J Ornithol (2005) 146: 176–183
DOI 10.1007/s10336-005-0077-6

ORIGINAL ARTICLE

Sin-Yeon Kim · Pat Monaghan

Effects of vegetation on nest microclimate and breeding performance of lesser black-backed gulls (*Larus fuscus*)

Received: 4 November 2004 / Revised: 24 January 2005 / Accepted: 2 February 2005 / Published online: 19 March 2005

Abstract For birds that breed in large colonies, the overall area occupied by the colony generally comprises several sub-areas that differ in physical and social features such as vegetation and breeding density. Birds arriving at a breeding colony select their nesting sites through a hierarchical process of selecting a sub-area, then a particular nest site with appropriate biotic and physical attributes. Optimal vegetation cover is one such important attribute. Many ground nesting gulls preferentially select nest sites that provide shelter during reproduction, but this presumably has to be balanced against any costs such as reduced visibility of potential predators. The effects of vegetation height in the sub-areas within a colony, and of the amount of vegetation in the immediate vicinity of the nest on nest microclimate were investigated in lesser black-backed gulls *Larus fuscus* in a colony in which overall vegetation height differed in different sub-areas and was patchily distributed within these areas. Tall vegetation did have a sheltering effect, and this was positively related with chick growth. However, this vegetation area was associated with lower breeding densities, relatively late laying birds and lower chick survival rate, suggesting that sub-areas with tall vegetation held more lower-quality or young breeders. Within the sub-areas, the birds preferentially selected nest sites with more surrounding vegetation, and this was positively correlated with their hatching success.

Keywords Breeding performance · Habitat selection · *Larus fuscus* · Microclimate · Nest vegetation

Communicated by P.H. Becker

S.-Y. Kim (✉) · P. Monaghan
Graham Kerr Building,
Division of Environmental and Evolutionary Biology, IBLS,
University of Glasgow, Glasgow, G12 8QQ, UK
E-mail: 0109783k@student.gla.ac.uk
Tel.: +44-141-330-6620

Introduction

In colonially breeding birds, the annual breeding cycle starts with the identification and selection of an appropriate breeding site within the colony that provides protection from physical and biotic components of the environment. Breeding in well sheltered sites can reduce the degree of exposure to extreme weather and predators (Partridge 1978). Since appropriate breeding habitat is often a limited resource, intraspecific competition for the best breeding sites may influence the spatial and temporal distribution of conspecifics within a colony (Fretwell 1972). Conspecific density is a key aspect of habitat quality, influencing the level of local competition and also the degree of protection against predators (Krause and Ruxton 2002).

Habitat selection is a hierarchical decision-making process (Block and Brennan 1993; Borboroglu and Yorio 2004). Birds with a wide distribution, such as most seabirds, select their breeding habitats at several different levels, for example the colony itself, sub-area within a colony and then nest site, in relation to density of conspecifics, protection from predators or accessibility of good foraging areas (Cody 1985).

For ground nesting birds, the height and distribution of vegetation is an important habitat feature. A number of studies have shown positive relationships between vegetation at the nest sites and breeding performance in various gull species (Miyazaki 1996; Bosch and Sol 1998). Since earlier breeders or higher quality individuals are more likely to occupy the best habitats with appropriate amounts of vegetation, the association between habitat and individual quality or timing of breeding has to be taken into account when examining the relationship between nest vegetation and breeding performance (Burger and Lesser 1980; Pierotti 1982; Becker and Erdelen 1986; Kim and Monaghan 2005). Vegetation close to the nest site may be important for the parents and offspring in providing protection from extreme weather (Becker and Erdelen 1982; Saliva and

Burger 1989), and in decreasing social conflicts by reducing visibility of conspecifics (Burger 1977; Bukacińska and Bukaciński 1993). However, nesting in an area with tall vegetation may make individuals more vulnerable to predation risk through its effect on visibility or movement of the breeding birds and their chicks (Ewald et al. 1980; Götmark et al. 1995; Borboroglu and Yorio 2004). In this study, we investigated the relationships amongst nest vegetation, nest site selection and breeding performance in lesser black-backed gulls.

Methods

Study area and species

This study was carried out from April to July 2003 at the South Walney Nature Reserve, Walney Island, Cumbria, UK (54°08′N, 03°16′W), a mixed colony of lesser black-backed gull *Larus fuscus* and herring gull *L. argentatus*. Approximately 13,000 pairs of lesser black-backed gulls and 4,300 pairs of herring gulls were recorded breeding at this site in 2003 (counts organised by Cumbria Wildlife Trust). The reserve is centred on an extensive sand dune system. Breeding gulls of the two species are generally spatially segregated throughout the colony depending on the topology and vegetation. Lesser black-backed gulls are generally considered to prefer topologically low areas with nettle *Urtica* sp., burdock *Arctium* sp. and thistles *Carduus* sp., *Cirsium* sp., while herring gulls most frequently nest in more open areas with marram grass *Ammophila* sp. (Calladine 1997; unpublished data). At the South Walney colony, the height of the vegetation in the areas occupied by lesser black-backed gulls is variable, and the patchy nature of the vegetation within different areas makes this a suitable site for a study of the relationship between vegetation and breeding success at different spatial scales.

Selection of study areas and measurement of nest vegetation

We selected three adjacent sub-areas, where lesser black-backed gulls nested, less than 300 m apart, with variable overall heights of vegetation cover (A, low; B, intermediate; C, tall vegetation). All three areas were located in low lying flat areas between sand dunes. To quantify and verify this assessment, we surveyed the height of vegetation in the three sub-areas using a square-quadrat (0.5×0.5 m), which was randomly thrown backwards 5–10 times in each sub-area. We measured the height of the tallest vegetation in the quadrat, which gave a good indication of vegetation height since this was generally homogeneous within the sub-areas. This was done before nest building (18 April 2003) and again during early incubation (23 May 2003). Figure 1 shows the average vegetation heights in each area.

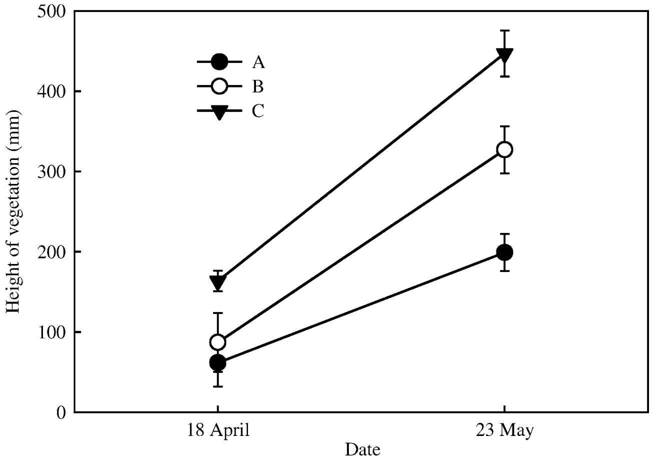

Fig. 1 Height of vegetation in different sub-areas with low (*A*), intermediate (*B*) and tall (*C*) vegetation (means ± SE). 18 April 2003: ANOVA: $F_{2,17} = 5.92$, $P < 0.05$; Tukey test: A and B: NS, A and C: $P < 0.05$, B and C: NS. 23 May: ANOVA: $F_{2,37} = 17.77$, $P < 0.001$; Tukey test: A and B: $P < 0.05$, A and C: $P < 0.001$, B and C: $P < 0.05$

On 23 May 2003, when all nests had been at least partially built, five square-quadrats (0.5×0.5 m, with 25 sub-quadrats) at nest sites and five at sites without nest-building activity were taken randomly in each of the three sub-areas to examine whether birds appeared to select nest sites in more vegetated patches within each sub-area. The number of the sub-quadrats containing vegetation was counted to estimate the percentage of vegetated area. We also examined the extent of vegetation surrounding nests using a round-quadrat divided into eight sectors. The quadrat was laid on the centre of the nest, and the number of sectors containing vegetation was counted. We investigated this at all the nests between 19 and 21 May 2003.

Nest microclimate and nocturnal egg cooling rate

During the incubation phase, we measured the microclimate at the nest site in a sample of nests in each sub-area. Air temperature was measured simultaneously at three nests, one in each sub-area, over 24 h, so that weather conditions did not affect the results when comparing microclimatic data among the three different sub-areas. We measured a total of 21 nests in each sub-area. We placed thermistors connected to TinyTag data loggers (Gemini Data Loggers, Chichester, UK) recording temperature at 1-min intervals at a 5-cm distance from the edge of nests and 3 cm above the ground, such that they were not in contact with parent birds and thus body temperature did not influence the measurements. We used the diurnal maximum temperature, nocturnal minimum temperature and average temperature during 24 h at each nest site for analyses. Wind speed and humidity at the nest site were measured at 26 nests each in areas A, B and C. Spot measurements were taken at a nest in each area separately within 30 min of each other using a Kestrel 3000 anemometer with additional humidity sensor (RS Components, Northants, UK). We placed the anemometer at 10 cm above the nest to measure wind speed and humidity every second for 40 s, and the maximum wind speed and the final record of humidity (to allow stabilisation of the sensor) were taken.

To examine the effect of the amount of vegetation surrounding the nest on its thermal properties, we measured the rate of heat loss from uncovered eggs at 13 nests in each of the sub-areas A and C, which had the lowest and tallest vegetation height, respectively. We selected a freshly completed nest without eggs in each area. Two fresh herring or lesser black-backed gull eggs of similar mass (paired *t* -test: $t_{12} = 1.09$, $P = 0.30$) that had been removed from the nests elsewhere in the colony for experimental purposes by other researchers (under licence from English Nature) were placed in each nest. Thermistors connected to TiniTag data loggers recording temperature at 5-s intervals were inserted 25 mm deep from the pointed apex of the two eggs, and they were warmed up to 35°C inside an incubator for about 6 h. We transported them in a warm box (maximum transport time 15 min) and placed them in the nests after sunset, so that sunlight did not influence the measurements of cooling rates. Eggs were protected from predators with open chicken wire. The data loggers and nest protectors were collected in the early following morning. We used linear egg cooling rate (slope of the linear regression line) during the first 120 min for analysis of variation in heat retention.

Field methods for breeding performance

To quantify the pattern of the nest site occupation, we surveyed the study areas once daily during egg laying. We marked each new nest containing eggs with numbered bamboo sticks. We recorded breeding performance at a sample of nests in each sub-areas (A: $n = 31$; B: $n = 40$; C: $n = 40$ nests). Eggs were individually marked with a permanent marker and weighed (to nearest 0.1 g) on the day of laying. We estimated nest density by measuring distance (to nearest cm) to the nearest neighbour when nest building was complete. We estimated the expected hatching date by adding 30 days to the first egg laying date and we checked each nest once daily beginning 2 days before the estimated hatching date until all the chicks were hatched. All chicks were marked using leg flags made with coloured tapes on the day of hatching (day 0) for identification within each brood. We visited each nest every 4 days until day 23 to record chick growth and survival. We weighed chicks (to nearest g) with 600-g and 1,000-g spring balances, and measured the total length of head and bill (to nearest 0.1 mm) with callipers. In most cases when mortality occurred, we found the corpse of the chick. Since chicks become much more mobile and move further from their nest sites as they grow, we were unable to continue the growth measurements after day 23. Linear growth rates, slopes of the linear regression lines of mass and head and bill length, were used for analysis. Linear growth rate of head and bill length was calculated from hatching to day 23, whereas that of mass was calculated from day 3 to day 23 since linear mass increase starts from day 3 onward in lesser black-backed gulls.

Statistical analyses

We used parametric tests unless the data distributions violated the assumptions, when equivalent nonparametric tests were used. Post hoc multiple comparisons were conducted with Tukey or nonparametric multiple comparisons (Zar 1999). All tests were two-tailed, and means ± SE are presented in the results. Influences of nest vegetation, area and laying date on egg mass were examined in ANCOVA using a linear model (Crawley 2003). Two nests that had abnormally small eggs without yolk (less than 20 g) were excluded from the analysis of egg mass. We examined the factors influencing laying date, clutch size, hatching success and chick survival rate using generalised linear models. The nests where no eggs hatched were excluded from the analysis of chick survival rate. The factors influencing chick growth were examined in mixed effect models with nest identity as a random effect (Crawley 2003). We compared breeding performance between the three sub-areas, with laying date and nest vegetation being taken into account. Differences between the sub-areas were identified using comparisons between the main model and sub-models with group combined (Crawley 2003). In separate analyses, we examined the effect of vegetation surrounding the nest within each sub-area.

Results

Differences in microclimate between sub-areas

There was a significant difference between the sub-areas in the microclimate during the incubation phase (Fig. 2). The diurnal maximum air temperature and wind speed at the nest sites in the sub-area with low vegetation (A) were significantly higher than those in the sub-areas with taller vegetation (B and C) (see Fig. 1). However, the average and nocturnal minimum air temperature and humidity at nest sites did not differ between the sub-areas. Heat loss from eggs at the nest sites was also related to vegetation, with heat loss in the low vegetation (A) being faster than in the tall vegetation (C); linear egg cooling rate during 120 min differed significantly between the two areas (means ± SE: $A = -0.185 \pm 0.007$°C/min, $C = -0.168 \pm 0.004$°C/min; Wilcoxon signed-ranks test: $T = 2.96$, $n = 13$ per area, $P < 0.01$).

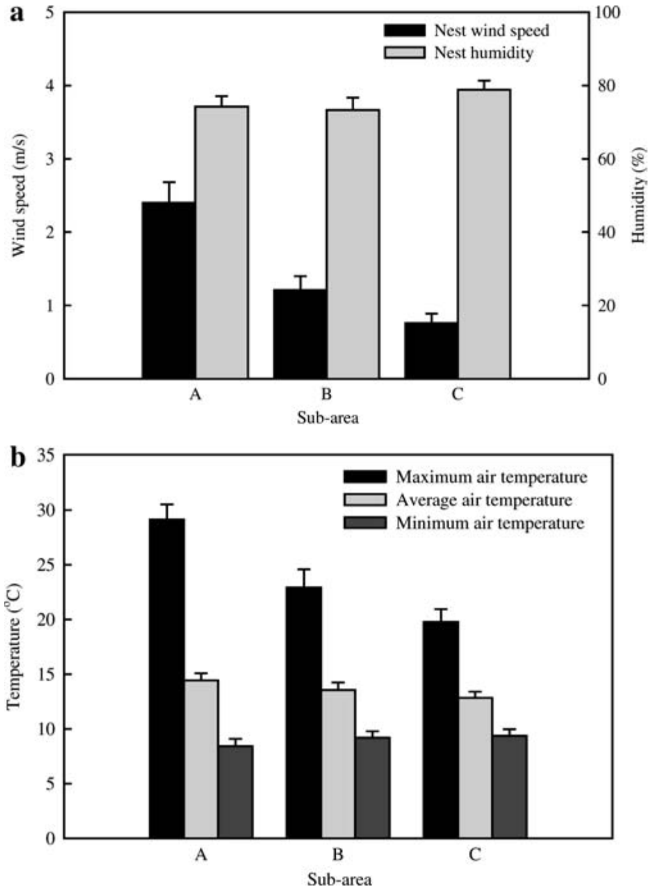

Fig. 2 Microclimate of lesser black-backed gull *Larus fuscus* nest site in different sub-areas. **a** Wind speed and humidity (means ± SE): wind speed: $F_{2,75} = 16.29$, $P < 0.001$, Tukey test: *A* and *B*: $P < 0.001$, *A* and *C*: $P < 0.001$, *B* and *C*: NS; nest humidity: $F_{2,75} = 1.02$, $P = 0.37$. **b** Air temperature (means ± SE): diurnal maximum nest air temperature: ANOVA: $F_{2,60} = 11.31$, $P < 0.001$, Tukey test: *A* and *B*: $P < 0.01$, *A* and *C*: $P < 0.001$, *B* and *C*: NS; average nest air temperature: $F_{2,60} = 1.60$, $P = 0.21$; nocturnal minimum nest air temperature: $F_{2,60} = 0.66$, $P = 0.52$

Table 1 Distance to the nearest neighbour and laying date of lesser black-backed gull *Larus fuscus* (expressed as number of days from 1 May = 1) in different sub-areas with low (A), intermediate (B) and tall (C) vegetation (means ± SE)

Area	*n*	Distance to the nearest neighbour (cm)	Laying date
A	31	371.3 ± 28.2	15.3 ± 1.1
B	40	349.0 ± 17.3	15.0 ± 0.9
C	40	573.8 ± 47.6	18.9 ± 0.9

Breeding performance

Nest density was lower, and laying date was later in the sub-area with tallest vegetation (C) than in the other two (Table 1; nest density: ANOVA: $F_{2,108} = 13.60$, $P < 0.001$; Tukey test: A and B: NS, A and C: $P < 0.001$, B and C: $P < 0.001$; laying date: generalised linear model with a Poisson error distribution and a log link: Deviance = 21.74, $df = 2$, $P < 0.001$). The first-laid eggs of clutches in the sub-areas with intermediate and tall vegetation (B and C) were significantly heavier than those from the sub-area with low vegetation (A) (means ± SE: A = 76.1 ± 1.4 g, B = 80.2 ± 1.1 g, C = 80.3 ± 1.1 g; ANCOVA: $F_{2,97} = 3.77$, $P < 0.05$; sub-model with A and B combined versus main model with separate groups: $F = 5.70$, $df = 1$, $P < 0.05$; sub-model with A and C: $F = 6.05$, $df = 1$, $P < 0.05$; sub-model with B and C: $F = 0.01$, $df = 1$, $P = 0.94$) when the effect of laying date was taken into account (ANCOVA: $F_{1,97} = 3.95$, $P < 0.05$) in a linear model. Clutch size did not differ significantly among the sub-areas (means ± SE: A = 2.7 ± 0.1, $n = 31$; B = 2.9 ± 0.1, $n = 40$; C = 2.8 ± 0.1, $n = 40$; generalised linear model with a Poisson error distribution and a log link: Deviance = 0.16, $df = 2$, $P = 0.92$), and laying date did not influence clutch size (Deviance = 0.33, $df = 1$, $P = 0.57$). Hatching success (proportion of eggs hatched) did not differ among the three sub-areas (means ± SE: A = 0.67 ± 0.08, $n = 31$; B = 0.83 ± 0.04, $n = 40$; C = 0.75 ± 0.05, $n = 40$; generalised linear model with a binomial error distribution and a logit link: $F = 1.51$, $df = 2$, $P = 0.22$), while it decreased as breeding season progressed ($F = 4.16$, $df = 1$, $P < 0.05$). Chick survival rate (proportion of chicks surviving to day 23) differed significantly among the sub-areas, being lower in the sub-area with tall vegetation than in the other two sub-areas (means ± SE: A = 0.58 ± 0.09, $n = 23$; B = 0.65 ± 0.07, $n = 39$; C = 0.40 ± 0.08, $n = 35$; generalised linear model with binomial error distribution and a logit link: $F = 3.17$, $df = 2$, $P < 0.05$; sub-model with A and B combined versus main model with separate groups: $F = 0.40$, $df = 1$, $P = 0.53$; sub-model with A and C: $F = 5.13$, $df = 1$, $P < 0.05$; sub-model with B and C: $F = 10.45$, $df = 1$, $P < 0.01$) when effect of laying date was taken into account ($F = 5.55$, $df = 1$, $P < 0.05$). The chicks in area A grew less well than those in areas B and C (Fig. 3; mixed models: mass: L. ratio = 10.07, $df = 2$, $P < 0.01$; head and bill length: L. ratio = 8.54, $df = 2$, $P < 0.05$).

Effects of nest vegetation on breeding

There was no difference in vegetation cover between nest sites and non-nest sites in the sub-area with low vegetation (A). However, nest sites had significantly more vegetation cover than non-nest sites in the sub-areas with intermediate (B) and tall vegetation (C) (Fig. 4), indicating that when vegetation is present in a breeding area, the birds build their nests close to it. The amount of vegetation immediately around the nest differed significantly among the sub-areas (means ± SE: A = 33.1 ± 5.5%, B = 52.8 ± 4.0%, C = 72.8 ± 3.6%; Kruskal-Wallis test: $H_2 = 30.19$, $P < 0.001$; nonparametric multiple comparison: A and B: $P < 0.05$, A and C: $P < 0.001$, B and C: $P < 0.01$). Overall, laying date was not correlated with surrounding nest vegetation (generalised linear model with a Poisson error distribution and a log link: Deviance = 0.63, $df = 1$, $P = 0.43$). Nest

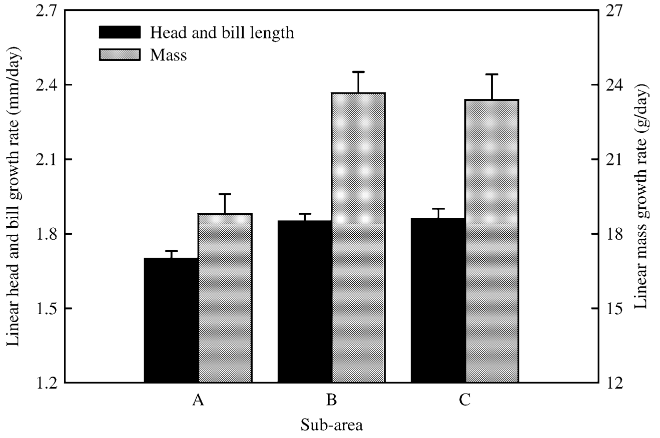

Fig. 3 Linear mass and head and bill length growth rates of chicks in different sub-areas

Table 2 Summary of generalised linear models examining relationships of nest vegetation (*nestveg*) and egg laying date (*laydate*) with clutch size, hatching success (proportion of eggs hatched) and chick survival rate (proportion of chicks survived to day 23) in different sub-areas

	Nestveg			Laydate			Nestveg:laydate		
	Deviance or *F*	*df*	*P*	Deviance or *F*	*df*	*P*	Deviance or *F*	*df*	*P*
Clutch size[a]									
A	0.10	1	0.76	0.43	1	0.51	0.01	1	0.94
B	0.003	1	0.96	0.02	1	0.90	0.03	1	0.87
C	0.04	1	0.85	0.05	1	0.82	0.38	1	0.54
Hatching success[b]									
A	0.71	1	0.40	8.93	1	<0.01	2.63	1	0.11
B	2.76	1	0.10	0.000	1	0.995	3.61	1	0.06
C	1.82	1	0.18	0.07	1	0.80	3.45	1	0.06
Chick survival rate[b]									
A	12.10	1	<0.001	0.52	1	0.47	0.76	1	0.38
B	5.58	1	<0.05	0.29	1	0.59	0.40	1	0.53
C	0.11	1	0.74	15.09	1	<0.001	5.05	1	<0.05

[a] Generalised linear model with a Poisson error distribution and a log link. The significance reported is the deviance when the explanatory variable of interest is dropped from the model

[b] Generalised linear model with a binomial error distribution and a logit link. The significance reported is the *F* value when the explanatory variable of interest is dropped from the model

vegetation did not influence egg mass (ANCOVA: $F_{1,97}=0.57$, $P=0.45$) in a linear model when sub-area and laying date were taken into account. Since differences between areas in the laying date suggest that the quality of birds may differ between areas, we examined the effects of the level of vegetation surrounding the nest on clutch size, hatching success and chick survival rate separately within each sub-area. Clutch size was not related to nest vegetation within any the three sub-areas when any effects of laying date were taken into account, nor were there any significant interactions between laying date and nest vegetation (Table 2). Overall, the proportion of eggs hatched increased as nest vegetation increased (Fig. 5; generalised linear model with a binomial error distribution and a logit link: $F=4.85$, $df=1$, $P<0.05$) although the effects were not significant in separate models in the three different sub-areas (Table 2). Nest vegetation did not correlate with chick survival rate overall (generalised linear model with a binomial error distribution and a logit link: $F=0.34$, $df=1$, $P=0.56$). However, the pattern of the effects varied in the three different areas. In the sub-area with low vegetation (A), chick survival rate was negatively correlated with nest vegetation, but the opposite trend occurred in the sub-area with intermediate vegetation (B) (Table 2). Nest vegetation did not influence growth rate of mass and head and bill length in any of the three areas, when laying sequence and laying date were taken into account (Table 3).

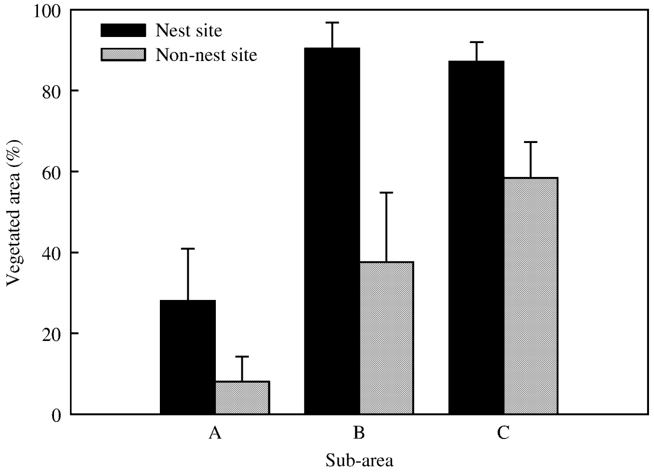

Fig. 4 Comparison in percentage of vegetation cover between nest and non-nest sites in different sub-areas. Area *A*: Mann-Whitney *U* test: $U=7.50$, $n_1=n_2=5$, $P=0.26$; *B*: $U=3.50$, $n_1=n_2=5$, $P=0.05$; *C*: $U=19.50$, $n_1=n_2=10$, $P<0.05$

Table 3 Summary of mixed effect models examining the effects of nest vegetation(*nestveg*), laying sequence and laying date (*laydate*) on linear growth rates of chicks. The significance reported is the Likelihood ratio when the explanatory variable of interest is dropped from the model

Variable	Mass			Head and bill length		
	L. ratio	*df*	*P*	L. ratio	*df*	*P*
Sub-area A						
Nestveg	0.03	1	0.87	0.001	1	0.97
Sequence	8.60	2	<0.05	9.35	2	<0.01
Laydate	0.51	1	0.47	0.03	1	0.85
Sub-area B						
Nestveg	0.53	1	0.47	0.44	1	0.51
Sequence	7.25	2	<0.05	7.39	2	<0.05
Laydate	0.21	1	0.65	1.32	1	0.25
Sub-area C						
Nestveg	0.12	1	0.73	0.25	1	0.61
Sequence	2.74	2	0.25	0.78	2	0.68
Laydate	0.22	1	0.64	1.60	1	0.21

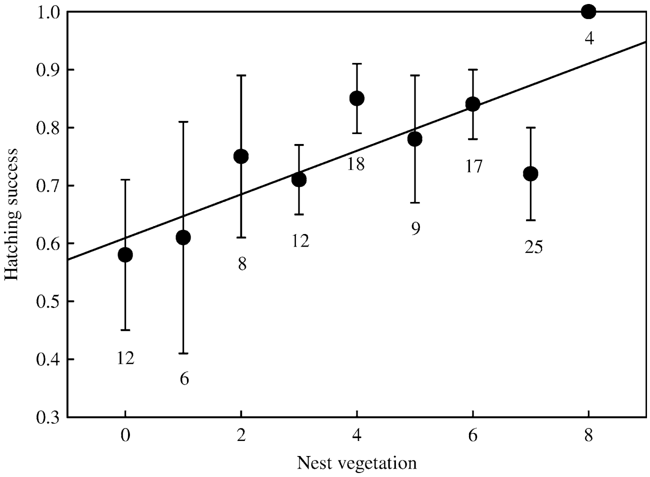

Fig. 5 Relationships of hatching success (proportion of eggs hatched) with nest vegetation (number of sectors containing vegetation in a round-quadrat; 0 = 0% to 8 = 100%)

Discussion

Vegetation can protect the incubating birds, eggs and chicks at the nest sites from diurnal heat gain, nocturnal heat loss and strong wind. Our results showed that lesser black-backed gull nests in sub-areas of the colony with intermediate and tall vegetation (around 100–400 mm) had lower diurnal temperature and wind speeds than those in the area with mainly very low vegetation (around 50–200 mm), indicating that vegetation height is an important factor moderating the microclimate experienced by the breeding birds. High temperature and strong wind at the nest site can stress the incubating birds and increase their energetic demands (Bartholomew and Dawson 1979; With and Webb 1993; Wiebe and Martin 1998). Heat and wind levels can also negatively influence the performance of the chicks and even cause chick mortality (Salzman 1982).

We did not detect any effect of vegetation on nocturnal minimum nest temperature. However, comparison of nocturnal egg cooling rate between relatively tall and low vegetation areas showed that vegetation reduced the rate of heat loss from uncovered eggs. While most gulls incubate their clutch continuously, they sometimes leave the clutch unguarded for a few hours, particularly during night when visibility is reduced and consequently predation risk decreases (Hébert and McNeil 1999). Unattended eggs at night may chill to temperatures which cause cessation of heart beat of the embryo (Bennett and Dawson 1979). Vegetation may therefore allow parents to be away for longer.

It is known that nest humidity influences water loss in eggs during incubation (Vleck et al. 1983; Swart et al. 1987) and in addition it may affect development and hatching of the eggs depending on species (Ar and Rahn 1980; Visschedijk 1980; Ar and Sidis 2002). In the present study, the vegetation was not related to the humidity of the nest sites. Vleck et al. (1983) reported that the difference in water-vapour pressure between an egg and its microenvironment is less in the ground nests of gulls and terns than it is in tree nesting species such as herons. In lesser black-backed gulls, therefore, water-vapour from the ground may be sufficient to control appropriate nest humidity even without nest cover, and as a result nest vegetation might not influence hatching success in terms of water loss.

Our results suggest that gulls have a clear preference for particular vegetation levels when selecting sub-areas of the colony and the nest site itself. The area with mainly tall vegetation was occupied on average by the latest laying birds, probably because this might obstruct the vision or movement of the breeders and affect anti-predator behaviour (Ewald et al. 1980; Götmark et al. 1995; Borboroglu and Yorio 2004). Many studies have shown positive relationships between habitat quality and breeding success of individuals in gull species (Bosch and Sol 1998; Rodway and Regehr 1999). The later laying date of birds in the sub-area with tall vegetation suggests that they may be younger or poorer quality individuals (Pierotti 1982; Becker and Erdelen 1986; Brouwer et al. 1995; Hipfner 1997). In an experimental study of herring gulls, we have shown that nest vegetation levels and breeder quality are linked (Kim and Monaghan 2005). In the present study, within an area of the colony with similar vegetation height and laying pattern, lesser back-backed gulls preferentially build their nests close to it. This suggests that vegetation levels around the nest are generally an important attribute of nest site selection for high and low quality birds throughout the season. Interestingly however, birds laid heavier eggs and chicks grew better in the sub-areas with intermediate (B) and tall vegetation (C) than those in the sub-area with low vegetation (A), even though the latest laying birds were in area C. Since gulls stay in their territory from pre-incubation phase to defend it (Butler and Janesbutler 1982), the habitat quality may influence the prelaying body condition of the female. Reduced prelaying energy costs in the taller vegetation area through reduced social conflict and microclimatic benefits might enable females to invest more in egg production (Houston et al. 1983; Gloutney and Clark 1997; Kilpi and Lindström 1997; Mawhinney et al. 1999; Kim and Monaghan 2005). As chicks grow bigger, the parents need to spend more time feeding and, as a consequence, the chicks are left unguarded for longer. Since cannibalism is an important mortality factor in gulls (Parsons 1971; Spaans et al. 1987) and aggression from neighbouring birds increases during this period (Ewald et al. 1980), chicks need shelter to avoid visual and physical contact with neighbouring adults. Since gull chicks are highly mobile and seek shelter by themselves, vegetation in the habitat surrounding the nest is likely to be more important in providing protection than that at the nest site itself. Such protection might reduce social harassment and predation risk, and enable the chicks to decrease stress and energy expenditure. The lower nesting density in the area with tall vegetation may also contribute to reduced neighbour aggression. However, chick survival rate was low in the tall vegetation area (C) compared to the other two sub-areas, even when laying date was taken into account. Tall vegetation might negatively influence visibility or movement of the chicks against predators, and consequently increase predation risk (Ewald et al. 1980; Götmark et al. 1995; Borboroglu and Yorio 2004). Alternatively, parental quality might cause the low chick survival rate in tall vegetation area (C), since poor-quality areas appear to be occupied by poor-quality individuals (Kim and Monaghan 2005).

The amount of vegetation around the nest site itself did not influence egg production in terms of clutch size and egg mass, as was also reported for the herring gull (Becker and Erdelen 1986), probably because the vegetation was still relatively short during the egg laying period. However, our results showed a positive relationship between hatching success and nest vegetation, indicating the potential importance of nest vegetation in incubation. While different parental quality might also influence hatching success, it would require an experimental approach to break the correlation between parental quality and vegetation levels to separate the two effects. During the incubation phase, nest vegetation can contribute to the provision of an appropriate microclimate for successful development of embryo and protect eggs from predators (Stauffer and Best 1986; Bekoff et al. 1989; Saliva and Burger 1989). Nest vegetation itself did not influence chick performance in terms of growth, probably due to their mobility as explained above. The effect of nest vegetation on chick survival rate varied in the different sub-areas, indicating that the habitat immediately surrounding the nest is more likely to be important than nest vegetation itself in overall reproductive output.

Zusammenfassung

Effekte der Vegetation auf das Mikroklima am Nest und die Brutbiologie der Heringsmöwe (*Larus fuscus*)

Große Vogelkolonien umfassen Teilbereiche, die sich durch verschiedene Merkmale wie Vegetation oder Brutpaardichte unterscheiden können. Bei der Ankunft am Koloniestandort suchen Individuen einen Nistplatz, indem sie in einem hierarchischen Prozess zunächst eine Subkolonie, dann einen bestimmten Nestplatz mit geeigneten biotischen und physikalischen Merkmalen auswählen. Ein wichtiges Charakteristikum dabei ist optimale Vegetationsdeckung. Viele am Boden nistende Möwenarten bevorzugen Neststandorte, die Schutz während der Reproduktion bieten, doch muss dieser Vorteil mit möglichen Nachteilen wie die reduzierte Sichtbarkeit potenzieller Prädatoren in Einklang gebracht werden. Diese Fragen wurden an einer Heringsmöwenkolonie (*Larus fuscus)* untersucht, deren Subkolonien sich in der durchschnittlichen Höhe der Vegetation unterschieden, die zudem fleckenartig verteilt war. Die Auswirkungen der Subkolonie-typischen Vegetationshöhe auf die Reproduktion und Massenentwicklung der Jungen sowie der Vegetationsdeckung in der unmittelbaren Nestumgebung auf das Mikroklima am Nest standen im Mittelpunkt der Studie. Hohe Vegetation hatte einen schützenden Effekt und war positiv mit dem Kükenwachstum korreliert. Die Subkolonie mit hoher Vegetation war aber durch geringere Brutdichten, relativ spät legende Vögel und reduzierte Überlebensraten der Küken gekennzeichnet. Das deutet darauf hin, dass sie überwiegend aus Brutvögeln geringerer Qualität oder jüngeren Alters bestand. Innerhalb der Subkolonien wurden Neststandorte mit mehr das Nest umgebender Vegetation bevorzugt, ein Parameter, der positiv mit dem Schlüpferfolg korrelierte.

Acknowledgements We are very grateful to Liliana D'Alba who provided invaluable help in fieldwork. We also thank Maria Bogdanova, Kampanat Tharapoom and Nanette Verboven for advice and help during field season, and Kevin Murphy for helpful discussion on the research protocol. Trish Chadwick and Mick Venters of the Cumbria Wildlife Trust kindly allowed S.-Y. Kim to carry out the research in the South Walney Nature Reserve. Peter H. Becker and Arie L. Spaans provided constructive criticism to improve the manuscript. S.-Y. Kim is funded by a University of Glasgow postgraduate research scholarship and the Overseas Research Scheme. The investigations we performed did not involve any licensed procedures and complied with the current laws of the UK. The eggs used for measurement of cooling rate were collected by M. Bogdanova and N. Verboven for their experimental manipulations under English Nature licenses.

References

Ar A, Rahn H (1980) Water in the avian egg: overall budget of incubation. Am Zool 20:373–384

Ar A, Sidis Y (2002) Nest microclimate during incubation. In: Deeming DC (ed) Avian incubation: behaviour, environment, and evolution. Oxford University Press, Oxford, pp 143–160

Bartholomew GA, Dawson WR (1979) Thermoregulatory behavior during incubation in Heermann's gull. Physiol Zool 52:422–437

Becker PH, Erdelen M (1982) Windrichtung und Vegetationsdeckung am Nest der Silbermöwe (*Larus argentatus*). J Ornithol 123:117–130

Becker PH, Erdelen M (1986) Egg size in herring gulls (*Larus argentatus*) on Mellum Island, North Sea, West Germany: the influence of nest vegetation, nest density, and colony development. Colon Waterbirds 9:68–80

Bekoff M, Scott AC, Conner DA (1989) Ecological analysis of nesting success in evening grosbeaks. Oecologia 81:67–74

Bennett AF, Dawson WR (1979) Physiological responses of embryonic Heermann's gulls to temperature. Physiol Zool 52:413–421

Block WM, Brennan LA (1993) The habitat concept in ornithology, theory and applications. Curr Ornithol 11:35–91

Borboroglu PG, Yorio P (2004) Habitat requirements and selection by kelp gulls (*Larus dominicanus*) in Central and Northern Patagonia, Argentina. Auk 121:243–252

Bosch M, Sol D (1998) Habitat selection and breeding success in yellow-legged gulls *Larus cachinnans*. Ibis 140:415–421

Brouwer A, Spaans AL, De Wit AAN (1995) Survival of herring gull *Larus argentatus* chicks: an experimental analysis of the need for early breeding. Ibis 137:272–278

Bukacińska M, Bukaciński D (1993) The effect of habitat structure and density of nests on territory size and territorial behaviour in the black-headed gull (*Larus ridibundus* L.). Ethology 94:306–316

Burger J (1977) Role of visibility in nesting behavior of *Larus* gulls. J Comp Physiol Psych 91:1347–1358

Burger J, Lesser F (1980) Nest site selection in an expanding population of herring gulls. J Field Ornithol 51:270–280

Butler RG, Janesbutler S (1982) Territoriality and behavioral correlates of reproductive success of great black-backed gulls. Auk 99:58–66

Calladine J (1997) A comparison of herring gull *Larus argentatus* and lesser black-backed gull *Larus fuscus* nest site: their characteristics and relationships with breeding success. Bird Study 44:318–326

Cody ML (1985) An introduction to habitat selection in birds. In: Cody ML (ed) Habitat selection in birds. Academic, New York, pp 3–56

Crawley MJ (2003) Statistical computing: an introduction to data analysis using S-Plus. Wiley, Chichester

Ewald PW, Hunt GL Jr, Warner M (1980) Territory size in western gulls: importance of intrusion pressure, defence investments, and vegetation structure. Ecology 60:80–87

Fretwell SD (1972) Theory of habitat distribution. In: Fretwell SD (ed) Populations in a seasonal environment. Princeton University Press, N.J., pp 79–117

Gloutney ML, Clark RG (1997) Nest-site selection by mallards and blue-winged teal in relation to microclimate. Auk 114:381–395

Götmark F, Blomqvist D, Johansson OC, Bergkvist J (1995) Nest site selection: a trade-off between concealment and view of the surroundings? J Avian Biol 26:305–312

Hébert PN, McNeil R (1999) Nocturnal activity of ring-billed gulls at and away from the colony. Waterbirds 22:445–451

Hipfner JM (1997) The effects of parental quality and timing of breeding on the growth of nestling thick-billed murres. Condor 99:353–360

Houston DC, Jones PJ, Sibly RM (1983) The effect of female body condition on egg laying in lesser black-backed gulls *Larus fuscus*. J Zool 200:509–520

Kilpi M, Lindström K (1997) Habitat-specific clutch size and cost of incubation in common eiders, *Somateria mollissima*. Oecologia 111:297–301

Kim S-Y, Monaghan P (2005) Interacting effects of nest shelter and breeder quality on behaviour and breeding performance of herring gulls. Anim Behav 69:301–306

Krause J, Ruxton GD (2002) Living in groups. Oxford University Press, Oxford

Mawhinney K, Diamond AW, Kehoe FP (1999) The use of energy, fat, and protein reserves by breeding great black-backed gulls. Can J Zool 77:1459–1464

Miyazaki M (1996) Vegetation cover, kleptoparasitism by diurnal gulls, and timing of arrival of nocturnal rhinoceros auklets. Auk 113:698–702

Parsons J (1971) Cannibalism in herring gulls. Br Birds 64:528–537

Partridge L (1978) Habitat selection. In: Krebs JR, Davis NB (eds) Behavioural ecology: an evolutionary approach. Blackwell, Oxford, pp 351–376

Pierotti R (1982) Habitat selection and its effect on reproductive output in the herring gull in Newfoundland. Ecology 63:854–868

Rodway MS, Regehr HM (1999) Habitat selection and reproductive performance of food-stressed herring gulls. Condor 101:566–576

Saliva JE, Burger J (1989) Effect of experimental manipulation of vegetation density on nest-site selection in sooty terns. Condor 91:689–698

Salzman AG (1982) The selective importance of heat stress in gull nest location. Ecology 63:742–751

Spaans AL, de Wit AAN, van Vlaardingen MA (1987) Effects of increased population size in herring gulls on breeding success and other parameters. Stud Avian Biol 10:57–65

Stauffer DF, Best LB (1986) Nest-site characteristics of open-nesting birds in riparian habitats in Iowa. Wilson Bull 98:231–242

Swart D, Rahn H, De Kock J (1987) Nest microclimate and incubation water loss of eggs of the African ostrich (*Struthio camelus* var. *domesticus*). J Exp Zool Suppl 1:239–246

Visschedijk AHJ (1980) Effects of barometric pressure and abnormal gas mixtures on gaseous exchange by the avian embryo. Am Zool 20:469–476

Vleck CM, Vleck D, Rahn H, Paganelli CV (1983) Nest microclimate, water-vapor conductance, and water loss in heron and tern eggs. Auk 100:76–83

Wiebe KL, Martin K (1998) Costs and benefits of nest cover for ptarmigan: changes within and between years. Anim Behav 56:1137–1144

With KA, Webb DR (1993) Microclimate of ground nests: the relative importance of radiative cover and wind breaks for three grassland species. Condor 95:401–413

Zar JH (1999) Biostatistical analysis. Prentice Hall, Upper Saddle River