Interacting effects of nest shelter and breeder quality on behaviour and breeding performance of herring gulls

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Physical attributes of a nest site can be important in determining the outcome of a breeding event. However, high-quality individuals may be more able to obtain particular sites, and thus habitat quality and individual quality are often confounded in correlative studies. We examined the potential sheltering effect of nest vegetation on the nest microclimate and on the behaviour and breeding performance of herring gulls, *Larus argentatus*. In addition to comparing birds at unmanipulated vegetated and unvegetated sites, we experimentally manipulated vegetation around nests to tease apart breeder quality and habitat effects. Birds nesting at unmanipulated vegetated sites had earlier laying dates, heavier eggs and more fledglings than those at comparable unvegetated sites. Vegetation provided shelter from weather conditions for the incubating birds and chicks; vegetated nest sites had on average milder air temperatures and lower wind speeds than unvegetated control nest sites. During incubation, breeders at naturally vegetated nests assumed alert postures less, and spent more time sleeping, than those at naturally unvegetated sites, indicating less disturbance from neighbours. In nests where vegetation was experimentally removed, both nest microclimate and breeder behaviour became similar to those at the naturally unvegetated nests; however, despite these changes, the absence of vegetation did not alter the higher breeding performance of birds at these sites. Therefore, nest microclimate alone is not responsible for the improved performance at vegetated sites; such sites appear to be occupied by better-quality individuals.

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The identification and selection of a suitable place to breed is an important component of an organism's life cycle. For most species, both physical and biotic features of the breeding area are likely to be important, influencing the degree of exposure to the elements and to predators and pathogens (Partridge 1978; Cody 1985). The spatial distribution of conspecifics will obviously be linked to variation in habitat quality, and in turn the presence of conspecifics will influence an individual's habitat choice. Conspecific density has both positive and negative effects on habitat suitability, influencing, for example, the level of local competition and also the degree of protection against predators (Krause & Ruxton 2002). Competition among individuals for the best breeding sites may result in a positive association between individual quality and habitat quality, with the more dominant individuals also occupying the best breeding areas. This makes it difficult to separate the effects of individual quality on breeding

performance from effects that are attributable to physical components of the breeding areas.

In colonially breeding birds such as gulls and terns, the association between habitat heterogeneity and breeding performance is often particularly marked, with individuals in certain areas of a colony often breeding more successfully than others (Nettleship 1972; Hudson 1982; Pierotti 1982; Bosch & Sol 1998). Where such areas also show differences in attributes such as vegetation cover, it is unclear whether the presence of vegetation is in itself contributing to variation in breeding performance. Vegetation close to the nest may be important in providing protection from extreme weather (Saliva & Burger 1989; Miyazaki 1996), a refuge in social conflicts with neighbours (Ewald et al. 1980; Bukacinska & Bukacinski 1993; Kilpi 1995) and protection from predators (Stauffer & Best 1986; Bekoff et al. 1989). However, vegetation may also make individuals more vulnerable to predation through its effect on visibility or movement (Ewald et al. 1980; Götmark et al. 1995; Wiebe & Martin 1998).

We investigated the effect of vegetation cover adjacent to the nest on the behaviour and breeding performance of herring gulls, *Larus argentatus*. We examined the sheltering effects of vegetation from weather conditions and also

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compared the pattern of occupation and performance of birds breeding at vegetated and unvegetated nest sites. By experimentally removing vegetation from a number of nest sites, we also disentangled the effect of individual quality from habitat quality in the observed variation in performance among birds nesting in vegetated and unvegetated sites.

METHODS

From early April to late July 2002 we studied a mixed colony of herring and lesser black-backed gulls, *Larus fuscus*, at South Walney Nature Reserve, Walney Island, Cumbria, U.K.(54°08′N, 03°16′W). Approximately 4400 pairs of herring gulls and 18 600 pairs of lesser black-backed gulls were recorded breeding at this site in 2002 (N. Verboven, personal communication). During the breeding season, herring and lesser black-backed gulls are generally spatially segregated in the Walney colony. Lesser black-backed gulls prefer topologically low areas with homogeneous thick vegetation such as nettles, *Urtica dioica*, or bracken, *Pteridium aquilinum*, whereas herring gulls most frequently nest in sand dunes with large clumps of marram grass, *Ammophila arenaria* (Harris 1964; Calladine 1997). Within the areas occupied by herring gulls, there is substantial variation in the amount of vegetation immediately surrounding the nest sites, and we therefore focused on this species to examine the interaction between nest shelter and breeder quality. The study was done under licence from English Nature.

To quantify the pattern of occupation of vegetated and unvegetated nest sites, we surveyed the study areas once daily during egg laying from 19 April to 16 May 2002. We marked each new nest containing eggs with numbered bamboo sticks and recorded the extent of vegetation cover. Nests with one or more marram grass clumps within a 30-cm radius of the edge of the nest cup were considered vegetated nests; nests that lacked grass clumps within this area were categorized as unvegetated nests. Since the grass clumps were large, this classification clearly distinguished between nests with and without potentially sheltering vegetation nearby. We recorded data for 157 vegetated nests and 186 unvegetated nests. At this preincubation stage, the marram grass vegetation was tall enough to recognize, and also a large proportion of clumps had dead grass remains from the previous year. Thus the gulls may be able to recognize that such habitat will become even more vegetated later in the season. To compare breeding performance, we recorded egg production and the outcome of the breeding event. The first-laid eggs were individually marked on the day of laying with a permanent marker and weighed at 127 randomly selected vegetated nests and 114 unvegetated nests among the recorded nests. Both vegetated and unvegetated nests were scattered over the same areas throughout the colony. Thus there was no difference in general environmental circumstances such as topology and nest density between the vegetated and the unvegetated nests.

We used a subset of these nests to examine the effect of experimental removal of vegetation by cutting all grass clumps within a 30-cm radius from the edge of the nest cup 3 days after clutch completion. To maintain the vegetation reduction, we cut the vegetation two or three times during the breeding period to prevent regrowth to more than 5 cm from the ground. We also visited the control nests on the same day for a similar period to ensure that the level of disturbance was the same at all sites. Unfortunately, we could not add vegetation to unvegetated sites, because the marram grass clumps were too large and deep rooted to be transplanted. Since timing of breeding may influence the results, for the experimental component of the study we standardized laying dates among the experimental treatment groups by allocating similar numbers of birds laying on the same day to each treatment, which were as follows: (1) vegetated control nests (VC), $N = 37$; (2) control nests that were not vegetated (NC), $N = 39$; and (3) vegetation-removed nests (VR), $N = 33$ (means of laying date $\pm$ SE expressed as number of days from 1 April = 1; VC: 31.11 ± 0.77; NC: 29.90 ± 0.56; VR: 30.24 ± 0.58; ANOVA: $F_{2,106} = 0.96$, $P = 0.39$). All study nests had three eggs initially.

We used subsamples of the experimental nests for microclimate measurements and behavioural observations as follows. During the incubation period, we measured air temperatures and wind speeds at the nest site in 22 VC nests, 22 NC nests and 22 VR nests at 4 and 19 days after clutch completion. The averages of these two measurements were used for data analyses. We measured the temperature at the same number of VC, NC and VR nests simultaneously over 24 h, so that weather conditions did not affect the results when we compared microclimate data among the groups. We placed thermistors connected to TinyTag data loggers recording temperature at 1-min intervals over 24 h (Gemini Data Loggers, UK Ltd, Chichester, U.K.) 5 cm from the edge of nests and 3 cm above the ground, such that they were not in contact with parent birds and we could record the air temperature of the habitat without the effect of individual body temperature. On two occasions, we noted wind speed at the same number of VC, NC and VR nests separately within 30 min of each other using a Kestrel electronic anemometer (RS Components, UK Ltd, Northants, U.K.). The anemometer was placed at 10 cm above the nest bottom to measure wind speed every 1 s for 10 s, and the maximum wind speed was recorded.

To investigate differences in social interactions between habitat types, we monitored the behaviour of parents for three or four 120-min observation periods using scan sampling at 5-min intervals. This was done for seven VC nests, seven NC nests and seven VR nests during incubation (mean total observation time per nest $\pm$ SE: 365.71 ± 17.52 min). We selected nests clearly visible from the observation hides for the observations and laying dates did not differ between the three groups (means of laying date $\pm$ SE expressed as number of days from 1 April = 1, VC: 29.14 ± 1.40; NC: 30.14 ± 1.47; VR: 28.00 ± 1.31; ANOVA: $F_{2,18} = 0.59$, $P = 0.57$). One of each type of nest was observed simultaneously. We categorized behaviours as sleeping, alert and aggression.

The proportion of the total number of scans in which the birds were engaged in each activity was estimated. We estimated the expected hatching date by adding 30 days to the laying date of the first egg 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 with leg flags made of coloured tapes on the day of hatching (day 0) for identification within each brood. We visited each nest every 4 days until day 31 to record chick growth and survival. We removed the leg flags of the chicks at the day of the last growth measurement. After this time, the by then large and mobile chicks became too hard to catch without causing undue disturbance and were presumed to fledge successfully. We weighed chicks with 600-g and 1000-g spring balances, and measured the total length of head and bill with callipers. Linear growth rates (slopes of the linear regression lines of mass and size from hatching to day 31) were used for analysis.

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 $\pm$ SE or medians $\pm$ 75 and 90 percentiles are presented in the results. We compared the mass of the first-laid eggs of clutches in vegetated and unvegetated nests, taking laying date into account in an ANCOVA using a linear model (Crawley 2003). To examine group effects on the number of chicks hatched and fledged, we used generalized linear models with a Poisson error distribution and a log link. Differences between groups were identified using comparisons between the main model and submodels with group combined (Crawley 2003). The factors influencing chick growth were examined in a mixed-effect model with nest identity as a random effect (Crawley 2003).

RESULTS

Nest Shelter and Habitat Preferences

In the total sample of unmanipulated nests, the distributions of laying dates did not differ from normal (Kolmogorov–Smirnov test: vegetated nests: $Z = 0.92$, $N = 157$, $P = 0.37$; unvegetated nests: $Z = 1.02$, $N = 186$, $P = 0.25$). Overall, herring gulls that occupied vegetated nest sites laid their clutches significantly earlier than those at unvegetated sites (mean laying dates expressed as number of days from 1 April = 1: vegetated nests: 32.07 ± 0.41, $N = 157$; unvegetated nests: 33.77 ± 0.42, $N = 186$; $t_{341} = -2.85$, $P < 0.01$), suggesting that earlier breeding birds were more likely to occupy vegetated nest sites.

The maximum air temperature of unvegetated nest sites (NC) was significantly higher than that of vegetated nests (VC) (Fig. 1). Overall, 45% of unvegetated nests were exposed to temperatures over 30°C, whereas only 5% of vegetated nests experienced such high temperatures. The minimum air temperature at unvegetated nests (NC) was lower than that at vegetated nests (VC), although the
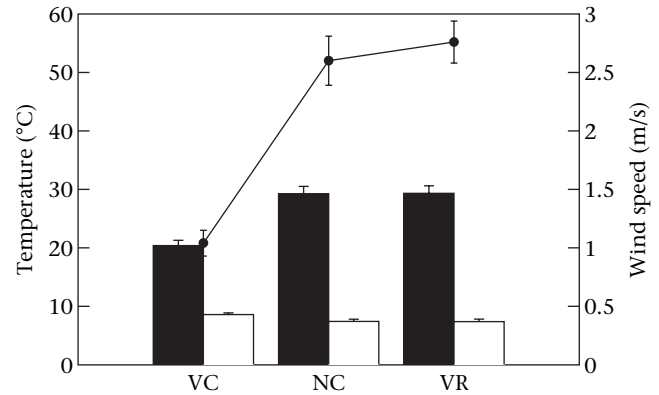

Figure 1. Microclimate parameters ($\overline{X} \pm$ SE; ■: maximum air temperature; □: minimum air temperature; ●: wind speeds) of nest sites from vegetated (VC), unvegetated (NC) and vegetation-removed (VR) groups. Maximum air temperature: ANOVA: $F_{2,63} = 19.67$, $P < 0.001$; Tukey tests: VC and VR: $P < 0.001$; VC and NC: $P < 0.001$; VR and NC: $P = 0.999$. Minimum air temperature: ANOVA: $F_{2,63} = 3.60$, $P < 0.05$; Tukey tests: VC and VR: $P = 0.06$; VC and NC: $P = 0.07$; VR and NC: $P = 0.997$. Wind speed: ANOVA: $F_{2,63} = 29.86$, $P < 0.001$; Tukey tests: VC and VR: $P < 0.001$; VC and NC: $P < 0.001$; VR and NC: $P = 0.81$.

effect was small and only marginally significant, whereas the wind speed was significantly higher (Fig. 1). The vegetated sites were thus well sheltered from extremes of temperature and wind.

Effects of Nest Shelter on Adult Behaviour

The behaviour of the breeding birds during incubation differed significantly between vegetated and unvegetated nests. Individuals at vegetated nests (VC) spent a significantly higher proportion of time sleeping than those at unvegetated nests (NC), and assumed alert postures less often (Fig. 2).
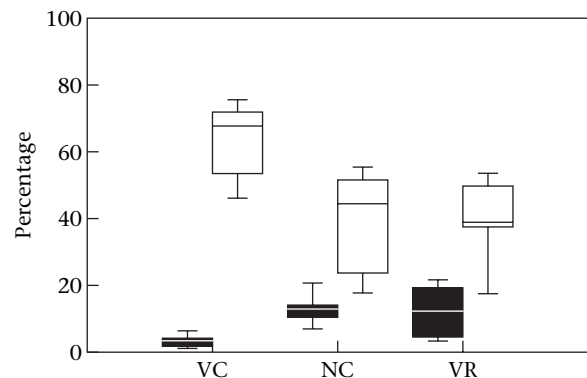
Figure 2. The percentage of time (median $\pm$ 75 and 90 percentiles) that individuals spent alert (■) and sleeping (□) in vegetated (VC), unvegetated (NC) and vegetation-removed (VR) groups. Alert: Kruskal–Wallis test: $H_2 = 9.89$, $P < 0.01$; nonparametric multiple comparison: VC and VR: $P < 0.05$; VC and NC: $P < 0.05$; VR and NC: NS. Asleep: Kruskal–Wallis test: $H_2 = 8.71$, $P < 0.05$; nonparametric multiple comparison: VC and VR: $P < 0.05$; VC and NC: $P < 0.05$; VR and NC: NS.

Nest Shelter and Breeding Performance

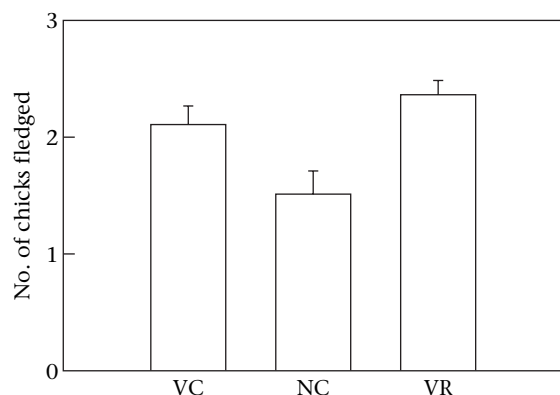The first-laid eggs of clutches in vegetated nests were significantly heavier (88.50 ± 0.60 g, $N = 127$) than those from unvegetated nests (85.49 ± 0.63 g, $N = 114$; ANCOVA: $F_{1,237} = 11.82$, $P < 0.001$). Laying date did not influence egg mass (ANCOVA: $F_{1,237} = 1.33$, $P = 0.25$), and there was no significant interacting effect of nest vegetation and laying date (ANCOVA: $F_{1,237} = 0.08$, $P = 0.77$). Furthermore, individuals at vegetated nests fledged their chicks significantly more successfully than did those at unvegetated nests (Fig. 3).

Separation of Shelter and Breeder Quality

In VR nests, both nest microclimate and the behaviour of the breeding birds changed after the manipulation, becoming similar to those of birds at unvegetated nests (Figs 1 and 2). However, reproductive performance did not change. There was no difference between groups in hatching success (generalized linear model: Deviance$_2 = 1.84$, $P = 0.40$). The percentage of all eggs that were predated among study nests was only 5.2% during the incubation period, and did not differ between groups. However, the chicks of both VC and VR groups were more likely to survive and fledge than those of the NC group (Fig. 3). Treatment group did not influence the linear growth rates of mass and head and bill length of surviving chicks (mixed-effect model with nest identity as a random effect: mass: likelihood ratio$_2 = 2.18$, $P = 0.34$; head and bill length: likelihood ratio$_2 = 1.52$, $P = 0.47$).

DISCUSSION

In birds, nest sites associated with the highest breeding success are often the first to be occupied in the spring (Brooke 1979; Bensch & Hasselquist 1991), and also such sites are occupied more frequently (Møller 1982; Andrén 1990). Since earlier breeders are often higher-quality individuals, the contributions of individual and habitat quality are difficult to tease apart in nonexperimental studies. In this study, on average, the gulls that occupied vegetated nest sites laid their clutches significantly earlier than did those that nested at unvegetated sites, suggesting that the birds breeding early preferentially selected vegetated nest sites. While the difference of 1.7 days in the timing of breeding is relatively small and may not in itself influence breeding performance, even small differences in laying date can indicate differences in breeder quality (Coulson & White 1958; Sydeman et al. 1991; Brouwer et al. 1995). This is further supported by eggs being heavier at vegetated nests, which again suggests that parental body condition is better at vegetated nests (Houston et al. 1983; Meathrel et al. 1987; Bolton 1991; Bolton et al. 1992; Risch & Rohwer 2000). Although reduced prelaying energy costs at vegetated nest sites may enable females to invest more in egg production, this seems unlikely since at such an early time in the season, the vegetation was still relatively short.

The nest vegetation moderated the microclimate of the nest sites and provided protection to the incubating birds on the nests from diurnal heat gain, nocturnal heat loss and strong wind. It is clear that the differences in microclimate between vegetated and unvegetated nests were due to the existence of the tall vegetation close to the nest, as removal of this vegetation resulted in the microclimate of vegetated nests becoming similar to that of unvegetated nests. In seabird species, weather conditions affect nesting habitat selection (Buckley & Buckley 1980), and our results suggest that protection from the weather is an important consequence of nesting at a vegetated site. By correlating behavioural responses (gaping, panting, extending the neck and elevating the scapulars or crown feathers) with thermal conditions, Bartholomew & Dawson (1979) showed that high temperature at the nest site could stress incubating adult gulls. We also observed that incubating adults showed the same thermoregulatory behaviours when the air temperature was high. Exposure to low temperature during the night or rainy weather and strong wind may also stress incubating birds and increase energy demands. Incubation can be a demanding phase of avian reproduction in terms of energy expenditure, and changes in energy expenditure can influence subsequent performance in the same reproductive event (Thomson et al. 1998; Reid et al. 2000; Tinbergen & Williams 2002).

Nest vegetation could also provide chicks with shelter from sun, wind and rain. In this study, chicks at vegetated sites fledged more successfully than those at unvegetated sites. However, there was no evidence that this was directly related to vegetation, since survival of chicks was not lower in the nests where vegetation had been removed before they hatched. Furthermore, there was no evidence that nest vegetation influenced chick growth. Studies on other *Larus* gull species have also shown that vegetation cover is not a dominant factor influencing chick mortality (Salzman 1982; Jehl & Mahoney 1987). The sheltering effects of nest vegetation may be important

Figure 3. The mean number of chicks fledged (number of chicks that survived until day 31) from vegetated (VC), unvegetated (NC) and vegetation-removed (VR) groups. Generalized linear model: Deviance$_2 = 7.59$, $P < 0.05$; submodel with VC and VR combined versus main model with separate groups: Deviance$_1 = 0.31$, $P = 0.58$; submodel with VR and NC combined: Deviance$_1 = 6.77$, $P < 0.01$; submodel with VC and NC combined: Deviance$_1 = 4.39$, $P < 0.05$.

only in extreme weather conditions, particularly when chicks are very young. However, adults brood very young chicks in the nest. Also, as chicks become more mobile, they can move to seek shelter, although this may result in increased aggression from neighbouring pairs.

Observations during incubation showed that the parent birds at vegetated nests assumed alert postures less and spent more time sleeping than those at unvegetated nests. This was not due to a difference in social conditions between the groups, since the three types of nests occurred in the same areas of the colony. Rather, it is likely that the vegetation reduced visual contact between neighbours (Burger 1974, 1977; Bukacinska & Bukacinski 1993). Overall, our results suggest that birds nesting at vegetated sites are less disturbed by their neighbours and, therefore, can rest more. There was no evidence that vegetation cover influenced predation rate of eggs and chicks at this colony. However, predation rate was very low in our study area once the individuals completed their clutches and started incubation.

The microclimate and behavioural differences between vegetated and unvegetated sites disappeared with the removal of vegetation. However, birds nesting at these manipulated sites still had relatively high breeding success. Hence, nest vegetation itself is not responsible for the higher reproductive success at vegetated nests. Higher-quality individuals, who tend to secure better habitat, are also likely to attain higher reproductive success (Goodburn 1991; Bunin & Boates 1994). Various studies have shown a positive relation between breeding performance and parental quality as reflected in egg size, age and breeding experience (Ollason & Dunnet 1978; Pugesek 1981; Coulson & Porter 1985; Bolton 1991; Sydeman et al. 1991; Ratcliffe et al. 1998; Daunt et al. 1999; Risch & Rohwer 2000). In the nests where vegetation was removed, individual quality appears to have overcome the relatively poor quality of the nesting habitat. However, while we detected no within-season effects on breeding performance when vegetation was removed, breeding in poorer habitats, exposure to poor micro-environmental conditions and high disturbance levels could result in long-term costs for the incubating individuals or their chicks.

References

Andrén, H. 1990. Despotic distribution, unequal reproductive success and population regulation in the jay *Garrulus glandarius* L. *Ecology*, **71**, 1796–1803.

Bartholomew, G. A. & Dawson, W. R. 1979. Thermoregulatory behavior during incubation in Heermann's gulls. *Physiological Zoology*, **52**, 422–437.

Bekoff, M., Scott, A. C. & Conner, D. A. 1989. Ecological analysis of nesting success in evening grosbeaks. *Oecologia*, **81**, 67–74.

Bensch, S. & Hasselquist, D. 1991. Territory infidelity in the polygynous great reed warbler *Acrocephalus arundinaceus*: the effect of variation in territory attractiveness. *Journal of Animal Ecology*, **60**, 857–871.

Bolton, M. 1991. Determinants of chick survival in the lesser black-backed gull: relative contributions of egg size and parental quality. *Journal of Animal Ecology*, **60**, 949–960.

Bolton, M., Houston, D. & Monaghan, P. 1992. Nutritional constraints on egg formation in the lesser black-backed gull: an experimental study. *Journal of Animal Ecology*, **61**, 521–532.

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

Brooke, M. D. L. 1979. Differences in the quality of territories held by wheatears (*Oenanthe oenanthe*). *Journal of Animal Ecology*, **48**, 21–32.

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

Buckley, F. G. & Buckley, P. A. 1980. Habitat selection and marine birds. In: *Behaviour of Marine Animals. Vol. 4: Marine Birds* (Ed. by H. E. Winn & B. L. Olla), pp. 69–112. New York: Plenum.

Bukacinska, M. & Bukacinski, 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.

Bunin, J. S. & Boates, J. S. 1994. Effects of nesting location on breeding success of Arctic terns on Machias Seal Island. *Canadian Journal of Zoology*, **72**, 1841–1847.

Burger, J. 1974. Breeding adaptations of Franklin's gull (*Larus pipixcan*) to a marsh habitat. *Animal Behaviour*, **22**, 521–567.

Burger, J. 1977. Role of visibility in nesting behaviour of *Larus* gulls. *Journal of Comparative and Physiological Psychology*, **91**, 1347–1358.

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

Cody, M. L. 1985. An introduction to habitat selection in birds. In: *Habitat Selection in Birds* (Ed. by M. Cody), pp. 3–56. New York: Academic Press.

Coulson, J. C. & Porter, J. M. 1985. Reproductive success of the kittiwake *Rissa tridactyla*: the roles of clutch size, chick growth rates and parental quality. *Ibis*, **127**, 450–466.

Coulson, J. C. & White, E. 1958. The effect of age on the breeding biology of the kittiwake, *Rissa tridactyla*. *Ibis*, **100**, 40–51.

Crawley, M. J. 2003. *Statistical Computing: An Introduction to Data Analysis using S-Plus*. Chichester: J. Wiley.

Daunt, F., Wanless, S., Harris, M. P. & Monaghan, P. 1999. Experimental evidence that age-specific reproductive success is independent of environmental effects. *Proceedings of the Royal Society of London, Series B*, **266**, 1489–1493.

Ewald, P. W., Hunt, G. L., Jr. & Warner, M. 1980. Territory size in western gulls: importance of intrusion pressure, defence investments, and vegetation structure. *Ecology*, **60**, 80–87.

Goodburn, S. F. 1991. Territory quality or bird quality? Factors determining breeding success in the magpie *Pica pica*. *Ibis*, **133**, 85–90.

Götmark, F., Blomqvist, D., Johansson, O. C. & Bergkvist, J. 1995. Nest site selection: a trade-off between concealment and view of the surroundings? *Journal of Avian Biology*, **26**, 305–312.

Harris, M. P. 1964. Aspects of the breeding biology of the gulls *Larus argentatus*, *L. fuscus* and *L. marinus*. *Ibis*, **106**, 432–456.

Houston, D. C., Jones, P. J. & Sibly, R. M. 1983. The effect of female body condition on egg laying in lesser black-backed gulls *Larus fuscus*. *Journal of Zoology*, **200**, 509–520.

Hudson, P. J. 1982. Nest site characteristics and breeding success in the razorbill *Alca torda*. *Ibis*, **124**, 355–359.

Jehl, J. R., Jr. & Mahoney, S. A. 1987. The roles of thermal environment and predation in habitat choice in the California gull. *Condor*, **89**, 850–862.

Kilpi, M. 1995. Further comments on nest density effects in large gulls. *Journal of Avian Biology*, **26**, 264–266.

Krause, J. & Ruxton, G. D. 2002. *Living in Groups*. Oxford: Oxford University Press.

Meathrel, C. E., Ryder, J. P. & Termaat, B. M. 1987. Size and composition of herring gull eggs: relationship to position in the laying sequence and the body condition of females. *Colonial Waterbirds*, **10**, 55–63.

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

Møller, A. P. 1982. Characteristics of magpie *Pica pica* territories of varying duration. *Ornis Scandinavica*, **13**, 94–100.

Nettleship, D. N. 1972. Breeding success of the common puffin (*Fratercula Arctica* L.) on different habitats at Great Island, Newfoundland. *Ecological Monographs*, **42**, 239–266.

Ollason, J. C. & Dunnet, G. M. 1978. Age, experience and other factors affecting the breeding success of the fulmar, *Fulmarus glacialis*, in Orkney. *Journal of Animal Ecology*, **47**, 961–976.

Partridge, L. 1978. Habitat selection. In: *Behavioural Ecology: an Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davis), pp. 351–376. Oxford: Blackwell Scientific.

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

Pugesek, B. H. 1981. Increased reproductive effort with age in the California gull (*Larus californicus*). *Science*, **212**, 822–823.

Ratcliffe, N., Furness, R. W. & Hamer, K. C. 1998. The interactive effects of age and food supply on the breeding ecology of great skuas. *Journal of Animal Ecology*, **67**, 853–862.

Reid, J. M., Monaghan, P. & Ruxton, G. D. 2000. Resource allocation between reproductive phases: the importance of thermal conditions in determining the cost of incubation. *Proceedings of the Royal Society of London, Series B*, **267**, 37–41.

Risch, T. S. & Rohwer, F. C. 2000. Effects of parental quality and egg size on growth and survival of herring gull chicks. *Canadian Journal of Zoology*, **78**, 967–973.

Saliva, J. E. & Burger, J. 1989. Effect of experimental manipulation of vegetation density on nest-site selection in sooty terns. *Condor*, **91**, 689–698.

Salzman, A. G. 1982. The selective importance of heat stress in gull nest location. *Ecology*, **63**, 742–751.

Stauffer, D. F. & Best, L. B. 1986. Nest-site characteristics of open-nesting birds in riparian habitats in Iowa. *Wilson Bulletin*, **98**, 231–242.

Sydeman, W. J., Penniman, J. F., Penniman, T. M., Pyle, P. & Ainley, D. G. 1991. Breeding performance in the western gull: effects of parental age, timing of breeding and year in relation to food availability. *Journal of Animal Ecology*, **60**, 135–149.

Thomson, D. L., Monaghan, P. & Furness, R. W. 1998. The demands of incubation and avian clutch size. *Biological Reviews of the Cambridge Philosophical Society*, **73**, 293–304.

Tinbergen, J. M. & Williams, J. B. 2002. Energetics of incubation. In: *Avian Incubation: Behaviour, Environment, and Evolution* (Ed. by D. C. Deeming), pp. 299–313. Oxford: Oxford University Press.

Wiebe, K. L. & Martin, K. 1998. Costs and benefits of nest cover for ptarmigan: changes within and between years. *Animal Behaviour*, **56**, 1137–1144.

Zar, J. H. 1999. *Biostatistical Analysis*. Upper Saddle River, New Jersey: Prentice Hall.