The Condor 99:634–641

CHARACTERISTICS AND COMPETITION FOR NEST CAVITIES IN BURROWING PROCELLARIIFORMES[1]

JAIME A. RAMOS[2], LUIS R. MONTEIRO, ENCARNACION SOLA AND ZITA MONIZ
Departamento de Oceanografia e Pescas, Universidade dos Açores, 9900 Horta (Azores), Portugal

Abstract. We examined the dimensions, nearest-neighbor distance, density, vegetation cover, shelter, and substrate of nest cavities in a multispecific colony of Procellariiformes: Cory's Shearwater (*Calonectris diomedea*), Little Shearwater (*Puffinus assimilis*), Bulwer's Petrel (*Bulweria bulwerii*), and Band-rumped Storm-Petrel (*Oceanodroma castro*). We investigated differences in nest cavity dimensions between species, the influence of nest cavity characteristics on hatching success of Cory's Shearwater and Band-rumped Storm-Petrel, and intra- and interspecific competition for nest cavities by using natural and artificial nests. Dimensions of nest cavities were highly correlated with species' body size. Physical features of the nests of Cory's Shearwater differed from those of small petrels. Physical features of the nests of small petrels overlapped extensively. Physical features helped to explain hatching success of Cory's Shearwater, and crowding influences contributed to hatching success of Band-rumped Storm-Petrel. Sheltered nest cavities had higher hatching success, but nest cavity characteristics interacted with the quality of breeders. Breadth and volume of eggs laid by Cory's Shearwater in artificial nests were significantly smaller than those in nearby natural nests, indicating that young breeders likely occupied artificial nests. Cory's Shearwater laid in half of the artificial nest cavities built for them, and excavated natural and artificial nest cavities of small petrels. We suggest that the breeding population of Cory's Shearwater includes high numbers of new breeders and is regulated by the availability of nest cavities. Results indicated that interference competition within and between Cory's Shearwater and small petrels is important in the structure of this procellariiform breeding community.

Key words: Procellariiformes, shearwaters, nest-site characteristics, population regulation, interference competition, hatching success, Azores.

INTRODUCTION

Colonial seabirds nest in crowded situations, often in mixed colonies, and both physical and social factors are important in selection of nest sites (Coulson 1968, Potts et al. 1980, Ramos and del Nevo 1995). If the selection of breeding habitats is adaptive, then nest site quality may be reflected in breeding success (Birkhead et al. 1985). Characteristics and competition for nest sites, and their influence on breeding success of colonial seabirds, have been described extensively for surface- and ledge-nesters such as terns *Sterna* spp. (Burger and Gochfeld 1988, Gochfeld and Burger 1988, Ramos and del Nevo, 1995), murres *Uria* spp. (Birkhead et al. 1985, Birkhead and Nettleship 1987, Olsthoorn and Nelson 1990), European Shags *Phalacrocorax aristotelis* (Potts et al. 1980, Olsthoorn and Nelson 1990), Black-legged Kittiwake *Rissa tridactyla,* Razorbill *Alca torda,* and Northern Fulmar *Fulmarus glacialis* (Olsthoorn and Nelson 1990). For burrowing Procellariiformes, there is some quantitative information on nest-site characteristics (Burger and Gochfeld 1991, Brandt et al. 1995), but very little quantitative information on nest-site competition (Warham 1990). Burrowing Procellariiformes show marked colony and nest site tenacity (Warham 1990, Forbes and Kaiser 1994), and competition for nest cavities may occur intra- and interspecifically.

We worked on Vila Islet, Azores, a colony composed of Cory's Shearwater (*Calonectris diomedea*), Little Shearwater (*Puffinus assimilis*), Bulwer's Petrel (*Bulweria bulwerii*), and Band-rumped Storm-Petrel (*Oceanodroma castro*). These species show a decreasing size gradient (average weight in g = 840, 172, 98, and 49, respectively), and some degree of overlap in their breeding seasons (Monteiro et al. 1996b): Band-rumped Storm-Petrel (August–February), Little Shearwater (January–May), Bulwer's Petrel (May–September), and Cory's Shearwater (March–October). Observations, such as the following by Monteiro et al. (1996a, 1996b), suggest that shortage of nest cavities may affect this

[1] Received 22 March 1996. Accepted 16 April 1997.
[2] Present address: Instituto Piaget, Escola Superior de Educação, 5340 Macedo de Cavaleiros, Portugal.

breeding community: (a) the same nest cavity is often used by different species overlapping in breeding phenology, (b) many broken eggs of Cory's Shearwater were found in very exposed nest cavities, which offer little protection in poor weather or against predators such as gulls (Zino 1971), and (c) the larger Cory's Shearwater exhibit high levels of daytime nest attendance in early March (23%, $n = 121$), fight to secure burrows, and excavate nests of smaller petrels.

On the basis of these observations, we investigated three factors that might explain the structure of this Procellariiform breeding community: (1) nest cavity dimensions, (2) hatching success, and (3) competition for nest cavities. We describe the dimensions of nest cavities, intra- and interspecific nest density, vegetation cover, and other features related to the shelter of nest cavities, and compared these variables between species.

The fact that most broken eggs were found in exposed nest cavities means that hatching success may be partly explained by nest cavity characteristics. Also, most eggs in open nest cavities may have been laid by young and inexperienced females, which are likely to lay smaller eggs (Brooke 1990). We correlated hatching success with nest cavity characteristics, and compared egg measurements and egg volume of hatched and nonhatched eggs, and artificial (see later) and nearby natural nests to explore this point.

Fights to secure a burrow, high levels of daytime burrow attendance, sharing of nest sites between species, and excavation of nests of smaller petrels by Cory's Shearwaters suggest strong intra- and interspecific competition for nest cavities. We built artificial nest cavities for Cory's Shearwater and smaller petrels, collected data on occupancy levels of these and natural nest cavities, and examined degree of excavation of natural and artificial nests by Cory's Shearwaters (especially those built for smaller petrels) to test the importance of competition for nest cavities. If there is a shortage of nest sites, we would expect a high number of artificial nest cavities to be occupied, as well as a high degree of natural nest-prospecting and excavation.

METHODS

Vila Islet, off Santa Maria, Azores, is a small islet (< 10 ha) with several habitat types: steep to medium rock slopes, medium soil slopes with rock and vegetation, small caves, and a well-vegetated soil plateau having few rocks. About 50 pairs of Bulwer's Petrel, 50 pairs of Little Shearwater, 200 pairs of Band-rumped Storm-Petrel (Monteiro et al. 1996a), and 350 pairs of Cory's Shearwater (pers. observ.) breed in this colony. All areas of the islet have been surveyed and nest cavities marked since 1993. Most nests of Cory's Shearwater are accessible, except for a few in narrow and deep caves. Some nests of small petrels (Little Shearwater, Bulwer's Petrel, and Band-rumped Storm-Petrel) may not have been discovered because entrances are difficult to find in rocky areas and among boulders. We concentrated our sampling in three habitat types (rock, soil with vegetation, mixed) where most birds nested; we are confident that the majority of the nest cavities of both Cory's Shearwater and the smaller petrels were found.

In 1995, all nest cavities with adults were checked during laying and incubation. Nest cavities were characterized a few days after the peak of hatching of each species: early January (Band-rumped Storm-Petrel), mid-March (Little Shearwater), and early August (Cory's Shearwater and Bulwer's Petrel). For the Band-rumped Storm-Petrel and the Cory's Shearwater, only the nest cavities used in 1995 were considered; hatching success was obtained for these two species. To increase the sample size for Bulwer's Petrel and Little Shearwater, some nest cavities from the 1993 and 1994 breeding seasons were included, but hatching success was obtained from a very small sample of them. Data were collected from 247 nest cavities of Cory's Shearwater, 61 of Band-rumped Storm-Petrel, 38 of Bulwer's Petrel, and 33 of Little Shearwater (10–15% of the described nest cavities were shared between small petrels). For each nest cavity, 12 variables were recorded: 7 continuous and 5 categorical (Table 1). Continuous variables reflected the dimensions of nest cavities, intra- and interspecific nest density, and vegetation cover around the nest entrance. Categorical variables represented factors related to shelter, substrate type, and orientation of the nest cavity. We used one-way ANOVA (for continuous variables) and median test (for categorical variables) to compare nest cavity characteristics between species. Continuous data were log $(x + 1)$ transformed, or square-root or arcsine transformed, in order to attain normality and homoscedasticity (Zar 1996).

TABLE 1. Variables recorded for each nest cavity.

Nest-site variable	Description
1 Nest width	Maximum width of nest cavity (m).
2 Nest height	Maximum height of nest cavity (m).
3 Nest length	Maximum length from entrance to back of nest cavity (m).
4 Neighbor distance, same species	Distance to nearest neighbor of the same species (m).
5 Neighbor number	Number of neighbors of the same species within 3 m.
6 Neighbor distance, different species	Distance to nearest neighbor of a different species (m).
7 Cover	Vegetation cover within 1 m of nest cavity entrance (%).
8 Shelter	Number of walls and roof around a nest site (1–5).
9 Chamber	Chamber at nest entrance: absent (0), small (0.5), large (1).
10 Curved entrance	Absent (0), present (1).
11 Nest type	Proportion of cavity sides bounded by rock: all rock, rock crevice (0); soil bed, soil crevice (0.5); all soil, burrow (1).
12 Orientation	West (+1), East (−1), North (−0.5), South (+0.5).

To determine which characteristics influenced hatching success of Cory's Shearwater and Band-rumped Storm-Petrel, a cavity was classified as successful or unsuccessful on the basis of whether clutches hatched or not. Thus, for each cavity we had a binary response variable together with the nest cavity variables. Logistic regression was used to assess the contribution of nest cavity characteristics in explaining hatching success (Manly et al. 1993). The parameters of the best model were obtained by the maximum likelihood method (Cox 1970).

We made a complete survey of Cory's Shearwater nests, measured about half the eggs (length and breadth), calculated egg volume index as length $\times$ breadth^2, and tabulated their hatching success in three habitats: rock, soil, and mixed. Hatching success and presence or absence of nest material were tabulated for Cory's Shearwater and Band-rumped Storm-Petrel. In addition to nest material, Cory's Shearwater nesting in rock crevices often place a large bed of pebbles at the entrance of the nest cavity. We recorded the area (cm^2) and maximum height (cm) of the pebble bed and investigated whether nests with pebbles have higher hatching success.

The degree of prospecting natural nests by Cory's Shearwater was examined by monitoring the occupants of 100 nests once a night, for one week in March and in May 1994, prior to egg laying. Between 6–10 March 1996, 28 artificial nest cavities for Cory's Shearwater and 20 artificial nest cavities for small petrels were built to investigate intra- and interspecific competition for nest cavities. Nest cavities for Cory's Shearwater were located within the two breeding areas composed of soil with vegetation, and mixed substrate. These nest cavities were 47–60 cm long, 11–29 cm wide and 15–28 cm high and placed at approximately 1- to 3-m intervals. Nest cavities for small petrels were located up to 20 m from their main breeding area, and built close to a large rock and prone to be excavated by Cory's Shearwaters; these nest cavities were about 12 cm wide and high, and about 25 cm long. Some were shorter but had a curved entrance. We recorded natural and artificial nests of small petrels that were excavated by Cory's Shearwater. We compared egg dimensions and volume index between eggs that hatched and did not hatch in natural nests, and between artificial nests and nearby natural nests (three to five nearest nests).

RESULTS

COMPARISON OF NEST CAVITY CHARACTERISTICS AMONG SPECIES

The characteristics of nest cavities were significantly different between species, except for vegetation cover (Table 2). The strongest effects of continuous variables were shown by the various dimensions of nest cavities: nest height, nest length, and nest width. These differed consistently between Cory's Shearwater and small petrels. Nest cavity dimensions of small petrels overlapped extensively (Table 2). The smaller petrels, Bulwer's Petrel and Band-rumped Storm-Petrel, had nest cavities of similar dimensions. Nests of small petrels differed from those of Cory's Shearwater in having a chamber and a curved entrance. Band-rumped Storm-Petrel

TABLE 2. Nest cavity characteristics of procellariiforms at Vila Islet, Azores. Variables defined in Table 1. Values tabulated are mean ± SE for continuous variables, and percentage of each category for categorical variables.

Variable	Cory's Shearwater (n = 247)	Little Shearwater (n = 33)	Bulwer's Petrel (n = 38)	Band-rumped Storm-Petrel (n = 61)	Statistic†
Nest width (m)	0.25 ± 0.01 A#	0.12 ± 0.01 B	0.17 ± 0.02 B	0.13 ± 0.01 B	22.5***
Nest height (m)	0.33 ± 0.01 A	0.20 ± 0.02 B	0.16 ± 0.03 BC	0.11 ± 0.01 C	40.1***
Nest length (m)	0.55 ± 0.01 A	0.46 ± 0.03 B	0.36 ± 0.02 C	0.34 ± 0.02 C	35.7***
Neighbor distance, same species (m)	3.13 ± 0.27 A	11.36 ± 3.06 B	8.94 ± 2.51 B	9.01 ± 1.62 B	13.9***
Neighbor number	1.91 ± 0.10 A	0.94 ± 0.16 B	1.11 ± 0.19 B	0.69 ± 0.11 B	15.3***
Neighbor distance, different species (m)	14.00 ± 1.16 A	1.64 ± 0.61 B	3.72 ± 0.10 B	3.45 ± 0.50 AB	7.8***
Cover (%)	24.17 ± 1.57	29.33 ± 4.18	21.98 ± 4.18	29.05 ± 3.78	1.1 ns
Shelter (%)					
1	0.8 A	0.0 A	2.6 A	0.0 B	37.0***
2	9.7	0.0	10.6	4.9	
3	34.8	9.1	26.3	14.8	
4	54.3	87.9	60.6	65.5	
5	0.4	3.0	0.0	14.8	
Chamber (%)					
Absent	73.7 A	48.5 B	60.6 B	39.3 B	30.0***
Small	16.6	39.4	28.9	47.6	
Large	9.7	12.1	10.5	13.1	
Curved entrance (%)					
Absent	92.3 A	48.5 B	81.6 C	80.3 C	47.5***
Present	7.7	51.5	18.4	19.7	
Nest type (%)					
Rock crevice	38.5 A	6.1 A	34.2 A	24.6 B	24.4***
Soil crevice	53.0	93.9	63.2	49.2	
Burrow	8.5	0.0	2.6	26.2	
Orientation (%)					
East	36.4 A	72.7 B	42.1 A	34.4 A	8.0*
North	13.4	6.1	10.6	24.6	
South	31.6	18.2	36.8	29.5	
West	18.6	3.0	10.5	11.5	

† F-values (one way ANOVA) were used for continuous variables, chi-square values (median test) were used in categorical variables.
# Entries in the same row that share the same letter are not significantly different (all comparisons $P < 0.05$, Tukey test for continuous variables and paired Median test for categorical variables).
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns = nonsignificant.

had a higher shelter index and percentage of burrow-nests. Larger nest cavities (mainly those of Cory's Shearwater) had fewer walls at the entrance, resulting in a lower shelter index. Nest type was correlated with nest width and length (birds nesting in rock crevices are unable to alter nest cavities) and cover (birds nesting in soil areas had a higher percentage of vegetation cover around nest entrances; all r_s between 0.22 and 0.25, $P < 0.05$). All compass directions were represented in the nests sampled, although those of Little Shearwater were less oriented towards the North (and West?).

RELATIONSHIP BETWEEN NEST CAVITY CHARACTERISTICS AND HATCHING SUCCESS

A complete survey of Cory's Shearwater nests indicated that nests are more abundant on mixed (n = 168) and rocky (n = 118) substrates than on soil (n = 25), but hatching success was much higher on soil (mixed = 52%, rock = 43%, soil = 88%, $\chi^2_2 = 16.6$, $P < 0.001$). Nest width, nest length, and chamber influenced hatching success (Table 3). Birds having longer nest cavities and an entrance chamber had significantly higher hatching success than those birds having shorter nest cavities lacking a chamber. Nest width had

TABLE 3. Parameter estimates of the maximum likelihood logistic regression model used to assess the contribution of nest cavity characteristics in explaining hatching success.

Variable	Cory's Shearwater	Band-rumped Storm-Petrel
Nest width	−2.66*	−4.52
Nest height	−0.79	−7.03
Nest length	3.20**	−2.08
Neighbor distance, same species	−0.07	−0.09
Neighbor number	−0.05	−2.94**
Neighbor distance, different species	0.00	−0.18
Cover	0.01	0.02
Shelter	0.08	0.46
Chamber	1.09*	1.38
Curved entrance	0.45	3.65*
Nest type	0.02	−0.91
Orientation	0.08	−0.21

* = $P < 0.05$, ** = $P < 0.01$; others $P > 0.05$.

TABLE 4. Relationship between Cory's Shearwater hatching success and nest features related to behavioral attributes of the parents. See Table 1 for definition of nest types.

Nest type	Number eggs (% hatched)	χ^2_1
Rock crevice		
Pebbles		
With pebbles	58 (71)	
Without pebbles	39 (28)	19.3***
Nest material		
With material	75 (65)	
Without material	22 (5)	22.8***
Soil crevice		
Nest material		
With material	112 (61)	
Without material	19 (0)	21.6***
Burrow		
Nest material		
With material	21 (90)	
Without material	0	

*** = $P < 0.001$.

a negative effect, i.e., birds with wider nest cavities had lower hatching success. Distance to the nearest neighbor of the same species had no effect on hatching success ($P < 0.1$).

For the Band-rumped Storm-Petrel, neighbor number and curved entrance were the only variables that influenced hatching success (Table 3). Birds nesting in cavities having a curved entrance had significantly higher hatching success, and those nesting in an intraspecific crowded situation had lower success.

Table 4 presents the relationship between hatching success of Cory's Shearwater and nest material for the three nest types. Both rock crevice and soil crevice nests with material had higher hatching success than those without material. All burrows had nest material, a possible influence of the vegetation present around the entrance. For Band-rumped Storm-Petrel, hatching success did not differ between nests with material (55.5%) and those without material (43.5%, n = 59; χ^2_1 = 2.2), but the sample size was much smaller.

In Cory's Shearwater, pebbles were present more at rock crevice nests (60%, n = 97) than soil crevice nests (21%, n = 131). The presence of pebbles at the entrance of rock crevice nests was associated with a significantly higher hatching success (Table 4). The mean (± SE) area of the pebble bed was 1,599 ± 173 cm^2 (n = 88) and the mean height was 3.2 ± 0.2 cm (n = 87). The mean area and height of pebbles of successful and unsuccessful nests were not significantly different (t_{86} = 0.89 and t_{85} = 1.50, respectively, both $P > 0.15$).

INTRA- AND INTERSPECIFIC COMPETITION FOR NEST CAVITIES

Burrow occupancy was high, but the incidence of breeding in occupied burrows was low. Egg laying was noted in only 46% (n = 28) of the Cory's Shearwater artificial nests, but all showed some signs of activity, e.g., fresh droppings and feathers, and night birds were seen within all but three nests. The hatching success of eggs laid in artificial nests was 31%. Such rapid occupation of artificial nests suggests strong intraspecific competition for nest cavities among Cory's Shearwater. The existence of intraspecific competition also may be inferred from the following observations: (1) many signs of digging activity occurred throughout the study area. We recorded 44 nest scrapes, but some could have been excavated in previous years. Of these, 93% were adjacent to a medium or large rock (length = 27–65 cm), seemingly used as a roof and to stabilize soil erosion; (2) of the 100 Cory's Shearwater nests that were monitored before laying, 5% had one bird, 37% always had the same pair, and 58% had more than a pair. Such high degree of digging and nest-prospecting should increase intraspecific encounters.

In natural nest cavities, egg breadth and vol-

TABLE 5. Comparison of measurements (mean ± SD) and volume index (= length × breadth^2) between hatched and nonhatched eggs in natural nests, and eggs laid in artificial and nearby natural nests for Cory's Shearwater.

	Length†	Breadth†	Volume†
In natural nests			
Hatched eggs (n = 100)	74.5 ± 3.08	49.7 ± 1.37	184.5 ± 13.44
Nonhatched eggs (n = 60)	74.1 ± 2.74	49.1 ± 1.63	178.6 ± 13.86
t-test	0.95	2.62**	2.63**
Eggs laid in			
Natural nests (n = 48)	73.9 ± 3.00	49.7 ± 1.28	183.0 ± 12.16
Artificial nests (n = 12)	74.7 ± 2.07	48.2 ± 2.21	173.7 ± 17.81
t-test	0.79	3.19**	2.13*

* = $P < 0.5$, ** = $P < 0.01$.
† Length and breadth are measured in mm, volume in cm^3.

ume of nonhatched eggs were significantly smaller than those of hatched eggs (Table 5). The same trend was found among artificial and nearby natural nests (Table 5). This suggests that clutches that did not hatch and those in artificial nests were mainly laid by younger breeders.

Of the 20 nests built for small petrels, 4 were excavated by Cory's Shearwater. In addition, of 76 active nests (with adult, egg or chick) of small petrels marked since 1993, in an area of mixed substrate (thus prone to be excavated), 47% were excavated by Cory's Shearwater. Ultimately, the latter bred in seven of these cavities in 1995. In this year, two Bulwer's Petrels, two Little Shearwaters, and two Band-rumped Storm-Petrels were found dead at the entrance of nests excavated by Cory's Shearwater. In general, only the entrance chamber was excavated, but if the ground was soft the nesting cavity also was destroyed. Furthermore, the presence of small petrels was noted on active nests of other small petrels in 1993/1994: Bulwer's Petrel = 51%, n = 55; Little Shearwater = 55%, n = 42; and Band-rumped Storm-Petrel = 6%, n = 131. These observations point to high levels of interference competition for nest cavities between Cory's Shearwater and small petrels, and within small petrels.

DISCUSSION

As expected, our data show that dimensions of nest cavities are strongly related to species body size. It is obvious that larger species such as Cory's Shearwater must nest in larger cavities, but it is not clear why small petrels do not breed in larger cavities. The explanation may be related to the fact that the present population size of small petrels is reduced (Monteiro et al. 1966a). Thus, small petrels occupy the smallest nest cavities, where they may achieve a higher degree of protection; plus appropriate large cavities are occupied by Cory's Shearwater. Cory's Shearwater seemed more opportunistic than small petrels because nests ranged from large and less sheltered cavities to long and protected ones. Wide entrances appeared to be the result of natural features (e.g., through soil erosion or natural cavities in rocky areas). Small petrels apparently specialize in the use of fairly sheltered and small cavities. Protection against rainfall, drainage and wind may be achieved with a curved entrance or a long cavity. In our study, nest length was important in explaining hatching success of Cory's Shearwater but not of Band-rumped Storm-Petrel. Longer small nest cavities are either under-represented in our sample or uncommon in this colony. In terms of shelter, the presence of a curved entrance may substitute for the effect of length. The Band-rumped Storm-Petrel should be able to occupy smaller natural nest cavities without excavation.

Petrels and shearwaters are constrained to breed in areas where the substrate provides crevices and opportunities to excavate, although burrowing Procellariiformes may prefer to nest in more crowded situations (Jones 1986). Physical features were more important in explaining the hatching success of Cory's Shearwater than the Band-rumped Storm-Petrel. Band-rumped Storm-Petrels breeding close to a high number of conspecifics apparently had lower hatching success. Number of neighbors was uncorrelated with shelter, nest width, height and length, and one likely explanation is that interference competition for adequate nest cavities influenced hatching success in the Band-rumped Storm-Petrel. This contrasts with surface-nesting seabirds in which the proximity of conspecifics enhances breeding success (Birkhead 1977, Wooler and Coulson 1977, Birkhead et al. 1985).

The pressure for nests among Cory's Shearwater was enormous and high levels of nest site competition were apparent: about 50% of the artificial nests were occupied in the first year, as opposed to 23% in the second year for Manx Shearwater *Puffinus puffinus* (Brooke 1990). Among some shearwaters, over half of the adults at a colony may be nonbreeders (Skira 1991), although these cease to visit the colony a few weeks after hatching begins.

The eggs laid by Cory's Shearwater in artificial nests were smaller than those in natural nests, which suggests that they were laid by young, inexperienced birds (Brooke 1990). Unlike the study of Mougin et al. (1990) on Cory's Shearwater of the Selvagem Grande, we found a positive relationship between hatching success and egg size. Other studies have shown that reproductive success in shearwaters is independent of egg size (Meathrel et al. 1993) and governed primarily by age and breeding experience (Wooler et al. 1990). However, age (Croxall et al. 1992) and breeding experience (Lequette and Weimerskirch 1990) may be closely related to egg size and, thus, the difference between our results and those of Mougin et al. (1990) could be due to the fact that our sample included a greater proportion of young, inexperienced breeders.

Therefore, although hatching success was related to some nest cavity characteristics, there is probably an interaction between the quality of breeding birds and characteristics of the nest cavities that they occupy. In cormorants, individuals tend to move to better quality sites when available, with a concomitant increase in breeding success (Potts et al. 1980). Mougin et al. (1990) showed that young Cory's Shearwaters change partners often, lose their egg, and forego reproduction for several years, but with experience, their performance improves. In our study, the importance of behavioral traits was highlighted by the fact that hatching success was highest in rock crevice nests with pebbles. Pebbles are added to the nest entrance every year; their area and height are related to the age and experience of the parents. These pebbles conceivably reduce the size of the nest entrance, thus reducing the area to be defended from conspecifics and increasing protection to the chick. Indeed, we recorded 18 chicks predated by Buzzards *Buteo buteo rothschildi* and, in the Selvages, Cory's Shearwater eggs are predated by gulls as well (Zino 1971).

Cory's Shearwater were more abundant, more plastic in their choice of breeding site, much larger, and more aggressive than small petrels, which are very vulnerable to predation (Tomkins 1985) and were displaced from nest cavities by Cory's Shearwater. We showed indirectly that nest cavities are in short supply for Cory's Shearwater and presented circumstantial evidence that they are in short supply for the smaller petrels too. We hypothesized that interference competition for nests cavities, which may lower hatching success, is important in this mixed-species colony.

High levels of intraspecific and interspecific interference competition for nest cavities may be a result of alteration of breeding habitat in historical times. Small petrels are now confined to three islets and inaccessible cliffs, following human colonization of the main islands, the introduction of predators, exotic vegetation, and exploitation (Monteiro et al. 1996a, pers. observ.); therefore breeding biotopes may be the limiting factor for the present populations of Procellariiformes. Ironically, the reduction in exploitation of Cory's Shearwater by humans may lead to greater pressure for nest cavities. This fact can be mitigated by building artificial nests for small petrels that are impossible to be excavated by Cory's Shearwater.

ACKNOWLEDGMENTS

This study was financed by the European Commission (contract LIFE B4-3200/95/351). José Maria Soares helped in access to the islet, Dan Chamberlain commented on an earlier draft, and David Ainley and two anonymous referees provided helpful comments on a previous version.

LITERATURE CITED

BIRKHEAD, T. R., E. GREEN, J. D. BIGGINS, AND D. N. NETTLESHIP. 1985. Breeding site characteristics and breeding success in Thick-billed Murres. Can. J. Zool. 63:1880–1884.

BIRKHEAD, T. R., AND D. N. NETTLESHIP. 1987. Ecological relationships between Common Murres, *Uria aalge*, and Thick-billed Murres, *Uria lomvia*, at the Gannat Islands, Labrador. II. Breeding success and site characteristics. Can. J. Zool. 65: 1630–1637.

BRANDT, C. A., J. K. PARRISH, AND C. N. HODGES. 1995. Predictive approaches to habitat quantification: Dark-rumped Petrels on Haleakala, Maui. Auk 112:571–579.

BROOKE, M. 1990. The Manx Shearwater. T. & A. D. Poyser, London.

BURGER, J., AND M. GOCHFELD. 1988. Nest site selection and temporal patterns in habitat use of Roseate and Common Terns. Auk 105:433–438.

BURGER, J., AND M. GOCHFELD. 1991. Nest-site selection by the Herald Petrel and White-tailed Tropicbird on Round Island, Indian Ocean. Wilson Bull. 103:126–130.

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.

COX, D. R. 1970. Analysis of binary data. Methuen, London.

CROXALL, J. P., P. ROTHERY, AND A. CRISP. 1992. The effect of maternal age and experience on egg-size and hatching success in Wandering Albatrosses *Diomedea exulans*. Ibis 134:219–228.

FORBES, L. S., AND G. W. KAISER. 1994. Habitat choice in breeding seabirds: when to cross the information barrier. Oikos 70:377–384.

GOCHFELD, M., AND J. BURGER. 1988. Nest-site selection: comparison of Roseate and Common Terns (*Sterna dougallii* and *S. hirundo*) in a Long Island, New York colony. Bird Behav. 7:58–66.

JONES, M. J. 1986. The relationship of chick-size and nest site occupancy with nest type and nesting density in Cory's Shearwater *Calonectris diomedea* on Selvagem Grande. Boletim do Museu Municipal do Funchal 38:110–119.

LEQUETTE, B., AND H. WEIMERSKIRCH. 1990. Influence of parental experience on the growth of Wandering Albatross chicks. Condor 92:726–731.

MANLY, B. F. J., L. L. MCDONALD, AND D. L. THOMAS. 1993. Resource selection by animals. Statistical design and analysis for field studies. Chapman and Hall, London.

MEATHREL, C. E., J. S. BRADLEY, R. D. WOOLER, AND I. J. SKIRA. 1993. The effect of parental condition on egg-size and reproductive success in Short-tailed Shearwaters *Puffinus tenuirostris*. Oecologia 93:162–164.

MONTEIRO, L. R., J. A. RAMOS, AND R. W. FURNESS. 1996a. Past and present status and conservation of breeding seabirds in the Azores. Biol. Conserv. 78:319–328.

MONTEIRO, L. R., J. A. RAMOS, R. W. FURNESS, AND A. J. DEL NEVO. 1996b. Movements, breeding, molt, diet and feeding of seabirds in the Azores. Colonial Waterbirds 19:82–97.

MOUGIN, J. L, CHR. JOUANIN, AND F. ROUX. 1990. Le rôle de l'âge et de l'expérience dans le déroulement et la réussite de la reproduction chez le Puffin Cendré *Calonectris diomedea borealis* de l'île Selvagem Grande. L'oiseaux et R. F. O. 60:39–49.

OLSTHOOR, J. C. M., AND J. B. NELSON. 1990. The availability of breeding sites for some British seabirds. Bird Study 37:145–164.

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. J. Anim. Ecol. 49:465–484.

RAMOS, J. A., AND A. J. DEL NEVO. 1995. Nest-site selection by Roseate Terns and Common Terns in the Azores. Auk 112:580-589.

SKIRA, I. 1991. The Short-tailed Shearwater: a review of its biology. Corella 15:45–52.

TOMKINS, R. J. 1985. Breeding success and mortality of Dark-rumped Petrels in the Galapagos, and control of their predators. Int. Council for Bird Preservation Tech. Publ. 3:159–175.

WARHAM, J. 1990. The petrels. Their ecology and breeding systems. Academic Press, London.

WOOLER, R. D., J. S. BRADLEY, I. J. SKIRA, AND D. L. SERVENTY. 1990. Reproductive success of Short-tailed Shearwaters *Puffinus tenuirostris* in relation to their age and breeding experience. J. Anim. Ecol. 59:161–170.

WOOLER, R., AND J. C. COULSON. 1977. Factors affecting the age of first breeding in the Kittiwake *Rissa tridactyla*. Ibis 119:339–349.

ZAR, J. H. 1996. Biostatistical analysis. Prentice-Hall, London.

ZINO, P. A. 1971. The breeding of Cory's Shearwater on the Selvage Islands. Ibis 113:212–217.