EGG PREDATION IN THE HERRING GULL Larus argentatus: WHY DOES IT VARY SO MUCH BETWEEN NESTS?

ALEWIJN BROUWER & ARIE L. SPAANS

Abstract We studied egg loss in Herring Gulls Larus argentatus on the Dutch Frisian Island of Terschelling. Conspecific egg predation was the main cause of egg loss. Late breeding, a small inter-nest distance and a low vegetation cover enhanced egg predation. Predation was more frequent in nests with small eggs than in nests with large eggs. The effect of egg volume on predation was experimentally investigated by exchanging clutches between pairs. Increasing differences in egg size between original and adopted clutches increased progressively the predation rate. Egg predation was strongly correlated to the original clutch volume (control and experimental pairs combined). No correlation was observed between egg predation and the volume of the adopted clutches. This excludes a possible predator-linked selection mechanism. It is suggested that lower quality birds not only lay smaller eggs but also exhibit less efficient parental care during the incubation period, resulting in an increased predation risk.

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INTRODUCTION

In many large Larus gulls, predation of eggs and chicks by conspecifics is a common cause of egg and chick loss (e.g. Brown 1967, Parsons 1971, Burger 1984). Cannibalistic behaviour is particularly severe in areas with a high nest density, thus favouring less densely populated colonies with larger territories (Pierotti 1982, Burger 1984). Since egg and chick predation is often prevalent, it can have important consequences for the total reproductive output of gulls.

We studied egg predation in Herring Gulls L. argentatus in a large mixed colony of Herring and Lesser Black-backed Gulls L. fuscus in The Netherlands. The study was originally initiated to establish a causal relationship between laying date and chick survival (Brouwer et al. 1995). For that study we exchanged complete clutches of three eggs between pairs which had started egg-laying at different dates. We used the data of egg predation on experimental and control clutches to investigate the effects of laying date, vegetation cover, nest density and egg volume on predation risk.

We also used the adopted clutches to determine whether the negative relationship we found between predation rate and clutch volume was due to predator selection or to the fact that clutch volume was linked to the care behaviour of the parents. In the first case we would expect a correlation between predation rate and the volume of the clutches as measured after the exchange (new clutch volume). In the second case we would expect predation rate to be correlated to the volume of the clutches as measured before the manipulation (original clutch volume). If both predation selection and care behaviour play a role, we would expect predation rate to be correlated to both the new and the original clutch volume.

STUDY AREA AND METHODS

The study was conducted in the Boschplaat nature reserve (4400 ha) on the eastern part of the Dutch Frisian Island of Terschelling. The reserve consists primarily of a series of low undulating dune complexes surrounded by saltmarshes, which are intersected by large tidal creeks. The dunes are
predominantly covered with marram grass *Amphiphila arenaria* and sea buckthorn *Hippophaë rhamnoides*, with local patches of lyme grass *Solanum dulcamare* and elder *Sambucus nigra*. The dunes are interspersed with small grassy valleys dominated by sea couch *Elymus pycnanthus*. Herring Gulls breed mainly in the dunes, while Lesser Black-backed Gulls nest predominantly in the valleys. The number of Herring Gulls on the island increased from 6000-8000 pairs in the late 1960s to 21,000-21,500 pairs in the early 1980s. From 1985 to 1990 numbers decreased to 15,800 pairs. Approximately 7 ha of typical nesting habitat used by Herring Gulls was selected as a study area (see Spaans et al. 1987, for further descriptive and topographical details of the study area).

From late April to late June 1990, the study area was searched for new clutches in such a way that the entire area was covered at least once every two days. During the laying and hatching stages, nests were checked daily. Each nest was marked with a small numbered stick as soon as the first egg was found in the nest. Eggs were individually marked a, b, and c, according to their laying sequence. Maximum length and width of the eggs were measured to the nearest 0.1 mm, using vernier callipers. Egg volume (V in cm³) was calculated using the formula: \[ V = 0.5035 \times \text{length} \times \text{width}^2 \] (Spaans & Spaans 1975).

Vegetation cover around each nest was scored on a scale from 1 (no, or hardly any cover around nest) to 5 (tall vegetation completely covering the nest). Vegetation cover depended mainly on the plant species present around the nest; vegetation growth during the season had little effect on the cover score. At the end of the egg-laying season, the inter-nest distance of each nest was calculated by averaging the distance from the three closest neighbours (Burger 1984). In doing this, we made no distinction between Herring and Lesser Black-backed Gulls.

For the purpose of a study on the effect of laying date on chick survival, 92 clutches of three eggs were exchanged between pairs. The difference in laying date between each set of pairs was six days. Exchange took place shortly after the last pair of each set of pairs had completed egg-laying. In 75 control nests, eggs were removed for approximately five minutes, which was as long as it took to exchange clutches from experimental pairs. In half of the control nests, eggs were temporarily removed just after clutch completion, whilst this was done six days later in the other half. Nests were never left empty, but were temporarily filled with three hard-boiled Herring Gull eggs. Experimental and control nests were chosen randomly.

Predation was scored from the moment of manipulation (exchange or temporary removal of clutches). This implies that during the experiment, half of the experimental and control groups was exposed to predation for 26 days (incubation period after the laying period), and half of the groups for 20 days. So the 167 clutches can be divided into four categories: control clutches exposed for 20 (CA) and 26 days (CB), respectively, and experimental clutches exposed for 20 (EA) and 26 days (EB), respectively.

For a statistical analysis of the data we used linear and logistic regression with a stepwise backward procedure (McCullagh & Nelder 1983). The logistic regression is designed to describe proportions as a function of one or more independent variables. The regression gives a maximum likelihood estimate of the exponent \( a \) in the form: \[ e^a/(1+e^a) \]. Significance of variables was tested using the \( F \) distributed change in deviance and the change in degrees of freedom when the variable was dropped from the full model. In visualising the relationship between predation rate and each significant variable, the effect of other variables is not taken into account.

**RESULTS**

**Natural trends**

We marked 348 clutches of which 167 had three eggs at the moment the clutch was exchanged or temporarily removed. From the remaining 181 clutches one or more eggs were
From the 167 complete clutches 105 eggs (25 times three eggs, 3 times two eggs, 24 times one egg) disappeared after the exchange or temporary removal of the clutch. The chance of losing an egg increased progressively from 0.14 for the first egg within a clutch to 0.89 of also losing the third egg. Within the group of partially robbed clutches predation was random with respect to the laying sequence of the eggs ($\chi^2 = 0.85, df = 2, NS$).

Using logistic regression, a model was constructed for the 167 clutches that had three eggs at the moment of manipulation. The model described the relationship between the proportion of eggs lost per nest, and laying date, vegetation cover, inter-nest distance and original clutch volume (volume of clutches before manipulation of the eggs). Each of these four variables significantly decreased the deviance (Table 1). The probability of egg predation decreased with an increase in cover, inter-nest distance and original clutch volume (Figs 1 & 2).

Because cover and inter-nest distance increased with laying date (linear regression, cover: $0.0485 \cdot \text{laying date} + 2.18, r^2_{165} = 0.08, P < 0.001$;...
Table 1. Logistic regression analysis of the proportion of Herring Gull eggs lost per clutch of three eggs for control and experimental pairs. The null model represents the constant only, the full model includes all significant predictor variables. For the null and full model the deviance and the degrees of freedom are given, for the significant variables the $F$ distributed change in deviance and the change in degrees of freedom are listed after stepwise dropping variables from the full model.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>$F$ (dev.)</th>
<th>Degrees of freedom</th>
<th>Estimates of coefficients</th>
</tr>
</thead>
<tbody>
<tr>
<td>Null model</td>
<td>411.3</td>
<td>166</td>
<td></td>
</tr>
<tr>
<td>Full model</td>
<td>314.9</td>
<td>158</td>
<td></td>
</tr>
<tr>
<td>Laying date</td>
<td>9.60**</td>
<td>+1</td>
<td>0.1094</td>
</tr>
<tr>
<td>Vegetation cover</td>
<td>9.13**</td>
<td>+1</td>
<td>-0.6306</td>
</tr>
<tr>
<td>Original clutch volume</td>
<td>8.34**</td>
<td>+1</td>
<td>-0.0856</td>
</tr>
<tr>
<td>Inter-nest distance</td>
<td>4.97*</td>
<td>+1</td>
<td>-3.4090</td>
</tr>
<tr>
<td>Clutch volume *</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>inter-nest distance</td>
<td>4.22*</td>
<td>+1</td>
<td>0.0123</td>
</tr>
<tr>
<td>Squared difference of clutch volumes</td>
<td>4.77*</td>
<td>+1</td>
<td>0.0005</td>
</tr>
</tbody>
</table>

$^{*} P < 0.05, ~** P < 0.01$

inter-nest distance: $0.0767 \times$ laying date + 3.83, $r^2_{165} = 0.033, P < 0.05$, a decrease in egg predation with laying date would be expected. However, egg predation also increased with laying date (Fig. 1, Table 1).

Considering all possible interactions, only the interaction between original clutch volume and inter-nest distance was significant (Table 1). The effect of clutch volume on predation rate increased with decreasing inter-nest distance (Fig. 3). All other two-way interactions between the parameters mentioned in Table 1 were not significant. To test non-linear relationships all parameters were squared and proven not to be significant either.

The effect of clutch transfer

As a next step the two experimental categories (EA, EB) and the two control categories (CA, CB) were added to the full model, as categorical variables. Neither of these variables, nor their interactions significantly decreased the deviance. This implies that within the model there were no significant differences in predation rate between the four categories.

In the experimental pairs, new and original clutch volume differed from each other in all cases; in the control pairs new and original clutch volume were of course identical. The squared difference between the original and new clutch volumes (dvol$^2$) significantly decreased the deviance.
Fig. 4. Mean predation rate of control (light grey, \(N = 75\)) and experimental clutches of Herring Gulls (E1-E3). Experimental clutches with increasing squared difference between the volume (cm\(^3\)) of the original clutch and that of the adopted clutch (dvol\(^2\): E1 = 56.25, \(SD = 50.57\), \(N = 30\), E2 = 364.6, \(SD = 161.6\), \(N = 30\), E3 = 1479, \(SD = 1020\), \(N = 30\)).

Prevalence risk increased with an increasing difference between original and new clutch volume (Fig. 4). As a result the experimental pairs (EA, EB) suffered a higher predation rate than the control pairs (nests: \(39.2%\) and \(21.3%\), respectively; eggs: \(27.2%\) and \(13.3%\), respectively). The effect of dvol\(^2\) was not significant when the difference between original and new clutch volume was investigated for the 92 experimental pairs only (\(F_{1,83} = 3.10\), NS).

**Clutch volume investigated experimentally**

In the full model (Table 1), we then replaced the variable original clutch volume with the new clutch volume for control and experimental pairs combined. In contrast to the original clutch volume, the coefficient of the new clutch volume did not significantly differ from zero (\(F_{1,159} = 2.97\), NS).

Finally, we constructed a new model including only the variables new clutch volume and ‘exchanged’ (categorical) and used the interaction term new clutch volume \(\times\) exchanged to establish a difference in slope between the original clutches (control and experimental pairs combined) and the adopted clutches in the relationship between predation and new clutch volume (Fig. 2). Controlling for new clutch volume, the interaction term new clutch volume \(\times\) exchanged significantly decreased the deviance (\(F_{1,161} = 4.79\), \(P < 0.05\)). Using the experimental pairs only, the coefficient of the new clutch volume did not significantly differ from zero (\(F_{1,88} = 1.0\), NS).

Controlling for original clutch volume, the interaction term original clutch volume \(\times\) exchanged did not significantly decrease the deviance (\(F_{1,161} = 2.18\), NS), indicating that in the relationship between predation and original clutch volume, the experimental pairs follow the same trend as the control pairs. From this we conclude that the original clutch volume affected the predation rate, whilst the new clutch volume did not. This means that predation rate is not directly related to egg size.

**DISCUSSION**

Egg predation by conspecifics was a common phenomenon in Herring Gulls on Terschelling in 1990, both during the laying and the incubation period. The high predation rate in 1990 was not exceptional. In 1983-1984, almost a quarter of all eggs produced was lost to predators (Spaans et al. 1987).

Once a clutch was fully incubated, egg predation was random with regard to the laying sequence of the eggs. This contrasts with a study conducted by Verbeek (1988), who found a selective predation for the c-egg in the Glaucous-winged Gull L. glaucescens in Canada. In Verbeek’s study, however, the c-egg was lighter coloured than the two other eggs, thus focussing the attention of predators on that particular egg (see also Verbeek 1990). On Terschelling there were no consistent colour differences between the eggs within a clutch.

The probability of losing another egg, once a pair fully incubating a c/3 had lost an egg, increased progressively. The same result was found experimentally by Baerends et al. (1970), who showed that a progressive egg loss is linked with
an increase in restlessness of the incubating bird and in a tendency to leave the nest more often.

The rate of predation increased in later laying birds, whilst the probability of losing eggs decreased with an increase in vegetation cover, inter-nest distance and clutch volume. The relationship to clutch volume was absent after clutches had been exchanged between pairs. Size differences between original and adopted eggs increased the predation rate progressively. Differences in contact between eggs and brood patch before and after the exchange may have induced an increased restlessness in the experimental birds, thus enhancing the increase in predation rate. Besides size differences, other tactile stimuli and visual features of the eggs could also have contributed to the effect of the manipulation (see Baerends & Hogan-Warburg 1982).

Since eggs are less easily seen as the vegetation becomes taller (Brown 1967, Burger 1984) the negative relationship we found between vegetation cover and predation rate was as expected. Later laying birds preferred progressively a tall vegetation such as sea buckthorn. If a tall vegetation is advantageous from the egg predation point of view, the question arises as to why early gulls do not choose nesting sites in this habitat more often. We suggest that nesting in a tall vegetation increases the adult's risk of being killed during laying and incubation by a mammalian predator. This is strengthened by the observation of Drent (1970) on nearby Schiermonnikoog that Herring Gulls nesting in tall and dense vegetation abandon their eggs and the colony during darkness for many more days after clutch completion than birds nesting in open habitat. As the season progresses an increasing number of gulls remain in the colony during darkness, thus probably facilitating later starting gulls to nest more in tall vegetation. Mammalian predators are lacking on Terschelling and Schiermonnikoog except for small numbers of stoats Mustela erminea (Terschelling 1930s-1980s, Schiermonnikoog 1980s, see Broekhuizen et al. 1992) and feral cats Felis catus (last few decades, State Forestry Service Terschelling and F.J.J. Niewold pers. comm.). It is therefore unknown whether the reluctance of early breeders to nest in tall vegetation has evolved under present predation pressure or that is has an ultimate basis.

If conspecific egg predation is so negatively correlated to inter-nest distance, one may ask why gulls do not nest more solitarily. Eggs placed by Burger (1984) in unattended experimental nests outside the colony, were, however, faster found and eaten by predators than eggs placed in the colony. This suggests that neighbouring gulls, though potential predators themselves, serve at least partially as a deterrent to potential robbers roaming the area. However, a tendency for solitary nesting as a result of severe egg loss has been described for the Yellow-footed Gull L. livens by Spear & Anderson (1989).

An increase in egg predation with an increasing nest density was also noticed by Fordham (1964) for the Southern Black-backed Gull L. dominicanus. Parsons (1976) and Burger (1984), however, found the lowest predation rate in Herring Gull territories of intermediate sizes. Burger (1984) argued that at a high nest density the gulls got too involved in neighbour-neighbour interactions, resulting in a waning of egg guarding. However, if the nest density was too low, gulls had frequent encounters with non-neighbour intruders that were attempting to establish a territory. Gulls with territories of intermediate sizes had the lowest aggressive interaction rate and therefore the highest reproductive output. The relationship between nest density and interaction rate with other gulls is, however, habitat dependent (Pierotti 1987). It is therefore difficult to make generalisations.

We found experimental evidence that within clutches of three eggs predation of eggs is not causally linked to clutch volume. Apparently, there is no predator selection with respect to clutch volume. The relationship between original clutch volume and predation rate must have been caused therefore by a factor correlated to clutch volume. Egg volume is directly affected by food supply (Hiom et al. 1991, Van Klinken 1992) and the physiological state of the female (Pierotti &
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Bellrose 1986, Meathrel et al. 1987). Mills (1979) showed that the most efficient foragers produce the largest eggs, suggesting that parental quality is related to egg size. A positive relationship between egg size and parental quality was clearly established by Bolton (1991), who performed a clutch transfer experiment in Lesser Black-backed Gulls by cross-fostering clutches of large eggs with clutches of small eggs. We suggest therefore that lower quality birds not only lay smaller eggs as a result of less efficient foraging practices but also show less efficient egg care behaviour (e.g. lower territory attendance) during the incubation period, resulting in an increased predation risk. We have no data on territory attendance or other parental care behaviour in relation to clutch volume. However, Herring Gulls that lose eggs, more frequently leave the colony for feeding (probably as a result of a lower hunting efficiency) than successful pairs. The former also leave their territory unguarded for longer periods of time than the latter (M. Bukacińska & D. Bukaciński, pers. comm.). These data indicate that parental care behaviour and breeding success on Terschelling are strongly related to each other. Burger (1987) and Morris (1987) came to the same conclusion for Herring Gulls nesting in North America.

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REFERENCES


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**SAMENVATTING**

Zilvermeeuwen *Larus argentatus* roven geregeld eieren uit nesten van soortgenoten. De kans op eierroof is niet voor ieder nest gelijk. In 1990 hebben wij op Terschelling onderzocht welke factoren van invloed zijn op deze eipredatie. Uit 167 legels met drie eieren werden in totaal 105 eieren geroofd. Alle eieren binnen een legsel hadden een even grote kans om te worden gepredieerd. Als er eenmaal een ei uit een nest was geroofd, nam de kans op verdere roof toe.

De kans op eipredatie nam af naarmate de vegetatie rond het nest hoger was en de nesten verder uit elkaar lagen. Naarmate het seizoen vorderde, ging de meeuwen steeds verder uit elkaar en in een hogere vegetatie nestelen. Desondanks nam de eipredatie toe naarmate de meeuwen later begonnen te leggen.

Nesten met kleine eieren hadden een grotere kans om gepredieerd te worden dan nesten met grote eieren. Door legels te verwisselen voor legels van soortgenoten, kon worden aangetoond dat er geen direct verband bestaat tussen eigrootte en de kans op predatie. Verondersteld wordt dat eigrootte en broedzorg beide in sterke mate worden bepaald door de kwaliteit van de oudervogel.