Hatching success in Lesser Black-backed Gulls *Larus fuscus* - an island case study of the effects of egg and nest site quality

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Abstract

Within an avian breeding population, there can be considerable variation in egg and nest site characteristics that have implications for individual reproductive success. Here we present a detailed case study of Lesser Black-backed Gulls *Larus fuscus* nesting on Flat Holm island, Wales, at a time when the colony was growing. This species is ground-nesting, with a modal clutch size of three. We surveyed 714 nests across the island during two consecutive years and recorded data on nest and egg characteristics, along with hatching success. We modelled how hatching success was associated with clutch size, egg volume, egg laying order and local habitat features, i.e. the amount of vegetation surrounding the nest and each nest's proximity to neighbouring nests. Eggs were most likely to hatch when they were laid in the middle of the season, were large in size, part of big clutches and in nests with a substantial amount of surrounding vegetation. Lesser Black-backed Gull productivity is currently low in many protected rural and coastal colonies throughout this species' range. Detailed information on factors influencing reproductive success could therefore indicate ways in which this species could be better managed to help maintain and conserve breeding populations.

Introduction

Two key components of a bird's reproductive success in any particular breeding attempt are hatching success and chick survival to fledging (Lack 1968). Although chick survival is often the more important factor determining reproductive success in seabirds that nest in the open (Nelson 1980; Camphuysen 2013), hatching success is also important (Paludan 1951; Schreiber 1970). The latter is influenced by intrinsic factors, including parental quality and condition, which in turn contribute to egg viability (e.g. Bolton 1991; Oro *et al*. 2014), together with extrinsic factors such as predation and climatic conditions (e.g. Jones *et al*. 2008; van de Pol *et al*. 2010). Many birds construct nests to protect their eggs, and thereby increase their reproductive success. In seabirds, nests can range from none at all e.g. the White Tern *Gygis alba* (Nelson 1980) to quite elaborate structures such as those made by kittiwakes *Rissa* spp. (Coulson 2011).

Nests of the Lesser Black-backed Gull *Larus fuscus*, like those of most gulls, tend to be simple, ranging from a scrape with little gathered nesting material, to a small bed of vegetation arranged in a shallow cup. These ground-nesting seabirds, which breed primarily in northwest Europe (Malling Olsen & Larsson 2004), have traditionally occupied colonies at coastal nesting sites on flat or moderately sloping ground, which may be towards the top of cliffs, or in open, sometimes low-lying areas. Nests are therefore often quite accessible, leaving eggs (and chicks) vulnerable to predation, for example by conspecifics and other gull species that often nest nearby, or by mammalian predators such as Red Foxes *Vulpes vulpes* (Davis & Dunn 1976; Camphuysen *et al*. 2010). Predation has been found to be responsible for up to 30% of Lesser Black-backed Gull egg losses at particular sites (Paludan 1951; Camphuysen 2013). This risk can be partially offset by the benefits of colonial defence and vigilance (e.g. Götmark & Andersson 1984; Beauchamp 2009), and by nesting close to vegetation that conceals eggs from potential predators (Haycock & Threlfall 1975; Hunt & Hunt 1975; Burger & Shisler 1978). Open nest sites also leave eggs exposed to cold and inclement weather conditions, and large numbers of eggs can fail to hatch because of this (Paludan 1951; Fox *et al*. 1978). However, pairs can again compensate by choosing to nest in an area with shelter, for instance tall vegetation around the nest (e.g. Kim & Monaghan 2005a). The extent to which gulls are able to counteract the disadvantages of their ground-nesting breeding behaviour is thought to be influenced by aspects of their phenotypic quality (Kim & Monaghan 2005b; Oro 2008).

Establishing and maintaining a breeding territory is energetically taxing for gulls. Competition can be intense, especially for first time breeders (Chabrzyk & Coulson 1976), whilst costly aggressive interactions, including fighting, calling and displacement activities such as grass pulling, are regularly seen between even established pairs (e.g. Tinbergen 1953; Butler & Janes-Bulter 1982; Pierotti & Annett 1994). These behaviours appear to be necessary throughout the season to prevent territorial encroachments, such as the theft of nesting materials, predation of eggs or chicks and extra-pair copulations (e.g. Burger & Beer 1975; Bukacińska & Bukaciński 1994). Poor quality birds not only struggle to secure and successfully breed at a nest site in habitats favoured by superior birds, but lack the surplus energy to produce and successfully incubate the large and fertile eggs and clutches necessary to match the reproductive success of high quality individuals. Measures of nesting habitat, egg size and hatching success can therefore indicate an individual's phenotypic quality.

Breeding Lesser Black-backed Gull numbers are currently declining at many 'traditional' rural coastal sites across this species' range, including in protected areas, while breeding populations in urban areas are increasing in number and range (e.g. Camphuysen *et al*. 2010; Balmer *et al*. 2013). A thorough understanding of this species' breeding ecology is necessary to facilitate effective conservation management (for a review, see Ross-Smith *et al*. 2014). This is especially vital given that Lesser Black-backed Gulls that breed on rooftops in urban areas (e.g. Raven & Coulson 1997; Rock 2005) are causing an increasing public nuisance, leading to calls for ever stricter controls.

In this study, we assessed Lesser Black-backed Gull hatching success, and explored the reasons underlying hatching failure, for approximately 350 pairs each year over two consecutive seasons, across a range of nesting habitats at an island breeding colony. This colony is free of mammalian predators, and at the time of this study, the breeding population was steadily increasing and there was no apparent food stress or other external pressures known to be detrimentally affecting breeding success (Ross-Smith *et al*. 2013). For each egg found, we measured a number of variables. We noted the size of the clutch it was part of, as eggs from small clutches are less likely to hatch than those from large clutches (Harris 1964; Brown 1967). We recorded laying date, as hatching success has been shown to vary throughout the breeding season (Brown 1967; Davis & Dunn 1976; García Borboroglu *et al*. 2008), along with laying order, as within-clutch variation in egg composition, with potential implications for egg outcome, has been demonstrated in a number of studies (e.g. Royle *et al*. 1999). We calculated egg volume, as large eggs are more likely to hatch than small eggs (Parsons 1970; Bolton 1991). We also measured the amount of vegetation around nests, because of its influence on hatching success, as discussed above, and we calculated how nests were distributed relative to others in the colony, as proximity to conspecific nests has been found to influence reproductive success in gulls (e.g. Ewald *et al*. 1980; Butler & Trivelpiece 1981). We discuss the relative importance of each factor in determining hatching success and place this information in a conservation context.

Methods

Fieldwork was carried out between early April and late June of 2007 and 2008 on Flat Holm, a 35 ha island in the Bristol Channel, Wales (51°23’N 3°07’W). At the time of study, about six people (island staff and researchers) lived on Flat Holm during the breeding season. The island also hosted day visitors in parties of up to 30 people a maximum of three times a week, and residential groups of up to 20 visitors staying for one or two nights about twice a month. Day and residential visitors did not normally visit the gull colony, and the area monitored in this study was set back from paths through the colony used by island staff. In 2007 and 2008, there were about 3,700 and 4,200 breeding pairs of Lesser Black-backed Gulls on Flat Holm, respectively. This breeding population was estimated to be 3% of the population of Lesser Black-backed Gulls in Great Britain during the last national seabird census (Calladine 2004). There were also around 400 breeding pairs of Herring Gulls *L. argentatus* present, although these were largely confined to the island’s edges, and one or two pairs of Great Black-backed Gulls *L. marinus* (Ross-Smith *et al*. 2013). The gull colony was occasionally visited by Common Buzzards *Buteo buteo* and Peregrine Falcons *Falco peregrinus*, and while these predators did not take eggs themselves, the disturbance resulting from their presence did offer opportunities for other gulls to do so.

A study area of 7,700 m^2 (110 m x 70 m) was monitored daily throughout each field season (except in very poor weather). This area included a range of nesting habitats from those in open, rocky sites with no vegetation at all, to nests in densely vegetated areas where they were almost completely concealed. The principal vegetation in the monitored region was a mixture of grass, Bracken *Pteridium aquilinum*, Wild Turnip *Brassica rapa*, Common Nettle *Urtica dioica*, Brambles *Rubus fruticosus* and Elder *Sambucus nigra* (Figure 1). Nest densities were very low in the thickest stands of the latter five species. The study area was surveyed systematically to check for nesting activity, by walking slowly through the colony along the same route each time to minimise disturbance to the breeding birds (Robert & Ralph 1975; Martínez-Abraín *et al*. 2008). We located every nest in the study area and measured every egg we found with digital callipers to the nearest 0.01 mm. We used this information to calculate egg volume (cm^3) as length (mm) x breadth (mm) x 0.000476 (Harris 1964). We used a marker pen with indelible, non-toxic ink to write the letter A, B, or C on each egg (to denote first, second and third laid eggs, respectively). Given the near-daily surveying, the date on which each egg was found was taken as its laying date. We also characterised the vegetation surrounding and contiguous with the edge of the nest at the time of clutch completion (sometimes this was a small clump of Common Nettles, sometimes the nest was in the midst of a large stand of mixed vegetation). Vegetation grew continuously through the season, reaching more than 1.5 m in height for some Common Nettles, Wild Turnip and Brambles. For analytical purposes, the vegetation surrounding the perimeter of the nest was recorded as follows. We divided the perimeter of the nest into six arcs of a circle (0˚–59˚, 60˚–119˚, 120˚–179˚, 180˚–239˚, 240˚–299˚, 300˚–360˚). A score of one was given for any vegetation over 10 cm high that was present around up to 59˚ of the nest perimeter, a score of two if between 60˚ and 119˚of the perimeter was surrounded by vegetation over 10 cm high and so on, up to a maximum score of six.

Clutch size was counted as the number of eggs produced per breeding attempt, so this value was not altered if an egg was lost. If a clutch was re-laid following breeding failure, we considered this a separate breeding attempt by the pair concerned, and we counted the replacement eggs again as A, B or C. Finally, every nest with eggs was recorded by a Cartesian coordinate system within the study area, such that each one could be easily relocated and nearest neighbour distance calculated.

Statistical treatment: Results were analysed in R version 3.2.2 (R Core Team 2015), with the use of additional packages 'nlme' (Pinheiro *et al*. 2015) and 'mgcv' (Wood 2006). Statistical tests were two-tailed, with a significance level of 0.05. All values are given as arithmetic mean ± S.E.

Figure 1 (opposite). Lesser Black-backed Gulls *Larus fuscus*, May 2008, on Flat Holm nested in open grassy areas (foreground), and in Bracken, Wild Turnip, Common Nettles, Brambles and Elder (background), as well as in rocky patches and on the shingle beach (not shown in photo). © *Viola Ross-Smith*.

Not all eggs we recorded were included in our analyses. We excluded all those laid after 1 June in each year, because the field seasons ended before their incubation period did. Even those eggs laid after 1 June that we knew to have failed (because they disappeared or were broken) were omitted to prevent bias in the analyses. We also excluded those eggs for which laying order could not be determined (which happened for eggs found laid in the same nest after days when the weather was too poor for monitoring). The hatching success of all other eggs was analysed using generalised additive mixed models (GAMMs) with a binomial error. The response variable was binary, with a code of 0 if an egg did not hatch, and 1 if an egg did. GAMMs with a binomial error were also used to examine the eggs that did not hatch. Our response variable was again binary, with eggs divided into those that disappeared from the nest before incubation was complete and 'non-viable eggs' that remained in the nest unhatched. We also ran linear mixed-effects models (LMMs) with egg volume as a response variable. In all models, the nest of origin was included as a random factor.

Explanatory variables in both models of egg outcome were: year (2007 or 2008), the amount of vegetation around the nest (as a factor with six levels), egg laying order, egg volume, clutch size, and the distance to the nearest nest. Laying date was fitted as a smooth term. The maximum degrees of freedom for the smooth term were initially set to 10 and the degrees of freedom were selected automatically by Generalised Cross Validation (GCV). The gamma penalty for the GCV optimisation was set at 1.4 (Wood 2006). Where the fitted relationship was not biologically reasonable, the maximum degrees of freedom were reduced. In all models, interactions were only fitted if they were thought to be informative and biologically meaningful to help reduce the problem of multiplicity of P values (Grafen & Hails 2002). Therefore, we fitted all two-way interactions but nothing of a higher order. Model simplification proceeded via stepwise deletion of non-significant terms (Crawley 2007). Reported P values for GAMMs are based on the 'gam' model output from the 'mgcv' package, after Wood (2006), and t values are reported for comparisons of different levels of a factor. Plots show the fitted GAM covariates for an average nest, setting all other covariates at their mean value. The random effect of nest was not included in these plots and the confidence intervals are therefore for an average nest.

Results

In total, 947 eggs in 348 nests were monitored in 2007 and 1,011 eggs in 366 nests in 2008. In 67% of cases, we found eggs in a clutch laid every other day, although different laying intervals were recorded (an interval of three days occurred 21% of the time). Overall incubation time was 27.0 ± 0.1 days in 2007 and 26.9 ± 0.1 days in 2008, and the modal clutch size was three in both years. Mean nearest neighbour distance was 2.59 ± 0.07 m in both years. Mean egg volume for all eggs recorded in the monitored area was 67.89 ± 0.23 cm^3 in 2007 and 68.48 ± 0.21 cm^3 in 2008 (Table 1) and not significantly different between years (LMM, $F_{1,1248} = 2.14$, $P = 0.144$).

Table 1. Clutch sizes and egg volumes for first-laid clutches (replacement clutches following breeding failure are excluded). Calculations made for nests containing eggs of known laying order (A, B or C) only (261 nests in 2007, 352 nests in 2008). * In each year, there was also a single clutch of four eggs of known volume and laying order.

Year	Clutch size*	Mean egg volume ± S.E. (cm^3)		
		A	B	C
2007	1 (n = 23)	67.82 ± 1.25		
	2 (n = 48)	69.70 ± 0.87	65.04 ± 0.97	
	3 (n = 190)	71.61 ± 0.47	69.27 ± 0.48	63.45 ± 0.43
2008	1 (n = 24)	68.09 ± 1.53		
	2 (n = 59)	68.68 ± 0.92	64.25 ± 0.99	
	3 (n = 269)	71.70 ± 0.36	70.24 ± 0.36	64.95 ± 0.36

Hatching success: Hatching success was modelled for 704 of the 947 eggs recorded in 2007, and 911 of the 1,011 eggs monitored in 2008. Hatching success was significantly positively associated with egg volume (GAMM, $P = 0.0006$) and clutch size ($P < 0.0001$), with eggs in clutches of two ($t = 2.70$, $P = 0.0071$) and three ($t = 4.13$, $P < 0.0001$) being significantly more likely to hatch than those in clutches of one (Figure 2a). Hatching success was significantly correlated with the day of the season, and the smooth relationship indicated a decline later in the season ($P = 0.0006$) (Figure 2b). There was also a significant effect of the amount of vegetation around the nests ($P = 0.0137$), with eggs in nests surrounded by more than 300° vegetation (i.e. at least 5/6 of the perimeter) significantly more likely to hatch than those in nests with less than 60° ($t = 2.18$, $P = 0.0296$) (Figure 2c). Laying order had a significant effect ($P < 0.0001$). There was no effect of year ($P = 0.9954$) or nearest neighbour distance ($P = 0.5480$) on hatching success. The random effect of nest had an estimated variance of 1.5410. This suggests that there was some correlation in the fate of eggs in the same nest.

Hatching failure: Hatching failures fell into two categories. 'Non-viable eggs' were classed as those that remained in the nest after they should have hatched (eventually the breeding pair responsible stopped incubating). These could have resulted from infertility (i.e. the eggs were not fertilised successfully), or failure later in incubation, perhaps due to chilling or developmental defects. Alternatively, eggs disappeared from the nest before they were due to hatch. There was no significant difference in the proportion of non-viable eggs (11.3% in 2007, 13.6% in 2008) or eggs that disappeared (12.9% in 2007, 13.0% in 2008) between the two years ($\chi^2{}_1 \leq 1.93$, $P \geq 0.16$ in both cases). Some eggs were found broken in the nest shortly before they disappeared. As with the hatching success model, the random effect variance of 2.6300 suggests that there was some correlation in the fate of eggs in the same nest. This can also be seen from the data. For example, when eggs disappeared from clutches of two, the other egg also disappeared 44.4% of the time. In clutches of three, 12.0% of disappearances concerned the whole clutch, and 22.2% of disappearances involved two of the three eggs in the clutch. Egg disappearance was significantly related to clutch size (GAMM, $P < 0.0001$; Figure 3a), with eggs from single clutches more likely to vanish than those from clutches of two ($t = -3.88$, $P =$

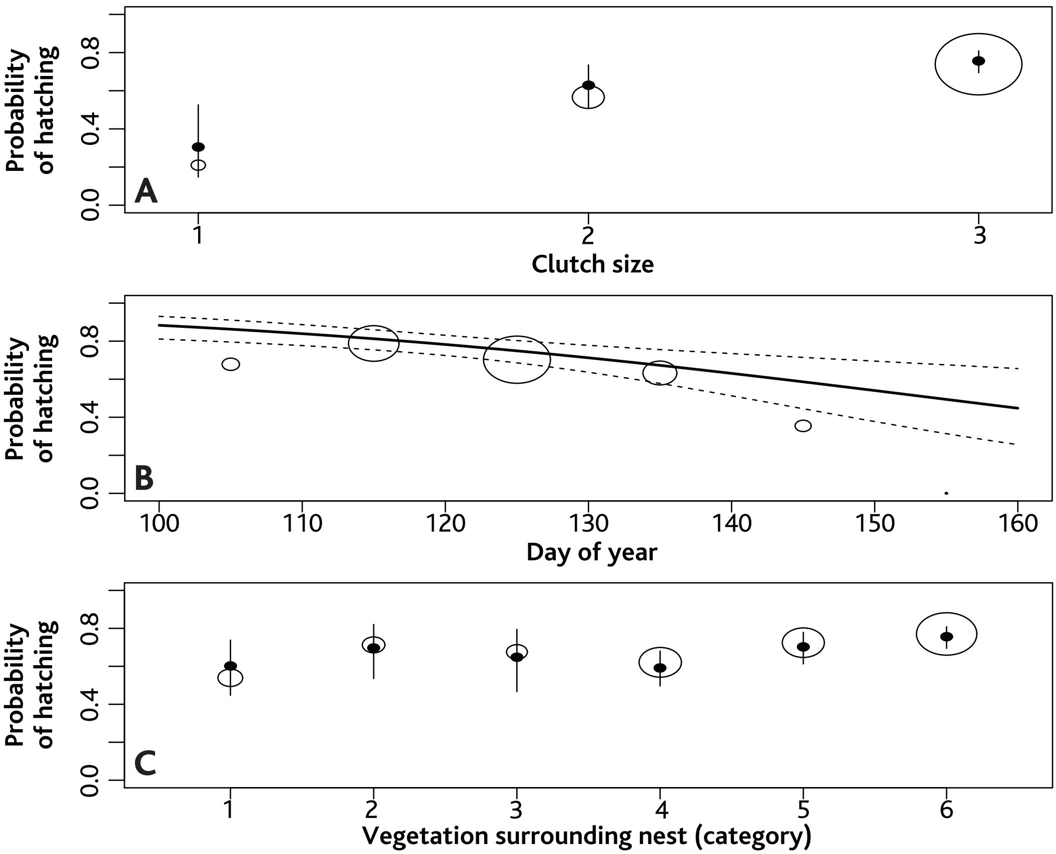

Figure 2. The modelled relationship between hatching success and a) clutch size; b) laying date; c) vegetation surrounding nest. Black dots and straight lines (solid and dashed lines in b) indicate the modelled estimate and 95% confidence interval for an average nest (not accounting for the random effect of nest). Open circles represent the average hatching success from the data with circle area proportional to sample size. The fitted marginal covariate effects (black) keep all other covariates at their mean value, whereas the average proportions in the data (open circles) have a range of covariate values. This difference can in some cases (particularly where there are smaller sample sizes) lead to a visual discrepancy between the fitted values and the data.

0.0001) or three ($t = -6.43$, $P < 0.0001$). There was also a significant effect of laying date (Figure 3b), as eggs had a higher probability of disappearing from the nest at the end of the breeding season than during the middle ($P < 0.0001$). There was also some evidence that there was a higher rate at the beginning of the breeding season, although the confidence limits were wider at the start and end of the breeding season, as we had fewer data and GAMs are often less precise towards the edges of the range of data. Finally, there was a significant effect of the nest vegetation ($P = 0.0103$), with eggs from nests surrounded by at least 300° vegetation being significantly less likely to disappear than eggs from nests with 60° surrounding vegetation or less ($t = -2.27$, $P = 0.0231$; Figure 3c). There was no significant effect of year ($P = 0.3994$), egg laying order ($P = 0.1166$), or distance to the nearest neighbouring nest ($P = 0.4765$). The effect of egg volume was almost significant, with larger eggs being more likely to disappear than smaller eggs ($P = 0.0501$).

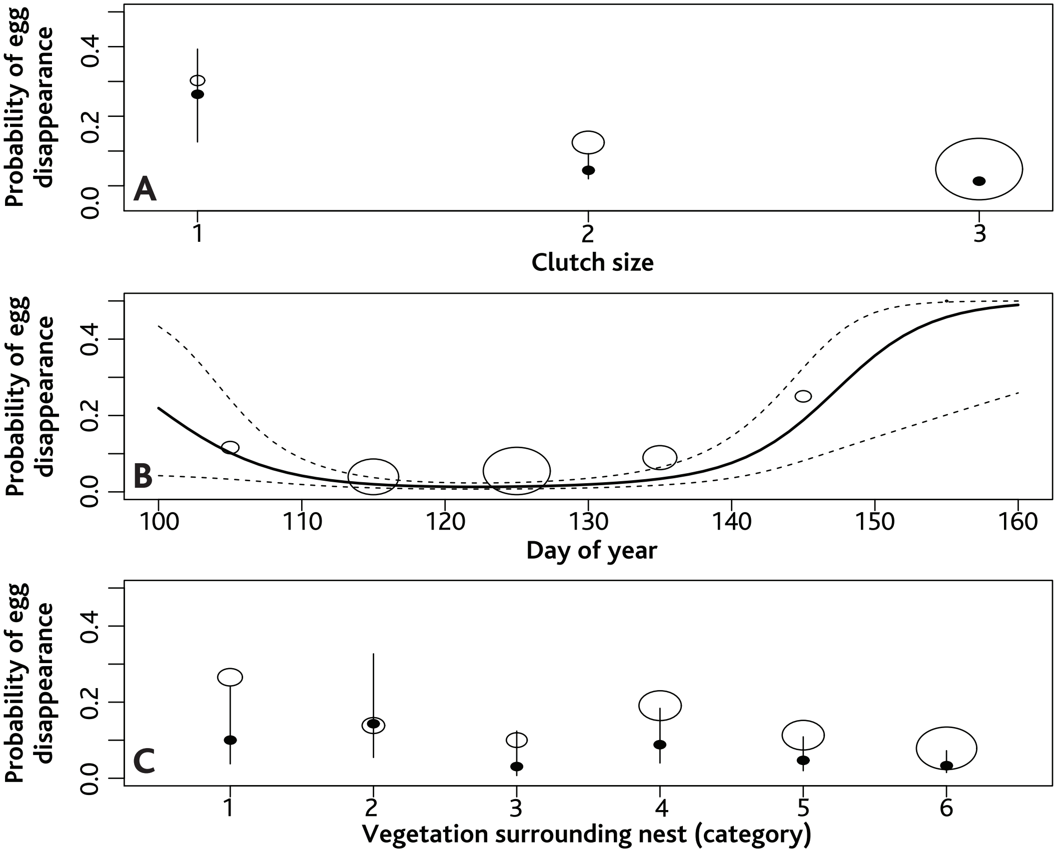

Figure 3. The modelled relationship between egg disappearance and a) clutch size; b) laying date; c) vegetation surrounding nest. Black dots and straight lines (solid and dashed lines in b) indicate the modelled estimate and 95% confidence interval for an average nest (not accounting for the random effect of nest). Open circles represent the average hatching success from the data with circle area proportional to sample size. The fitted marginal covariate effects (black) keep all other covariates at their mean value, whereas the average proportions in the data (open circles) have a range of covariate values. This difference can in some cases (particularly where there are smaller sample sizes) lead to a visual discrepancy between the fitted values and the data.

Discussion

In this study we present an assessment of hatching success and egg failure from an island-nesting breeding population of Lesser Black-backed Gulls. The hatching success of Lesser Black-backed Gulls breeding on Flat Holm was significantly positively associated with egg volume, clutch size, egg laying order and the amount of vegetation cover around the nest. The probability of successful hatching also varied significantly with laying date, as eggs laid towards the end of the season were less likely to hatch than those laid earlier. Overall, the present findings largely agree with those from studies of this or closely related gull species, at other colonies, although the reduction in hatching success with decreasing egg size has not been consistently observed (Nager *et al*. 2000). Seasonal declines in hatching success have been reported for Kelp Gulls *L. dominicanus* (García Borboroglu *et al*. 2008) and Herring Gulls (Brown 1967), as well as for Lesser Black-backed Gulls at other British colonies (Brown 1967; Davis & Dunn 1976). Similarly, eggs from smaller clutches have been found to be less likely to hatch in Herring Gulls (Parsons 1975), Western Gulls *L. occidentalis* (Harper 1971), Glaucous-winged Gulls *L. glaucescens* (Murphy *et al*. 1992), American Herring Gulls *L. smithsonianus* (Haycock & Threlfall 1975) and Lesser Black-backed Gulls (Harris 1964; Brown 1967), and an association between egg laying order and hatching success has been observed in Western Gulls (Pierotti & Bellrose 1986). The relationship we found between hatching success and vegetation quantity was similar to that found in Kelp Gulls by García Borboroglu and Yorio (2004), and was also consistent with the results of Good (2002), who reported that the addition of artificial nest cover improved hatching success in the Western Gull/Glaucous-winged Gull hybrid complex. Brown (1967) studied Lesser Black-backed Gulls and observed that eggs next to cover were more likely to hatch than those that were not, but did not quantify the amount of cover involved, while Camphuysen and Gronert (2010) found a positive correlation between hatching success and nest cover in Lesser Black-backed Gulls and Herring Gulls. The absence of nearest neighbour effects on breeding success is also consistent with a number of other gull studies (e.g. Dexheimer & Southern 1974; Hunt & Hunt 1975; Jehl 1994).

Analysis of eggs that failed to hatch showed that those that disappeared from the nest were more likely to originate from smaller clutches than non-viable eggs that remained in the nest after they were due to hatch. Eggs that disappeared were also more likely to be found in open nests or those with sparse vegetative cover, and to be laid either before or primarily after the peak of the laying period. The increased egg disappearance seen both very early and late in the season, combined with the reported vulnerability of open gull nests to predators (Haycock & Threlfall 1975; Hunt & Hunt 1975; Burger & Shisler 1978) and direct observation of gulls on Flat Holm (VR-S pers. obs.), suggests that intraspecific predation played a role in the disappearance of eggs. The marginally non-significant effect of egg size on disappearance also supports this suggestion, as larger eggs might be more appealing than smaller ones for gulls that have specialised in feeding on other birds' eggs (e.g. Camphuysen 2013). As many eggs that disappeared were produced before and after peak laying, they would not have benefited fully from the reduction in predation conferred by synchronised laying (Fetterolf 1984). Infanticide and cannibalism of eggs and chicks is a major cause of offspring mortality in several gull species (e.g. Hunt & Hunt 1975; Montevecchi 1977; Brouwer *et al*. 1995; Camphuysen 2013), and can therefore be a drawback of colonial breeding (Davis & Dunn 1976). Synchronisation lowers the risk of such losses (Fetterolf 1984) as gulls engaged in caring for their own clutch are less likely to seek opportunities to predate neighbours. Since it has been found that the pairs that have fallen victim to egg robbery turn to this behaviour themselves in Lesser Black-backed Gulls (Davis & Dunn 1976), eggs laid late in the season might be especially vulnerable to theft.

On Flat Holm, 12.9% of eggs disappeared in 2007 and 13.0% in 2008. These proportions are very similar to an island Lesser Black-backed Gull colony in the Netherlands, where 15.0% and 14.4% of eggs were predated in 2007 and 2008 respectively (Camphuysen 2013). However, not all the eggs that disappeared on Flat Holm were predated. We found some of these eggs cracked in the nest prior to their disappearance and we also observed damaged eggs (that had previously been incubated in their broken state) on the edge of the nest, where they had apparently been pushed by their parents, shortly before they vanished. This suggests some eggs that disappeared might have been abandoned or destroyed by their parents once they were recognised as damaged. Undamaged eggs might also have been destroyed or accidentally pushed out of the nest if the parent was suddenly disturbed, or because of inadequate incubation behaviour. Beer (1961, 1965) noted that gulls with fewer than three eggs rise and resettle on the nest more often than those with three (the modal clutch size for most gulls), and spend less time sitting on their eggs. These frequent movements might increase the likelihood of egg damage, while periods of inattentiveness might allow fluctuations in egg temperature that reduce the likelihood of hatching success, as well as providing opportunities for egg predation. Vegetation around the nest would help to offset this, both by concealing eggs from predators and helping to provide and maintain the correct microenvironment for successful incubation (Kim & Monaghan 2005a, 2005b). However, it seems possible that gulls are adapted to incubate the modal clutch size for the species (see also Niizuma *et al*. 2005), and that any other number of eggs does not provide the correct stimulus to bring about optimal incubation behaviour, contributing to the observed disappearance of eggs in small clutches on Flat Holm.

As the factors associated with increased egg disappearance (small clutch size, late laying date and exposed nests) have been found to vary with parental age, i.e. birds of intermediate age produce bigger clutches earlier in the year than first-time parents or very old birds (Davis & Dunn 1976; Oro *et al*. 2014) and young birds are more likely to nest in open areas than older birds (Reid 1988; Oro 2008), the egg loss we observed could have been the result of inadequate incubation and brood defence by either young and inexperienced parents, or old, senescent parents. Young breeders have been found to suffer high levels of intraspecific nest predation in Yellow-legged Gulls *L. michahellis* (Oro 2008). It is also possible that the pairs affected by egg disappearance were of a low phenotypic quality, and were therefore unable to lay either large or early clutches, and were similarly incapable of territorial defence under the pressure of competition from, or predation by, superior quality birds. Indeed, clutch size has been shown to honestly reflect parental quality in Western Gulls (Sydeman *et al*. 1991), and the tendency we found for whole clutches to fail or succeed suggests some pairs are less capable of incubating clutches to hatching than others.

Conclusions

The Lesser Black-backed Gull has undergone population redistribution in recent decades, with birds moving out of rural colonies and into built-up areas (e.g. Balmer *et al*. 2013). In common with other large gull species capable of nesting in urban areas, Lesser Black-backed Gulls are unpopular residents of towns and cities in the breeding season, leading to calls for drastic control measures (Rock 2005). As this population redistribution has been accompanied by population decline, particularly at protected sites (e.g. JNCC 2014; Ross-Smith *et al*. 2014), it seems prudent to reduce the need for population control by encouraging birds to nest away from human settlements. This could potentially be achieved through optimising the habitat and other conditions required for breeding at 'traditional', rural, coastal colonies, including at protected sites.

We cannot easily manage the intrinsic factors affecting hatching success, e.g. clutch size and egg volume. However, the vegetation in gull colonies can be managed to help maintain the breeding population. Plants that provide adequate cover could be encouraged and nests could be monitored and given some artificial shelter in open areas to help protect eggs (and chicks). One issue not measured in this study is the harmful effect of overgrowth of vegetation on breeding gull numbers. Although gulls clearly benefit from the shelter provided by some vegetation, they avoid nesting in very densely vegetated areas (e.g. Davis & Dunn 1976; Burger & Shisler 1978; Bosch & Sol 1998; García Borboroglu & Yorio 2004b; Skórka *et al*. 2006), and this was also seen on Flat Holm. Our results show substantial nest cover is beneficial, but nests were absent from areas where gulls could not easily fly or walk in or out, such as thick Brambles. Since this study took place, the vegetation on Flat Holm has become denser and in some places pairs are apparently unable or unwilling to nest in sites that were previously occupied (VR-S pers. obs.). Controlling vegetation outside the breeding season to thin it out when it has got too dense could also therefore help improve gull breeding performance.

The Lesser Black-backed Gull is on the Birds of Conservation Concern Amber List in the UK (Eaton *et al*. 2015), primarily because of the breeding population's concentration at a small number of breeding sites. While the nationally important colony on Flat Holm was gradually increasing in the years up to and including those in this study, it is now in decline (unpublished data). This recent downturn suggests Flat Holm's Lesser Black-backed Gull population might be starting to follow the trajectory of important breeding populations at other British sites, for instance Skomer (Pembrokeshire, Wales) and South Walney (Cumbria, England), where low productivity is thought to be a key factor in the decline (Perrins & Smith 2000; Kim & Monaghan 2006). Although chick mortality has been shown to be the primary driver of reproductive success for Lesser Black-backed Gulls breeding on certain other colonies (e.g. on Texel, The Netherlands; Camphuysen 2013) and this was not measured in our study, hatching success is also an important component of productivity in this species (Paludan 1951). The levels of hatching success and measures of egg volume found in this study on Flat Holm might represent those that need to be attained or exceeded if population stability is to be maintained, or growth achieved (in the absence of other factors, such as mammalian predation). The work described here concerned only the initial stages of the breeding process, i.e. egg production and hatching success, and no data were gathered on fledging success or recruitment. Also, the relationships we found between egg outcome and nest vegetation might differ for chick survival. Nevertheless, our results do show how certain simple observations can predict reproductive success in this early part of the breeding process, and this information could be valuable to conservationists at a time when the population of the Lesser Black-backed Gull (and related species) is subject to heated debate and in appreciable decline.

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