Effects of intraclutch variation in egg size and hatching asynchrony on nestling development and survival in semi-precocial Herring Gulls

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ABSTRACT. Intraclutch egg size variation may non-adaptively result from nutritional/energetic constraints acting on laying females or may reflect adaptive differential investment in offspring in relation to laying/hatching order. This variation may contribute to size hierarchies among siblings already established due to hatching asynchrony, and resultant competitive asymmetries often lead to starvation of the weakest nestling within a brood. The costs in terms of chick mortality can be high. However, the extent to which this mortality is egg size-mediated remains unclear, especially in relation to hatching asynchrony which may operate concomitantly. I assessed effects of egg size and hatching asynchrony on nestling development and survival of Herring Gulls (Larus argentatus), where the smaller size and later hatching of c-eggs may represent a brood-reduction strategy. To analyze variation in egg size, I recorded the laying order and laying date of 870 eggs in 290 three-egg clutches over a 3-yr period (2010–2012). I measured hatchlings and monitored growth and survival of 130 chicks from enclosed nests in 2011 and 2012. The negative effect of laying date ($\beta = −0.18 \pm SE 0.06, P = 0.002$) on c-egg size possibly reflected the fact that late breeders were either low quality or inexperienced females. The mass, size, and condition of hatching Herring Gulls were positively related to egg size (all $P < 0.0001$). C-chicks suffered from increased mortality risk during the first 12 d, identified as the brood-reduction period in my study population. Although intraclutch variation in egg size was not directly related to patterns of chick mortality, I found that smaller relative egg size interactively increased differences in relative body condition of nestlings, primarily brought about by the degree of hatching asynchrony during this brood-reduction period. Thus, the value of relatively small c-eggs in Herring Gulls may lie in reinforcing brood reduction through effects on nestling body condition. A reproductive strategy Herring Gulls might have adopted to maintain a three-egg clutch, but that also enables them to adjust the number of chicks they rear relative to the prevailing environmental conditions and to their own condition during the nestling stage.

RESUMEN. Efectos de la variación del tamaño de los huevos dentro de la nidad y la eclosión asincrónica, sobre el desarrollo y la supervivencia de pollos semi-nidifugos de Larus argentatus

La variación en el tamaño de los huevos dentro de la nidad puede no ser el resultado adaptativo como consecuencia de limitaciones nutricionales o energéticas, que actúan sobre hembras en puesta, o puede ser el reflejo adaptativo diferencial en la progenie en relación al orden de la puesta o eclosión. Esta variación puede contribuir a jerarquías de tamaño entre hermanos previamente establecidas debido a la eclosión asincrónica y la competitividad asimétrica resultante usualmente conduce hacia la inanición del polluelo más débil dentro de la nidad. El costo en términos de mortalidad de los polluelos puede ser alto. Sin embargo, la importancia relativa que tiene el tamaño del huevo sobre esta mortalidad aún no es claro, especialmente en relación con la eclosión asincrónica que puede operar de forma concomitante. Evalué los efectos del tamaño del huevo y la eclosión asincrónica sobre el desarrollo y la supervivencia de los pollos de Larus argentatus, en donde los tamaños pequeños y eclosión tardía de huevo-c pueden representar una estrategia de reducción de la progenie. Para analizar la variación del tamaño del huevo registre el orden y la fecha de la puesta de 870 huevos en 290 nidadas de tres huevos a lo largo de un periodo de tres años (2010–2012). Medi pollos y monitoreé el crecimiento y la supervivencia de 130 pollos de nidos cubiertos en el 2011 y 2012. El efecto negativo de la fecha de la puesta ($\beta = −0.18 \pm SE 0.06, P = 0.002$) sobre el tamaño de los huevos-c puede ser un reflejo del hecho de que las aves que se reproducen tardíamente son de baja calidad o son hembras con poca experiencia. La masa, la edad y la condición de los pollos de L. argentatus estuvieron positivamente relacionados con el tamaño del huevo (todos $P < 0.0001$). Los pollos-c sufrieron un mayor incremento de riesgo de mortalidad durante los primeros 12 días, lo cual fue identificado como el periodo de reducción de la progenie en mi población de estudio. Aunque la variación del tamaño del huevo dentro de la nidad no estuvo directamente relacionado con los patrones de mortalidad de pollos, encontré que tamaños de huevos proporcionalmente más pequeños aumentan de manera interactiva las diferencias en la condición corporal relativa de los pollos.

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principalemente promovido por el grado de asincronía durante los periodos de reducción de la progenie. Por lo tanto, el valor relativo de los pequeños huevos-c en *L. argentatus* puede estar reforzando la reducción de la progenie por medio de efectos sobre la condición corporal de los polluelos. Una estrategia reproductiva que *L. argentatus* puede haber adaptado para mantener un tamaño de nidada de tres huevos, pero que también le impide ajustar el número de polluelos que pueden criar relativo a las condiciones ambientales predominantes y a su propia condición durante la etapa de polluelos.

**Key words:** adaptive, body condition, body size, breeding strategy, brood reduction, constraints, investment pattern, *Larus argentatus*

Among birds, egg size varies both among and within clutches. Egg size may be positively correlated with hatching size, mass, condition, and nestling growth rate and survival and, hence, could have important fitness consequences (Christians 2002, Risch and Rohwer 2000, Krist 2011). Although egg size variation between clutches accounts for most observed variation (Christians 2002), intrACLutch variation may affect fitness more than the former because smaller chicks that hatch from smaller eggs must compete with larger siblings during early development (Aparicio 1999, Maddox and Weatherhead 2008). Although the relative size of the egg from which a nestling hatches is known to affect its probability of fledging, the causes of intrACLutch variation in egg size and the nature of the relationships with offspring survival remain unclear (Amat et al. 2001, Hargitai et al. 2005, Whittingham et al. 2007, Maddox and Weatherhead 2008, Forbes and Wiebe 2010, Svagelj and Quintana 2011, Parejo et al. 2012). For instance, intrACLutch variation in egg size could either reflect an adaptive maternal strategy to improve reproductive success or, alternatively, be a non-adaptive consequence of maternal constraints.

If intrACLutch variation in egg size has adaptive value, this variation may be related to laying order and ultimately to the hatching order of offspring (Slagsvold et al. 1984). In this context, parents often start incubating before clutch completion and eggs laid first will then be among the first to hatch (i.e., hatching asynchrony) and, consequently, have a head start on their siblings (Stenning 1996). The resulting size and strength advantage creates a hierarchy among siblings, and the ensuing competitive asymmetries can often initially lead to a poorer relative body condition and ultimately cause the death of the weakest, last-hatched chick(s) in a brood (Kim et al. 2010, Gilby et al. 2011, Merkling et al. 2014). Regardless of the adaptive value of hatching asynchrony (Kim et al. 2010), female birds may adaptively vary egg size to modify the effects of hatching asynchrony (Slagsvold et al. 1984). For instance, an increase in egg size with laying order would counteract competitive asymmetries imposed by hatching asynchrony (brood survival hypothesis, Howe 1978), whereas a decrease in egg size would accentuate competitive differences established by asynchronous hatching (brood reduction hypothesis, Parsons 1970).

Asynchronous hatching and the smaller size of the c-egg of gulls have potential adaptive value because, during periods with unfavorable environmental conditions (e.g., food scarcity), being able to reduce brood size and allocate available resources to fewer young by preferentially provisioning larger, high-quality young may be beneficial (Slagsvold et al. 1984, Stenning 1996, Hilström et al. 2000). However, the results of previous studies of Larids have been contradictory. Comparing synchronous and asynchronous broods, Hébert and McNeil (1999) found reduced survival of c-chicks in asynchronous broods, whereas other investigators have reported either reduced survival of c-chicks in synchronous broods (Sydeman and Emslie 1992, Hillström et al. 2000) or no difference in c-chick survival between synchronous and
asynchronous broods (Royle and Hamer 1998, Bradbury and Griffiths 1999). In addition, the results of several studies have revealed a positive relationship between small c-egg size and increased mortality rate in c-chicks (Parsons 1970, Hébert and Barclay 1986, Risch and Rohwer 2000), whereas other investigators have reported that small terminal egg size did not influence c-chick survival (Nager et al. 2000, Kim et al. 2010). Nevertheless, c-chick mortality can be very high and the extent to which this mortality is egg size-mediated, especially in relation to hatching asynchrony, remains unclear.

My objective was to examine the importance of egg size variation in clutches of a coastal population of Herring Gulls, while simultaneously considering the effect of hatching asynchrony on chick survival because both might operate concomitantly (Maddox and Weatherhead 2008). Of previous studies of Larids, only Kim et al. (2010) modeled the effects of hatching asynchrony and egg size on chick survival simultaneously, but only did so for Herring Gull chicks up to 10 d old. Because most chick mortality in Herring Gulls (Kilpi et al. 1996) occurs before this age, particularly for c-chicks (Hillström et al. 2000), I also examined whether this period coincides with the brood-reduction period, that is, the period post-hatching where offspring mortality most strongly varies with laying order (Mock 1994).

Within a constraints-adaptation conceptual framework, I also examined the extent to which absolute egg size was negatively affected by laying date. In my study population, inexperienced and lesser-quality birds start breeding later in the season (Van Waeyenberghe et al. 2002, D. S. Bosman, unpubl. data). Risch and Rohwer (2000) found that parental quality of Herring Gulls was reflected in the capacity to lay large eggs, and Davis (1975) found that older birds laid larger eggs. Additional objectives were to determine if (1) absolute egg size is positively correlated with one or more absolute measures of individual offspring development (i.e., mass, size, and condition at hatching and nestling growth rate), (2) patterns of intraclutch variation in egg size and hatching asynchrony are directly associated with patterns of chick mortality, (3) intraclutch variation in egg size and hatching asynchrony are indirectly related to nestling survival through effects on relative body condition, and (4) the effect of intraclutch variation in egg size (direct or indirect) encompasses the whole chick-rearing period or is restricted to the brood-reduction period.

METHODS

Field work was carried out during the breeding seasons of 2010–2012 in a mixed breeding colony of Herring Gulls and Lesser Black-backed Gulls (L. fuscus graellsii) at the outer port of Zeebrugge (Belgium, 51°21′N, 03°11′E). Each year, from mid-April until the end of May, I searched selected sub-colonies daily for new nests. New nests were marked with an individually coded stick and visited daily to record laying order. For each new egg, I recorded the laying date, expressed as the number of days after 1 December of the previous year (i.e., the earliest recorded arrival date of a breeding bird in my study population; Bosman et al. 2013). Eggs were measured with calipers (±0.01 mm; maximum length and width) and marked with a non-toxic, water-resistant marker in relation to their laying order (Mock 1994).

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From the end of May until mid-June, enclosed nests were visited daily to record hatching dates. To assign each chick to its egg of origin, egg teeth of chicks were marked with nontoxic ink during the pipping stage. The level of hatching asynchrony of a chick was calculated as the time (in days) elapsed since the hatching of the first chick of the same brood and was set to 0.5 d for eggs that hatched on the same day if there was an unambiguous difference in timing of hatching (i.e., assessed by dry versus still-wet plumage). Because chicks generally hatched in the same order eggs were laid (see results), laying order and hatching order were treated as synonymous. Using laying order in statistical analyses allowed me to differentiate between chicks with a hatching spread of less than half a day.

Once hatched, all chicks were marked with individually coded insulation tape around the tarsus, weighed with a digital balance, and measured every third day. Only individuals measured on the first day of hatching were included in the analyses. Because single trait measures were earlier shown to provide poor proxies of overall body size in gulls (Bosman et al. 2012), I measured tarsus length, head length, bill length, and bill depth of each chick with calipers (±0.01 mm), and quantified body size as the first axis of a principal component analysis (PC1) in SPSS statistics Ver. 21 (IBM Corporation, Armonk, NY). PC1 explained 98% of the body size variation in nestlings and had high positive loadings for tarsus length (0.97), head length (0.99), bill length (0.98), and bill depth (0.98). Chick growth rates were calculated for the period of linear growth as the slope of the linear regression of body size on age (in days) performed in SPSS statistics (Bolton 1991). When calculating growth rates, only chicks that survived until 23 d old and where I had at least four measurements between days 3 and 23 post-hatching were included (Bogdanova and Nager 2008, Hauber and Moskat 2008). Body mass was regressed on body size, and the standardized residuals were used as a measure of body condition (GLM, $r = 0.29$, $P < 0.0001$; Green 2001). Relative body condition was calculated as the deviance from the average body condition of siblings measured on the same day.

To analyze variation in egg size, I only used three-egg clutches because it was impossible to determine if eggs in clutches of one or two eggs had been lost to predation or cannibalism. One four-egg clutch was also excluded from further analysis, resulting in a sample size of 870 eggs from 290 nests for which both laying date and egg size were measured. In addition, hatching order was recorded for 93 nests (Table 1). Because multiple eggs from a single nest are not statistically independent, I fitted a series of linear mixed-effects models (LMM; Littell et al. 1996) in SAS 9.3 (SAS Institute Inc., Cary, NC) with nest-specific (i.e., random) intercepts and slopes and with nest nested in year (Schielzeth and Forstmeier 2009). Absolute egg size was modeled as the dependent variable, laying order (treated as a continuous variable) and laying date and their interaction as fixed effects, and year as random factor. Levels of significance of all fixed variables and their two-way interactions were tested in a stepwise backward selection procedure, and the Kenward–Roger method was applied for estimating the degrees of freedom (not necessarily integers; Kenward and Roger 1997). When laying order significantly interacted with laying date, analyses were split by laying order. To compare group means, post-hoc tests were carried out with Tukey’s tests. To explain variation in hatching size, mass, and condition, I analyzed the effect of laying order, laying date, absolute egg size and their two-way interactions on these traits for 115 hatchlings. I also tested the relationships of these independent variables with growth rates of 75 nestlings.

To analyze how patterns of chick survival (N = 130 chicks) were directly affected by relative egg size and hatching asynchrony, I fitted a mixed-effects Cox regression in R Ver. 2.15.3 (package coxme; Therneau 2012, R Core Team 2014) with laying date, laying order, absolute egg size and their two-way interactions on these traits for 115 hatchlings. To test how patterns of chick survival were indirectly influenced by relative egg size and hatching asynchrony, I applied a three-step procedure. First, I determined the brood-reduction period, defined as the period during which offspring mortality most strongly varied with laying order (Mock 1994). To determine this period, I fitted a series of mixed-effects Cox regressions with a change point (Pons 2003),...
Table 1. Within-clutch variation in timing of egg laying and hatching, and related variation in egg size in a Herring Gull colony. The a-egg is the first-laid, the b-egg the second-laid, and the c-egg the last-laid egg in a clutch. Values of laying and hatching are mean ± SE relative to the laying day of the a-egg (day 0). Values for egg size are mean ± SE.

<table>
<thead>
<tr>
<th></th>
<th>a-egg</th>
<th>b-egg</th>
<th>c-egg</th>
<th>N (clutches)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Laying (d)</td>
<td>NA</td>
<td>2.2 ± 0.04</td>
<td>4.5 ± 0.06</td>
<td>295</td>
</tr>
<tr>
<td>Hatching (d)</td>
<td>0.01 ± 0.01</td>
<td>0.6 ± 0.1</td>
<td>2.1 ± 0.1</td>
<td>93</td>
</tr>
<tr>
<td>Hatching first</td>
<td>92/93</td>
<td>1/93</td>
<td>0/93</td>
<td>–</td>
</tr>
<tr>
<td>Hatching last</td>
<td>0/93</td>
<td>0/93</td>
<td>93/93</td>
<td>–</td>
</tr>
<tr>
<td>Egg size (cm³)</td>
<td>81.46 ± 0.39</td>
<td>79.66 ± 0.41</td>
<td>73.66 ± 0.35</td>
<td>290</td>
</tr>
<tr>
<td>Largest egg size</td>
<td>184/290</td>
<td>103/290</td>
<td>3/290</td>
<td>–</td>
</tr>
<tr>
<td>Smallest egg size</td>
<td>11/290</td>
<td>21/290</td>
<td>258/290</td>
<td>–</td>
</tr>
</tbody>
</table>

*NA, not applicable.

Such models divide data into two discrete time steps, which allowed me to test the effect of laying order on chick mortality during discrete time periods before and after this change point. Because chick survival was monitored daily from hatching to fledging, I shifted the setting of this change point from one Cox regression to the next on a daily basis as well. If brood reduction is restricted to the early period of the nestling stage, I would expect a time step that divides the brood-reduction period (i.e., significant effect of laying order) from the non-brood-reduction period (i.e., no significant effect of laying order; Shizuka and Lyon 2013). Second, I modeled two additional mixed-effects Cox regressions with the change point set at the dividing time step (see Results) to test for relationships between relative body condition and chick survival. In the first model, I tested whether chick survival varied with relative body condition during the brood-reduction period (N = 78 chicks with an average age of 5.4 ± 2.5 [SD] d). In the second model, I tested whether chick survival after the dividing time step/change point varied with relative body condition of the survivors during the non-brood reduction period (N = 60 chicks with an average age of 21.8 ± 6.9 [SD] d). Finally, I ran two LMMs (SAS 9.3) to determine relationships of hatching asynchrony, relative egg size, and the two-way interaction with relative body condition during the brood reduction and the non-brood reduction periods, respectively. In these analyses, I modeled hatching asynchrony and relative egg size as fixed effects (independent of their levels of statistical significance) and laying order as a covariate. Because hatching asynchrony, relative egg size and laying order may be highly correlated, modeling these variables simultaneously might produce problems with collinearity. To determine the severity of the latter among independent variables in my dataset, I used the COLLIN, VIF, and TOL Options (SAS 9.3) to obtain condition indices, variance inflation factors, and tolerance values, respectively, that is, collinearity diagnostics (see Results). Values are presented as means ± SE.

RESULTS

I recorded the laying order and laying date of 870 eggs in 290 three-egg clutches (2010: 122 nests, 2011: 103 nests, 2012: 65 nests). Egg-laying started on 26 April in 2010, 2 May in 2011, and 1 May in 2012. For 93 three-egg clutches (2010: 41 nests, 2011: 36 nests, 2012: 16 nests), I also recorded the hatching date for all eggs. The last egg hatched on 19 June in 2010, 18 June in 2011, and 19 June in 2012. In 2011 and 2012, I monitored survival until fledging (i.e., the latter half of July) for 130 chicks (2011: 86 chicks, 2012: 44 chicks) in enclosed nests (N = 75 nests) where all three eggs hatched. Most chicks that did not survive simply disappeared and were probably predated. In 2011, an unknown proportion of chicks (including near-grown fledglings) died from an unidentified infection. Although I cannot formally analyze it, I have no reason to believe that either predation or disease rates differed between enclosed and non-enclosed nests (pers. obs.). Few chicks died of starvation.

Variation in egg traits. Eggs were laid every second day on average, although both
shorter and longer laying intervals regularly occurred (mean = 2.24 ± 0.03 d, range = 0–7 d). Eggs generally hatched in the order they were laid (Table 1), and hatching asynchrony was significantly related to laying order (LMM, $F_{1,165} = 346.4, P < 0.0001$). Although the timing of hatching differed significantly for a-, b-, and c-chicks (Tukey, $P < 0.0001$), a- and b-chicks often hatched on the same day (56.9%, $N = 93$) and the hatching asynchrony between them was lower than expected from the laying interval (0.63 ± 0.09 d). The laying span between a- and c-eggs averaged 4.48 ± 0.06 d, but the hatching span of 2.06 ± 0.12 d was significantly shorter (paired t-test: $t_{56} = 16.7, P < 0.0001$). Absolute egg size decreased with laying order (LMM, laying order, $\beta = 3.9 ± 0.2, F_{1,584} = 566, P < 0.0001$; Table 1) and a-, b-, and c-eggs differed significantly in size (Tukey, $P < 0.0001$).

When jointly modeling the effects of laying date and laying order on absolute egg size, the two-way interaction was significant (LMM, $\beta = -0.09 ± 0.03, F_{1,582} = 12.3, P = 0.0005$). Splitting the data by laying order revealed a significant negative relationship between laying date and the absolute size of c-eggs ($\beta = -0.18 ± 0.06, F_{1,266} = 9.7, P = 0.002$), but not a-eggs ($\beta = -0.06 ± 0.07, F_{1,154} = 1.0, P = 0.33$) and b-eggs ($\beta = -0.05 ± 0.07, F_{1,288} = 0.5, P = 0.49$). Relative egg size of c-eggs was negatively related to mean egg size of a clutch (GLM, $r = -0.28, P = 0.02$).

**Variation in offspring development.** Hatchling mass was positively correlated with absolute egg size (LMM, $\beta = 0.81 ± 0.09, F_{1,735} = 68.9, P < 0.0001$). The positive sign of the laying date*laying order interaction ($\beta = 0.34 ± 0.11, F_{1,109} = 9.3, P = 0.003$) indicated that the loss in mass with laying date decreased later in the laying sequence. Interactions of absolute egg size with both laying order and laying date were not significant and were therefore removed from the final model (all $P ≥ 0.67$).

Hatchling size increased with absolute egg size (LMM, $\beta = 0.005 ± 0.001, F_{1,109} = 22.9, P < 0.0001$) and decreased with laying order ($\beta = -0.02 ± 0.008, F_{1,852} = 7.1, P = 0.009$), but was not related to laying date ($\beta = -0.001 ± 0.001, F_{1,883} = 1.0, P = 0.32$). None of the two-way interactions between absolute egg size, laying order, and laying date were significant (all $P ≥ 0.39$).

Hatchling condition increased with absolute egg size (LMM, $\beta = 0.07 ± 0.01, F_{1,679} = 28.7, P < 0.0001$). The positive sign of the laying date*laying order interaction ($\beta = 0.04 ± 0.02, F_{1,101} = 5.9, P = 0.02$) indicated that the negative relationship with late laying date decreased with increasing laying order. Two-way interactions of absolute egg size with laying order and laying date were not significant (all $P ≥ 0.83$).

Hatchling growth was inversely related to laying date (LMM; $\beta = -0.0008 ± 0.0004, F_{1,434} = 4.0, P = 0.05$), but was not influenced by either absolute egg size ($\beta = 0.0002 ± 0.0004, F_{1,662} = 0.2, P = 0.7$) or laying order ($\beta = 0.003 ± 0.003, F_{1,515} = 0.7, P = 0.39$). Two-way interactions were not significant (all $P ≥ 0.10$).

**Variation in offspring survival and relative body condition.** I assessed the degree of correlation between the predictor variables in the following models using a collinearity analysis. However, there is no formal criterion for determining a threshold value for the condition index (CI), the tolerance value (TOL), or the variance inflation factor (VIF). Conventionally, a CI greater than 30, a TOL less than 0.1, or VIF greater than 10 roughly indicates significant and high multi-collinearity (Jeeshim and KUCC625 2003). Collinearity diagnostics revealed no severe symptoms of collinearity among independent variables in my dataset (all CI ≤ 9.6, all TOL ≥ 0.4, all VIF ≤ 2.9).

Nestling mortality increased with laying order (mixed-effects Cox regression; $Z = 3.3, P = 0.0008$), but I found no effect of laying date ($Z = 1.6, P = 0.10$), hatching asynchrony ($Z = -0.1, P = 0.91$), or relative egg size ($Z = -0.03, P = 0.98$) on nestling mortality. None of the two-way interactions were significant (all $P ≥ 0.24$). When fitting mixed-effects Cox regressions with a change point (Table 2), laying order predicted chick survival during the first 12 d after hatching (to the left of the dashed line in Fig. 1; $Z = 3.0, P = 0.003$), but no such relationship occurred during the period between 12 d post-hatching and fledging ($Z = 1.2, P = 0.23$; Fig. 1).

During the brood-reduction period (first 12 d post-hatching), chick mortality tended to be negatively related with relative body condition ($Z = -1.9, P = 0.06$). A significant positive interaction between hatching asynchrony and relative egg size (LMM, $\beta = 0.03 ± 0.01$,
Table 2. Results of a mixed-effects Cox regression with change point on survival rates of Herring Gull nestlings. For each model, I tested the effect of laying/hatching order on chick survival before and after the change point. Day 12 is the earliest point at which I detected a switch between laying/hatching-order-based survival to laying/hatching-order-independent survival. Only the results for the period from 8 to 14 d post-hatching are shown. Bold data indicate significant p-values.

<table>
<thead>
<tr>
<th>Change point</th>
<th>Before change point</th>
<th>After change point</th>
</tr>
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<tbody>
<tr>
<td></td>
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<td>P</td>
</tr>
<tr>
<td>Day 8</td>
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<tr>
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<tr>
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</tr>
<tr>
<td>Day 12</td>
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</tr>
<tr>
<td>Day 13</td>
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</tr>
<tr>
<td>Day 14</td>
<td>3.1</td>
<td>0.002</td>
</tr>
</tbody>
</table>

Fig. 1. Laying/hatching order effect on chick survival over time in a Herring Gull colony (N = 130 chicks). Kaplan–Meier curves demonstrate that chick survival varied with the laying/hatching order, with b- and (especially) c-chicks showing lower survival probabilities. Although this effect was evident before day 12, chicks that survived the brood-reduction period (first 12 d post-hatching as indicated by the dashed line) had equal probability of survival afterward.

$F_{1,47} = 7.5, P = 0.009$ on relative body condition further indicated that the negative effect of increasing hatching asynchrony (Fig. 2A) was strengthened by a smaller relative egg size. Relative body condition decreased with laying order ($\beta = -0.25 \pm 0.08, F_{1,47} = 11.5, P = 0.001$; Fig 3A).

After the brood-reduction period (first 12 d post-hatching), chick mortality was not affected by relative body condition ($Z = 0.8, P = 0.43$). Relative body condition improved with increasing hatching asynchrony ($\beta = 0.18 \pm 0.07, F_{1,43} = 8.4, P = 0.008$; Fig 2B), whereas relative egg size ($\beta = 0.03 \pm 0.02, F_{1,42} = 1.6, P = 0.22$) and the interaction between hatching asynchrony and relative egg size did not explain additional variation ($\beta = 0.0007 \pm 0.0234, F_{1,40} = 0.01, P = 0.98$). In addition, relative
Fig. 2. Changes in competitive asymmetries within broods as reflected by the relative body condition of Herring Gull nestlings (A) during and (B) after the brood-reduction period (78 and 60 chicks, respectively). Plots show individual body conditions as deviance from mean body conditions in a brood on a given day. Chicks from any given brood are measured on the same day. Trendlines with 95% confidence bands are shown, but statistical analyses incorporated nest as a random effect. (A) During the brood-reduction period, relative body condition declined with increasing hatching spread/asynchrony. (B) After the brood-reduction period, relative body condition improved with increasing hatching spread/asynchrony.

body condition did not vary with laying order ($\beta = 0.28 \pm 0.19$, $F_{1,41} = 2.3$, $P = 0.14$; Fig. 3B).

**DISCUSSION**

My results revealed consistent intrACLutch variation in egg size with laying order in Herring Gulls, with c-eggs being smallest in most (89%) clutches. B-eggs were similar in size to a-eggs in many clutches, and were the largest eggs in 35% of all clutches. The negative effect of laying date on absolute size of c-eggs in my study suggests that many late breeders may have been low quality or inexperienced females more limited in their breeding effort. Laying smaller eggs is assumed to reflect lower individual quality in gulls, that is, reduced foraging efficiency due to limited competitive abilities (Bolton 1991, Risch and Rohwer 2000). Likewise, reduced foraging efficiency due to a learning curve effect and lack of previous breeding experience of younger birds (not necessarily of lower quality) might also negatively influence their body condition (nutritional and energetic reserves) and reduce their reproductive investment (Sydeman and Emslie 1992). In gull species in particular, nutritional and energetic demands of egg formation are believed to be relatively high because egg size is about 15.6% of adult body size and energy requirements of egg laying reach 170% of their basic metabolic rates (Ricklefs 1974).

Female Herring Gull use stored lipids for egg production to a large extent (Hario et al. 1991). For late breeders that may be more energy-limited due to inexperience or poor body condition, these reserves probably cannot be replenished in time for production of the c-egg because delayed laying has costs related to a seasonal decline in reproductive success (Brouwer et al. 1995). Furthermore, intrACLutch egg size variation, and particularly the relative size of the c-egg, has previously been shown to reflect energetic and nutritional constraints in other species of gulls (Pierotti and Bellrose 1986, Bolton et al. 1992, Sydeman and Elsmie 1992, Kilpi et al. 1996).

My results provide additional empirical evidence that the mass, size, and condition of hatchling Herring Gulls are positively related to egg size. Egg size has previously been shown to be an important measure of egg “quality” in Herring Gulls and other bird species, probably
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because larger eggs contain more nutrient reserves for chicks during embryonic development (Parsons 1972, Hébert and Barclay 1986, Risch and Rohwer 2000, Krist 2011). In contrast, I found no significant relationships between egg size and growth rates of nestlings. Significant positive correlations are often found between egg size and nestling growth rates (Williams 1994, Krist 2011). However, Viñuela (1997) found no such relationship in nestling Black Kites, and argued that the effect of egg size on nestling growth could have been masked by other factors such as hatching order, feeding rate, type of food, or laying date.

Hatchling growth rates were inversely related to laying date in my study. Growth rates of young Herring Gulls have previously been shown to reflect parental quality through variation in the amount or quality of food provisioned (Risch and Rohwer 2000), possibly related to laying date because inexperienced or low-quality individuals may initiate clutches later (Bogdanova et al. 2007).

Is intraclutch variation in egg size adaptive in Herring Gulls? Despite the negative relationship between laying date and c-egg size, the small relative size of the last-laid egg in my study was likely not the sole result of energetic and nutritional constraints on late-laying inexperienced or lesser-quality female Herring Gulls because small terminal egg size should then have been more marked in females laying smaller eggs, reflecting their more limited reserves available for reproduction (see above; Pierotti and Bellrose 1986, Kilpi et al. 1996, Viñuela 1997). To the contrary, I found an inverse relationship between a clutch’s mean egg size and the relative size of c-eggs in my study population. This was unexpected because Parsons (1976) reported that female Herring Gulls that laid larger eggs also laid the most similarly sized eggs. However, Parsons (1970, 1972, 1976) also noted that Herring Gulls apparently have a lower size limit for eggs, below which hatchability abruptly drops, so very small eggs are not laid. In addition, Kim et al. (2010) argued that smaller eggs might be more vulnerable to suboptimal conditions such as exposure to cold temperature during periods of neglect. If so, c-eggs may need to exceed a minimum size threshold to be viable, and this may explain why females laying smaller-sized...
three-egg clutches might have been more limited in the degree to which they could reduce the relative size of their small terminal egg.

The relative body condition of c-chicks in my study was negatively impacted by an interaction between hatching asynchrony and relative egg size. Increasing hatching asynchrony reduced the relative body condition of c-chicks, particularly for c-chicks that hatched from smaller eggs. Furthermore, the relative body condition of nestlings in my study was positively related to their probability of survival during the first 12 d post-hatching and c-chicks had the highest mortality rates. Similarly, Hillström et al. (2000) reported a lower survival rate of c-chicks in Herring Gulls during the first 10-d post-hatching (see also Kilpi et al. 1996, Kim et al. 2010). This pattern is highly consistent with a brood-reduction strategy, that is, reduction of the survival probability of last-hatched chicks by laying relatively small final eggs (Slagsvold et al. 1984). After this brood-reduction period, however, relative body condition was no longer related to egg size, but was still related to hatching asynchrony, suggesting a longer-lasting effect of the latter.

My results suggest that the three-egg clutches of Herring Gulls, with smaller c-eggs, allow parents to adjust the number of chicks reared during the nestling stage (Slagsvold et al. 1984). Given some variation based on laying date, female Herring Gulls could, when sufficient food is available, reduce the degree of hatching asynchrony by delaying the onset of effective incubation (Kim et al. 2010) and, by doing so, increase the likelihood of the c-chick surviving the first 12 d post-hatching. However, when food is scarce, initiating effective incubation sooner likely increases the likelihood that c-chicks will die, allowing parents to direct more food to the surviving chicks and maximize their reproductive success relative to prevailing environmental conditions and to their own breeding condition (Slagsvold et al. 1984).

I found that the relative body condition of chicks only influenced nestling survival during the brood-reduction period whereas the degree of hatching asynchrony appeared to affect relative body condition throughout the nestling period. Although increased hatching asynchrony had a strong negative effect on relative body condition during the brood-reduction period, it affected relative body condition positively afterwards, albeit less strongly, but still to an extent that c-chicks were in the same or slightly better condition than a- or b-chicks. Although the latter result sounds counterintuitive, parents may allocate more food to c-chicks after they have survived the brood-reduction period, as recently observed in American Coots (Fulica americana) where late-hatched survivors equaled or exceeded their older siblings in size prior to independence because they received more food from parents (Shizuka and Lyon 2013).

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