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Nesting success of common eiders *Somateria mollissima* as influenced by nest-site and female characteristics in the Gulf of the St. Lawrence

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In the common eider *Somateria mollissima* as well as in many other bird species, nesting success has been associated with female reproductive characteristics and predator accessibility to the nest site. In this study, we tested the following predictions on nesting common eiders: 1) female and nest-site characteristics are correlated within a colony, where those with the highest ranked reproductive traits nest where the environment provides best protection, 2) females nesting on forested islands generally exhibit better reproductive traits than females nesting on open islets (hereafter habitats) because the former provide the best nest protection, and consequently, 3) colonies located on forested islands have higher nesting success than those on open islets. During the summers of 1995 and 1996, we recorded nesting success at 270 eider nests on two forested islands and four open islets. Simultaneously, we measured several variables describing nest (nest concealment, vegetation height, distance to shore and density of associated nesting gulls) and female (laying date and clutch size) characteristics. Using factor analysis to relate nest-site and female characteristics, we found a correlation between factor scores within four of the six colonies monitored. This correlation indicated that females with largest clutch size and early laying were associated with nest sites of low concealment that were close to shore. However, female score did not differ with habitat. Nesting success did not differ between habitats when controlled for female and nest scores, but was related to female score, and marginally to nest-site score. Because nesting success was principally related to female characteristics rather than to nest-site characteristics, we suggest that eiders rely on nest attendance rather than on nest concealment to protect their nests. Nesting close to shore may shorten incubation recesses and improve hatchling survival when leaving the nest.

Key words: common eider, female, Gulf of St. Lawrence, human disturbance, nest, nest concealment, nest success

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In studies of birds, especially waterfowl, nesting success correlates with female and nest-site characteristics. Females with better body condition lay larger clutches, nest earlier in the season, have shorter incubation periods, give better protection to their clutches, and are associated with higher reproductive success (Aldrich & Raveling 1983, Hatchwell 1991, Forslund & Larsson 1992, Rockwell et al. 1993, Black & Owen 1995). Reproductive success is also related to female age or nesting experience (Afton 1984, Dow & Fredga 1984, Hamann & Cooke 1987, Gauthier 1989). Nesting success is generally related positively to vegetative concealment (Giroux 1981, Hines & Mitchell 1983, Hill 1984, Jackson et al. 1988, Crabtree et al. 1989). Birds sometimes benefit from nesting in association with other species which provide extra protection (Young & Titman 1986, Robertson 1995). Female and nest-site characteristics seem related as birds of greater experience use more productive habitats (Hildén 1965, Riddington & Gosler 1995).

Female common eiders *Somateria mollissima* seemingly display similar relationships among nesting success, female characteristics and nest-site characteristics. Female eiders with the best reproductive traits are associated with the greatest nesting success (Choate 1967, Milne 1974, Spurr & Milne 1976, Baillie & Milne 1982, Gerell 1985, Hario & Selin 1988, Laurila & Hario 1988, Erikstad et al. 1993). In addition, vegetative concealment has been associated with greater nesting success (Choate 1967, Bourget 1970, Milne 1974, Schmutz et al. 1983), and eiders prefer to nest under vegetation of medium height and near shore (Norberg 1950, Schmutz et al. 1983). Since eiders often nest in association with gulls, their primary egg predators (Paynter 1951, Choate 1967, Ahlén & Andersson 1970, Bourget 1970, Mehlum 1991), nest-site concealment may be of considerable importance to protect eggs. Clutch size is related to nest concealment or forest canopy (Gerell 1985, Götmark & Ålhund 1988, Kilpi & Lindström 1997). These observations on female and nest-site characteristics suggest that they should be related within an eider colony, where females with the best reproductive traits also should be

associated with nest sites offering the best nest protection. Eiders are often found nesting on forested islands and small rocky islets close to one another (Reed 1975, Kilpi & Lindström 1997). Islands with a forested canopy offer nest cover while being generally avoided by nesting gulls. Females exhibiting better reproductive traits are experienced and apparently choose better nest sites. Recognizing these factors, we predicted that females with better reproductive traits would be associated with colonies located on forested islands and would exhibit better nesting success than those with poorer traits and located on rocky islets.

Common eiders often nest in association with gulls which poses a significant challenge to the collection of field data on eider nesting features. Nest monitoring leads to disturbance of incubating birds one or more times. Consequently, several researchers believe that their field activity has affected eider nest success because gulls or other egg predators benefit from easy access to unprotected nests (Cooch 1965, Choate 1967, Alhen & Anderson 1970, Milne & Reed 1974, Swennen 1983). Timing of visits during incubation and gull density have the greatest impact upon this disturbance (Bolduc & Guillemette 2003a). Human disturbance not only reduces nesting success, but it also affects individual success unevenly within a colony because earlier nesters have greater success when visits occur later in their incubation. Therefore, one has to ensure that the timing of disturbance is uniform for all monitored birds to obtain an unbiased estimate of the relationships among female and nest-site characteristics, and nesting success.

We monitored eider nesting success in six colonies during two summers, where we measured associated gull density, nest concealment, vegetation height, distance to shore, clutch size and laying date. We subsequently condensed these variables using factor analysis, and we used factor scores to test whether 1) eider female and nest-site characteristics are correlated within colony, where those with better reproductive traits nest where the environment provides best protection, 2) females nesting on forested islands generally exhibit better repro-

ductive traits than females nesting on open islets (hereafter habitats) because the former provide the best nest protection, and consequently, 3) colonies located on forested islands have higher nesting success than those on open islets. For this last test, we only used nests disturbed similarly to ensure that the timing of human disturbance did not affect nesting success of birds unevenly monitored. The disturbance regime was moderately severe (visits at 3-day intervals beginning in the first half of the incubation period), to obtain a large variability in nest survival.

Material and methods

Study area

We conducted our study in the Mingan Archipelago National Park Reserve during the summers of 1995 and 1996. This park reserve is located along the north shore of the Gulf of St-Lawrence, Québec, Canada. Paradis (1993) estimated that > 5,000 female eiders nested there in 1989. Eider colonies monitored in the course of our study were located in the area surrounding Ile à la Chasse (50°40'N, 63°07'W) and comprised approximately 3,500 nests. We monitored six colonies in the course of our study; four were located on small open islets (0.83-2.95 ha, with a vegetative cover mainly composed of herbaceous plant species) and two on forested islands (19.40 and 29.11 ha, with balsam fir *Abies balsamea* and white spruce *Picea glauca* as main tree species and with mosses *Pleurozium schreberi* covering the soil surface).

Sampling design

We monitored all eider colonies each summer, except for those on forested islands that we monitored during one summer only, one per year, to avoid too high an impact of nest monitoring on the local eider population (large forested islands including the largest share of the local nesting population). Visits occurred at various timing and frequencies during the incubation period in the context of another study on the effect of disturbance on nesting success (Bolduc & Guillemette 2003a). During one of the two summers, visits occurred every three days and began during the first half of incubation. Colonies on Ile du Milieu, Pogomo and Ste-Genevieve were monitored on this schedule in 1995, and those on Ile au Rapace, Trou Noir and Innu in 1996. We verified that monitored nests were in their first half of incubation at first visit by estimating laying dates (see below). Nests associated with a different timing of disturbance were discarded from analyses of nest success.

We monitored all nests in small colonies and system-

atically sampled nests (e.g. one of every three) on open islets with large numbers. On forested islands, nests were selected along a transect 10 m wide. Open islets were Ile du Milieu, Pogomo, Ile au Rapace and Trou Noir; forested islands were Ste-Genevieve and Innu.

Variables

Density of nesting gulls

Upon each visit to an eider colony, we counted gull nests occurring there (both greater black-backed gulls *Larus marinus* and herring gulls *L. argentatus* mixed). We used the maximum number of nests recorded on all visits as an estimate of gull density (nests/ha).

Nest concealment

We measured concealment provided (dead or live vegetation and rocks) at each eider nest by taking a photograph (using a 28 mm lens) from the bottom of the nest and looking upward. For each photograph, we evaluated the total portion of visible sky using a scale of 1-10 (10 corresponding to highest concealment).

Vegetation height

We measured the maximum height of vegetation in a one-meter radius around a nest using a measuring tape (± 5 cm) or a graduated stick.

Distance to shore

We measured distance between a nest and the seashore using a measuring tape (± 50 cm). On forested islands, we estimated this parameter from aerial photographs (1:10,000) using locations along the transect line.

Clutch size

Upon each visit to an eider nest, we marked each new egg with a felt pen to determine the total number of eggs laid and assess partial predation. Clutches of > 6 eggs were exceptions.

Laying date

Laying dates were estimated by measuring egg density loss during incubation (Baillie & Milne 1982). For clutches of known laying date, we measured width and length of each egg using a vernier caliper (± 0.1 mm), and then weighed them with a pesola scale (± 0.5 g) at various times during incubation. We computed a mean density index (weight/length*width²) for each clutch at each visit, and regressed the mean density index (MDI) against days since the first egg was laid (DAYS). We used the regression equation (DAYS = 146.8 - 256105.4 MDI, R² = 0.793, P < 0.0001) to estimate nest laying dates when unknown.

Nesting success

We considered a nest hatched when at least one egg membrane or duckling was found. Predated nests were those found empty, or those where only shell fragments with blood occurred or from which the egg membranes could not be distinguished. Almost no nests were classified as abandoned (cold eggs) although some could have been depredated between abandonment and our next visit. Each eider nest was marked with a wooden stake (1 m long).

Statistical analysis

We used factor analysis to condense nest-site and female variables for subsequent analyses. First, we transformed ($\log [x + 1]$) variables to meet normality assumptions (Sokal & Rohlf 1995) and to express all variables on a similar scale (Tabachnick & Fidell 1989). We used principal component extraction to evaluate factor eigenvalues (Tabachnick & Fidell 1989). The number of components with eigenvalues over 1 corresponded to the number of factors to be extracted from the factor analysis (Tabachnick & Fidell 1989). We extracted individual factor scores using the regression method (Tabachnick & Fidell 1989), and the factor analysis was conducted using SPSS 4.0 (SPSS Inc. 1986).

We tested whether nest-site and female factor scores were correlated within colonies using a correlation *z*-test (PROC CORR, SAS Institute, Inc. 1990). Secondly, we tested for difference in female score between habitats using a mixed model analysis of variance. We considered the variables habitat and year as fixed effects, and colony (nested within habitat) as a random effect (PROC MIXED; Littell et al. 1996). Finally, we tested for difference in nesting success between habitats using a generalized linear model for data with binomial distribution (GLIMMIX macro of PROC MIXED; Littell et al. 1996), with habitat as a fixed effect, nest-site scores,

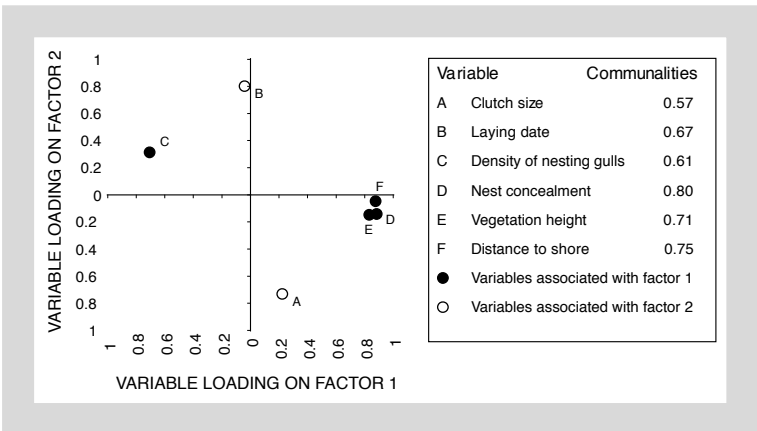


Figure 1. Variable factor loadings (with their associated communalities in legend) on the first two factors. The analysis included 270 eider nests monitored in the Mingan Archipelago National Park Reserve during the summers of 1995 and 1996.

female scores and their interaction as covariates (also fixed effects), and colony (nested within habitat) as a random effect. We back-transformed estimates of success probabilities from the logit scale to their original scale (MU) using the formula: $\text{exponential}(\text{logit estimate}) / 1 + \text{exponential}(\text{logit estimate})$. Associated standard errors were back-transformed using the formula: $\text{square root}([MU(1-MU)^2] * [\text{logit estimate}])$; Littell et al. 1996). We analyzed data using SAS 8.1 (SAS Institute, Inc. 1996).

Results

The factor analysis consolidated variables into two factors that explained 68.2% of the data set variation (50.8 and 17.4%, respectively), and 57-80% of each original variable variance (Fig. 1, communalities). Variables describing the nest-site environment were correlated with each other in the first factor (see Fig. 1, nest-site factor). Nests farther from the shore were associated with taller surrounding vegetation and were better concealed by the environment. These nests were mainly found on islands associated with gull colonies of low density. Variables

Table 1. Correlation between female and nest-site scores for eider colonies monitored in the Mingan Archipelago National Park Reserve during the summers of 1995 and 1996.

Habitat	Colony	N	Correlation coefficient	Z - value	P - value
Forested	Innu	46	-0.02	-0.11	0.91
	Ste-Genevieve	50	0.48	3.60	< 0.001
Open	Milieu	38	0.40	2.52	< 0.02
	Trou noir	43	0.53	3.73	< 0.001
	Pogomo	17	-0.06	-0.23	0.82
	Rapace	76	0.32	2.87	< 0.01

describing the female (clutch size and laying date) were inversely correlated with each other in the second factor (see Fig. 1, female factor), where nests of smaller clutch size were laid later in the breeding season.

Female and nest-site factor scores were correlated in four of the six colonies (Table 1). However, correlation coefficients were sometimes low (see Table 1). This indicated that generally nests of low female score (early laying date and large clutch size) were associated with low nest-site score (nest sites near to shore, with lower concealment and associated with shorter vegetation). Densities of nesting gulls were equal among nests within colonies, and therefore had no influence on this relationship. We found no differences in female score between habitats ($df = 1$, $F = 1.54$, $P = 0.3537$) or years ($df = 1$, $F = 0.01$, $P = 0.9360$), or their interaction ($df = 1$, $F = 0.88$, $P = 0.4548$). However, it is interesting to note the strong difference in female score among colonies within habitats (random effect, $df = 3$, $P < 0.0001$).

Of 270 nests that were included in the factor analysis, 108 nests were visited at a 3-day interval with the first visit occurring in the first half of incubation and only those nests were included in the generalized linear model testing for the effect of habitat, and nest-site and female score on nesting success. We found no effect of habitat ($df = 1$, $F = 0.02$, $P = 0.8935$), or nest-site score ($df = 1$, $F = 2.39$, $P = 0.1255$) on nesting success, but a strong effect of female score ($df = 1$, $F = 15.71$, $P = 0.0001$), and a marginal effect of the nest-site*female score interaction ($df = 1$, $F = 3.16$, $P = 0.0783$). Success probabilities increased with a decreasing female score, but at equal female score, success probabilities increased with increasing nest-site score except when female score was very low (Table 2).

Table 2. Predicted success probability of nesting common eiders on forested islands at specific levels of female score, nest-site score and their interaction from generalized linear model equation: $\log(\text{success probability}/1 - \text{success probability}) = -0.80 - 1.67 \times \text{Female score} + 1.05 \times \text{nest-site score} + 0.70 \times \text{female} \times \text{nest site interaction}$. See Methods for backtransformation equation from logit scale.

Female score	Nest score	Female*nest interaction	Success probability	SE
2	-2	-4	0.000	0.039
1	-1	-1	0.015	0.108
0	0	0	0.311	0.159
1	1	1	0.328	0.161
-1	-1	1	0.628	0.141
2	2	4	0.682	0.105
-1	1	-1	0.773	0.171
-2	2	-4	0.863	0.133
-2	-2	4	0.963	0.097

Discussion

The correlation between factors within colonies reveals that female characteristics are related to nest-site characteristics. For four of the six colonies, it seems that females with better reproductive traits (low scores, i.e. early laying and largest clutches) used nest sites having low scores, i.e. sites with low concealment and vegetation, and located near the shore (density of nesting gulls did not influence nest-site scores within colonies). Therefore, our results suggest that nest sites with low score had advantages related to nesting success under normal nesting conditions, or at least before any disturbance occurred. However, previous studies have shown that nest concealment is positively related to nesting success in the common eider (Choate 1967, Bourget 1970, Milne 1974, Schmutz et al. 1983, Gerell 1985), which suggests that nesting sites of highest concealment are selected to improve nest protection. Considering that eiders are highly sensitive to human disturbance (Bolduc & Guillemette 2003a), the importance of concealment for nest success may have been the result of the disturbance rather than nest-site selection by eiders. Egg predators probably benefited from easy access to eider nests during disturbance, with those less concealed being found first.

Eiders often nest in an open habitat where there is little nest concealment and where avian predators are common, e.g. in the Arctic. To be successful in these harsh conditions, eiders have evolved nesting behaviours to protect their clutch. Female eiders fast during incubation, when they lose 35–45% of their body mass (Korschgen 1977, Parker & Holm 1990, Bolduc & Guillemette 2003b), which allows them to exhibit the highest nest attendance recorded among waterfowl (Afton & Paulus 1992, Bolduc & Guillemette 2003b). Recesses from the nest occur mostly at night (Swennen et al. 1993, Bolduc & Guillemette 2003b), which is important at latitudes where darkness occurs at night during summertime and where most egg predators are diurnal birds. Gulls are rarely able to drive a female eider off her nest (Götmark & Åhlund 1988, Mehlum 1991, Swennen et al. 1993). Therefore, there is probably little need to select highly concealed nest sites since they protect their nests well. If nest concealment and vegetation height do not benefit female eiders, perhaps a shorter distance between the nest and the shore does. It has been found that eiders prefer to nest close to shore (Norberg 1950, Schmutz et al. 1983). For example, in Finland, Norberg (1950) recorded that 82% of nests were located within 50 m of the shore. Short distances between nest and shore could shorten the duration of nest recesses and thus the time that nests are left unprotected. It may also be important

when hatchlings leave the nest for the sea as they are more vulnerable to predators while on land.

We found no difference in female score between habitats, but there was a large variation in female score among colonies within habitat. However, colonies were not equal in female score, suggesting that another factor may influence distribution of females among islands. Nevertheless, it seems that there is no advantage for a female with better reproductive traits to seek nest concealment on a forested island.

Our analysis of the effect of habitat, nest-site and female score on nesting success indicated that nesting success increased with a decreasing female score, with some partial interaction with nest-site score, where greater nest-site score generally increased success probability. These results contradict our previous statement on the correlation between nest-site and female score because one would expect that if low-score females used low-score nest sites to improve their reproductive success, then successful eiders should be associated with lowest nest-site scores. However, as stated earlier, we believe that human disturbance produced this female*nest-site score interaction, where gulls prey upon eider nests left unguarded during daytime and where less concealed nests were taken first. For example, Bolduc & Guillemette (2003a) recorded eider nesting success at levels up to 100% in both types of habitat when disturbance occurred late during incubation. The effect of female characteristics on nesting success is more difficult to interpret because laying date or clutch size does not provide any direct mechanism for nest protection. Potentially, female characteristics are related to nest attendance, as observed in Canada geese *Branta canadensis* where females with smallest clutch sizes also have lowest nest attentiveness (Aldrich & Raveling 1983). Female eiders with larger clutch sizes may invest more energy into their annual reproductive effort to ensure success (Hanssen et al. 2003).

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