.004
Precipitation	-0.207	-0.409	-0.005

short-term mortality (until fledging) there was a pronounced reduction in mortality for offspring from large propagules under heavy precipitation (Fig. 1a). A negative relationship between clutch size and offspring mortality (Table 1b) might reflect differences in quality among parents which positively affect offspring fitness (Both et al. 1998, Pettifor et al. 2001, Koch and Meunier 2014). There was a trend for a positive effect of propagule size on fledgling body mass (Table 2). This result conforms to the general pattern that the relationship between propagule size and body mass of nestlings is strong at hatching and weakens towards fledging due to variation in the growth and development of nestlings (Williams 1994, Krist 2011).

Previous studies have suggested that there is a monotonic increase in offspring fitness with increasing propagule size (Williams 1994, Einum and Fleming 1999, Hendry et al. 2001, Krist 2011, Rollinson and Hutchings 2013b). This is based on the observation that large propagules contain more energy and nutrients and hatch nestlings with high fat reserves (Williams 1994). In the present study, a large propagule size reduced mortality until fledging when there was heavy precipitation (Fig. 1a). Thus, increased fat reserves from large propagules probably facilitated reduced mortality in periods of high precipitation and low food supply in the short-term (Öberg et al. 2015), but does not carry an advantage under more benign conditions. In the long-term, nestlings from large propagules had lower mortality until recruitment than nestlings from small propagules during cold temperatures (Fig. 1b). However, the pattern was reversed under high temperatures where small propagules were favoured (Fig. 1b). Large nestlings in high temperatures could experience accelerated growth rates compared to smaller nestlings, which could result in an accumulation of oxidative damage and telomere attrition (Ringsby et al. 2015), and potentially reduced life expectancy (Ricklefs 2006). An interaction effect between temperature and fledgling body mass on offspring survival has been found by Nord and Nilsson (2016). In their experiment with blue tits *Cyanistes caeruleus*, offspring survival increased with body mass at low and intermediate incubation temperatures and decreased with body mass at high incubation temperatures (Nord and Nilsson 2016). Our results are consistent with previous suggestions that propagule size is most important for offspring fitness under harsh environmental conditions, such as heavy precipitation or temperatures in the upper or lower end of the scale (Fig. 1, Einum and Fleming 1999, Fox and Czesak 2000, Krist 2011, Rollinson and Hutchings 2013a).

The interaction between propagule size and environment on offspring mortality (Table 1, Fig. 1) could provide the basis for adaptive eco-evolutionary dynamics. Under unpredictable environmental conditions, parents may increase their geometric mean fitness (i.e. decrease their variance in fitness) at the expense of reduced arithmetic mean fitness by adopting a diversifying bet-hedging strategy in propagule size (Marshall et al. 2008, Olofsson et al. 2009, Sæther and Engen 2015). In other words, by producing propagules of different sizes within their clutch, parents may increase

the probability that at least some offspring survive. On the other hand, in a more predictable environment a different strategy may be favoured. Then parents could increase their mean fitness by adaptive plasticity in mean propagule size (Einum and Fleming 1999, Fox and Czesak 2000, Marshall et al. 2008, Kvalnes et al. 2013). Females would then produce propagules of the size which under the prevailing environmental conditions minimize the probability of offspring mortality. Previously it has been shown that females in our population actually produce smaller propagules when temperature is high during the breeding season (Kvalnes et al. 2013). Accordingly, our results suggests that females adopt adaptive plasticity in propagule size as a strategy to deal with the seasonal changes in environmental conditions.

In the study area, temperature and precipitation also vary considerably among years (Ringsby et al. 2002). Thus, the optimal propagule size for offspring fitness may be subject to environmentally induced temporal variation both within and among years. For a parent, this variation is likely to be affected by both predictable and unpredictable elements in the environment. Accordingly, the relative importance of bet-hedging and adaptive plasticity in propagule size should be investigated for parents fitness to understand how populations maintain high mean fitness in fluctuating environments. The interaction and possible tradeoffs between propagule size, offspring fitness and other life-history traits, such as clutch size and parental survival, will then determine the optimal propagule size (Hendry et al. 2001). Such knowledge may advance our understanding of the eco-evolutionary dynamics of parental investment in life history theory and enable us to predict how different populations and species might respond to environmental changes in the future.

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Author contributions – TK and AÅR are joint first authors. TK and AÅR equally contributed to analyse the data and write the paper, in close collaboration with THR. THR, HJ, BES and TK came up with the idea and concepts. HH, HJ, HP, THR and TK carried out the fieldwork. HJ and TK carried out the genetic parentage analyses. All authors contributed when writing up the manuscript through conceptual discussions, edits and inserts.

Conflicts of interest – We have no competing interests.

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Supplementary material (Appendix jav-01786 at <www.avianbiology.org/appendix/jav-01786>). Appendix 1.