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Mismatching between nest volume and clutch volume reduces egg survival and fledgling success in black-tailed gulls

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Abstract

A longstanding suggestion posits that parents prefer to match nest volume and clutch size (clutch volume), but few studies have tested this in colonial seabirds that nest in the open. Here, we demonstrate the effects of nest–clutch volume matching on egg survival, hatching, and fledgling success in black-tailed gulls *Larus crassirostris* on Hongdo Island, Korea. We show that the volume mismatch, defined as the difference between nest volume and total egg volume (the sum of all eggs' volume in the clutch), was positively related to egg and chick mortality caused by predation, but was not significantly related to hatching success incurred by insulation during the incubation period. Although nest volume was negatively related to laying date, we found that the mismatch was positively related to laying date. Our results support the claim that well-matched nest–clutch volume may contribute to survival of eggs and chicks, and ultimately breeding success.

Key words: black-tailed gulls, clutch size, egg survival, fledgling success, nest volume.

Natural selection maximizes fitness by acting on life-history characteristics that involve trade-offs (Roff 2002). Optimal resolution of trade-offs is contingent on environmental conditions (Arlt and Part 2007) such that mismatches between parental reproductive decisions and the optimum under particular environmental conditions could have negative fitness consequences (Visser et al. 1998; Kotiaho 2001; Dunn et al. 2011). Thus, decisions that are made during one stage of reproduction have important consequences for subsequent stages of the same reproductive event.

Parent birds must allocate acquired or accumulated resources to costly reproductive activities, such as migration to breeding habitat, nest building or laying eggs (Stearns 1992). The costs might be optimized by parents laying the size of clutch which maximizes their individual recruitment of offspring (i.e., individual optimization hypothesis; Perrins and Moss 1975). Parents should select for the optimal level of reproductive investment in a given environment.

Nest building is such a costly reproductive activity (Mainwaring and Hartley 2013; Deeming and Mainwaring 2015). Several studies have suggested that nest construction may reflect trade-offs between

nest qualities (benefits) such as insulation to keep eggs or chicks warm (Sclurine and Kern 1980; Mainwaring et al. 2014), and costs such as predation risk during nest building due to nest conspicuousness (Slagsvold 1984; Mainwaring et al. 2015). These costs may vary in space and time (Cresswell et al. 2004). For example, birds in high-predation nesting areas may choose to limit insulation in order to decrease conspicuousness (Møller 1990). Furthermore, nest-building behavior is also associated with breeding behavior and pair formation in birds because males can usually use nest sites and nest material to attract a mate (Collias and Collias 1984; Hansell 2000).

In a similar manner, individuals could adjust nest volume and clutch size (as well as clutch volume) to each other as appropriate to the environment (Møller et al. 2014). According to previous studies, there may be two possible costs associated with mismatched nest volume and clutch size. First, unstable insulation condition (i.e., flexible temperature) caused by the mismatched volume may negatively affect embryo development and consequently reduce hatching success (Vleck and Kenagy 1980) or delay hatching (Boersma 1982), both of which have negative effects on the early growth of chicks

(DuRant et al. 2010). Soler et al. (2001, 2007) suggested that nest building could be used to assess parental quality because the difference between nest size (nest volume) and clutch size could alter insulation (Williams 1996) and therefore impact embryonic development (Webb 1987; Møller 1984). Second, high nest volume relative to clutch size may attract higher predator pressure (e.g., Weidinger 2004). Møller (1990) found that in blackbirds *Turdus merula*, a larger volume mismatch, i.e., a larger spatial gap between the nest walls and eggs, has been shown to cause a higher rate of predation because a small number of eggs in large nest may be well revealed exposed to predator (also see Weidinger 2004). However, in colonial seabirds with open nests, such as gulls, it is unclear whether well-matched nest volume and clutch size will offer reproductive benefit (e.g., higher hatching success or reduced mortality) or what the relative importance of incubation and nest conspicuousness are.

The hypothesis that well-matched nest volume to clutch size (or volume) is advantageous (Collias and Collias 1984) has never been tested in colonial seabirds as ground-open nesters. Unlike passerine birds that usually develop in nests over a long period (altricial species), seabirds mainly need nests for laying and incubating eggs and early growth period posthatching (precocial species; Schreiber and Burger 2002; Starck and Ricklefs 1998). Therefore, we expected that the effects of well-matched nest volume to clutch size on incubation performance (i.e., egg survival) may be greater than the effects on early growth or survival after hatching. We test this hypothesis in a population of black-tailed gulls *Larus crassirostris* on Hongdo Island, Korea. We predict that well-matched nest volume with clutch volume will increase egg survival and fledgling success.

Materials and Methods

Species and study area

Black-tailed gulls *L. crassirostris*, one of the most common seabirds in Korea (Lee et al. 2010), breed colonially on island or rocky cliffs and forage for food (e.g., fish, bait, and fishermen's garbage) near their breeding areas (Kwon 2004). They build an open nest on the ground either in the open or on vegetation. They line the nest with grass, weeds, and feathers. Sedge *Carex boottiana* is the most common nesting material (Lee et al. 2006). The clutch, which normally consists of 1–3 eggs (mean clutch size is 1.9 ± 0.6, Kwon 2004), was laid in the middle of April–early May, and the incubation period lasts for approximately 28 days. Both sexes participate in nest building, incubation, brooding, and feeding of chicks.

During the breeding season (April–August) in 2003, this study was carried out on Hongdo Island, Gyeongsangnam-do, Korea (34°31'87"N, 128°43'88"E). The island is located 23 km from the mainland. The highest point of the island is 115 m above sea level and the area is 9.84 ha. Cliffs with a slope of over 45° surround the coastline (Kwon 2004). There are 2 different habitats on the island: grass and rocky cliff (Lee et al. 2008). The rocky-cliff habitat occurs on the outside margin of the island and consisted of granitic cliff and soil, whereas the grass habitat on the island is in the center of the island. The grass habitats are mainly composed of sedge, but also include other plants, mainly Japanese camellia *Camellia japonica*, cactus pear *Opuntia ficus-indica*, aster *Aster spathulifolius*, and dandelion *Taraxacum mongolicum*. There is a nesting population of black-tailed gulls on the island numbering around 20,000 breeding pairs, which is the largest colony in Korea (Lee et al. 2005). Potential nest predators are a breeding pair of Peregrine falcons *Falco peregrinus*, neighbor gull adults, and a feral cat *Felis catus*

(Lee et al. 2005). During the breeding season (April–July) in 2003, the mean temperature was 19.7 ± 2.8 °C and the mean precipitation was 56.1 ± 9.9 mm (Korea Meteorological Administration 2003).

Measurement of nest volume

On 7 April 2003, we began to check marked nests used during the last breeding season (2002) to find signs (e.g., scraped ground or vegetation, gathered weed) of nest building every day. A nest was considered complete when scraped ground was fully covered by materials such as weeds and the gulls laid their first egg (average time to first egg $= 6.2 \pm 0.8$ days after nest completion). Once the nest building was completed, we measured the smallest diameter (centimeter), largest diameter (centimeter), and depth of the nests (centimeter) to the nearest 0.5 cm (Figure 1). We calculated nest volume (cubic centimeter) after Møller (1982),

$$\text{Nest volume} = \frac{4}{3}\pi\left(\frac{1}{2}a\right)\left(\frac{1}{2}b\right)hx = \frac{1}{3}\pi abhx \qquad (1)$$
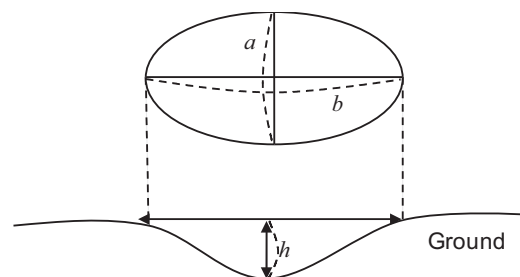
where a is the smallest and b is the largest diameters (centimeter) of the ellipsoid, h is the height (nest depth), and x is a fraction (nest shapes were approximated as a quarter of an ellipsoid, $x = 0.25$; see Soler et al. 1998; Figure 1).

Breeding performance

We visited 128 nests at the same time every day and recorded laying date once we found an egg. All eggs were marked using a permanent pen and weighted with an OHAUS portable scale to the nearest 0.05 g. The length and breadth of each egg were measured with a caliper to the nearest 0.01 mm. Egg volume was calculated as:

$$\text{Egg volume} = 0.476 \cdot LB^2 \qquad (2)$$

where L is the length and B is the breadth (Harris 1964, Tomita et al. 2009). Volume mismatch is defined as *nest volume – total egg volume*. We recorded clutch size (total number of egg laid at first clutch), which can be used as an indicator of female investment to reproduction (Møller 1982). We recorded the hatching date and banded all hatchlings, first with a color ring on the tarsus for identification, and then replaced the color ring with a metal ring with a unique number 2 weeks later. Hatching success was calculated as hatched eggs divided by laid eggs. We visited nests every day to check egg or chick survival and recorded the date and cause of mortality (e.g., predation, disappear, or starvation, etc.). If a chick disappeared when we visited a nest, we revisited the next day. The chick was recorded as a failed fledgling if the chick was not in the nest for next 3 days. We calculated fledgling success, defined as the

Figure 1. Illustration of measuring nest volume (*a* is the smallest diameter and *b* is the largest diameter [in centimeters] of the ellipsoid, and *h* is the height [nest depth]).

proportion of successful chicks, those which survived until 15 days after hatching.

Statistical analysis

In order to examine how habitat type, laying date, and clutch size were related to nest volume and the difference between nest volume and total clutch volume (sum of all eggs' volume in the clutch), we used linear mixed effect (LME) models with habitat type (rocky cliff or grass) as a fixed effect and laying date (1 = 1 April 2003) and clutch size as covariates, plus all interactions among variables. We ran separate analyses using nest volume and volume mismatch (nest volume – total egg volume per each clutch) as the response.

To assess the spatial gap between nest volume and total clutch volume, we first calculate the difference between nest volume and total clutch volume. To examine the association between the volume mismatch and variables describing breeding success (egg survival [related to egg predation], egg hatching [related to insulation], or chick survival in early life), habitat type (rocky cliff or grass) was included as independent factor in separate binary logistic regressions.

All means are presented with standard errors and all analyses were performed using R version 3.2.2 (R development core team 2015). All field works were performed under the permission of The Cultural Heritage Administration of Korea.

Results

A total of 128 pairs laid 252 eggs during the breeding season of 2003. On average, the first egg in each sampled nest was laid on 15 April 2003; mean (± standard error [SE]) clutch size was 1.97 ± 0.05 eggs. Mean nest volume was $402.62 \pm 14.12 \, cm^3$. Mean single egg volume was $66.90 \pm 0.99 \, cm^3$, and mean total clutch volume was $128.46 \pm 3.02 \, cm^3$. The significant predictors of nest volume were laying date (Figure 2A) and clutch size (Figure 2B; Table 1).

Mean volume mismatch was $274.15 \pm 13.61 \, cm^3$. The volume mismatch was positively related to laying date (Table 2; Figure 3). However, there were no significant effects of habitat type, clutch size, and all interactions on nest volume (Table 2).

During the breeding season in 2003, hatching and fledgling success were 0.73 ± 0.03 and 0.60 ± 0.04, respectively. The probability of a nest having at least 1 egg preyed on was strongly positively related to volume mismatch ($\beta = -0.007$, $\chi_1^2 = 19.016$, $P < 0.001$; Figure 4A): the probability of egg survival was higher when the volume mismatch was lower, i.e., clutch volume was well matched to the nest volume. However, there was no significant effect of the volume mismatch on hatching success ($\beta = 0.006$, $\chi_1^2 = 2.818$, $P = 0.093$). Similarly, the proportion of fledglings from chicks hatched (chick survival early in life) was strongly and negatively related to the volume mismatch ($\beta = -0.007$, $\chi_1^2 = 11.073$, $P = 0.001$; Figure 4B): there was lower proportion of fledglings when the mismatch was higher, i.e., when clutch volume was poorly matched to the nest volume.

Discussion

Our results show that there was higher egg survival and proportion of fledglings from chicks hatched when parents had nest volume that match the volume of their clutches. Parents laying eggs earlier built larger nests than parents laying eggs later. In addition, the

spatial gap between nest volume and total clutch volume was smaller in parents laying eggs earlier.

We have highlighted that mismatching between nest volume and total clutch volume had negative impact on both egg and fledging survival related to predation. Weidinger (2004) found that increasing nest size (keeping the same artificial clutches, original nest replaced by nest of the larger species) was positively related to predation, whereas predation was declined when decreasing nest size
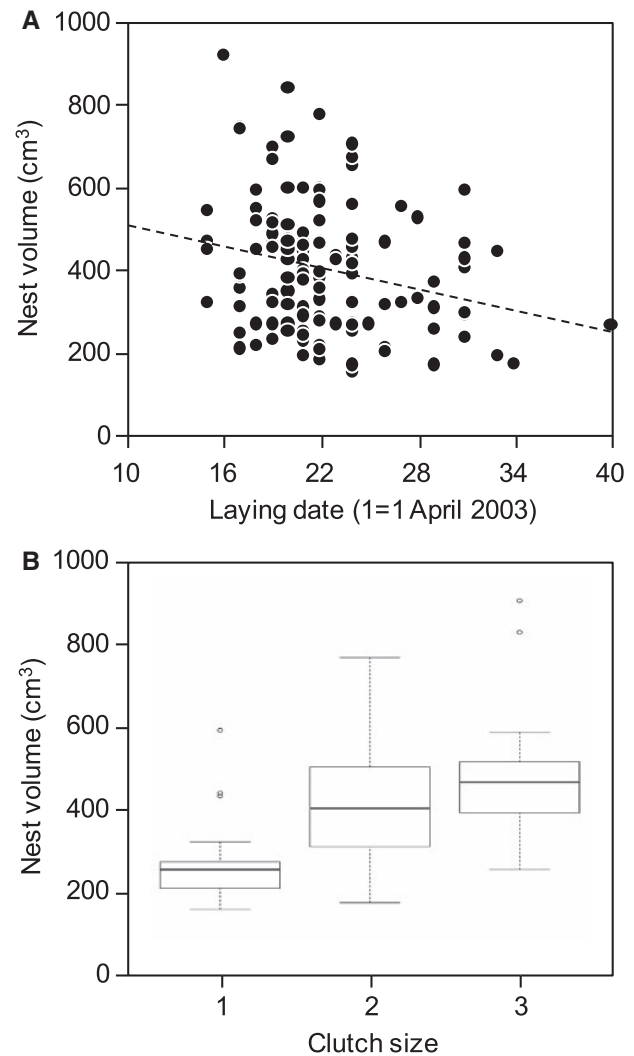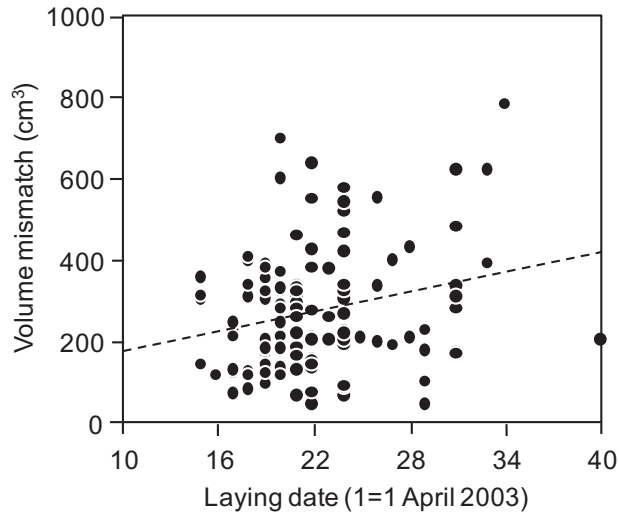

Figure 2. Relationship between nest volume and (A) laying date (1 = 1 April 2003) or (B) clutch size in black-tailed gulls. Nest volume was measured once nest building was completed at the onset of breeding season in 2003.

Table 1. The LME models for final nest volume as a function of habitat type (rocky cliff or grass) as a fixed effect, covariates of laying date (1 = 1 April 2003) and clutch size, plus all interactions

Model	F	df	P
Habitat type (rocky cliff or grass)	0.24	1, 119	0.623
Laying date	15.78	1, 119	<0.001
Clutch size	9.67	1, 119	0.002
Habitat type × laying date	1.01	1, 119	0.316
Habitat type × clutch size	2.13	1, 119	0.147
Laying date × clutch size	0.22	1, 119	0.643
Habitat type × laying date × clutch size	0.40	1, 119	0.529

Table 2. The LME models for volume mismatch as a function of habitat type (rocky cliff or grass) as a fixed effect, covariates of laying date (1 = 1 April 2003) and clutch size, plus all interactions
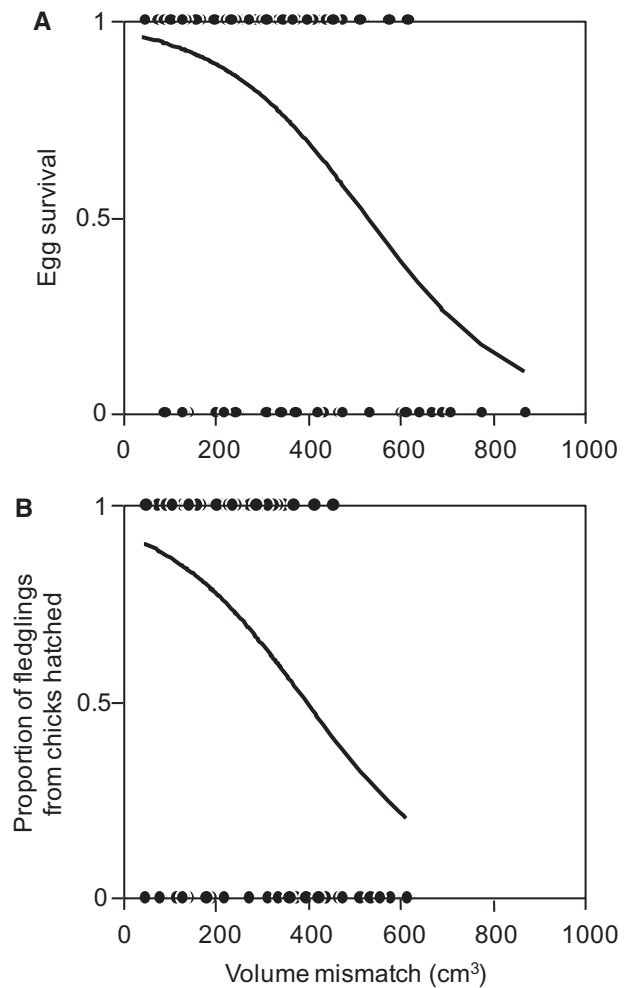
Model	F	df	P
Habitat type (rocky cliff or grass)	0.29	1, 119	0.591
Laying date	3.51	1, 119	0.049
Clutch size	0.86	1, 119	0.357
Habitat type × laying date	0.15	1, 119	0.702
Habitat type × clutch size	0.07	1, 119	0.785
Laying date × clutch size	0.18	1, 119	0.674
Habitat type × laying date × clutch size	0.01	1, 119	0.925

Figure 3. Relationship between laying date and volume mismatch. Nest volume was measured once nest building was completed at the onset of breeding season in 2003.

Figure 4. Logistic regression of (A) probability of egg survival ($n = 127$; 0 = eggs preyed on or 1 = eggs not preyed on, regardless of hatching success) and (B) proportion of fledglings from chicks hatched (chick survival by 15 days posthatching; $n = 104$; 0 = at least 1 chick died from predator or attack by neighbor adults or 1 = all chick survived) in black-tailed gulls in relation to volume mismatch. Probabilities were calculated using the formula: (A) Pr(egg survival) $= 1(1 + \alpha)$, where $\alpha = \exp(3.334 - 0.007*$volume mismatch), and (B) Pr(chick survival in early life) $= 1/(1 + \alpha)$, where $\alpha = \exp(2.508 - 0.007*$volume mismatch).

(replacement by nest of the smaller species), suggesting larger gap between nest size and egg volume may have potential effects on predation risk. Similarly, Møller (1990) showed that the rate of nest predation in blackbirds *T. merula* was significantly larger in the group with increased nest size with fixed clutch size. These support that it is especially true of open nests that are exposed to predators (Collias and Collias 1984; Schreiber and Burger 2002), where if there were a small number of eggs or young chicks in large nest or overabundance eggs in small nest. In this study, we had no data of the body volume of hatched chicks, but the gap between nest size and chick volume may be parallel with the gap between nest size and total clutch mass because it is well documented that larger eggs produced hatchlings that were both heavier and larger (Schreiber and Burger 2002; Dzialowski and Sotherland 2004). In previous studies (Lee et al. 2006, 2010), we showed that black-tailed gulls preferred nests that were more concealed by vegetation and so benefits of vegetation were related to chicks' survival as a shelter. In addition, young (usually, <5 days after hatching) chicks in black-tailed gulls crouched motionless on their nest instead of running to a shelter because the color pattern of chicks' fluffy down (soft feather) provide excellent camouflage (Kwon 2004). Therefore, our results here suggest that larger spatial gap between nest volume and total clutch volume as a visual cue increases probability of egg and chick predation.

It is known that parents of higher quality and greater breeding experience in seabirds arrive early on breeding islands to select nest sites

with specific physical factors that are associated with higher breeding success (Lack 1968; Cézilly and Quenette 1988). Thus, the positive relationship between laying date and the volume mismatch may imply that higher quality parents with greater breeding experience in black-tailed gulls built well-matched nests with their clutch volume (highly closeness of volume matching between nest and egg/chicks). In addition, the physiological condition of females before laying and breeding may affect the degree of volume matching between nests (as experience) and clutches (as condition) because the determination of clutch size by females in several hole nesting birds is apparently affected by available space for the future chicks (see Murphy and Haukioja 1986 for a review). Hongdo Island has two major habitat types with different consequences for breeding gulls: the rocky cliffs with higher clutch size and earlier laying date, and the grassy areas with lower clutch size and later date (Lee et al. 2008). However, there was no effect of habitat types on egg survival. This result suggests that the matching is probably one of the defensive strategies selected by parents for increasing survival of eggs.

Many studies have suggested that the volume mismatch between nest size and clutch size could reduce hatching success through unstable insulation condition (Slagsvold 1982, 1989; Grubbauer and Hoi 1996; Vergara et al. 2010). However, we found that volume mismatch was not related to hatching success. To prevent egg cooling causing negative effect on embryo development (ultimately, hatching success), in general, parents can modify how long they stay away from the nest to rewarm eggs (Williams 1996; Deeming and Mainwaring 2015), lined the nest with insulating materials, or improve the nest thickness (Reid et al. 2002). If there was not enough material at the beginning of the breeding season (appropriate vegetation does not grow well until the hatching period; Kwon 2004), parental efforts to line the nest and improve nest thickness might have less of an effect than cooling during parents' foraging trips on hatching success in black-tailed gulls, but further studies are needed.

In conclusion, this study showed that the well-matched nest and total clutch volumes could lead to better egg survival and fledging success in open nested seabirds, though the direct mechanisms underlying these effects remain unclear. In black-tailed gulls, especially, the matching between nest volume and total clutch volume has been more related to defense against predation than the insulation during the incubation period because open nest may be not good for keeping eggs warm in the first place (poor insulation; e.g., Pinowski et al. 2006). Moreover, we showed a negative relationship between laying date and nest volume, but a positive relationship between laying date and volume mismatch, suggesting that nest volume and the degree of volume matching could be related to parental condition during breeding. Soler et al. (1998) and Møller (2006) found that female barn swallows Hirundo rustic preferred long-tailed males and that these males built larger nests. Recent studies (e.g., Lambrechts et al. 2012) showed the links between phenotypical quality of the building parents and the size of their nests; experimental work would be required to demonstrate how parental physiological condition is related to the difference between nest volume and clutch volume.

Acknowledgments

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