Effects of microhabitat preferences on kelp gull *Larus dominicanus* breeding performance

Pablo García-Borboroglu and Pablo Yorio

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We examined microhabitat preferences and their adaptiveness for the kelp gull *Larus dominicanus* in one of its largest colonies in Patagonia. We quantified 13 habitat variables at 104 and 92 nest-sites and at 70 and 60 random points in 1998 and 1999, respectively. We recorded egg laying dates, hatching success, number of chicks fledged and breeding success at 92 of these nests in each of the study seasons. Compared to random points, nest sites had more vegetation cover and were closer to the nearest available bush, but they were located further from the nearest clearing for flight take-off, all variables included in the "vegetation" principal component. Nests were built on substrates with lower slopes and higher percentages of silt-clay, but with lower percentages of rock. In both years, hatching success, number of chicks fledged and breeding success were related positively to the vegetation principal component. Substrate slope and composition contributed to explain the variation in hatching and breeding success in 1998 and 1999, respectively. Our study shows that some kelp gull breeding parameters are affected by nest-site habitat characteristics. These associations were in most cases influenced by the timing of breeding, with earlier breeders being more successful. Vegetation effects and substrate characteristics were important variables in distinguishing random sites from nest sites, and in explaining variation in breeding performance, showing that their habitat preferences are adaptive and allowing us to detect both the pattern and process in kelp gull habitat selection.

P. García-Borboroglu (correspondence) and P. Yorio. Centro Nacional Patagónico, (CONICET), Blvd Brown s/n, (9120) Puerto Madryn, Chubut, Argentina, and Wildlife Conservation Society, 2300 Southern Boulevard, Bronx, New York, NY 10460, USA. E-mail: pgborbor@cenpat.edu.ar

Organisms often breed at sites that are selected non-randomly from the available habitat (Rotenberry and Wiens 1998, Clark and Shutler 1999). Selection of suitable nesting habitat is critical for most animals because it directly affects fitness (Partridge 1978, Cody 1985). Habitat preferences are assumed to be adaptive, such that fitness is higher in selected microhabitats, causing natural selection to maintain preferences if they have a genetic basis (Jaenike and Holt 1991, Martin 1998, Chase 2002). If the chance of nest failure is consistently related to certain nest site characteristics, then nest-site preferences based on those characteristics should be favored by natural selection (Martin 1993, Chase 2002). Habitat selection studies have usually first addressed questions regarding the *patterns* in habitat use

(Wiens 1989, Clark and Shutler 1999), trying to find differences between selected and available habitats. Yet, a second key step is to study the *process*, exploring the way in which unsuccessful and successful nest sites differ (Clark and Shutler 1999). Variations in habitat characteristics between unsuccessful and successful nests may be less evident than those between non-nesting and nesting habitat, because short-term selection typically produces less distinct patterns than long-term selection (Dawkins 1986).

Several seabird studies have shown that habitat differences can affect both breeding success (Calladine 1997, Hamer et al. 2002) and adult survivorship (Saliva and Burger 1989). In gulls, breeding habitat selection involves a set of choices where physical cues are very

important. Nest site selection is a function of the characteristics within the immediate vicinity of the nest, as well as characteristics of the habitat patch surrounding the nest (Saliva and Burger 1989). Features of the microhabitat should be important in providing protection against factors such as inclement weather conditions, predation and intra- or inter-specific social interference (Buckley and Buckley 1980, Burger and Gochfeld 1981, Saliva and Burger 1989).

Kelp gulls *Larus dominicanus* are widely distributed in the Southern Hemisphere, breeding in South America, southern Africa, Australia, New Zealand, Subantarctic islands and on the Antarctic Peninsula (Burger and Gochfeld 1996). In Argentina, this species is the most widely distributed and the third most abundant seabird breeding along the Atlantic coast (Yorio 2000). Few nest-site selection studies have been conducted on this species in the Southern Hemisphere, (Burger and Gochfeld 1981 in South Africa and Quintana and Travaini 2000 in Antarctica), and only one study analyzed the relationship between breeding success and microhabitat (Yorio et al. 1995), but they only considered the vegetation cover variable.

In this study we tested the hypothesis that nest microhabitat preferences are adaptive in kelp gulls at one of its biggest colonies in Patagonia. To achieve this goal we first tested whether there is evidence of long-term natural selection by analyzing differences in habitat characteristics between nest-sites and random points. As a second step, we tested for evidence of ongoing natural selection by examining the relationship between these habitat variables and breeding parameters.

Methods

Study area

Research was conducted during the 1998 and 1999 breeding seasons at the kelp gull colony of Vernaci Sudoeste Island (45° 11′S, 66° 31′W; Fig. 1). This colony is located near the mouth of Caleta Malaspina, San Jorge Gulf, Chubut (Fig. 1). It is a low island of approximately 6.4 ha, 500 m long and less than 200 m wide. Beaches have gentle slopes composed of sand, gravel and shell. Vegetation consists mainly of bushes of *Atriplex* spp., *Suaeda divaricata* and *Lycium chilensis*. The kelp gull is the most abundant seabird at Vernacci Sudoeste Island, with 8,200 breeding pairs spread throughout 5.61 ha (87.6% of island area; Yorio and García Borboroglu 2002). Nests were built among and under bushes, or on open ground.
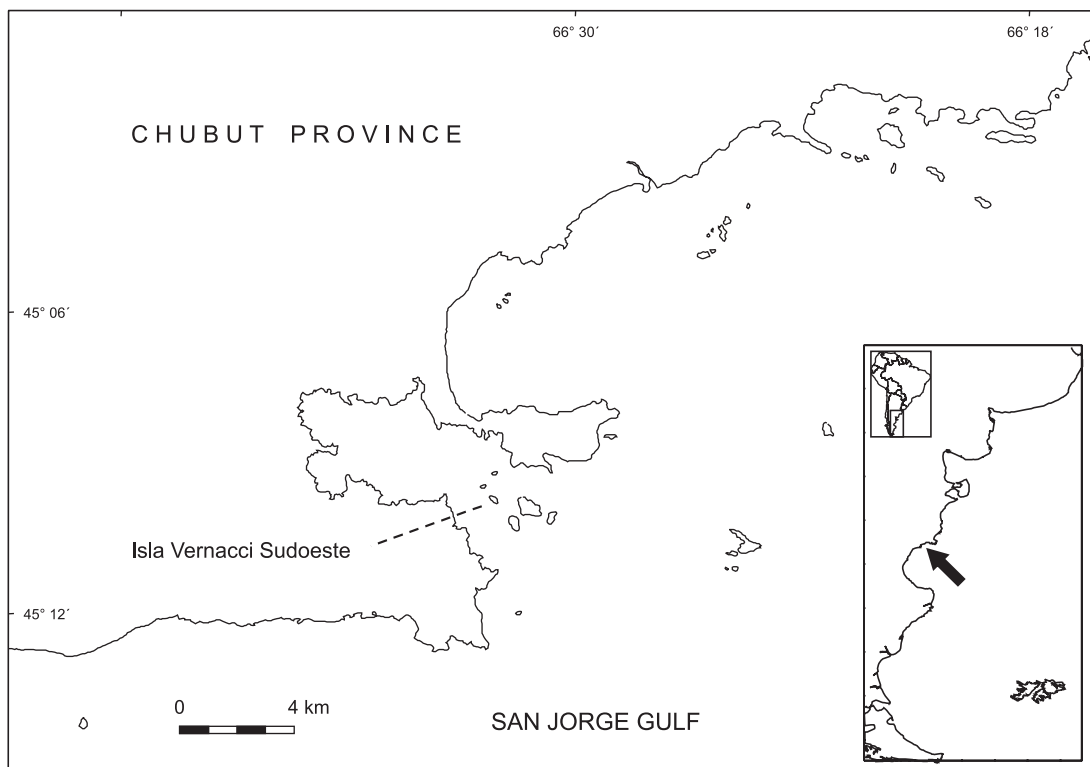

Fig. 1. Geographical location of Isla Vernaci Sudoeste, Chubut, Argentina.

Habitat measurements

We quantified 13 habitat variables at 104 and 92 nest-sites and at 70 and 60 random points in 1998 and 1999, respectively. We selected these habitat variables because they have been shown to affect reproductive success in studies of gulls and other seabirds (Burger and Gochfeld 1981, Quintana and Travaini 2000). We gathered information during late incubation (December). Random points within each colony (that is, the area enclosed by the peripheral nests) were selected using tables of random numbers to generate the x and y coordinates (Burger and Gochfeld 1985, Bosch and Sol 1998). Nest-site habitat data were collected from all nests located in 3 distinct study areas established within the gullery (see breeding parameters section for description). At each nest-site and random point we estimated the percentage of substrate components in the surface layer (top 5 cm). Substrate components were classified as (1) silt-clay, (2) sand, (3) shell (shell fragments), (4) gravel and rock fragments, and (5) rock (exposed bedrock; see Stokes and Boersma 1998). We measured the slope of the substrate using a Suunto type PM-5/060 PG clinometer. We recorded the percentage of shrub vegetation cover within a 1- and 5-m radius around the nest or random point, the distance to the nearest vegetation and its height, and the distance to the nearest clearing from which gulls could take flight from when threatened. Finally we measured the distance to nearest high-tide line and altitude over the sea level.

Breeding parameters

During 1998 and 1999 we followed all nests located in areas of approximately 200 m² placed in three different sectors of the gullery and separated by at least 100 m. To determine breeding parameters we selected all nests located in the study areas, totalling 92 nests in each of the study seasons. We measured habitat variables for these nests and included the data in the nest-site selection analysis. We surrounded each of the study areas with nets of 0.6 m height to facilitate counting the number of chicks attaining one month of age. Study areas were large enough to avoid constraining the ability of chicks to search out shelter, and to allow us to check and measure chicks with minimal disturbance. We marked all nests with stones wrapped up with numbered tapes. During both seasons, we visited the colony every two to three days from the beginning of October to late December, and then every two to five days (2.6 ± 1.4) until mid February. During visits we recorded egg laying dates, hatching success and breeding success. We defined hatching success as the proportion of eggs laid that hatched per nest, and breeding success as the proportion of eggs that resulted in fledged chicks per nest. We also calculated the number of fledged chicks as the number surviving to at least the fourth week of age per nest

where eggs were laid. We measured tarsus length of first chicks at 31 ± 3 days of age with calipers to the nearest 0.1 mm. Chick sizes were only obtained during 1998. Tarsus length has been used because it is the only chick measurement that reaches an asymptote before fledging (Yorio and García Borboroglu 2002). We marked chicks at hatching with the nest number and hatching order using a labelled fiber-tape band. We used the laying date of the first egg in the clutch as an indicator of timing of breeding (Day 1 = November 10 and 13 in the two years). We recorded nearest neighbour distance for each nest as an indicator of nesting density, using a meter tape to the nearest cm.

Statistical analyses
Habitat variables

The variables were transformed prior to analysis using log $(x+1)$ or arcsine transformation to approximate normality. A principal components analysis (PCA) was used to summarize the patterns of covariation present in the 13 habitat variables measured at random points. Both random points and nest sites were then scored on the resulting principal components (see Rotenberry and Wiens 1998, Chase 2002). This technique allowed us to summarize the measured dimensions of variation present in available habitat, and then scores each nest-site along those dimensions. All components that met the broken-stick criterion recommended by Jackson (1993) were retained. Hence, we only present the components (axes) where the broken-stick eigenvalue is less than the actual eigenvalue for the axis, meaning that that axis contains more information than expected by chance and should therefore be considered for interpretation.

To determine which predictor variable should be included in the final multivariate model of nest-site selection, we applied the following model-building strategy. Univariate comparisons of the habitat variables yielded by the PCA were made between the nest-sites and random points. The variables that were significant in the univariate analysis at $P < 0.025$ were then included in an initial multivariate logistic regression model, following Hosmer and Lemeshow (1989). A forward likelihood ratio method was applied, consisting of a forward stepwise selection with entry testing based on the significance of the score statistic, and removal testing based on the probability of a likelihood-ratio statistic (LRS), based on the maximum partial likelihood estimates. Scores, LRS and their significances are reported. All statistical procedures were performed with the SPSS statistical package.

Nest success

We used Generalized Linear Models (GLM) using GLM software (Baker and Nelder 1978, Crawley 1993), to

assess simultaneously which explanatory variables and/or their interactions better explained the variation in hatching success, number of fledged chicks, the proportion of eggs that resulted in fledged chicks per nest, and tarsus length of first chick at fledging. We considered a normal distribution of errors for the response variables after testing its distribution with the Kolmogorov Smirnov test.

The response variables were tested in separate GLM analyses against the following explanatory variables: PC1 scores, PC2 scores, PC3 scores, timing of laying, distance to the nearest neighbour, and finally, the interactions between each principal component against timing and distance. We performed separate analysis for 1998 and 1999, except for tarsus length, since chicks were only measured in 1998.

Apart from testing the significance of linear trends, we also tested if curvilinear relationships between explanatory and response variables were statistically significant to be retained by the models.

We fitted each of the explanatory variables to the observed data using the Forward Stepwise Branching Modelling Procedure (Bustamante 1997, Tella et al. 1999). This is a modification of the traditional forward stepwise procedure in which each variable is tested in turn for significance, and only those significant at the 5% level are included in the model. The modification of the procedure employed allows testing the alternative models that were obtained when the second or third most significant variables were included, instead of the most significant one at each of the steps (Bustamante 1997). The Forward Stepwise Branching Modelling Procedure eventually produces a set of different models, but in most instances these converge into a single model (Donázar et al. 1993). To select the model that best fits the data we used the Akaike's information criterion (AICs; Burnham and Anderson 1992).

Results

Variation in habitat availability

The PCA of 13 habitat variables measured on 130 randomly selected points yielded three components that met the broken-stick criterion (Jackson 1993), collectively accounting for 71.5% of the total variation in the original data (Table 1). The first principal component is related with the proximity to the beach, combining the distance to the high-tide line with the percentages of shell and gravel in the substrate with the altitude over the sea level. The amount of shell and gravel increases as both the distance to the beach and the altitude above sea level decrease. The second component clearly represents the effects of vegetation, with positive loadings for shrub vegetation cover within a 1- and 5-m radius and the distance to the nearest clearing from

Table 1. Factor loadings, total and cumulative percent variance explained for principal components analysis of habitat variables measured in 130 random points at Vernaci Sudoeste Island. Factor loadings with absolute values > 0.3 are shown in bold.

Habitat variables	Component		
	I	II	III
Rock (%)	− 0.02	− 0.18	**+ 0.48**
Silt-clay (%)	+ 0.22	+ 0.26	**− 0.47**
Shell (%)	**+ 0.34**	− 0.02	− 0.19
Sand (%)	− 0.23	− 0.23	+ 0.15
Gravel (%)	**+ 0.38**	− 0.01	− 0.04
Slope	− 0.27	+ 0.02	**+ 0.51**
1-m radius vegetation cover (%)	− 0.14	**+ 0.47**	+ 0.14
5-m radius vegetation cover (%)	− 0.18	**+ 0.45**	+ 0.11
Vegetation height	− 0.20	− 0.22	− 0.18
Distance to nearest vegetation	− 0.21	**− 0.38**	− 0.08
Distance to nearest open	− 0.17	**+ 0.44**	+ 0.13
Distance to high tide line	**− 0.37**	+ 0.08	− 0.28
Altitude over sea level	**− 0.39**	+ 0.08	− 0.23
Eigenvalue	4.21	3.19	1.89
Percent total variance	32.35	24.57	14.59
Cumulative variance	32.35	56.92	71.51

which gulls could take flight from when threatened, contrasting with a negative loading for the distance to the nearest vegetation. The third component is a "substrate characteristics" component, since it relates slope to substrate rock and silt-clay composition, contrasting sites with high percentages of rock on higher slopes with sites with high percentages of silt-clay on lower slopes. Taken together, these components served to define three new, synthetic variables that described the principal independent dimensions of variation in the breeding habitat available to kelp gulls at this colony throughout the 2-year period of our study. Random points and nest sites were then scored using these components, and theses scores were then used in the analyses of nest-site selection and nest success.

Nest-site selection

Univariate analyses of the three components generated by the PCA comparing nest sites with random points, indicated that PC2, "vegetation" component hereafter and PC3, "substrate" characteristics component hereafter, were statistically different (Mann-Whitney U test, P = 0.006 and 0.012 for PC2 and PC3, respectively), while PC1, "beach proximity" component hereafter, did not differ significantly (Mann-Whitney U test, P = 0.07). The final multivariate model of nest-site selection included the vegetation and substrate components, indicating that nest sites presented more vegetation cover, were placed closer to the nearest available bushes, and hence, were placed further from the nearest clearing to take flight from when escaping in comparison to random points (Table 2). Moreover, the model shows that nests were built on substrates with lower slopes and higher percentages of silt-clay, but with lower percentages of rock than random points (Table 2).

Table 2. Results of multivariable logistic regression of kelp gull nest-site selection (random = 0, used = 1) on habitat variables at the Vernaci Sudoeste Island colony.

	Coefficient ± SE	Entry test		Removal test	
		Score statistic	P	LRS	P
PC2	− 0.19 ± 0.07	7.550	0.006	8.026	0.005
PC3	+ 0.24 ± 0.09	3.343	0.012	6.721	0.009
Constant	− 0.29 ± 0.12				

In order to examine if inter-nest distance was related to the visibility from the nest we performed regression analyses between inter-nest distance and vegetation cover. The slope of these relations were negative, but not statistically significant (P > 0.05 in all cases).

Nest success

In all cases, only linear relationships were statistically significant as to be retained in the models. The best significant GLM model obtained for hatching success during 1998 (Table 3) included two interaction terms: (1) between the vegetation component and timing of laying, and (2) between the substrate component and timing of laying. The vegetation component was positively associated with hatching success, while the substrate component and timing of laying were negatively associated with hatching success. The final model, therefore, showed that hatching success increased as the vegetation component scores increased and as the substrate component scores decreased. These relationships were influenced by the timing of breeding, with earlier breeders being more successful. In 1999 the model included the vegetation component and also its interaction term with the timing of laying. It showed that hatching success was positively related to the vegetation component and also that timing of laying is influencing this relation, with higher hatching success for earlier breeders (Table 4).

Table 3. Generalized Linear Model (GLM) for hatching success, number of fledged chicks, breeding success and chick size at Vernacci Sudoeste Island during 1998.

Response variable	Explanatory variable	Parameter estimate	SE	% of deviance explained
Hatching success	Constant	0.927	0.085	
	PC2 × timing	− 0.007	0.003	
	PC3 × timing	0.019	0.006	10.40
Number of chicks fledged	Constant	0.836	0.211	
	PC2	0.495	0.129	
	PC2 × timing	− 0.040	0.008	26.14
Breeding success	Constant	0.768	0.170	
	PC2	0.194	0.056	
	PC2 × timing	− 0.018	0.003	
	Nearest nest distance	− 0.354	0.145	28.57
Chick size	Constant	83.64	2.17	
	PC2	3.523	1.529	
	PC2 × timing	− 0.334	0.150	
	Timing	− 0.484	0.150	
	Nearest nest distance	− 1.706	0.809	51.36

Table 4. Generalized Linear Model (GLM) for hatching success, number of fledged chicks and breeding success at Vernacci Sudoeste Island during 1999.

Response variable	Explanatory variable	Parameter estimate	SE	% of deviance explained
Hatching success	Constant	0.259	0.368	
	PC2	0.330	0.162	
	PC2 × timing	− 0.013	0.003	22.64
Number of chicks fledged	Constant	1.659	0.263	
	PC2	1.312	0.342	
	PC2 × timing	− 0.083	0.031	
	PC3 × timing	0.036	0.009	41.17
Breeding success	Constant	0.623	0.094	
	PC2	0.463	0.122	
	PC2 × timing	− 0.029	0.011	
	PC3 × timing	0.014	0.003	42.08

In the resulting model for the size of month-old first chicks the vegetation component entered with a positive sign while both timing of laying and nearest nest distance entered with negative signs. This GLM showed that the chick size increased as the vegetation component scores increased and both the nearest nest distance and the timing of breeding decreased. The interaction term retained indicates that the effect of vegetation was more pronounced for early breeders.

In both years, the models for the number of fledged chicks included the vegetation component with a positive sign, the timing of laying with negative sign, and their interaction term. The results show that the number of fledged chicks increased with an increase in the vegetation component scores and that the strength of this relationship declined as the season progressed. In addition, the substrate component-timing interaction term also contributed to explain the variation in the number of chicks fledged in 1999, showing that more chicks fledged at nests with lower scores for the substrate component. Again, this relation was influenced by the timing of breeding. In both years, the models for breeding success included the vegetation component with a positive sign and the interaction terms with timing of laying with a negative sign (determined by the negative sign of timing). This results indicated that breeding success was related positively to the vegetation component in both years, and this relation was more beneficial for early breeders. In 1998, breeding success also increased as the nearest nest distance decreased, while in 1999 it was affected by the substrate component-timing interaction term.

Discussion

Kelp gulls placed their nests nonrandomly with respect to microhabitat characteristics, and their preferences appeared to be adaptive. Overall, kelp gulls nest-site selection appeared to be influenced by both the effects of vegetation and substrate characteristics. In general terms, kelp gulls showed preferences for building nests at sites with higher vegetation cover, located in close proximity to bushes, but relatively far from the nearest clearing to take flight. In addition, nests tended to be placed on flat surfaces with high proportion of silt and clay, but low percentages of rock. This is consistent with what was observed for kelp gulls in other locations in Patagonia (P. García-Borboroglu and P. Yorio unpubl. data), where individuals select particular nest-sites from the available habitat mainly with respect to variables related to vegetation and substrate slope. These variables were also reported as important cues used by kelp gulls when choosing nesting sites in other regions (Burger and Gochfeld 1981, Quintana and Travaini 2000).

At Isla Vernaci, nests with more vegetation cover, closer distance to bushes and greater distance to clearings, showed higher hatching success, larger one-month-old chick size and higher breeding success. For many seabirds, including gulls, cover is an important factor increasing breeding performance (Lemmetynen 1973, Hudson 1982, Stokes and Boersma 1998). Studies on herring gulls *Larus argentatus* and lesser black-backed gulls *L. fuscus* have shown that these species were more successful, at least concerning some breeding parameters, when nesting at sites that included cover (Brown 1967, Burger 1979, Becker and Erdelen 1986, Calladine 1997). Kelp gull preference for sites in close proximity to vegetation and a higher breeding success at more covered sites have been previously reported for a colony north of our study area (Yorio et al. 1995). Cover determines the thermal properties of the nest and influences the risk of predation (Burger and Gochfeld 1981, Jehl and Mahoney 1987). Its positive effects result mainly from reduced exposure of nest contents to predators, by reducing visibility, and from avoidance of heat stress, by offering shade.

The presence of vegetation yields benefits that take place throughout the breeding cycle. In many seabirds, adults attend their nests almost permanently during the incubation period, offering shade and protection against predators and intruders. If nests are left unattended, eggs or small chicks located in areas devoid of vegetation cover are more exposed to predation and heat stress. Predation is an important cause of offspring mortality in the study colony, mostly by skuas *Catharacta antarctica* and other kelp gulls (Yorio and García Borboroglu 2002). Predation could be reduced by parental defense and/or concealment of chicks by vegetation (Calladine 1997, Stokes and Boersma 1998). As the breeding season progresses, attendance at the nest site and vigilance by parents decrease and therefore the risk of predation increases, at least until chicks are too large to be taken by predators. In addition, most of the chick-rearing period coincides with the highest temperatures in summer, when ambient temperatures can reach 40°C (Servicio Meteorológico Nacional unpubl. data), with higher temperatures closer to the ground. Kelp gull chicks from covered sites may spend a higher proportion of their time near their nests, whereas chicks from exposed nests may seek protection from the sun by moving under nearby bushes, as have been observed in other gull species (Paynter 1949, Davis and Dunn 1976, Burger and Shisler 1978). While seeking protection against solar radiation and predators, chicks from nests without, or with very low vegetation cover have to trespass on neighbouring gull territories, and may in this way be injured or occasionally killed (Emlen 1956, Yorio et al. 1995). Aggression towards kelp gull chicks by adults from neighbouring territories has been observed

even in the absence of human disturbance (Fordham 1964, P. Yorio unpubl. data).

Substrate characteristics appeared to also affect both hatching and breeding success, although the effects on the former were only observed in 1998 and the effects on the latter only during 1999. The main variable included in the substrate component was slope of the terrain. Kelp gulls breeding in South Africa also showed a strong preference to nest on the most level sites (Burger and Gochfeld 1981). Even though on the Antarctic Peninsula, Quintana and Travaini (2000) found that gulls nested on higher slopes than random points, selected slopes lay within the range observed in our study and by Burger and Gochfeld (1981). Nests at lower slopes were associated with higher percentages of silt-clay and lower percentages of rock in the substrate. Eggs and chicks are less likely to roll or fall from level nests and a soft substrate reduces the probability of egg breaking in comparison to the hard surface provided by rock.

Our study shows that some kelp gull breeding parameters are affected by nest-site habitat characteristics. These associations were in most cases influenced by the timing of breeding, with earlier breeders being more successful. Timing of breeding can have significant effects on fitness in a wide number of bird species (Perrins 1970, Moreno 1998), including kelp gulls breeding at Golfo San Jorge (P. García-Borboroglu et al. unpubl. data). Much of the information about parental quality is expressed by the time the eggs are laid (Nisbet et al. 1998) and, in several seabird species, there is evidence that variation in parental quality contributes significantly to variation in performance (Ryder 1980, Coulson and Thomas 1985, Bolton 1991, Bollinger 1994). Higher-quality or the most competitive individuals would be the first ones to settle down, selecting the best or most suitable habitats. Parental quality would also be reflected in a better ability to obtain food for chicks. Unfed chicks are more active and move further from their territories than do well fed chicks (Hunt and McLoon 1975, Hunt and Hunt 1976, Brouwer et al. 1995), thus increasing the probability of being attacked by neighbouring pairs, if they lack adequate cover for protection. Hence, the effects of both the individual and the habitat quality would combine to result in a higher egg and chick survival and growth, in accordance with the results obtained in this study. Unless experimental studies are conducted, the effects of nest site and individual quality on breeding parameters remain difficult to separate.

Only during the first study season was nesting density a determinant of breeding success, with higher densities being more beneficial at the individual level. In other gull species, breeding performance was highest where nests were most dense, but this occurred in vegetated habitats where natural screens blocked the nearest neighbor (Good 2002). Physical barriers to visibility, such as vegetation, can increase the number of birds breeding in an area since inter-nest distance is directly related to visibility (Burger 1977). However, even though in our study inter-nest distances decreased with an increase in vegetation cover, this relation was not statistically significant.

We found evidence that might suggest directional selection in the case of the variables included in the vegetation and substrate components. Evidence of directional selection may exist when higher nest failure occurs at one end of the habitat gradient (Clark and Shutler 1999), which is the case for these two synthetic variables. Vegetation effects and substrate characteristics were important variables in distinguishing random points from real nest sites, and in explaining variation in breeding performance, thus allowing us to detect the process, as well as the pattern, in kelp gull habitat selection.

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