

# Disentangling egg and parental effects on chick quality

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## Abstract

Variation in rearing conditions is known to affect fitness later in life, but the underlying mechanisms of this relationship remain elusive. Egg size impacts offspring quality and is therefore a candidate mechanism, but exactly how egg size causes effects on offspring performance remains unclear. This research aims to unravel the correlation between egg size and offspring mass (a quality marker), by testing if (i) egg size itself or (ii) the shared parental or environmental quality, explained the observed correlation. We performed a cross-foster experiment using a natural population of Jackdaws, *Corvus monedula*, where we swapped whole clutches. We found that the correlation between egg size and day 5 mass was explained by egg size itself, but not by parental or environmental quality. Intra-clutch variation in egg size also partially explained the correlation between egg size and day 5 mass. Intriguingly, the slope of the correlation between egg size and day 5 mass is higher ( $1.7 \text{ g/cm}^3$ ) than the slope between egg size and day 1 mass ( $0.7 \text{ g/cm}^3$ ) indicating that the egg quality has carry-over effects on the growth rate of the chicks. We conclude that the correlation in egg size and chick quality is, at least in early development, only caused by egg effects and that this is not only caused by nutrients in the egg, but that the egg also influences the growth rate of chicks in an unknown way.

## Introduction

Early life development can among others be determined by genes, the environment or parental, non-genetic, effects. The quality differences resulting from early life development can have important long-term fitness consequences (Lindström 1999). Maternal effects, like egg size, have been shown to affect offspring quality (Krist 2011, Monteith et al. 2012, Bosman 2014, Krist and Munclinger 2015). Understanding the underlying mechanism behind this relationship is important to understand the effect these life-history traits have on fitness. It may be that egg size actually reflects parental or environmental effects, instead of that egg size itself is influencing offspring quality, or that egg size reflects both egg size effects as well as parental or environmental effects. Until now, quite a few studies have tried to separate these factors, but found different results. Blomqvist et al. (1997), Hipfner and Gaston (1999), Styrsky et al. (1999), Hipfner (2000), Pelayo and Clark (2003), Krist (2009) and Reed et al. (2009) found only egg effects and no effect of parental or environmental quality. Bize et al. (2002) and Van De Pol et al. (2006) found only parental effects and no direct egg effects. Bolton (1991), Amundsen et al. (1996), Risch and Rohwer (2000), Arnold et al. (2006), Silva et al. (2007) and Hadfield et al. (2013) found egg effects as well as parental effects. All of these researches were performed with birds. In burying beetles, Monteith et al. (2012) found an effect of egg size on offspring quality, but they also showed that this effect was usually masked by the effect of the parental quality. So, there is not one unambiguous conclusion and there needs to be a causation for that. It could be that in birds, just as in the burying beetle experiment, one of both effects is stronger than the other and therefore the weaker one might be undetectable in a normal mixed effects model. Therefore, we propose a method that we think is more suitable to detect weak effects.

Many studies on this subject did not take into account the possibility of parental or environmental factors making up this correlation, but instead try to understand if the correlation is based on actual

egg size (large eggs give large chicks) or on relative egg size (relatively large eggs within a clutch give larger chicks) (Erikstad et al. 1998, Amat et al. 2001, Bosman 2014, Krist and Munclinger 2015, Gibson and Williams 2017). It is of course possible that this correlation is found because of a within clutch effect, but then one would expect more egg size variation within clutches than between clutches. In our population however, we found three times more variance between clutches than within. Therefore, we do not consider this as a fourth hypothesis explaining the whole correlation, but we do correct for within clutch effects in our models.

In this study, we performed a cross-foster experiment in a natural population of jackdaws, *Corvus monedula*, in which we swapped whole clutches. We expect to find only an effect of egg on chick quality (H1), only an effect of the parents or the environment on chick quality (H2) or an effect of both on chick quality (H3). Throughout the whole article standard errors are given with averages.

## Method

### Study population

We studied free-living jackdaws breeding in nest boxes in six colonies, each containing 12 to 22 nest boxes, south of Groningen, the Netherlands (53.1708° N, 6.6064° E). The data used in this paper were collected in 2015, 2016 and 2017. In our study population, jackdaws lay one clutch per year and have an average clutch size of 4.5 ( $\pm 0.03$ ). In jackdaws there is no extra-pair paternity (Liebers and Peter 1998, Henderson et al. 2000). With the start of the breeding season, all nest boxes were regularly checked (every 3 days) for new eggs to approximate the laying order. Found eggs were marked with a felt tip pen to identify from which egg a chick hatched and their length and width were measured to the nearest 0.1 mm using a calliper. The egg volume (V), in  $\text{cm}^3$ , was calculated using the formula:  $V = \pi * W^2 * L * K / 6$ . Where W is the egg width (mm), L is the egg length (mm) and K is a constant, in jackdaws  $K = 0.00096$  (Soler 1988). Eighteen days after the first egg was laid the nests were checked daily for newly hatched chicks. Hatched chicks were weighed to the nearest 0.1 grams and one or more nail tips were clipped in a specific combination for individual identification. On the fifth day after the first egg had hatched (from now on called day 5) all the chicks were weighed again, to the nearest 0.5 grams. Eggs that had not hatched were then removed. When it was unknown from which egg a chick had hatched, the average egg volume of all the eggs with unknown chick from a clutch was used as its egg volume. Thirty days after the first hatch date the chicks were ringed with a metal ring and a unique colour ring combination. Un-ringed breeding adults were also ringed with a metal ring and a unique colour combination. Before the breeding season birds were identified using a telescope and were assumed to breed in a box when they were seen multiple times flying in and out a specific box. In the breeding season as much parents were caught as possible, to check if ring combinations were correct and to take some general measurements and a blood sample.

### Cross-foster experiment

To separate egg (H1) and parental effects (H2) from egg size on day 5 mass we swapped clutches ( $n=100$ , containing in total 462 eggs) with the same clutch size and laying date ( $\pm 1$  day). Apart from these conditions the swaps were done randomly, (Fig. 1).  $7(\pm 0.18)$  days after the last egg was laid the swaps were performed, to make sure the clutch was completed. An average incubation time is approximately 18 days and birds do not always start incubating immediately after laying all eggs. All chicks from eggs that were laid in the period that the swapped eggs were laid were included in the statistical analysis, also the ones that were not from a swapped clutch (total  $n=624$  chicks, of which 308 were from swapped clutches). We used linear mixed models to statistically test our hypotheses. For the statistical analysis R 3.4.1 was used, with the packages lme4, lmerTest and ggplot2.

To answer our question, we made two models. The first one will show us the observed correlation between egg size and day 5 mass from our study population, but without intra-clutch variation, so the correlation between the average egg size per clutch and the day 5 mass:

$$D5mass = B_0 + \alpha * E_{gp} + e_0$$

Where  $B_0$  is the intercept,  $\alpha$  the dependency of day 5 mass (D5mass) on the average egg volume of the genetic parents ( $E_{gp}$ ) and  $e_0$  is the residual variance. The second model is to understand which factor determines the correlation between the average egg volume and the day 5 mass. In this model we included the average egg volume of the foster parents ( $E_{fp}$ ) and the difference in egg volume between the genetic and the foster parents ( $\Delta E_{gp-fp}$ ).

$$D5mass = B_0 + \beta * E_{fp} + \gamma * \Delta E_{gp-fp} + e_0$$

Where  $\beta$  is the dependency of day 5 mass on the average egg volume of the foster parents and  $\gamma$  is the dependency of day 5 mass on the difference in egg volume between the genetic and foster parents. If there is only a direct egg effect (H1) one would expect that eggs placed by foster parents would still grow into chicks with the mass that belongs to their eggs, (Fig. 2) and therefore, the observed slope ( $\alpha$ ) should be the same as the slope of the difference in egg volume between the genetic and foster parents ( $\gamma$ ). Actually, all three slopes should be the same ( $\alpha=\beta=\gamma$ ) if H1 is true, since by definition the average egg volume of the genetic parents is equal to the sum of the average egg volume of the foster parents and the difference in egg volume between the genetic and foster parents. Therefore, if there only is an egg effect one could replace the average egg volume of the genetic parents in model 1 with the sum of the other two:

$$D5mass = B_0 + \alpha * E_{gp} + e_0 = B_0 + \alpha * (E_{fp} + \Delta E_{gp-fp}) + e_0 = B_0 + \alpha * E_{fp} + \alpha * \Delta E_{gp-fp}$$

If there is only an effect of parental or environmental quality (H2) one would expect that chicks would grow as large as is predicted by their foster parent's egg size, (Fig. 2). Therefore, the slope ( $\gamma$ ) of the difference in egg size between the genetic and the foster parent should be 0, but the slope of the average egg volume of the foster parents should not be 0, so in this case we would predict that  $\gamma=0$  and  $\beta \neq \gamma$ .

If there is both an egg effect and a parental or environmental effect (H3), one would expect the difference in egg volume between the genetic and foster parents ( $\Delta E_{gp-fp}$ ) to have a slope in between 0 and the observed slope ( $\alpha$ , the slope from the average egg volume of the genetic parents), (Fig. 2). So if this hypothesis is true, we would expect  $\alpha \neq \beta \neq \gamma$  and  $\gamma > 0$ . Depending on the slope from  $\Delta E_{gp-fp}$  one can determine the relative importance of both effects. The closer this slope is to 0, the more important parental or environmental effects are and the closer this slope is to the slope from  $E_{gp}$ , the more important egg effects are.

### Separating within and between clutch variation

As mentioned in the introduction, it could be that the effect of the relative egg size also partially explains the correlation between egg size and chick quality (relative large eggs within a clutch produce larger chicks than relative small eggs in the same clutch). To correct for this, an extra term is added to our model: The difference between an egg's own volume and the clutch average ( $\Delta E_{e-gp}$ ). If its slope ( $\delta$ ) is significantly different from 0, then there is also a relative effect of egg size on chick size.

### Final models

Not all chicks are five days old at day 5, therefore the relative hatch date ( $HD_{rel}$ ) was also added in the model, to correct for age differences within broods. The relative hatch date is the difference in days between an chick's own hatch date and the hatch date of the first egg of the clutch that has hatched.

Since laying order highly correlated with relative hatch date, we did not include this in the model.

Because not all measurements are completely independent, female ID, colony and clutch swap code (CSC, to link together two nests which clutches are swapped) are also added to the model. These random effects together also specify year and clutch identity, which were therefore not included in the model (when added the estimates changed only slightly and the conclusions stayed the same).

Thus, our final models are:

$$D5mass = B_0 + \alpha * E_{gp} + \delta * \Delta E_{e-gp} + \varepsilon * HD_{rel} + a * FemID + b * Colony + c * CSC + e_0 \quad (1)$$

$$D5mass = B_0 + \beta * E_{fp} + \gamma * \Delta E_{gp-fp} + \delta * \Delta E_{e-gp} + \varepsilon * HD_{rel} + a * FemID + b * Colony + c * CSC + e_0 \quad (2)$$

## Results

### Separating egg and parental effects

From all chicks that were used in the data analysis (n=624) 308 were from swapped clutches. The models revealed significant slopes for the average egg volume of the genetic parents ( $1.72 \pm 0.43$  g/cm<sup>3</sup>, p<0.01), the average egg volume of the foster parents ( $1.74 \pm 0.51$  g/cm<sup>3</sup>, p<0.01) and the difference in egg volume between the genetic and foster parents ( $1.70 \pm 0.46$  g/cm<sup>3</sup>, p<0.01) and these slopes tested not to be significantly different (Fig. 3). This indicates that the effect egg size has on day 5 chick mass was caused by the egg itself (H1) and not the parental or environmental quality (H2) or by both egg and parental effects (H3). The effect of average egg volume on day 5 mass is shown in figure 4.

### Within and between clutch effects

As shown above, there is a clear between-clutch effect of egg volume on day 5 mass (H1). However, the within-clutch effect of egg volume on day 5 was also tested and the difference between the average egg volume of a clutch and the volume of a specific egg ( $\Delta E_{e-gp}$ ) had also a significant effect on the day 5 mass, which, as expected, was very similar in both models ( $2.35 \pm 0.93$  g/cm<sup>2</sup>, p=0.01 and  $2.26 \pm 0.95$  g/cm<sup>3</sup>, p=0.02, respectively). This indicates that also the relative egg volume within a brood has a positive effect on the day 5 mass (Fig. 5), which is even stronger than the between clutch effects. For all estimates of both models, see table 1.

## Discussion

The aim of our study was to understand if the effect of egg size on chick quality was due to an effect of egg size, an effect of parental or environmental quality or an effect of both. Our results show that this correlation is solely based on egg quality and not on parental or environmental quality, since the three slopes were not significantly different. This positive effect of egg volume on day 5 mass is as well true for the actual size of the egg as well as its relative size in its clutch and is independent of hatching order.

Our results agree with Blomqvist et al. (1997), Hipfner and Gaston (1999), Styrsky et al. (1999), Hipfner (2000), Pelayo and Clark (2003), Krist (2009) and Reed et al. (2009) who also only found egg effects. However in the articles that found both egg- and parental effects (Bolton 1991, Amundsen et al. 1996, Risch and Rohwer 2000, Arnold et al. 2006, Silva et al. 2007, Hadfield et al. 2013), it was common that in the early development egg effects were either most or only important and only later in the development parental and environmental effects became more important. So our results might still be in agreement with theirs as well. Only Bize et al. (2002) and Van De Pol et al. (2006) found parental effects and no egg effects. However, both studies only had data on longer term chick

survival, so it might be that the egg effects were already overshadowed by then or were not important anymore. In Van De Pol et al. (2006) there were very large differences in territory quality, so this could make the environmental effects more important and thus it could overshadow any egg effect more easily.

Relative egg size within a clutch was in our study also an important predictor of chick quality, since its slope (2.3) was much higher than the slope of the average egg size of a clutch (1.7). This result is in accordance with Erikstad et al. (1998), Amat et al. (2001), Bosman (2014), Krist and Munclinger (2015) and Gibson and Williams (2017).

One major shortcoming of this research, is that we cannot correct for genetic effects that theoretically could both influence egg size and growth rate. If there are such genes, the effect egg size seems to have on chick quality might actually be explained by the effect of these genes. This is not an easy problem to solve, since it would need a much deeper understanding of the effect of single genes and their gene networks on life history traits.

In this research we clearly found that larger eggs have a positive effect on chick quality, so why are there still differences in egg size found in nature? This question is commonly answered with the brood reduction theory (Howe 1976, O'Connor 1978, Fischer et al. 2011), which says that parents invest differently in their chicks, because they cannot predict the environment in the whole breeding season and it is less bad to lose a chick that is less invested in than a chick where a lot is invested in. This theory agrees with our finding that relative egg size is important for chick quality. However, this can never be the only answer to the question why there is still variation in egg size, because we also found a lot of between clutch variation in egg size which was also determining for chick quality.

To answer this question it is important to look at it from the perspective of the mother and not from the perspective of the offspring, because egg size is a trait of the mother and an individual will always do what is best for its own inclusive fitness and this is not always in accordance with what is best for the fitness of its offspring, especially when there are trade-offs. For example in our study population there was a correlation found between the female condition and egg size (Verhulst and Salomons 2004), implicating that when females are in good condition they have more reserves that they can use in reproduction than females in bad conditions. So it could be that only when females are in good enough condition, they will lay eggs of the optimal size. However, still then it could be that females do not lay eggs of optimal size for the chicks, for example because she has to change her (pelvic or ovary) anatomy for that and this could have costs for her survival. Next to that, there is a trade-off between the quality and quantity of eggs (Sinervo and Licht 1991, Hendry et al. 2001, Fischer et al. 2011). Hendry et al. (2001) found in freshwater fish that it is actually more beneficial for an individual's fitness to increase the number of eggs instead of the size of the eggs, so it might be true in birds as well that for a mother's fitness it is better to lay more eggs than it is to optimize the egg size to the optimal for the chicks. Monaghan et al. (1998) also found a trade-off between egg size and rearing capacity of parents. When parents were experimentally manipulated to lay an extra egg, their foster chicks had a significantly lower mass when fledging and they also had less foster chicks that survived until fledging. So especially in altricial birds parents could choose to decrease their egg size when they are not in optimal condition, to make sure they at least have enough energy to rear their chicks. However, as said before, in our study we found that the parental quality does not have an effect on chick quality. This would imply that parents should still invest in bigger eggs than in rearing capacity, even with this trade-off. So, how this trade-off works and how important it is in this population is still unclear.

Also, there is a trade-off between current and future reproduction (Williams 1966, Schaffer 1974, Hirshfield and Tinkle 1975, Pianka and Parker 1975, Bell 1980, Martin 1995). So it might be that females who invest in optimizing eggs from their current clutch are less able to survive or to invest in future clutches. Therefore it could be more beneficial to not optimize a current clutch, but instead

invest this energy in survival until future reproduction or in a future clutch.

Quite a lot of papers use the egg size of the foster parents as a measurement of their quality (for example: Bolton 1991, Amundsen et al. 1996, Blomqvist et al. 1997, Monaghan et al. 1998, Hipfner and Gaston 1999, Styrsky et al. 1999, Risch and Rohwer 2000, Bize et al. 2002, Silva et al. 2007, Krist 2009), but is this a legit assumption? Concluding from our research, we can say it is a good proxy. Actually, already the fact that there is a correlation between egg size and chick quality means that high quality parents lay large eggs and that therefore egg size can be used as a measurement for parental quality. Our results show that the high quality of these parents partially is expressed in their egg size and therefore egg size is not only a good proxy for parental quality based on a correlation, but also based on a partial causation, which makes it an even better predictor.

Our most intriguing result however, is the value of the slope, 1.7, we found between the average egg volume of the genetic parents and the day 5 mass. The slope of the correlation between the average egg volume of the genetic parents and the day 1 mass (the mass at the day the chicks hatched) is only 0.7, see table s1. This 0.7 slope means that the nutrients in the egg are not for a hundred percent effectively transmitted into body weight, but that chicks get 0.7 grams heavier for every added cubic centimetre of egg volume. Since the slope with day 5 mass is steeper than the slope with day 1 mass, the egg does not only influence the mass of the chicks by the nutrients in it, but it also influences the growth rate of the chicks. It could be that the parents have a certain laying strategy and give larger eggs to chicks that have genes for a high growth rate and small eggs to chicks with genes for a low growth rate. A second possibility is that eggs contain something, like hormones, that influence the growth rate of the chicks and that chicks with larger eggs thus get more from this and therefore grow faster. It would be interesting to find out if other (bird) species show a similar contribution of egg size on chick growth and to understand how eggs influence the growth rate.

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Figures and Tables

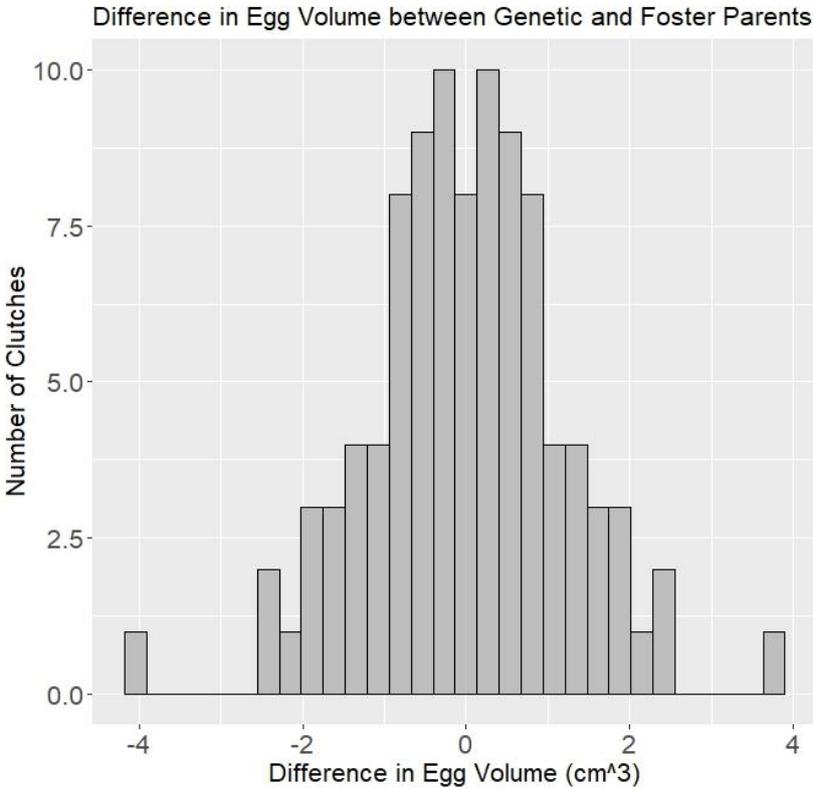


Figure 1: A histogram from the cross-fostered clutches of the difference in average egg volume between the genetic and foster parents. Clutches were swapped according to their clutch size and laying date, but it was tried to cross-foster randomly with respect to egg volume.

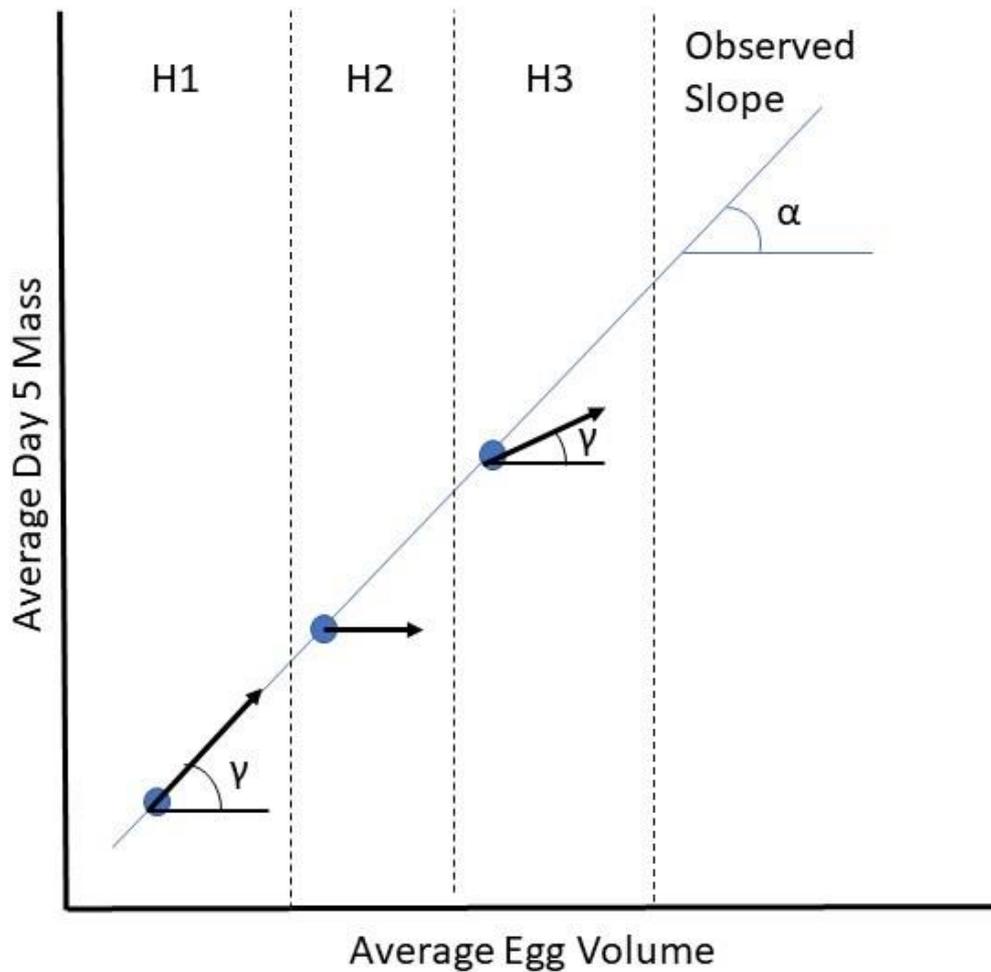


Figure 2: The expected slopes for every hypothesis (H1, H2 and H3). The dots are parents which are given a foster clutch with an average higher egg volume than their own (genetic) clutch. When only direct egg effects influence day 5 mass (H1) one would expect that the foster chicks from these parents would develop according to their own egg size and not according to their foster parents clutch size. Thus, the slope of the difference in egg volume between the genetic and foster parents would have the same slope as the observed slope. When only parental or environmental effects influence day 5 mass (H2) one would expect that the foster chicks from these parents would develop according to the foster parents (or foster environment) quality and not according to their egg volume. Therefore, the slope of the difference in egg volume between the genetic and foster parents would be 0. If both egg effects and parental (or environmental) effects influence day 5 mass (H3), one would expect the slope of the of the difference in egg volume between the genetic and foster parents to be in between the observed slope and 0.

Table 1: Model 1 and 2. Day 5 mass in relation to the egg volumes of the genetic and foster parents, their difference, the relative egg volume and the relative hatch date (n=624).

Model	Fixed Effect	Slope	Standard Error	p-value
1	Average egg volume genetic parents ( $E_{gp}$ )	1.7208	0.4274	0.000123
	Relative egg volume ( $\Delta E_{e-gp}$ )	2.3494	0.9337	0.012253
	Relative hatch date (RelHD)	-13.5012	0.5476	$<2 \cdot 10^{-16}$
2	Average egg volume foster parents( $E_{fp}$ )	1.7407	0.5099	0.000972
	Difference in egg volume between genetic and foster parents ( $\Delta E_{gp-fp}$ )	1.6951	0.4595	0.000465
	Relative egg volume ( $\Delta E_{e-gp}$ )	2.2600	0.9541	0.018331
	Relative hatch date (RelHD)	-13.4969	0.5501	$<2 \cdot 10^{-16}$

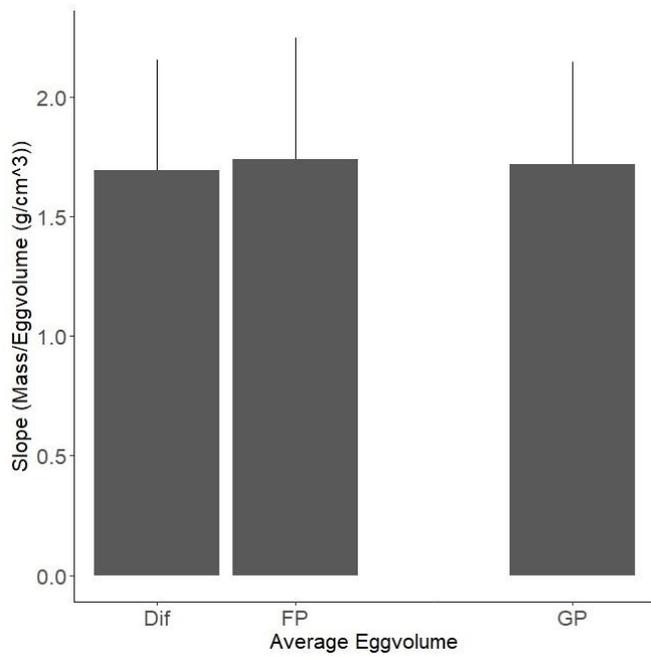


Figure 3: The values of the slopes from both models. These slopes are the effects on day 5 mass of: the average egg volume of the genetic parents (GP) from model 1, the average egg volume of the foster parents (FP) from model 2 and the difference in egg volume between the genetic and the foster parents (Dif), all with their standard errors.

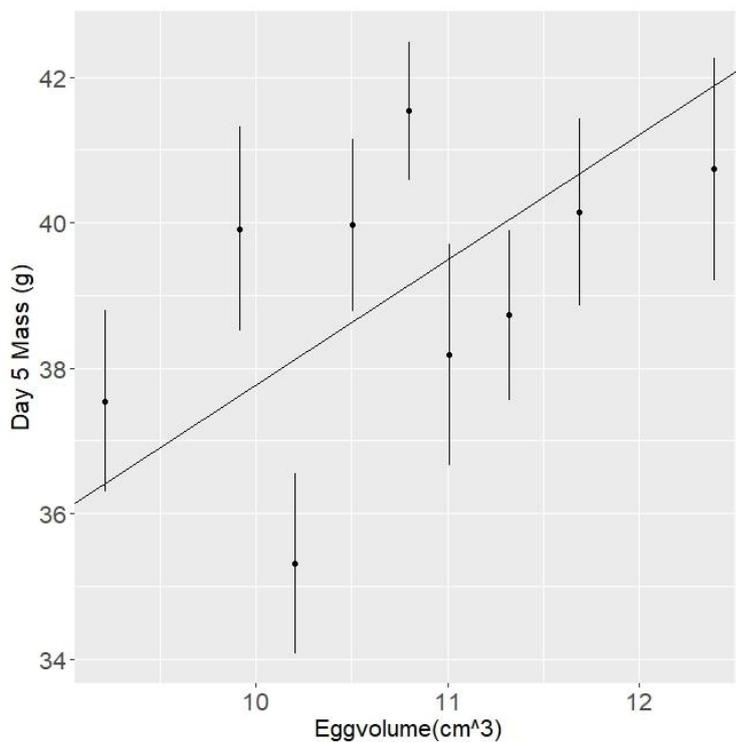


Figure 4: The between clutch effect of egg volume on day 5 mass. The average egg volume per clutch is plotted against the average day 5 mass per clutch. Clutches were sorted according to egg volume and divided in 9 groups for clarity, each averaging 25 or 26 clutches. The line has the slope estimated by model 1.

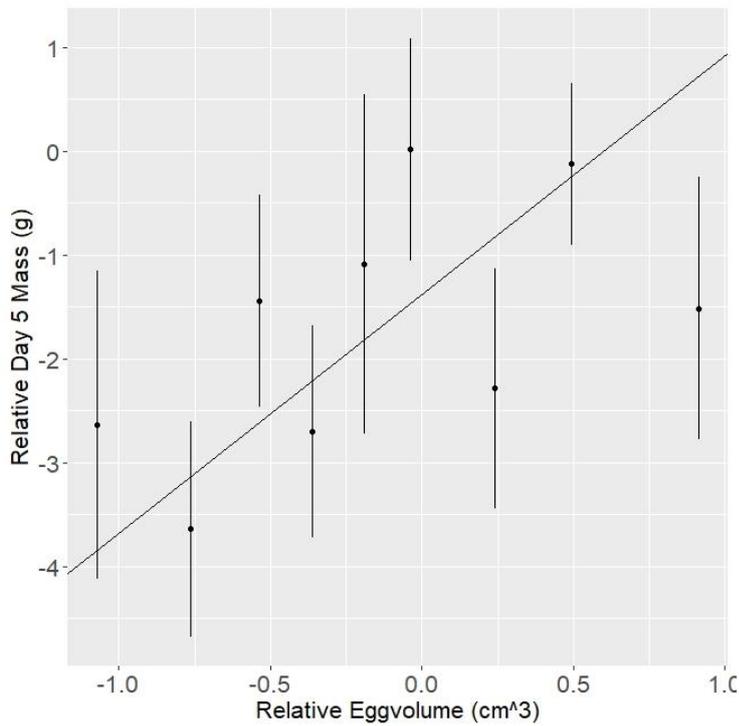


Figure 5: The within clutch effect of egg volume on day 5 mass. For this figure only the chicks from known eggs were used (n=136). The relative egg volume of these chicks is plotted against their relative day 5 mass, both relative to the clutch average. Chicks were sorted according to their relative egg volume and grouped accordingly in 8 groups for clarity, each averaging 17 chicks. The line has the slope estimated by both models (2.3).

Table S1: The effects on day 1 mass of the average egg volume of the genetic parents, the relative egg volume within a clutch and the relative hatch date. As random effects, female ID, colony and clutch swap code (to link together 2 clutches that were swapped) were added. n=612 nestlings in 178 broods.

<b>Fixed Effects</b>	<b>Estimate</b>	<b>Standard Error</b>	<b>P-value</b>
Average egg volume of the Genetic parents	0.69151	0.07483	5.33*10 <sup>-15</sup>
Relative hatch date	-0.05203	0.11856	0.66103
Relative egg volume within a clutch	0.58734	0.20660	0.00468
<b>Random Effects</b>	<b>Variance</b>	<b>Standard Deviation</b>	<b>Number of groups</b>
Clutch Swap Code	0.0002	0.01316	106
Female ID	0.0383	0.1958	90
Colony	0.0591	0.2432	7
Residual	1.8015	1.3422	