Nest-Site Characteristics, Occupation and Breeding Success in the European Shag

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Abstract.—The European Shag (*Phalacrocorax aristotelis*) breeds in a wide range of nest-sites depending on the locality, such as crevices under fallen rocks, open ground caves and open ledges on craggy cliffs. In this paper the habitat selection of shags breeding in cavities on the coastal slopes of Islas Cíes (Galicia, Northwest Iberian Peninsula) are examined. Shags selected sites with more lateral and overhead cover, with better drainage and with average visibility. In addition, sites where breeding was successful differed from unsuccessful sites. Nest-site characteristics especially affected the hatching success. In this colony, shags showed adaptive responses to site-quality variability. Thus, nest-site quality declined with density and with seasonal occupancy. Shag colonies seem to follow an ideal despotic distribution, where some individuals monopolize high quality sites and prevented other individuals from settling in the good sites. Further studies are required to assess the proximal mechanisms used for nest-site selection in this species. *Received 24 April 2003, accepted 10 September 2003.*

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Bird nests are not distributed randomly among potential breeding sites, and it is generally accepted that non-random distribution patterns are the result of natural selection (Cody 1985). Factors affecting breeding success can vary among habitats and, in this situation, fitness effects resulting from habitat differences can be expected to influence the evolution of habitat selection (Partridge 1978; Orians and Wittenberger 1991). Natural selection occurs when there are habitat differences between successful and unsuccessful sites, and this may modify habitat use for nesting over evolutionary time (Martin 1998). Short-term selective pressures, such as weather or predation, can oscillate unpredictably, and then nest-site selection may reflect long-term optima that may be neutral or maladaptive in the short term (Clark and Shutler 1999). Thus, a crucial step in nest-site selection studies is to identify temporal and spatial variations in the differences between selected and unselected sites, and also between successful and unsuccessful sites.

When individuals of a species have equal competitive abilities the individuals should be distributed within a habitat in such a way as to have equal expected fitness ("ideal free distribution"; Fretwell and Lucas 1970; Bernstein *et al.* 1991; Newton 1998). However, when individuals have different competitive abilities, the settlement patterns can vary between classes of individuals (e.g., older birds may obtain more suitable sites). Dominant or early breeding individuals are able to gain higher quality sites than subordinate or later breeding individuals relegated to low quality sites ("ideal despotic distribution"; Fretwell and Lucas 1970; Bernstein *et al.* 1991; Sutherland 1996; Newton 1998). When reproductive output varies between nest sites, the territories are occupied in the order of suitability (Sutherland 1996). Over a period of years, sites can vary in the frequency of use in low-density years, and only the best territories should be occupied when individuals show adaptive responses in habitat selection (Newton 1991; Shuterland 1996). The settlement pattern depends on the knowledge by individuals of the quality of each site (Pulliam and Danielson 1991). Thus, when the knowledge is imperfect, adaptive responses are expected to be weaker.

The European Shag (*Phalacrocorax aristotelis*) is a colonial seabird that breeds in the western Palaearctic. Potts *et al.* (1980) showed that the shags on the Farne Islands in England were regulated by the availability of breeding sites. These authors classified nest sites according to four quality indices (protection from high tides, protection from the rain, ability to shelter the brood and accessibility from to the sea for escape). They also showed that mean nest quality declined when the number of birds increased. During their research, in 1968, there was a catastrophic mortality. In 1969, nest-site quality and reproductive success increased, especially among young breeders. These young birds, which are generally relegated to poor quality sites, were able to breed in top quality sites during that year, thereby experiencing a greater reproductive success. When the population recovered, the proportion of birds that used poorer sites increased again and the average nest success declined. Thus, this species is an example of a socially induced density-dependent regulation associated with variation in quality of nest-sites.

The European Shag breeds in a wide range of nest-sites depending on the locality, such as cavities under fallen rocks and open ledges on craggy cliffs (Snow 1960; Cramp and Simmons 1977; Velando and Freire 2001). Habitat selection has been studied in several British colonies on cliff ledges (Potts *et al.* 1980; Aebischer 1985; Olsthoorn and Nelson 1990). Nevertheless, the physical factors that affect the breeding success on cliffs may be different from those operating in rocky cavities. European Shags seem to show labile responses to local nest-site availability. Thus, this species uses different types of nest-sites in the same colony and between nearby colonies. In Islas Cíes (NW Iberian Peninsula), European shags breed mainly (96%) in cavities under fallen granite rocks on slopes of rugged cliffs. In contrast, in the nearest colony (Isla de Ons, 15 km away) most of nest-sites (91%) are located on open ledges on the cliffs (Velando 1997).

Some of the factors used by Potts *et al.* (1980) in their study on Farne Islands to score the habitat quality may be inappropriate for scoring the sites in cavities. For example, in Cíes, cavities are large enough to raise the brood, and are protected from high seas because they are on slopes approximately 100 m above the sea. In order to understand the differences in nest-site characteristics among colonies, we studied the physical characteristics of nest sites used by shags at Islas Cíes. We examined nest-site preferences of shags breeding on Islas Cíes, using data from a five-year study. We tested whether: (1) occupied sites differed from non-occupied sites, as evidence for long-term selection; (2) successful sites differed from unsuccessful sites, evidence for ongoing selection pressures (3) site quality varied inversely with annual breeding density; evidence for density-dependent occupation, and (4) early breeders chose better nest sites than later breeders.

METHODS

Site Characteristics and Breeding Parameters

The data set included all sites in three adjacent areas on the Isla do Faro (Islas Cíes, Galicia, NW Iberian Peninsula) used by the European Shag in 1994-1998. Sites where the shags laid eggs and those where the shags only accumulated some material, but did not lay, were included. The breeding density varied during the study, especially in 1998 when there was a low occupation rate, with some adults not breeding (Velando and Freire 2002). In 1998, some rock falls during winter restricted our access to some sites and we could not visit these during the breeding season, resulting in a smaller sample size in that year. For each nest with eggs, the laying date, clutch size, number of hatched eggs and number of fledged chicks (defined as number of chicks surviving to 50 days) were recorded in 1994-1996 (Velando *et al.* 1999). In 1998, most of the shags abandoned clutches during incubation.

The nest-sites in the study area were underneath large landslides of granite boulders on the slopes. We divided the cavities into three sections: the entrance, the gallery (passageway connecting the entrance to the nest chamber) and the chamber. Four nest-site dimensions were measured: *entrance area*: measured to nearest cm^2, *gallery length*: measured to nearest cm, *chamber width*: measured to nearest cm, *chamber volume*; measured to nearest cm^3. In addition, the following variables were recorded: *Lateral cover*: the number of lateral walls (from 0 to 4) surrounding and isolating the chamber; *Overhead cover*: an index of the amount of cover over the chamber (1 for chamber almost totally exposed to 4 for nest totally covered); *Drainage*: the walls surrounding the chamber may be concave (slanting from top to bottom toward the chamber), straight, or convex; the concave walls increase the risk of flooding because the water flows through the wall to the nest-site. The nest-sites with more concave walls were found waterlogged after a downpour. Drainage was measured as a count of concave walls (from 0 for chambers with four concave walls, to 4 for chambers with no concave walls), which indicates the degree of drainage of the nest-site hollow; *Accessibility*: difficulty for the shag to enter into the chamber (from 1 for accessible in a straight line, to 4 for a labyrinth with more than two bends); *Structure of the Chamber*, many of the chambers have small cavities and different compartments (from 1 for only one cavity, to 4 for several cavities); *Visibility*, the ability to observe from chamber other shags or predators (from 0 for no visibility, to 4 for full visibility).

Statistical Analyses

Since most of the variables were not normally distributed (Shapiro-Wilks test), we used univariate non-parametric analyses of the data (Mann-Whitney test and Spearman rank correlation). The effects of site characteristics on the annual occupation, success and seasonally occupancy were investigated using Generalized Linear Models (GLM; Wedderburn 1974; McCullagh and Nelder 1989). We tested for multicollinearity among the descriptor variables using principal component analysis. The first component explained little of the variation in the data (25%), implying that the original variables were orthogonal (Jackson 1993). Only the correlation between the overhead and lateral cover was significant, but explained only the 16% of the variance. Hence, we use the original variables in the GLM models.

In order to avoid pseudo-replication, we considered the nest-site as the unit for statistical analysis. Then, site selection, differences in the reproductive success and seasonal occupancy of nest sites were tested using the proportion of years that a single nest-site was occupied, the mean standardized site success (using the Z distribution for each year) and the mean laying date for each site (standardized with respect to the first egg laid per season), respectively. The link function and error distribution in the GLM models were applied, after taking into account the presumed error distribution of the data (McCullagh and Nelder 1989) and selecting those that minimized the deviance in the model (Crawley 1993; Herrera 2000). Site occupation was fitted to a binomial distribution, mean reproductive success did not differ from a normal distribution, and time of breeding was fitted to a gamma distribution (with the variance function of the quadratic mean response with a constant coefficient of variation rather than a constant variance; see McCullagh and Nelder 1989). We fitted each explanatory variable to the observed data by following a traditional forward stepwise procedure. Each variable was tested for significance in turn. The variable that contributed to the largest significant change in deviance from the null model was then selected and fitted. Once a variable was fitted to the model we tested whether the addition of a second variable significantly improved the model. Variables were accepted into the model when they explained more than 5% of deviance. It has been stated that the stepwise procedures are not necessarily able to select the most influential variable from a subset of variables (James and McCulloch 1990). We use a modification of a stepwise procedure to test alternative models that were obtained when the second or the third most significant variable was included instead of the first most significant one at each step. This branching procedure could produce a set of different models, but in most instances it converged into a single model or to a set of models from which similar relationships could be inferred. Quadratic relationships and interaction between response variables were examined.

RESULTS

Nest-site Occupation

European Shags used 132 sites in the study area during 1993-1998. The annual site occupation rate varied from 68% in 1995 to 34% in 1998. There were significant inter-annual differences in site characteristics between occupied and unoccupied sites during the period studied (Table 1). The occupied sites in all years of study had significantly more walls, a higher roof and less number of concave walls than unoccupied sites. Nest-site visibility was significant lower in unoccupied than in selected sites during low-occupation years (1996-98: Table 1, Fig. 1).

The model, fitted with stepwise procedure incorporated the variables of lateral cover, drainage and visibility (quadratic function), explained 44% of the deviance. Thus, these variables had significant effects on the probability of site occupation. It showed that shags used for nesting those sites with a greater lateral cover, better drainage and average visibility. None of the interaction terms significantly improve the model. The overhead cover had a significant influence on the occupation pattern, explaining as single variable 17% of deviance, and it was the third most significant variable. The overhead cover was correlated with lateral cover ($r_{s132} = 0.40$, $P < 0.001$). Alternative models that included the overhead cover in the first step also included the walls (Table 2). The remaining variables were not included in the alternative models. In all, 21% of all nest sites in the study area had the highest possible scores for lateral and overhead cover and drainage.

Nest-site Quality and Annual Breeding Density

The mean nest-site characteristics varied among years and their scores increased in years with low shag density (Fig. 1). The four variables affecting the probability of the site being occupied varied with annual breeding density. The variables of lateral and overhead cover showed most difference between low-density years (1997 and 1998) and high-density years (1994-1996). Most sites selected had high overhead cover scores and the mean-annual score was close to the maximum score (4) in low-density years (Fig. 1). Visibility was the variable with the highest correlation with density.

Table 1. Variables describing physical characteristics (mean ± SE) measured at unoccupied (U) and occupied (O) sites of European Shags in each year of study in Islas Cíes. Mann-Whitney test of the differences between occupied and unoccupied: *P < 0.05, **P < 0.01, ***P < 0.001.

	1994		1995			1996		1997		1998		
	Occupied	Unoccupied	Occupied	Unoccupied		Occupied	Unoccupied	Occupied	Unoccupied	Occupied	Unoccupied	
Number of sites											54	
Lateral cover		2.39 ±0.13	2.70 ±0.08	2.40 ±0.15		2.76 ±0.09	2.39 ±0.12	2.91 ±0.08	2.35 ±0.11	2.92 ±0.11	2.62 ±0.09	
Overhead cover		3.52 ±0.09	3.78 ±0.05	3.50 ±0.07	**	3.80 ±0.05	3.54 ±0.08	3.89 ±0.04	3.53 ±0.07	3.91 ±0.05	3.70 ±0.07	
Drainage		2.58 ±0.13	2.85 ±0.10	2.50 ±0.16		2.94 ±0.12	2.51 ±0.12	3.05 ±0.10	2.49 ±0.10	3.35 ±0.14	2.59 ±0.13	***
Visibility		1.60 ±0.12	1.64 ±0.08	1.59 ±0.00		1.82 ±0.09	1.39 ±0.09	1.89 ±0.11	1.42 ±0.08	2.03 ±0.13	1.59 ±0.11	
Accessibility		1.37 ±0.12	1.26 ±0.06	1.44 ±0.11		1.42 ±0.08	1.34 ±0.09	1.35 ±0.07	1.41 ±0.09	1.29 ±0.09	1.29 ±0.08	
Chamber structure		1.39 ±0.08	1.68 ±0.08	1.45 ±0.13		1.76 ±0.09	1.42 ±0.11	1.77 ±0.11	1.50 ±0.10	1.67 ±0.16	1.55 ±0.10	
Gallery length (m)		0.71 ±0.09	0.81 ±0.09	0.69 ±0.05		0.72 ±0.06	0.74 0.08	0.69 ±0.08	0.76 ±0.05	.0.58 ±0.06	0.59 ±0.07	
Entrance area (m^2)		0.26 ±0.03	0.25 ±0.02	0.26 ±0.02		0.25 ±0.02	0.27 ±0.03	0.23 ±0.02	±0.27 ±0.03	0.22 ±0.02	0.25 ±0.03	
Chamber width (m)		0.59 ±0.04	0.57 ±0.02	0.65 ±0.06		0.62 ±0.04	0.56 ±0.03	0.63 ±0.05	0.57 ±0.03	0.58 ±0.04	0.57 ±0.04	
Chamber volume (m^3)		0.40 ±0.09	0.35 ±0.05	0.51 ±0.17		0.47 0.10	0.29 ±0.04	0.46 ±0.11	0.33 ±0.06	0.31 ±0.05	0.39 ±0.12	

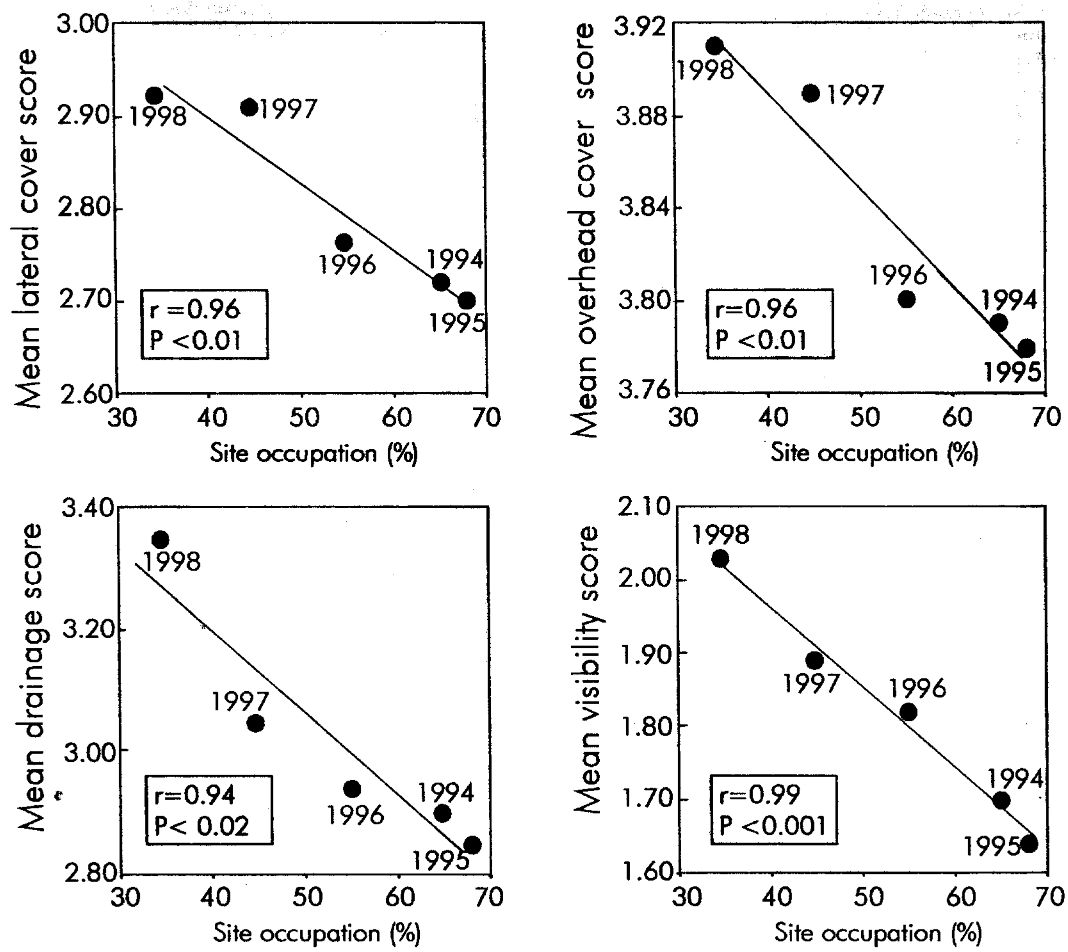

Figure 1. Mean of annual site quality scores (lateral and overhead cover, drainage and visibility) of European Shag nests on Islas Cíes in relation to annual breeding density, measured as the percentage of nest sites occupied on the study-area during five years.

Nest-site Characteristics and Breeding Success

The reproductive success varied between years but it was significant correlated with site characteristics every year (Table 3, Fig. 2). On average, the number of young hatched was 77%, 70%, 61% and 72% higher in nest sites with the highest scores than in those with the lowest scores for lateral cover, overhead cover, drainage, and visibility, respectively.

The relationships between site characteristics and reproductive success were due more to hatching success than to chick survival (Table 3). Some brood reduction in Islas Cíes was due to food limitation during adverse weather events during the chick-rearing period, probably caused by reduced underwater visibility and because the sand-eels (sandlance, Ammodytidae), the most important prey (Velando and Freire 1999), are buried in the sea bed sediment (Velando *et al.* 1999). We examined the breeding performance at new sites from the previous season by pooling 1995 and 1996 data (there were no annual differences in reproductive success). The reproductive success in new sites correlated with lateral cover ($r_{s40} = 0.36$, $P < 0.02$) and drainage ($r_{s40} = 0.38$, $P < 0.02$). In new sites, the number of fledglings in sites with only two lateral walls was 32% less than in sites with four lateral walls, and in sites with four concave-slanted walls was 33% less than in sites with one slanted wall. The re-

Table 2. Generalized Linear Models for nest-site selection of European Shags in Islas Cíes assuming a binomial distribution of errors and a logistic link. The proportion of years that a nest site was selected during 1994-1998 was used as the response variable.

		Multivariate models[d,e]			
	Univariate models[b,]	Stepwise model		Alternative model[5]	
Variable[a]	Change in deviance	Model coefficient	SE	Model coefficient	SE
Constant		-6.44	1.91	-7.22	2.24
Lateral Cover	10.0***	0.85	0.33	0.71	0.38
Overhead Cover	8.3***			0.35	0.52
Drainage	9.5***	0.41	0.27	0.38	0.28
Visibility	3.8**	2.73	1.50	2.72	1.51
(Visibility)^2	2.6**	-0.56	0.35	-0.57	0.35
Residual deviance		25.4		24.9	
d.f.	87	85		84	

[a]The remaining variables (see Table 1) were not significant.
[b]Univariate GLM: **P < 0.01, ***P < 0.001.
[c]Deviance in the null model = 45.3.
[d]Variables were included in the model at 5% level.
[e]Model that included the Overhead Cover in the first step.

maining site characteristics did not correlate with the reproductive success of sites selected for first time.

The stepwise procedure produced a significant model that included drainage, visibility, and lateral and overhead cover. Thus, these variables correlated independently on the mean nest site success. The model explained 42% of the deviance in the null model. Other alternative models only differed in the order in which the different explanatory variables were included and finally converged with this same model. None of the quadratic and interaction terms were significant. The remaining variables measured were not included in the models due to their non-significant effect on the mean reproductive success.

Table 3. Spearman rank correlation between nest-site characteristics and reproductive success, hatching success and chick mortality of European Shags in Islas Cíes. Only significant correlations are shown. **P < 0.01, ***P < 0.001.

	Reproductive success[a]			Hatching success[b]			Chick mortality[c]		
	1994	1995	1996	1994		1996	1994	1995	1996
Sample size	85	90	79	85	90	79	61	65	62
	0.30**	0.31**	0.34**	0.30**	—	0.36***			
		0.47***	—	—	0.44***	0.30**			
		0.41***	0.50***	—	0.37***	0.50***			
	0.28**	0.33**	—	0.40***	0.26**	—			
								-0.36**	

[a]Reproductive success measured as number of chicks fledged per pair that laid eggs.
[b]Hatching success measured as the proportion of hatched eggs by clutch.
[c]Chick mortality measured as the proportion of chicks that died.

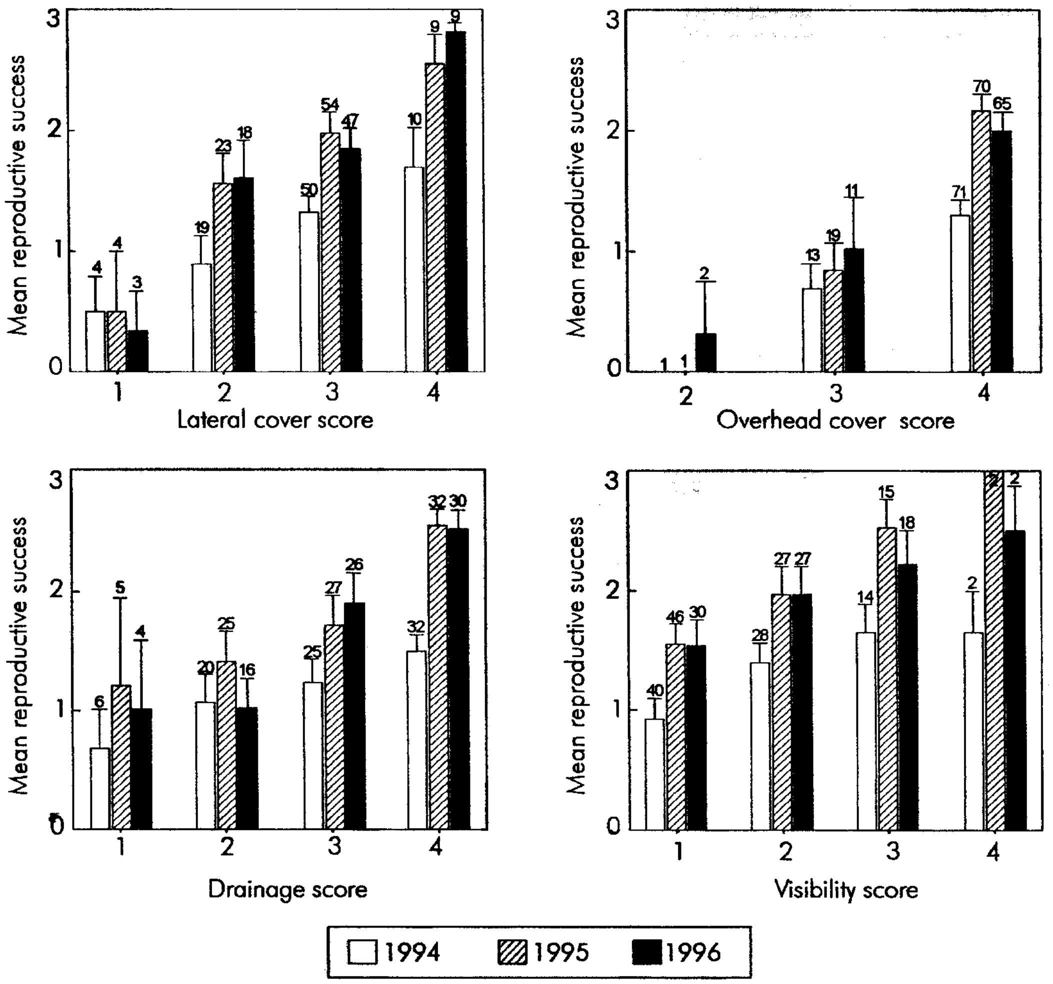

Figure 2. Mean (±SE) reproductive success, measured as number of chicks fledged per pair, of European Shag nest-sites on Islas Cíes in relation to the site quality score (lateral and overhead cover, drainage and visibility) for three study years.

Nest-site Quality and Seasonal Occupation

Significant differences between years occurred in the laying date of the European Shag on the Islas Cíes (1994 to 1996; One-way ANOVA: $F_{2,256} = 12.9$, $P < 0.001$). A post hoc analysis (LSD) indicated that the 1996 laying date was significant earlier than 1994 and 1995 (mean Julian days: 92, 91 and 83 in 1994, 1995 and 1996, respectively). There were significant differences in the laying date related to nest-site characteristics (Fig. 3). After correction for year, the laying date in three years was significant earlier at sites with more lateral cover and with better drainage (Fig. 3). There were significant differences in laying dates between sites according with their visibility and overhead cover only in 1995, the year with highest density (Fig. 3). The stepwise model included drainage, lateral cover and visibility. The model explained the 33% of deviance in the null model (Table 5), and indicated that sites with more lateral cover, better drainage and better visibility were occupied earlier. An alternative model included the overhead cover when this variable was introducéd in the first step. Quadratic and interaction terms were all non-significant.

The effect of site characteristics on mean reproductive success after controlling for season was also significant. The GLM models

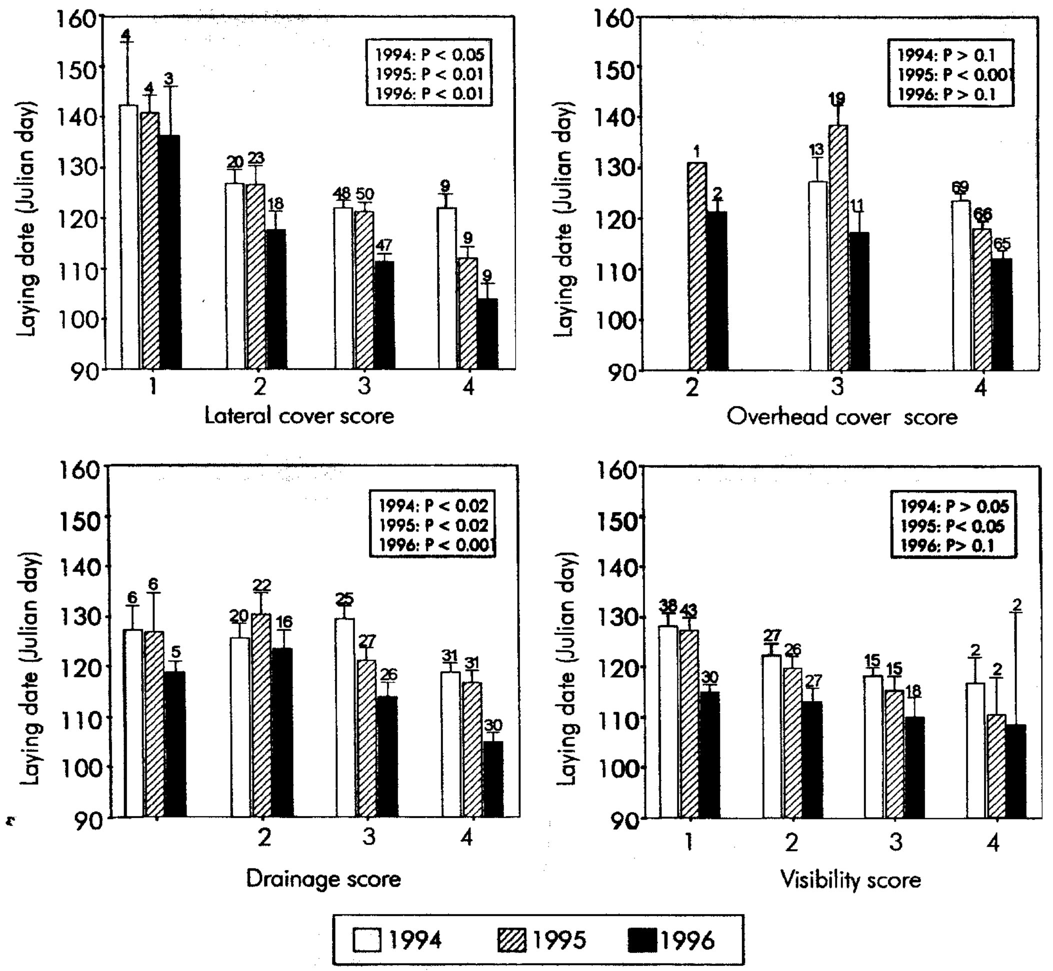

Figure 3. Mean (±SE) laying dates, measured as Julian day, of European Shag nest-sites on Islas Cíes in relation to the site quality score (lateral and overhead cover, drainage and visibility) for three study years. Results from Kruskall-Wallis tests for differences in laying dates among sites with different scores each year are given.

for the effect of site characteristics on mean reproductive success including the mean standardized laying date on the first step ($F_{1,112}$ = 50.1, P < 0.0001) was significant for lateral cover ($F_{1,111}$ = 7.0, P < 0.01), overhead cover ($F_{1,111}$ = 10.8, P < 0.001), drainage ($F_{1,111}$ = 15.9, P < 0.0001), and visibility ($F_{1,111}$ = 9.36, P < 0.002). Thus, these physical variables explained a significant proportion of reproductive success variance after controlling the seasonal effects.

DISCUSSION

European Shags were selective in the choice of nesting sites; thus physical characteristics of occupied sites differed from unoccupied sites in the years studied. Moreover, we found that some characteristics affected the reproductive success, suggesting ongoing selection pressures. Nevertheless, the correlations between site characteristics and reproductive success do not necessarily reveal whether they are due to the sites themselves or to attributes of the organisms in them (Coulson 1968; Porter 1990; Ens *et al.* 1992; Harris *et al.* 1997; Stokes and Boersma 1998). The oldest or more experienced individuals are able to hold the preferred sites (Potts *et al.* 1980), and then the higher success in these sites may simply be a result of the positive correlations between bird quality and site

Table 4. Generalized Linear Models of the breeding success of each nest site of European Shag in Islas Cíes in relation to site characteristics assuming a Gaussian distribution of errors. The mean standardized reproductive success for each nest site during 1994-1996 was used as the response variable.

	Univariate models[b,c]	Multivariate model[d]	
Variable[a]	Change in deviance	Model coefficient	Standard error
Constant	—	-0.69	0.17
Drainage	2.1***	0.10	0.02
Lateral cover	1.7***	0.12	0.03
Visibility	1.4***	0.07	0.03
Overhead cover	1.4***	0.09	0.05
Residual deviance		5.7	
d.f.	87	84	

[a]The remaining variables (see Table 1) were not significant.
[b]Univariate GLM: **P < 0.01, ***P < 0.001.
[c]Deviance in the null model = 31.7.
[d]Variables were included in the model at 5% level.

characteristics. The European Shag is a seasonally breeding bird with marked seasonal differences in reproductive success due the age and experience (Potts *et al.* 1980; Aebischer 1993; Aebischer *et al.* 1995; Daunt *et al.* 1999; Velando *et al.* 2001). After controlling the laying date, site characteristics (overhead and lateral cover, drainage and visibility) had a significant effect on reproductive success. Moreover, the site characteristics (lateral cover and drainage) significantly influenced the reproductive success of sites occupied for first time, probably occupied by young and inexperienced birds (Aebischer *et al.* 1995; Velando 1997). The characteristics of selected sites seem to increase the reproductive success, however experimental data are required to confirm these findings. On present evidence, there is concordance between site preferences (occupation) and selective pressures on nest-site selection (hatching success), suggesting that these preferences have been selected to be maintained (Martin 1998; Clark and Shutler 1999).

The study also revealed that hatching success was related to site characteristics the but not chick mortality. On the Islas Cíes, many nests were flooded during incubation by heavy rain in this period. Flooding of a nest usually results in loss of the nest con-

Table 5. Generalized Linear Models for the seasonal occupation of each nest site of European Shag on Islas Cíes in relation to site characteristics assuming a gamma distribution of errors and identity link. The mean laying date for each nest site (standardized with respect to first egg laid within seasons) during 1994-1996 was used as the response variable.

	Univariate models[b,c]	Multivariate model[d]	
Variable[a]	Change in deviance	Model coefficient	Standard error
Constant	—	68.97	6.09
Lateral Cover	5.9***	-6.74	1.40
Drainage	4.9***	-4.01	1.18
Visibility	2.2**	-3.02	1.16
Overhead Cover	2.5**	—	—
Residual deviance	—	21.1	
d.f.	114	112	

[a]The remaining variables (see Table 1) were not significant.
[b]Univariate GLM: **P < 0.01, ***P < 0.001.
[c]Deviance in the null model = 31.7.
[d]Variables were included in the model at 5% level.

tents. Thus, greater lateral and overhead cover and better drainage prevent the nest-sites from flooding. Protection of nest content from predation is another benefit of selected sites with greater lateral and overhead cover. Shags nesting in cavities with these characteristics avoid predation by Yellow-legged Gulls (*Larus cachinnans*). No other predators are known on Islas Cíes. Good visibility from the nest may be linked to social interactions (protection of the mate or nest site, attraction of females) and better escapes routes (Burger and Gochfeld 1981; Götmark *et al.* 1995; Velando and Marquez 2002).

Protection against predators and visibility may be characteristics that are inherent in the location of the nests on the ledges of vertical cliffs. In the British colonies, shags nesting on open ledges usually use large, well-drained sites protected from predators, with low probability of attack and located distant from the sea spray (Potts *et al.* 1980, Aebischer 1985; Olsthoorn and Nelson 1990). These results point to general characteristics of nesting sites in this species. The structure of the sites are different in different localities, but the functional effects of the sites selected seem to be the same: shags use sites that protect them from atmospheric conditions, predators, and intra-specific interference. Many seabirds select sites that protect them from predators and atmospheric conditions (Nettleship 1972; Hudson 1982; Burger and Gochfeld 1985; Burger and Gochfeld 1987; Seddon and Davis 1989; Bosch and Sol 1998; Velando and Marquez 2002).

An interesting result, confirming previous studies, is that the quality of nest sites increased in years with low density (Fig. 1). Thus in years with high density, shags on average occupied less suitable sites due to competition for nest sites. This effect is similar to the density-dependent decline in reproductive performance associated with the variation in the quality of nest sites reported for shags nesting on the Farne Islands (Potts *et al.* 1980). Moreover, the early pairs showed a general preference for high quality sites in the study years, the same pattern observed on the Farne Islands (Potts *et al.* 1980). Therefore, high quality individuals monopolized high quality sites and prevented other individuals from settling in the best places following an "ideal despotic distribution" (Fretwell and Lucas 1970). Thus, despite the different type of nest-sites used, in both colonies the shags showed adaptive responses to site quality.

European Shags select different nest-sites in nearby colonies. Thus, on the Isla de Ons (15 km from Islas Cíes) the shags choose open ledges on the cliffs. The geomorphology of the two islands is different: the cliffs on the Islas Cíes are c. 200 m high and their slopes are covered of falling granite rocks; on the Isla de Ons, the cliffs are low (<50 m) and have vertical, earth walls. The availability of different types of breeding sites differs between the two islands, but the adaptive responses to availability of different nest sites depend on how birds obtain the knowledge of nest-site quality. In Islas Cíes, 83% of second-year breeders nest on sites not previously occupied (Velando 1997). Young shags can recognize site quality but they are relegated to poor sites by older shags (Potts *et al.* 1980). According to this hypothesis, in Islas Cíes and Farne Islands, site quality increased in years with fewer breeding pairs (Fig. 1; Potts *et al.* 1980). Thus, the shags seem to recognize site quality, so there is a need to understand the proximal mechanisms of nest-site selection.

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LITERATURE CITED

Aebischer, N. J. 1985. Aspects of Biology of the Shag (*Phalacrocorax aristotelis*). Unpublished Ph.D. dissertation, Durham University. Durham.

Aebischer, N. J. 1993. Immediate and delayed effects of a gale in late spring on the breeding of the Shag *Phalacrocorax aristotelis*. Ibis 135: 225-232.

Aebischer, N. J., G. R. Potts and J. C. Coulson 1995. Site and mate fidelity of Shags *Phalacrocorax aristotelis* at two British colonies. Ibis 137: 19-28.

Bernstein, C., J. R. Krebs and A. Kacenlik. 1991. Distribution of birds amongst habitats: theory and relevance to conservation. Pages 317-345 *in* Bird Population

Studies, C. M. Perrins, J. D. Lebreton and G. J. M. Hirons (Eds.). Oxford University Press, Oxford.

Birkhead, T. R. and R. W. Furness. 1985. Regulation of seabirds populations. Pages 145-167 *in* Behavioural Ecology, R. M. Sibly and R. H. Smith (Eds.). Blackwell Scientific Publications, Oxford.

Bosch, M. and D. Sol. 1998. Habitat selection and breeding success in Yellow-legged Gulls *Larus cachinnans*. Ibis 140: 415-421.

Burger, J. and M. Gochfeld. 1981. Nest site selection by Kelp Gulls in Southern Africa. Condor 83: 243-251.

Burger, J. and M. Gochfeld. 1985. Nest site selection by Laughing Gulls: comparison of tropical colonies (Culebra, Puerto Rico) with temperate colonies (New Jersey). Condor 87: 364-373.

Burger, J. and M. Gochfeld 1987. Colony and nest-site selection in Silver Gulls *Larus novaehollandiae* in Queensland, Australia. Bird Behaviour 7: 1-21.

Clark, R. G. and D. Shutler 1999. Avian habitat selection: pattern from process in nest-site use by ducks? Ecology 80: 272-287.

Cody, M. L. 1985. Habitat Selection in Birds. Academic Press, London.

Coulson, J. C. 1968. Differences in the quality of birds nesting in the centre and on the edges of a colony. Nature 217: 478-479.

Cramp, S. and E. L. Simmons. 1977. The Birds of the Western Palearctic. Vol I. Oxford University Press, Oxford.

Crawley, M. J. 1993. GLIM for Ecologists. Blackwell Scientific Publications, Oxford.

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

Ens, B. J. Kersten, M. Brenninkmeijer, and J. B. Hulscher. 1992. Territory quality, parental effort and reproductive success of Oystercatchers (*Haematopus ostralegus*). Journal Animal Ecology. 61: 703-715.

Fretwell, S. D. and H. L. Lucas, Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. 1. Theoretical development. Acta Biotheoretical. 19: 1-36.

Furness, R. W. and P. Monaghan. 1987. Seabird Ecology. Blackie, Glasgow.

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

Harris, M. P., S. Wanless, T. R. Barton and D. A. Elston. 1997. Nest site characteristics, duration of use and breeding success in the Guillemot *Uria aalge*. Ibis 139: 468-476.

Herrera, C. M. 2000. Flower-to-seedling consequences of different pollination regimes in an insect-pollinated shrub. Ecology 81: 15-29.

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

Jackson, D. A. 1993. Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. Ecology 74: 2204-2214.

James, F. C. and C. E. McCulloch. 1990. Multivariate analysis in ecology and systematics: panacea or Pandora's box? Annual Review of Ecology and Systematics. 21: 129-166

Klopfer, P. H. 1963. Behavioral aspects of habitat selection: the role of early experience. Wilson Bulletin 75: 15-22.

McCullagh, P and J. A. Nelder. 1989. General Linear Models. Chapman and Hall, London.

Martin, T. E. 1998. Are microhabitat preferences of coexisting species under selection and adaptive? Ecology 79: 656-670.

Nettleship, D. N. 1972. Breeding success of the Common Puffin *Fratercula arctica* (L.) on different habitats at Great Island, Newfoundland. Ecological Monographs 42: 239-268.

Newton, I. 1991. Habitat variation and population regulation in Sparrowhawks. Ibis 133: S76-S88.

Newton, I. 1998. Population limitation in Birds. Academic Press, London.

Olsthoorn, J. C. M. and J. B. Nelson. 1990. The availability of breeding sites for some British seabirds. Bird Study 37: 145-164.

Orians, G. H. and J. F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. American Naturalist 137: S29-S49.

Porter, J. M. 1990. Patterns of recruitment to breeding group in the kittiwake *Rissa tridactyla*. Animal Behaviour. 40: 350-360.

Potts, G. R., J. C. Coulson and I. R. Deans 1980. Population dynamics and breeding success of the shag, *Phalacrocorax aristotelis*, on the Farne Islands, Northumberland. Journal Animal Ecology 49: 465-484.

Pullian, H. R. and B. J. Danielson. 1991. Sources, sinks and habitat selection: a landscape perspective on population dynamics. American Naturalist 137: S50-S66.

Seddon, P. J. and L. S. Davis. 1989. Nest-site selection by Yellow-eyed Penguins. Condor 91: 653-659.

Snow, B. 1960. The breeding biology of the Shag *Phalacrocorax aristotelis* on the Island of Lundy, Bristol Channel. Ibis 102: 554-575.

Stokes, D. L. and P. D. Boersma. 1998. Nest-site characteristics and reproductive success in Magellanic penguins (*Spheniscus magellanicus*). Auk 115: 34-49.

Sutherland, W. J. 1996. From individual behaviour to population ecology. Oxford University Press, Oxford.

Velando, A. 1997. Ecología y Comportamiento del Cormorán Moñudo *Phalacrocorax aristotelis* en las Islas Cíes y Ons. Unpublished Ph.D. dissertation, University of Vigo, Vigo.

Velando, A. and J. Freire. 1999. Intercolony and seasonal differences in the breeding diet of European shags on the Galician coast (NW Spain). Marine Ecology Progress Series 188: 225-236.

Velando, A. and J. Freire. 2001. Can the central-periphery distribution become general in seabird colonies? Nest spatial pattern in the European Shag. Condor 103: 544:554.

Velando, A. and J. Freire. 2002. Population modelling of European shag at their southern limit: conservation implications. Biological Conservation: 107: 59-69.

Velando, A. and J. C. Marquez. 2002. Predation risk and habitat selection in the inca tern (*Larosterna inca*). Canadian Journal of Zoology 80: 1117-1123.

Velando, A., J. E. Ortega-Ruano and J. Freire. 1999. Chick mortality in European Shag *Stictocarbo aristotelis* related to food-limitations during adverse weather events. Ardea 87: 51-59.

Velando, A., J. Graves and J. E. Ortega-Ruano. 2001. Sex ratio in relation to timing of breeding, and laying sequence in a dimorphic seabird. Ibis 144: 9-14.

Wedderburn, R. W. M. 1974. Quasilikelihood functions, generalized linear models and the Gauss-Newton method. Biometrika 61: 439-447.