

HOW GENERAL IS THE CENTRAL-PERIPHERY DISTRIBUTION AMONG SEABIRD COLONIES? NEST SPATIAL PATTERN IN THE EUROPEAN SHAG

ALBERTO VELANDO^{1,3} AND JUAN FREIRE²

¹Departamento de Ecología e Biología Animal, Universidade de Vigo, 36200 Vigo, Spain

²Departamento de Biología Animal, Biología Vegetal e Ecología, Universidade da Coruña, 15071 A Coruña, Spain

Abstract. The central-periphery distribution model of nest dispersion suggests that nests located in the center of a colony are less accessible to predators and that birds breeding in the central area are of better physical quality and have greater reproductive success. Another hypothesis, the central-satellite distribution model, suggests that low-quality birds build their nests near those of high-quality pairs, which do not necessarily settle in the colony's center. Advantages of this type of association include increasing the opportunity for extra-pair copulation by low-quality females and increasing the potential for low-quality individuals to obtain a better breeding site or partner in the following season. Here we test these hypotheses on two colonies (Portelo and Faro) of the European Shag (*Phalacrocorax aristotelis*) on the Cíes Islands, Galicia, northwest Spain. Spatial distribution of pairs differing in quality was analyzed using residuals of reproductive success, eliminating the effect of physical quality of the nest site. A negative autocorrelation of these residuals between nests at short distances was detected for the Portelo colony. In Faro there was no evidence that nest distribution differed from a random distribution. Occupation of nest sites (measured as new nest or reoccupied nest) showed negative autocorrelation at short distances, implying that there was an association between new and reoccupied sites. These results demonstrate that nest distribution of European Shag colonies does not fit the central-periphery model, but rather corresponds to either the central-satellite model or to a random distribution.

Key words: central-satellite, coloniality, European Shag, nest site, *Phalacrocorax aristotelis*, seabirds, spatial autocorrelation.

¿Es Generalizable el Modelo Centro-Periferia a Todas las Colonias de Aves Marinas? Distribución Espacial de los Nidos en *Phalacrocorax aristotelis*

Resumen. La distribución de los nidos en aves coloniales puede ser explicada por dos modelos. El modelo centro-periferia implica que las aves que crían en el centro de una colonia son menos accesibles a los depredadores, poseen una mejor condición y tienen un mayor éxito reproductivo. En cambio, el modelo centro-satélite sugiere que aves de baja calidad construyen sus nidos cerca de parejas de alta calidad para obtener ventajas como un mayor número de cópulas extrapareja por parte de hembras de baja calidad o un mejor sitio de cría o pareja en la siguiente estación de cría. En el presente estudio, nosotros contrastamos estos modelos con la distribución de la calidad de las parejas de *Phalacrocorax aristotelis* en dos colonias (Portelo y Faro) de las Islas Cíes situadas en Galicia, noroeste de España. Hemos utilizado como indicador de la calidad de la pareja los residuales del éxito reproductor, eliminando el efecto de la calidad del sitio de nido. En la colonia del Portelo se observó una correlación negativa entre la calidad de las parejas a una distancia menor de 4 m; en el Faro, en cambio, no hubo evidencias de una distribución diferente al azar. Además, se encontró una correlación espacial negativa entre los sitios de nido en los que se construyó un nido por primera vez y los sitios que fueron reocupados. En global, estos resultados muestran que la distribución de las colonias del *P. aristotelis* no corresponde al modelo centro-periferia, sino más bien al modelo centro-satélite o en todo caso, a una distribución al azar.

INTRODUCTION

Nest defense against potential predators has long been suggested as an important force in the evo-

lution of coloniality in birds (Lack 1968, Gotmark and Andersson 1984). Nests located in the more densely populated areas of colonies are more sheltered from predation than those at the periphery (Wittenberger and Hunt 1985). In the context of this relationship between nest density and predation, the central-periphery distribution

Manuscript received 24 February 2000; accepted 7 March 2001.

³ E-mail: avelando@uvigo.es

hypothesis (called "periphery model" in this paper) was first proposed by Coulson (1968) in his study of a colony of Kittiwakes (*Rissa tridactyla*), where he found that birds breeding in the central area were of better physical quality and had higher reproductive success than those nesting at the periphery. Moreover, subsequent studies showed that this population is regulated by the availability of central sites (Porter and Coulson 1987) and that birds breeding in the center have a higher survival rate (Aebischer and Coulson 1990). The periphery model predicts that variation in survival arises because central individuals are less accessible to predators (Hamilton 1971, Vine 1971).

Several studies on seabirds report nest distributions that fit the periphery model, and this model is the generally accepted explanation for nest dispersion patterns in seabird colonies (Wittenberger and Hunt 1985, Furness and Monaghan 1987, Kharitonov and Siegel-Causey 1988). However, there are some examples where this model is not fulfilled. Ryder and Ryder (1981) found a colony of Ring-billed Gulls (*Larus delawarensis*) in which there was no variation in reproductive success between central and peripheral areas, while in another colony, Pugsek and Diem (1983) observed that differences in reproductive success were determined by different spatial distributions of age groups. Scolaro et al. (1996), in a study on a colony of the South American Tern (*Sterna hirundinacea*), found that birds' nest site selection is at first random, and then uniform, but not in the central-periphery pattern. Research on the Blue-eyed Shag (*Phalacrocorax atriceps*) carried out by Shaw (1985, 1986) showed that neither the spatial distribution of reproductive success nor the age of breeders followed the periphery model; as in most studies, this author did not specify the type of distribution that did occur.

In a study on the behavior of Kittiwake recruits in a colony in North Shields, Porter (1990) found that first-time breeders prefer more densely populated sites, with poorer quality birds being relegated to peripheral zones. Danchin et al. (1991) reported that recruits are directly attracted by successful sites and that they visit these sites during the prospecting season. Wagner et al. (1996) suggested that in colonial birds, females that mate with young males may be at an advantage if they breed near older males, because they may obtain extra-pair fertilizations

and perhaps change mates during a following season. Moreover, males may acquire better sites in the area surrounding their own nest site in subsequent years (Aebischer et al. 1995). Thus, "commodity selection" has been proposed to explain colonial breeding, in that animals that breed colonially are actually choosing commodities such as breeding habitats or mates, which in turn creates breeding aggregations (Wiley and Poston 1996, Danchin and Wagner 1997).

In the context of commodity selection, it is therefore possible to put forth an additional hypothesis for social distribution within seabird colonies that is dependent upon habitat heterogeneity and the desirability of good breeding sites. This central-satellite distribution model (herein called "satellite model") may occur in species that are attracted to breed near the best nest sites, both to achieve extra-pair copulations and to acquire a better site or mate in the following season. The term central-satellite refers to the spatial association of pairs differing in quality (i.e., poorer-quality pairs cluster around a central, high-quality pair).

In the Great Cormorant (*Phalacrocorax carbo*), recruits are attracted to and build their nests close to successful sites (Schjørring et al. 1999). Snow (1963) observed that newly formed pairs of European Shags (*Phalacrocorax aristotelis*) breed close to nests that are already established. Adults do not venture very far from the site of their first breeding and they occupy better sites as they get older (Aebischer et al. 1995). In this socially monogamous species, males pursue a mixed-mating strategy, pairing with one female while copulating with others (Graves et al. 1993). Thus, in years with high reproductive success, extra-pair paternity is evident at 18% of nests (Graves et al. 1993). Males choose breeding sites and attract females to their nest sites (Graves and Ortega-Ruano 1994) and males of highest quality (those that breed successfully and have a good nest site) are more successful in attracting females to their territories for extra-pair copulations (Graves et al. 1993, Graves and Ortega-Ruano 1994).

This paper tests the two models of nest distribution in space in two colonies of the European Shag on the Cíes islands, Galicia, northwestern Spain. As indicators of pair quality we used residuals of reproductive success and laying date from a regression of these variables on the physical quality of the nest site. The pair-

quality indexes allowed us to compare the spatial distribution of low and high quality nesting pairs to predictions made by the periphery and satellite models.

METHODS

The Cíes Islands have a nesting population of around 1000 pairs of shags that build their nests mostly in cavities formed by fallen granite rocks (Velando, Docampo, and Alvarez 1999). From 1994 to 1996, we studied all sites where nests were built in two areas, Portelo and Faro, which are far enough away from other breeding areas to be considered isolated colonies. For each nest with eggs, laying date and number of fledged chicks (defined as number of chicks surviving to 25 days) were recorded (Velando, Ortega-Ruano, and Freire 1999), as were variables describing the physical habitat.

A general linear model with Poisson errors and log link (a logarithmic linear model where the response variable has Poisson distribution, Crawley 1993) was used to calculate an index of physical quality of the nest site relative to cumulative reproductive success between 1994 and 1996 in each nest site: Physical Quality Index = $-1.62 + 0.27 \times \text{Visibility} + 0.29 \times \text{Covering} - 0.34 \times \text{Walls} + 0.57 \times \text{Roof}$ ($R^2 = 0.43$, $P < 0.0001$; Velando, unpubl. data). In this model, *Visibility* ranks the possibility of observing other shags or predators from the nest, from 1 for total visibility to 4 for no visibility. *Covering* is the number of walls (from 0 to 4) surrounding and isolating the nest ledge. The walls may be concave (slanting toward the nest), straight, or convex. *Walls* is a count of concave walls (from 0 to 4) that indicates the degree of drainage of the nest hollow; the more concave walls, the greater the risk of flooding. *Roof* indexes the amount of cover over the nest (from 1 for nest or ledge almost totally exposed to 3 for nest or ledge totally covered).

As indices of quality of breeding pairs, we used residuals from a linear regression between either reproductive success or laying date on the index of physical quality of the nest site in each season. All nest sites in the two areas were marked each year and mapped during the summer of 1996. Coordinates (in m) were determined for all nest sites, with the x-axis corresponding to a horizontal line parallel to the cliff edge and the y-axis a vertical line perpendicular to the coastline. Degree of slope (mainly in the

direction of the y-axis) was not taken into account.

Simulations of the two models of nest distribution were made to determine statistical characteristics of their spatial structure and to contrast them with the indices of pair quality obtained in each colony. In addition, a random model with random distribution was considered. Simulations under each of these three models examined pattern of nest distribution in a colony, assuming similar physical quality and 40% nest success (pair quality).

Spatial structure of nest distribution according to the three models and of indices of nest site quality and pair quality were analyzed using techniques of geostatistical analysis (Rossi et al. 1992). Spatial structure was analyzed by calculating the experimental variogram, which represents semivariance between pairs of points (nest sites) separated by a lag (distance) h :

$$y(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [z(x_i) - z(x_i + h)]^2$$

where $y(h)$ is the semivariance estimated for lag h , $N(h)$ is the number of pairs separated by lag h , $z(x)$ and $z(x_i + h)$ are values of the variable on two points separated by lag h . Lag was set to 4 m with a tolerance of ± 2 m. The semivariance was standardized by dividing it by the total variance of all points. When standardized semivariance is low (< 1), the points separated by this distance have similar values, whereas if semivariance is high (> 1), there are great differences between pairs of points.

Spatial autocorrelation of pair quality in each colony was tested statistically by product-moment correlation coefficients in the first lag calculated as

$$r(h) = \frac{1}{N(h)} \frac{\sum_{i=1}^{N(h)} [z(x_i) - m_{-h}][z(x_i + h) - m_{+h}]}{S_{-h}S_{+h}}$$

where $r(h)$ is the product-moment correlation coefficient estimated for lag h , S_{-h} and S_{+h} are standard deviations of values of tail and head of the vector, respectively, and m_{-h} and m_{+h} are mean values of points pertaining to the tail and head of the vector, respectively, in interval h . Autocorrelations were calculated at the first lag (from 0 to 4 m). Mean distance \pm SE to the closest nest was 3.4 ± 1.0 m. Additionally, directional pattern of reproductive parameters was

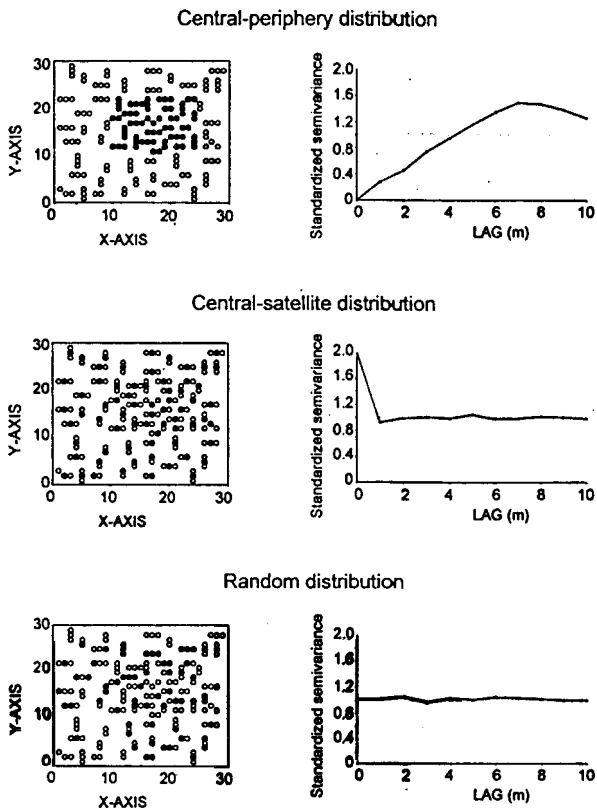


FIGURE 1. Theoretical distribution of pair quality (as indexed by residuals of reproductive success) in three nest distribution models. Spatial distribution of residuals is shown at left. Filled circles stand for positive residuals (high pair quality) and unfilled circles negative residuals (low pair quality). Standardized variograms for each model are shown at right (dotted line indicates standardized total variance). Standardized semivariances are shown in each lag (distance between nests); high semivariance values indicate a negative autocorrelation and low values indicate a positive autocorrelation.

studied at Portelo. Autocorrelations were calculated for nests grouped into 45° (±22.5°) categories based on their x-y coordinates. For example, the 0° group included all nests on the same horizontal plane; the 90° grouping included all nests directly above or below each other. At Faro the number of pairs of points per lag was extremely low, and therefore directional patterns were not analyzed. Significance of spatial autocorrelation was determined by *t* statistic for product-moment correlation coefficient (Sokal and Rohlf 1995). The variograms and correlograms were obtained using the geostatistical software VARIOWIN (Pannatier 1996). Data are expressed as means ± SE.

TABLE 1. Predictions of spatial autocorrelation of pair quality as indexed by reproductive success or its residuals, given random or aggregated nest-site quality, for each of three distribution models. Note that predictions using reproductive success do not allow discrimination among hypotheses, whereas reproductive success residuals make clearly different predictions.

Distribution of nest site quality	Distribution models of pair quality	Spatial autocorrelation predicted	
		Reproductive success	Reproductive residuals
Aggregated	Central-periphery	+ / 0	+
	Central-satellite	- / 0	-
	Random	0	0
Aggregated	Central-periphery	++	+
	Central-satellite	0	-
	Random	+	0

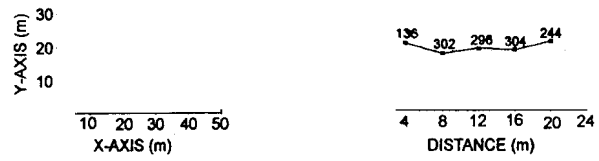
RESULTS

PREDICTIONS OF THE THEORETICAL MODELS OF SOCIAL DISTRIBUTION

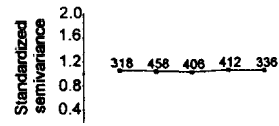
In the periphery model, high-quality birds tend to occupy a central position around which other pairs arrange themselves (Fig. 1, Table 1). In this model, the semivariance of pair quality, measured as reproductive success in the model, given homogeneous nesting habitat, results in low values at short lags and increasing values as lags become greater. This model predicts a positive spatial autocorrelation of reproductive parameter residuals at short lags. In the satellite model, low-quality birds are attracted to nest near better-quality birds. At short lags the standardized semivariance is much higher than 1, then drops quickly as the lag increases, resulting in values close to 1. At short lags a negative autocorrelation is predicted. The random model assumes no spatial relationship in distribution of pair quality. The semivariance has values close to 1 at all lags and a lack of spatial autocorrelation (Fig. 1).

SOCIAL DISTRIBUTION IN EUROPEAN SHAG COLONIES: A TEST OF THE PREDICTIONS OF THE THEORETICAL MODELS

The Portelo colony had more occupied nests (42–47) per season and a higher mean nest-site quality each year (yearly means ranged from



Portelo colony



	Portelo		Faro	
	1994	1996	1994	1996
Reproductive success				
Laying date				
Reoccupation				

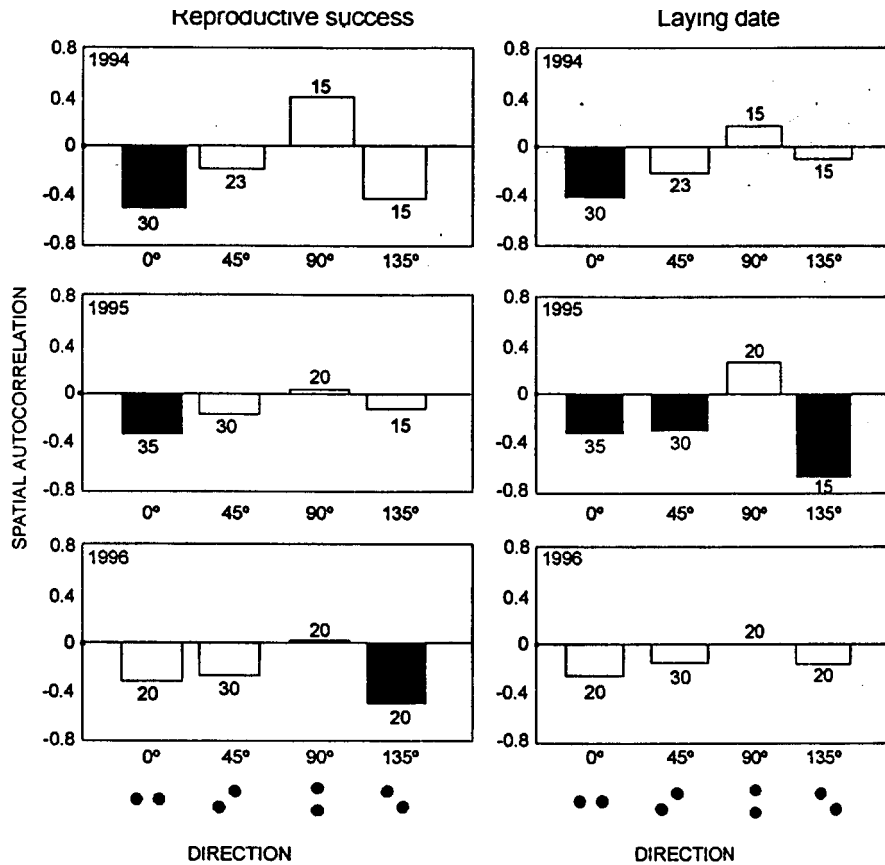


FIGURE 3. Directionality of nest distribution of the European Shag in the Portelo colony, Cíes Islands, Spain. Directional autocorrelation shown (every $45^\circ \pm 22.5^\circ$, considering x-axis as 0° – 180° and y-axis 90° – 270°) in the first lag (4 m) of residuals of reproductive success and laying date. Black bars indicate significant autocorrelation index ($P < 0.05$). Number of pair comparisons given in each case. (Dots in x-axis labels indicate orientation on the cliff face of pair-nest comparisons for each category).

both Portelo and Faro (Table 2), implying that there is an association between new and reoccupied sites at these distances.

DISCUSSION

We found that the two European Shag colonies studied do not fit the periphery model proposed by Coulson (1968). Instead, there is a contrasting relationship with birds of differing quality or age nesting in proximity to each other. In the Portelo colony there was significant negative association of residuals of reproductive success (which indicate pair quality, after removing the effect of physical quality of the site) for nests within 4 m in two of the three years studied. High-quality individuals breed earlier (Aebischer 1985, Velando 1997), and in this colony in two of the years of study there was a negative autocorrelation of residuals of laying date at short lags. Distributions

of reproductive parameters in the Faro colony appeared to be random, and only in 1995 was there a negative correlation in laying date at short lags. In this colony, nest-site quality is low. Mean quality of nest sites in the Portelo colony was high, but there are a limited number of good sites for breeding (only 7 of 59 nest sites were of high quality, Fig. 2). Poor-quality or younger birds could select any of these lower-quality sites (random distribution), or be relegated to the peripheral zones due to competition for the central sites (Porter and Coulson 1987). However, at Portelo there was an association between the poorer and better quality birds, suggesting a satellite model.

In the European Shag, age is one important factor causing differences in breeding success (Potts et al. 1980). Shags gradually attain better breeding sites as they get older (Aebischer et al.

1995). Young and poor-quality breeders return late to the colony and nest in poor-quality sites (Potts et al. 1980, Aebischer 1985, Velando 1997). In the Cíes Islands the laying season is very long, from February to June, but successful pairs lay before 20 April (Velando 1997, 2000). In many cases late or young breeders build nests at new sites (Velando 1997), but close to high-quality pairs.

In the European Shag, males vary more than females in reproductive success, with males in better condition obtaining more extra-pair copulations than poorer-condition males (Graves et al. 1993). There may be two selective pressures that induce low-quality or young birds to breed close to high-quality birds in the same season. One is the opportunity for females and males to obtain extra-pair copulations, and the other is the possibility of changing mates or breeding sites in the next season (Wagner 1993, Wagner et al. 1996). There is evidence that the frequency of extra-pair copulations correlates with distance between individuals and colony size (Møller 1991, Birkhead and Møller 1992), and there is also evidence that mate changes may be caused by extra-pair copulations (Ens et al. 1993). In birds, the choice of nest location could be influenced by conspecific attraction based on mating tactics (Ramsay et al. 1999). In the European Shag, females seeking extra-pair copulations can use the male dart-gape behavior and his nest site as clues to his quality (Graves et al. 1993). In the Isle of May the poor-quality males, occupying nest sites of poor quality, increased their dart-gape frequency when squatting near high-quality nests (Ortega-Ruano, unpubl. data). Moreover, individuals that breed close to high-quality pairs can obtain information about environment, nest, or mate quality at a local scale that can be useful in the next season (Boulinier et al. 1996). In the European Shag, changes of mate and nest site between seasons have been found to be dependent on distance between nest sites (Aebischer et al. 1995). Therefore, both sexual partners and nest sites ("commodities") can explain the satellite model distribution shown in shag colonies.

The attraction to conspecifics can generate central-satellite patterns in patchy environments, but in homogeneous habitats aggregation can generate other spatial patterns (Dan-

chin and Wagner 1997). Many seabirds breed on homogeneous open ground with low variability in nest-site quality. In this type of habitat, birds can choose to nest very close to others because the quality of breeding habitat depends only on the presence of nesting conspecifics, and density offers protection against predators (Birkhead and Harris 1985). This may explain why species in homogeneous environments breed in high-density colonies (Table 3). Habitat selection in the European Shag and in seabirds in general can be determined by two sometimes opposing forces: one, the attraction to breed near others (both for protection against predators and for social factors); and the other, the drive to seek out sites of high quality for protection (both against predators and adverse weather conditions, Velando 1997). The satellite model may apply in patchy environments with low breeding-bird density and high-quality nest sites (Table 3); in contrast, the periphery model appears to apply to species that breed in dense colonies. An example may be the ledges of the warehouse studied by Coulson (1968), where Kittiwakes bred on identical windowsills. This was also the case in the anthropogenic constructions used for nesting by the Cape Cormorant (*Phalacrocorax capensis*; Berry 1976). In these two examples, the driving force of selecting high-quality nest-sites is not present; therefore only the benefits of breeding close to others come into play, as was pointed out by the above authors.

In species offered a wide variety of habitats differing in quality, selection favors individuals that choose better habitats. Young birds or those in poorer physical condition will be relegated to the less favorable sites (Porter 1990). However, poorer sites are abundant, which may be why individuals breed close to other pairs in better condition. These cases may fit a satellite model, as we propose here. In our study, this distribution was evident on some occasions, particularly when direction was taken into account. Parallel to the coastline (x-axis), there was a negative correlation between residuals for nests at a distance of 4 m. Potts et al. (1980) report that European Shags are not affected by the activity of other individuals at greater distances. The absence of autocorrelation along the vertical axis (y-axis) may be due to the inclination of the slope in places where large

TABLE 3. Social distribution, environment type, density, and quality of nest site for selected seabird species. Nesting habitat is classified according to patchiness. Quality of nest site indicates protection level from predators and bad weather. Question marks denote species in which habitat type or social distribution is not clear.

Species	Nesting habitat ^a	Quality of nest site	Social distribution ^b	Source
<i>Pygoscelis adeliae</i>	H	Medium-high	P	Tenaza 1971
<i>Spheniscus magellanicus</i>	H	Medium-high	P	Gochfeld 180
<i>Pygoscelis antarctica</i>	H	Medium-high	P?	Barbosa et al. 1997
<i>Pelecanus occidentalis</i>	H	High	P	Blus and Keahcy 1978
<i>Sula variegata</i>	H	High	P	Duffy 1983, Velando, unpubl. data
<i>Sula nebowxii</i>	P	Low	S	Nelson 1978, Velando, unpubl. data
<i>Morus bassanus</i>	H	High	P	Montevocchi and Wells 1984
<i>Phalacrocorax capensis</i>	H	High	P	Berry 1976
<i>Phalacrocorax atriceps</i>	P	Medium	R?	Shaw 1986
<i>Phalacrocorax aristotelis</i>	P	Low	S/R	This study
<i>Phalacrocorax auritus</i>	H?	High	P	Leger and MacNeil 1987, Siegel-Causey and Hunt 1981
<i>Phalacrocorax pelagicus</i>	P	Low	S?/R?	Siegel-Causey and Hunt 1981
<i>Phalacrocorax gaimardi</i>	P	Very low	S?	Coker 1919, Murphy 1936
<i>Larus argentatus</i>	H?	Medium-high	P	Chabrzyk and Coulson 1976, Burger and Shisler 1980
<i>Larus delawarensis</i>	H?	Medium-high	P?/R	Dexheimer and Southern 1974, Pugsek and Diem 1983
<i>Rissa tridactyla</i>	H?	High	P	Coulson 1968
<i>Sterna hirundo</i>	H	High	P	Burger and Lesser 1978, Burger 1991
<i>Fratercula arctica</i>	P?	Medium-high	P	Harris 1980
<i>Uria aalge</i>	H?	High	P	Nettleship 1972

^a Nesting habitat: H = homogeneous, P = patchy.

^b Social distribution: P = periphery model, S = satellite model, R = random.

rocks fallen from higher ground have settled. The arrangement of the large rocks as a vertical barrier makes the interacting distance between individuals greater on the y-axis than on the x-axis. Thus, the interactions with shags nesting above or below a nesting pair are reduced relative to interactions with shags nesting on the same horizontal line.

Aebischer (1985) studied reproduction of the European Shag in central and peripheral areas of a colony on the Isle of May. This author did not find any differences in reproductive success between zones; however, nest-site quality was higher in peripheral areas. This could imply colonization of new zones, however, since most of the problems in studies of center and periphery stem from definitions of "center" and "periphery." Aebischer (1985) did not present a clear definition of periphery. The two colonies studied on the Cíes Islands are relatively isolated from others, but it may also be argued that we have studied relationships within a central area that has a periphery in less dense areas. In any case, regardless of the definition used, the colonies studied did not fit the model in which high-quality individuals nested close together, but rather the opposite held true. This model is probably best applied to those habitats where protection against predators is due to nest-site quality and not density of individuals. We predict that homogeneous habitats having a low level of protection are likely to fit the periphery model proposed by Coulson (1968). However, in heterogeneous habitats where high-quality nest sites are scarce, the quality of neighboring nests may be inversely related. That is, high-quality individuals are likely to occupy the few best nest sites, while low-quality individuals select the ample poor quality sites that surround high-quality breeders.

ACKNOWLEDGMENTS

We thank Manolo Alvarez and Beatriz Gamallo for their assistance during the data collection. We are grateful to Xunta's Wildlife Service (Servicio de Medio Ambiente Natural, MAN) for helping in this study. We thank Professor J. Coulson, J. E. Ortega-Ruano, and two anonymous reviewers for their comments and suggestions to previous drafts of this paper. We also appreciate the improvements in English usage made by P. Lowther through the Association of Field Ornithologists' program of editorial assistance. This study was partially supported by the Shag Management Plan of the Xunta de Galicia.

LITERATURE CITED

- AEBISCHER, N. J. 1985. Aspects of biology of the Shag (*Phalacrocorax aristotelis*). Ph.D dissertation, Durham University, Durham, UK.
- AEBISCHER, N. J., AND J. C. COULSON. 1990. Survival of the kittiwake in relation to sex, year, breeding experience and position in the colony. *Journal of Animal Ecology* 59:1063-1071.
- 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.
- BARBOSA, A., J. MORENO, J. POTTI, AND S. MERINO. 1997. Breeding group size, nest position and breeding success in the chinstrap penguin. *Polar Biology* 18:410-414.
- BERRY, H. H. 1976. Physiological and behavioural ecology of the Cape Cormorant *Phalacrocorax capensis*. *Madoqua* 8:59-62.
- BIRKHEAD, T. R., AND M. P. HARRIS. 1985. Ecological adaptations for breeding in the Atlantic Alcidae, p. 205-232. In D. N. Nettleship and T. R. Birkhead [EDS.], *The Atlantic Alcidae*. Academic Press, London.
- BIRKHEAD, T. R., AND A. P. MÖLLER. 1992. Sperm competition in birds: evolutionary causes and consequences. Academic Press, London.
- BLUS, L., AND J. A. KEAHEY. 1978. Variation in reproductive success with age in the Brown Pelican. *Auk* 95: 128-134.
- BOULINIER, T., E. DANCHIN, J. Y. MONNAT, C. DOUTRELANT, AND B. CADIOU. 1996. Timing of prospecting and the value of information in a colonial breeding bird. *Journal of Avian Biology* 27:252-256.
- BURGER, J. 1991. *The Common Tern: its breeding biology and social behavior*. Columbia University Press, New York.
- BURGER, J., AND F. LESSER. 1978. Selection of colony sites and nest sites by Common Terns *Sterna hirundo* in Ocean County, New Jersey. *Ibis* 120: 433-449.
- BURGER, J., AND J. K. SHISLER. 1980. The process of colony formation among Herring Gulls *Larus argentatus* nesting in New Jersey. *Ibis* 122:15-26.
- CHABRZYK, G., AND J. C. COULSON. 1976. Survival and recruitment in the herring gull. *Journal of Animal Ecology* 44:187-203.
- COKER, R. E. 1919. Habits and economic relations of the guano birds of Peru. *Proceedings of United States Natural Museum* 56:449-511.
- 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.
- CRAWLEY, M. J. 1993. *GLIM for ecologists*. Blackwell Scientific Publications, Oxford, UK.
- DANCHIN, E., B. CADIOU, J. Y. MONNAT, AND R. RODRIGUEZ ESTRELLA. 1991. Recruitment in long-lived birds: conceptual framework and behavioural mechanisms. *Proceedings of the International Ornithological Congress* 20:1641-1656.
- DANCHIN, E., AND R. H. WAGNER. 1997. The evolution of coloniality: the emergence of new perspectives. *Trends in Ecology and Evolution* 12:342-347.

- DEXHEIMER, M., AND W. E. SOUTHERN. 1974. Breeding success relative to nest location and density in Ring-billed Gull colonies. *Wilson Bulletin* 86: 288-290.
- DUFFY, D. C. 1983. Competition for nesting space among Peruvian guano birds. *Auk* 100:680-688.
- ENS, B. J., U. N. SAFRIEL, AND M. P. HARRIS. 1993. Divorce in long-lived and monogamous oystercatcher *Haematopus ostralegus*: incompatibility or choosing the better option? *Animal Behaviour* 45:1129-1217.
- FURNESS, R. W., AND P. MONAGHAN. 1987. Seabird ecology. Blackie, Glasgow.
- GOCHFELD, M. 1980. Timing of breeding and chick mortality in central and peripheral nests of Magellanic Penguins. *Auk* 97:191-193.
- GOTMARK, F., AND M. ANDERSSON. 1984. Colonial breeding reduces nest predation in the Common Gull (*Larus canus*). *Animal Behaviour* 32:485-492.
- GRAVES, J., AND J. E. ORTEGA-RUANO. 1994. Patterns of interaction in the courtship behaviour of shags (*Phalacrocorax aristotelis*). *Etología* 4:1-9.
- GRAVES, J., J. E. ORTEGA-RUANO, AND J. B. SLATER. 1993. Extra-pair copulations and paternity in shags: do females choose better males? *Proceedings of the Royal Society of London Series B* 253: 3-7.
- HAMILTON, W. D. 1971. Geometry for the selfish herd. *Journal of Theoretical Biology* 31:295-311.
- HARRIS, M. P. 1980. Breeding performance of puffins *Fratercula arctica* in relation to nest density, laying date and year. *Ibis* 122:193-209.
- KHARITONOV, S. P., AND D. SIEGEL-CAUSEY. 1988. Colony formation in seabirds. *Current Ornithology* 5: 223-272.
- LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.
- LEGER, C., AND R. MCNEIL. 1987. Choix de l'emplacement des nids de cormorant aigrettes (*Phalacrocorax auritus*) aux îles de la madeleine, Quebec. *Canadian Journal of Zoology* 65:24-34.
- MØLLER, A. P. 1991. Preferred males acquire mates of higher phenotypic quality. *Proceedings of the Royal Society of London Series B* 245:179-182.
- MONTEVECCHI, W. A., AND J. WELLS. 1984. Fledging success of Northern Gannets from different nest-sites. *Bird Behaviour* 5:90-95.
- MURPHY, R. C. 1936. Oceanic birds of South America. Vol. I. Macmillan, New York.
- NELSON, J. B. 1978. The Sulidae: gannets and boobies. Oxford University Press, Oxford, UK.
- 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.
- PANNATIER, Y. 1996. VARIOWIN 2.2. The User Guide. Springer-Verlag, New York.
- PORTER, J. M. 1990. Patterns of recruitment to breeding group in the kittiwake *Rissa tridactyla*. *Animal Behaviour* 40:350-360.
- PORTER, J. M., AND J. C. COULSON. 1987. Long-term changes in recruitment to the breeding group, and the quality of recruits at a kittiwake *Rissa tridactyla* colony. *Journal of Animal Ecology* 56: 765-690.
- 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 of Animal Ecology* 49:465-484.
- PUGESEK, B. H., AND K. L. DIEM. 1983. A multivariate study of the relationships of parental age to reproductive success in California Gulls. *Ecology* 64: 829-839.
- RAMSAY, S. M., K. OTTER, AND L. M. RATCLIFFE. 1999. Nest-site selection by female Black-capped Chickadees: settlement based on conspecific attraction? *Auk* 116:604-617.
- ROSSI, R. E., D. J. MULLA, A. G. JOURNEL, AND E. H. FRANZ. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. *Ecological Monographs* 62:277-314.
- RYDER, P. L., AND J. P. RYDER. 1981. Reproductive performance of Ring-billed Gulls in relation to nest location. *Condor* 83:57-60.
- SCHJØRRING, S., J. GREGERSEN, AND T. BREGNBALLE. 1999. Prospecting enhances breeding success of first-time breeders in the great cormorant, *Phalacrocorax carbo sinensis*. *Animal Behaviour* 57: 647-654.
- SCOLARO, J. A., S. LAURENTI, AND H. GALELLI. 1996. The nesting and breeding biology of the South American Tern in northern Patagonia. *Journal of Field Ornithology* 67:17-24.
- SHAW, P. 1985. Age-differences within breeding pairs of Blue-eyed Shags *Phalacrocorax atriceps*. *Ibis* 127:537-543.
- SHAW, P. 1986. Factors affecting the breeding performance of Antarctic Blue-eyed Shags *Phalacrocorax atriceps*. *Ornis Scandinavica* 17:141-150.
- SIEGEL-CAUSEY, D., AND G. L. HUNT JR. 1981. Breeding-site selection and colony formation in Double-crested and Pelagic Cormorants. *Auk* 103:230-234.
- SNOW, B. 1963. The behaviour of the shag. *British Birds* 56:77-103, 164-186.
- SOKAL, R. R., AND F. J. ROHLF. 1995. Biometry. 3rd ed. W. H. Freeman and Company, New York.
- TENAZA, R. 1971. Behavior and nesting success relative to nest localization in Adelie Penguin (*Pygoscelis adeliae*). *Condor* 73:81-92.
- VELANDO, A. 1997. Ecología y comportamiento del cormorán moñudo *Phalacrocorax aristotelis* en las islas Cíes y Ons. Ph.D. dissertation, University of Vigo, Vigo, Spain.
- VELANDO, A. 2000. The importance of the hatching date on dominance of young shags. *Animal Behaviour* 60:181-185.
- VELANDO, A., F. DOCAMPO, AND D. ALVAREZ. 1999. The status of European Shag *Phalacrocorax aristotelis* population on the Atlantic coast of Iberian Peninsula. *Atlantic Seabirds* 1:105-114.
- 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.
- VINE, I. 1971. Risk of visual detection and pursuit by

- a predator and the selective advantage on flock behaviour. *Journal of Theoretical Biology* 30:405-442.
- WAGNER, R. H. 1993. The pursuit of extra-pair copulations by female birds: a new hypothesis of colony formation. *Journal of Theoretical Biology* 163:333-346.
- WAGNER, R. H., M. D. SCHUNG, AND E. S. MORTON. 1996. Condition-dependent control of paternity by female Purple Martins, implications for coloniality. *Behavioural Ecology and Sociobiology* 38:379-389.
- WILEY, R. H., AND J. POSTON. 1996. Perspective: indirect mate choice, competition for mates, and coevolution of the sexes. *Evolution* 50:1371-1381.
- WITTENBERGER, J. F., AND G. L. HUNT JR. 1985. The adaptive significance of coloniality in birds. p. 1-78. *In* D. S. Farner, J. R. King, and K. C. Parkes [EDS.], *Avian biology*. Vol. VIII. Academic Press, New York.