
Black Rats, Island Characteristics, and Colonial Nesting Birds in the Mediterranean: Consequences of an Ancient Introduction

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Abstract: *The devastation of island faunas by alien species has been instrumental in raising concerns about the global threat to biological diversity. Colonial nesting species, often restricted to islands, have been affected severely. Eradication of introduced species as a means to alleviate the problem is usually done with little or no understanding of the mechanisms governing interactions between introduced and native species. Such an understanding could help target management action. We analyzed how island area, rock substrate, bird species biology, and presence of an introduced species, the black rat (*Rattus rattus*), interact to explain the distribution and abundance of colonial nesting birds on a set of 72 islands from six archipelagos in the western Mediterranean. Rats were introduced to this region over 2000 years ago, and these communities have had time to reach an equilibrium. Using general linear models, we show that rats have affected species distributions more on the smaller islands and on islands with an acidic or neutral rock substrate; larger bird species are more resistant. On the smaller islands, where rat densities are highest, larger colonial birds are negatively affected. On larger islands, where rat densities are lower and fluctuate from year to year, larger colonial birds can maintain healthy populations despite the presence of rats. Although rats caused local extinction or reduction in bird abundance, the presence of islands varying in size and/or substrate allowed most archipelagos to retain their suite of colonial nesting bird species, despite a presumably reduced abundance for most species.*

Ratas Negras, Características de Islas, y Nidación Colonial de Aves en el Mediterráneo: Consecuencias de una Introducción Ancestral

Resumen: *La devastación de las faunas isleñas por especies forasteras ha sido instrumental en lo que respecta a elevar preocupaciones sobre la amenaza global contra la diversidad biológica. Las especies de nidación colonial, frecuentemente restringidas a islas, han sido severamente afectadas. La erradicación de especies introducidas como un medio para aliviar el problema es generalmente realizada con poco o ningún entendimiento de los mecanismos que gobiernan las interacciones entre las especies nativas y las introducidas. Este tipo de entendimiento podría ayudar a enfocar medidas de manejo. Nosotros analizamos como el área, el substrato rocoso, la biología de la especie de ave, y la presencia de una especie introducida, la rata negra (*Rattus rattus*), interactúan para explicar la distribución y abundancia de aves con nidación colonial en 72 islas de seis archipiélagos en el Mediterráneo occidental. Las ratas fueron introducidas a esta región hace más de 2000 años y estas comunidades han tenido tiempo suficiente para alcanzar un equilibrio. Mediante el uso de modelos lineales generales mostramos que las ratas han afectado más la distribución de especies en las islas pequeñas y en las islas grandes con un substrato rocoso ácido o neutro (textura burda), que en aquellas islas con caliza y textura fina. Las especies de aves más pequeñas son más sensibles a las ratas, más frecuentemente ausentes de las islas con ratas y sistemáticamente ausentes de islas con ratas y un substrato rocoso de estructura burda. Las especies de aves más grandes son más resistentes. En las islas más pe-*

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queñas, donde la densidad de las ratas es mayor, las aves coloniales grandes son afectadas negativamente. En islas más grandes, donde las densidades de ratas son menores, y fluctúan de un año al otro, las aves coloniales grandes pueden mantener poblaciones saludables a pesar de la presencia de las ratas. No obstante que las ratas causaron extinciones locales o reducciones en la abundancia de aves, la presencia de islas que varían en tamaño y/o substrato permite que la mayoría de los archipiélagos mantengan su grupo de especies de aves de nidación colonial, a pesar de una presumiblemente reducida abundancia en la mayoría de las especies.

Introduction

Since Darwin and Wallace, patterns of species distribution on islands have been the subject of considerable attention and have led to major advances in ecology and biogeography (e.g., MacArthur & Wilson 1967; Lack 1976). More recently, the devastation of island ecosystems by introduced species has been instrumental in raising awareness of the global threat that human-driven dispersal of species is posing to biological diversity (Bright 1998). Islands are essential for many species, especially for colonial nesting birds. On islands the latter can find a combination of suitable habitats (e.g., Lack 1968; Ashmole 1971; Ricklefs 1990) and the absence of predators (including humans; review in Burger & Gochfeld 1994). Indeed, the introduction of alien predators on islands has led to the extinction of numerous animal populations (Atkinson 1996; for Mediterranean beetles, Palmer & Pons 1996), including colonial species (Atkinson 1985; Collar et al. 1994).

Rats (Polynesian, *Rattus exulans*; black, *R. rattus*; and Norway, *R. norvegicus*) have been among the first and most successful predators introduced to oceanic islands by humans. Their impact, notably on colonial birds, has been enormous (Moors & Atkinson 1984; Moors et al. 1992). Significant efforts to restore island ecosystems through rat eradication have been made and are continuing in several archipelagos (e.g., Taylor & Thomas 1989; 1993; Chapuis et al. 1994; Siorat & Pascal 1995; Kaiser et al. 1997). In contrast to these efforts, only moderate attention has been paid to understanding how introduced rats actually interact with native species. When and why will certain species go extinct, decline, or persist in the presence of rats? What will be the long-term effect of the alien species on the indigenous community? How is this effect influenced by island characteristics?

We analyzed how black rats affect the distribution and abundance of colonial birds on islands of the western Mediterranean. Current rat distribution in the Mediterranean is well documented, and reliable information exists on the time of colonization (Audouin-Rouzeau & Vigne 1994). The introduction of the black rat to this region at least 2000 years ago makes it of special interest because it is likely that the invaded communities have reached some level of equilibrium. This is not necessarily the case in many of the isolated islands or archipelagos that

have been invaded much more recently. We focused on colonial nesting species, which are prey of high potential benefit to rats. We considered colonial nesting species as those species that nest in aggregated clumps and do not exhibit helping behavior (e.g., Wittenberger & Hunt 1985; Brown & Brown 1996). On these islands, colonial nesting birds span a range of body size and taxa that can help in understanding the relationships among predation risk, prey size, and prey biology. We also used experimental analysis to assess interaction between rats and two colonial bird species on these islands (Thibault 1995; Penloup et al. 1997). We tested four predictions: (1) the risk of extirpation by rats decreases with increasing prey body size; (2) for larger species, the presence of rats affects population size in a density-dependent manner; (3) independent of prey body size, the effects of rats on distribution and abundance of cavity nesters depends on island area, and (4) on substrate through variation in the availability of breeding sites safe from rats.

Current Regional Geography of Rats and Colonial Nesting Birds

The western Mediterranean basin spreads from Gibraltar to the Sicily channel (Fig. 1). It covers about one-third of the 2.9 million km² of the Mediterranean Sea, and it includes several hundred islands and islets. Of those, 471 occur around the Balearics, Corsica, Sardinia, and offshore Provence, France. The black rat, native to eastern Asia, reached Palestine around 3000 B.P. (Tchernov 1986). Evidence of rats in the western Mediterranean has been found on Corsica dating to 2400 B.P. (Vigne & Valladas 1996). At that time most of the islands surrounding Corsica and Sardinia were already separated from one another by the sea rise that followed the last glacial period (van Andel 1990; Laborel et al. 1994). On Menorca, records date to 2200 B.P. (Reumer 1986), and on Zembra, Tunisia, to the fifth or sixth century A.D. (Vigne 1988). Sanges and Alcover (1980) found rat bones on Sardinia in layers dating to 5500 B.P., but this date is still under debate (Audouin-Rouzeau & Vigne 1994). Only a few islands are close enough to the main islands to be accessible by natural dispersal (Cheylan 1986a), and the colonization process was probably de-

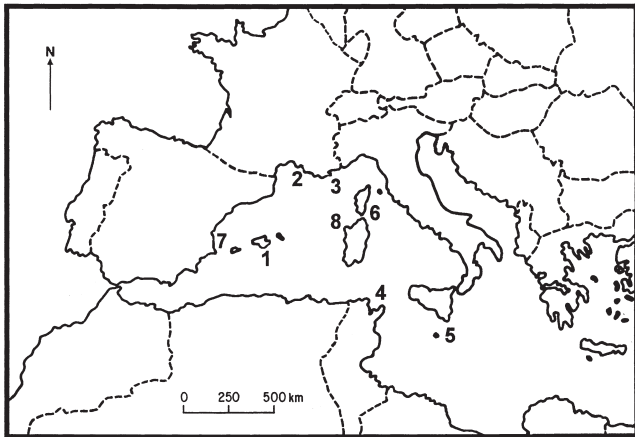


Figure 1. Map of the western Mediterranean region with location of sites studied: 1, Cabrera Archipelago; 2, Riou Archipelago; 3, Hyères Islands; 4, Zembra Islands; 5, Maltese Islands; 6, Bonifacio Strait Islands; 7, Benidorm Island; 8, Foradada Island.

pendent mostly on human movements by boat (Vigne 1994; for archeological data on boat transport of the Norway rat, see Vigne & Villié 1995). Consequently, rat populations from Corsica, Sardinia, and neighboring islands form a genetically homogeneous group suggesting a common origin (Cheylan et al. 1998).

Today black rats are widespread and abundant on most Mediterranean islands (Cheylan 1984; Audouin-Rouzeau & Vigne 1994). The species is common in forests and shrublands up to 1080 m elevation (Corsica; Salotti 1984) and is well adapted to micro-insular habitats (Norman & Baudinette 1969). At a regional scale there is no significant distribution gap. At a local scale, however, rats are absent from over 50% of the islands smaller than 5 ha and are present on most islands larger than 10 ha (Corsica; Guyot 1989; Appendix 1). The more isolated the smaller islands, the higher the probability of their being rat-free (Cheylan 1988). Other factors explaining the presence of rats are (1) human activities that may or may not facilitate their arrival and (2) the diversity and productivity of the flora that will decrease or increase chances that an established population of rats will persist (Cheylan 1988). On islets smaller than 20 ha, black rat densities tend to be higher and show less pronounced fluctuations than on larger islands (Cheylan 1986a, 1988; Granjon 1987; Granjon et al. 1992). These observations are consistent with studies of other rodents (Gliwicz 1980). The black rat is the only rat species encountered on the islands we studied.

At the regional scale, there are six common colonial nesting seabirds. They usually display nonuniform distribution patterns (Zotier et al. 1992, 1999). The Mediterranean Shearwater (*Puffinus yelkouan*), the Yellow-legged Gull (*Larus cachinnans*), and the Shag (*Phalacrocorax aristotelis*) are more abundant in confined basins (such as

the Balearic or Tyrrhenian Sea), whereas the Audouin's Gull (*Larus audouinii*) breeds mainly in the Alboran Sea (east of Gibraltar), although it has recently colonized the Balearic Sea (Oro & Martinez-Vilalta 1992). Cory's Shearwater (*Calonectris diomedea*) has a wide distribution and gathers in large colonies in relatively open seas (such as the central and southern Mediterranean), as does the Storm Petrel (*Hydrobates pelagicus*) but usually in smaller colonies (Zotier et al. 1999). The regional distribution of marine birds is often correlated with the distribution of oceanographic parameters such as thermal fronts, water temperature, and salinity (Zotier et al. 1999). The larger colonies of Cory's Shearwater, for example, are established close to summer thermal fronts, areas of the Mediterranean where summer winds are most frequent. More coastal species (e.g., Shag, Mediterranean Shearwater) are more abundant in areas with colder waters, such as those near the mouth of large rivers.

The distribution of most nonmarine colonial nesting birds tends to be restricted to islands relatively close to the mainland or to the main islands. Among the five main species, the Rock Dove (*Columba livia*) breeds mainly around Corsica, Sardinia, Sicily, and the Balearics (Cramp 1985; Hagemeyer & Blair 1997). It also occurs on islets or rocks if they are <5 km from open foraging habitats situated on the mainland or on larger islands (unpublished data). Pallid Swifts (*Apus pallidus*) are well distributed on small coastal islands (Cramp 1985; Hagemeyer & Blair 1997), but less so on remote islands or in the vicinity of colonies of Eleonora's Falcon (*Falco eleonora*). Alpine (*A. melba*) and Common swifts (*A. apus*) are less widespread and occur in smaller colonies. The patchy distribution of Eleonora's Falcon nesting colonies corresponds to areas where migrant passerines are concentrated in autumn, most colony sites being in the eastern Mediterranean (Mayol 1996).

Methods

We collected data on the abundance and distribution of colonial species in six main groups of islands, for a total of 72 islands (about 15% of all islands), situated in the western Mediterranean (Fig. 1). These islands range in size from 0.17 to 24,500 ha. They belong to (1) the Riou Archipelago in Provence, France, (2) the Hyères Islands in Provence, (3) the islands in the Bonifacio Strait between Corsica and Sardinia, (4) the Cabrera Archipelago of Balearics, Spain, (5) the Maltese Archipelago, and (6) the Zembra Islands, Tunisia, and two isolated islands off the Spanish and Sardinian coasts. For each island we assessed presence or absence of rats (Appendix 1).

For each island, we recorded the area, which is known to influence both the occurrence and the abundance of rats, and type of rock substrate (coarse texture such as granite, gneiss, schist versus smooth texture with cliffs

Table 1. Result of general linear model analysis of the effect of island area and presence of rats on the distribution and abundance of colonial nesting birds on the islands of the Bonifacio Strait and of the Cabrera Archipelago.*

Location and species	Variables and interactions		
	area (p)	rat (p)	area × rat (p)
Bonifacio Strait			
Cory's Shearwater	<0.01	n.s.	n.s.
Storm Petrel	n.s.	<0.001	n.s.
Yellow-legged Gull	n.s.	n.s.	n.s.
Pallid Swift	<0.05	<0.001	n.s.
Shag	n.s.	n.s.	n.s.
Audouin's Gull	n.s.	n.s.	n.s.
Rock Dove	n.s.	n.s.	n.s.
Cabrera Islands			
Cory's Shearwater	n.s.	<0.05	n.s.
Mediterranean Shearwater	n.s.	n.s.	n.s.
Storm Petrel	—	—	<0.05
Yellow-legged Gull	n.s.	n.s.	n.s.
Audouin's Gull	n.s.	n.s.	n.s.
Shag	n.s.	n.s.	n.s.
Eleonore's Falcon	n.s.	n.s.	n.s.
Common Swift	<0.01	n.s.	n.s.

*All 26 islands selected in the Bonifacio Strait have an acidic rock substrate (coarse texture, see methods). Rats are present on 19 islands and absent from 7. Only variables or interactions with significant effects are shown. All islands of the Cabrera Archipelago are of limestone (smooth) substrate; rats are present on four of them. Only variables or interactions with significant effects are shown. n.s., nonsignificant; —, variables that cannot be tested alone because of significant interaction with other variables.

such as limestone), which influences the number of cavities (higher on limestone islands) available to the cavity-nesting species as well as the difficulty of cavity access for rats. To single out the respective role of each of these three variables, we defined three groups of islands characterized by different combinations of the variables.

To understand how island area and presence of rats affect the distribution and abundance of colonial birds on islands with coarse-textured rock substrate, we analyzed the abundance and distribution of seven colonial nesting bird species that breed on the 26 granitic islands in the Bonifacio Channel (Fig. 1). These islands range in size from 0.5 to 420 ha. Nineteen of them have rats; seven have no rats.

Similarly, to analyze the effect of island area and of presence of rats on the distribution and abundance of colonial bird species on islands with smooth-rock substrate, we studied the distribution and abundance of eight colonial nesting bird species commonly found on 16 limestone islands of 0.17 to 1154 ha in the Cabrera Archipelago (Fig. 1). Four of these islands have rats; 12 have no rats.

To analyze the relationships among rock substrate, presence of rats, and colonial birds we analyzed the abundance and distribution of the six species common on 17 of the 18 islands studied in Provence. These islands belong to the Hyères and Riou archipelagos and range from 0.2 to 1254 ha. All have rats; eight have a coarse (acidic or neutral) rock substrate and nine a smooth limestone substrate. At a broader geographic scale, we studied the distribution and abundance of the four colonial nesting species that were observed in all

the archipelagos we studied in relation to three variables: presence of rats, island area, and rock substrate.

We used a generalized linear model (GLIM 3.77; Payne 1985) to analyze and test the statistical significance of the effect of the presence of rats, island area, and rock substrate (explanatory variables) and their effects on species abundance (the response variable) for the different data sets. Species' abundances and island area were log-transformed, and island area was treated as a continuous variable, whereas substrate and rat presence were treated as categorical variables (factors) with two categories each. Having log-transformed species abundance, we assumed normal errors for the response variable and used the identity link. We tested the significance-of-variable effect using the *F* statistic, and we verified the homoscedasticity of the data by examining the residuals for each analysis, the relation between residuals and estimated values as well as normality of residual distributions.

To interpret these results graphically and to qualify the role of the variables, we plotted the species' abundances against island area (log-transformed values) for those species that were affected significantly (GLM analysis) by the explanatory variables or by their interactions. We labeled islands with different symbols according to their value for the rat or substrate variables.

Results

Eleven common colonial nesting bird species breed on the islands we studied (Appendix 1). These include six

seabirds (Cory's Shearwater, Mediterranean Shearwater, Storm Petrel, Shag, Yellow-legged Gull, Audouin's Gull), one raptor that preys on migrating songbirds (Eleonora's Falcon), three aerial insect feeders (Common, Pallid, and Alpine swifts), and one terrestrial bird (Rock Dove).

Influence of Island Area and Rat Presence on Bird Abundance

Seven colonial nesting bird species breed on the granitic islands studied in the Bonifacio channel (Table 1). The abundances of three of these seven species, Cory's Shearwater, Storm Petrel, and Pallid Swift, were significantly affected by the explanatory variables. Island area had a significant effect on the abundance of Cory's Shearwater and Pallid Swifts. Rat presence significantly affected the abundance of Storm Petrels and Pallid Swifts (Table 1). There was no significant effect of the interaction between rat and area.

When all islands were considered, the abundance of Cory's Shearwater increased significantly with increasing island area, and rats had no significant effect (Table 1; Fig. 2). If we restrict the analysis to the islands where Cory's Shearwater was present, its abundance tended to be higher on islands with no rats than on islands of similar area that had rats (Fig. 2; GLM restricted to the 13 smaller islands with shearwaters: rat effect significant, $p < 0.05$; four islands without and nine with rats). Storm petrels were missing from all islands with rats and were present on most islands without rats (Fig. 2). There was a nonsignificant trend for decreasing abundance of Storm Petrels with increasing island area for the set of four islands where the species was present (Fig. 2). Finally, the abundance of Pallid Swifts increased significantly with island area on islands both with and without rats (Table 1; Fig. 2), but for a given island area abundance was significantly higher (Table 1) on islands without rats (Fig. 2).

Eight colonial species breed on the limestone Cabrera Islands (Table 1). The abundances of three of them, Cory's Shearwater, Storm Petrel and Common Swift, were significantly affected by one of the explanatory variables. The abundance of Cory's Shearwater was significantly affected by the presence of rats. The abundance of the Storm Petrel was significantly affected by the interaction between rat presence and island area. The variation in abundance of the third species, Common Swift, was significantly and positively correlated with variation in island area.

In contrast to islands with a coarse substrate (Bonifacio Channel), area variation on the limestone islands had no significant effect on the abundance of Cory's Shearwater (Table 2); furthermore, this species was missing from all four islands with rats. On islands without rats, the abundance of Cory's Shearwater was highly variable within a given area range (Fig. 3). As in the previous example, the Storm Petrel was missing from all islands with rats,

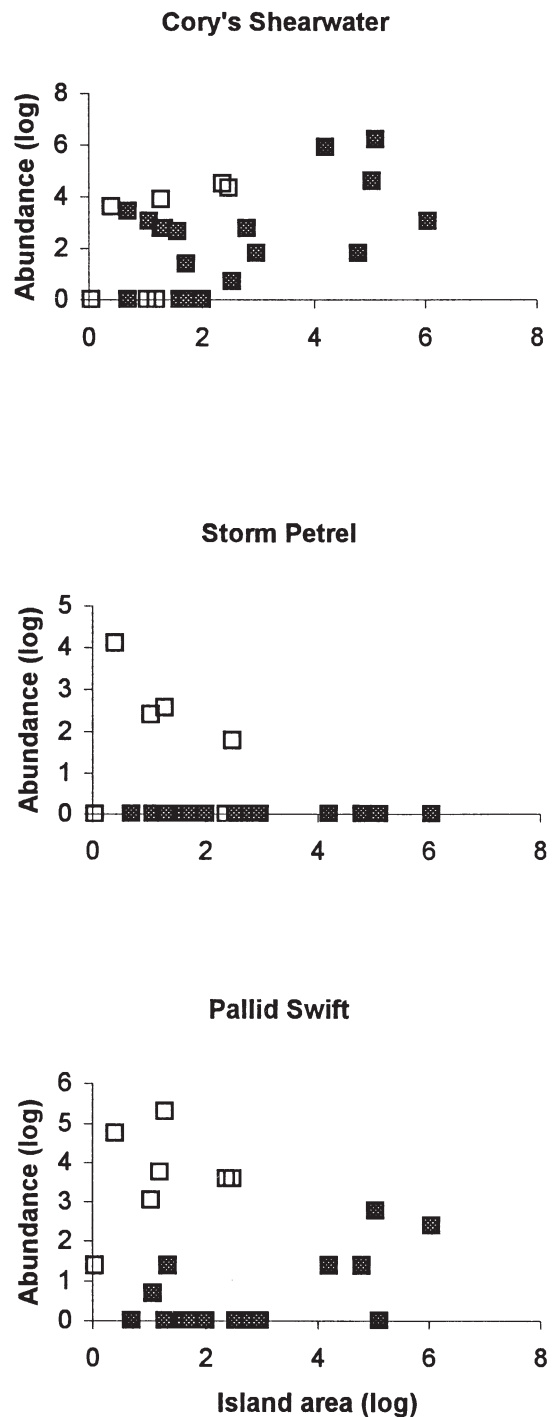


Figure 2. Variation in nesting bird species abundance in relation to island area and presence of rats on the islands of the Bonifacio Strait. All islands have an acidic or neutral rock substrate (coarse texture). Open squares, islands with no rats; filled squares, islands with rats.

whatever their area (Fig. 3), but the abundance of the Storm Petrel on islands without rats increased with island area. Hence, there was a significant effect of the interaction between island area and presence of rats on

Table 2. Result of general linear model analysis of the effect of island area and rock substrate (limestone vs. acidic or neutral) on the distribution and the abundance of colonial nesting birds on the Provence Islands.*

Species	Variables	
	area (p)	substrate (p)
Cory's Shearwater	<0.001	<0.05
Mediterranean Shearwater	<0.001	n.s.
Storm Petrel	n.s.	<0.001
Yellow-legged Gull	<0.001	<0.001
Pallid Swift	<0.001	<0.01
Alpine Swift	<0.001	n.s.

*Rats are present on all islands. Only variables or interactions with significant effects are shown; n.s., nonsignificant.

Storm Petrel abundance (Table 2). The abundance of Common Swifts increased with island area independently of the presence of rats (Table 2; Fig. 3).

Influence of Rock Substrate and Island Area on Bird Abundance

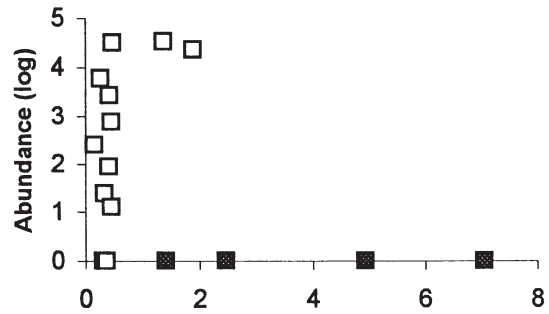
Six colonial bird species breed on the Provence Islands (Table 3). Except for the Storm Petrel (Table 3), the abundance of these birds varied significantly with area. Substrate had a significant effect on the abundance of four species: Cory's Shearwater, Storm Petrel, Yellow-legged Gull, and Pallid Swift (Table 3).

All species except the Storm Petrel had higher abundances on larger islands (Fig. 4). The Storm Petrel was entirely absent from larger islands and from all islands with a coarse substrate. Its abundance increased with island area on the smaller islands with a smooth limestone substrate. All species with a significant link between substrate and abundance (Cory's Shearwater, Storm Petrel, Yellow-legged Gull, and Pallid Swift) were on average more abundant on limestone islands, regardless of island area (Table 3; Fig. 4).

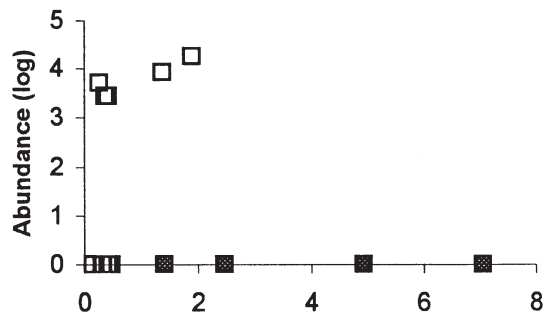
Regional Relationships among Bird Species Abundance, Rat Distribution, and Island Features

Cory's Shearwater, Mediterranean Shearwater, Storm Petrel, and Yellow-legged Gull were sufficiently widespread across the islands to be used for an overall analysis that would not be overly dependent on variation in the geographic distribution of species. Despite this precaution, the GLM analysis indicated that the abundance of three of these four species was still significantly linked to geography, as indicated by a significant effect of the explanatory variable "archipelago" (Table 3). Island area had a significant effect on species abundance in all species, either directly (Cory's Shearwater, Yellow-

Cory's Shearwater



Storm Petrel



Common Swift

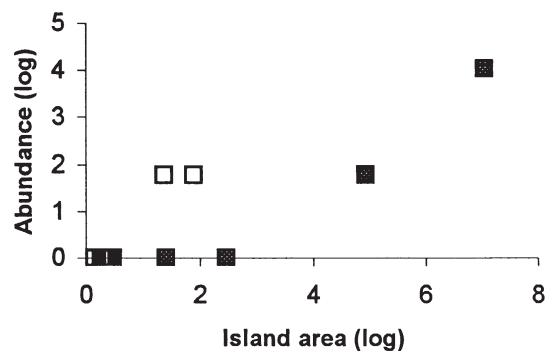


Figure 3. Variation in nesting-bird species abundance in relation to island area and presence of rats on the Cabrera Islands. All islands have a limestone rock substrate (smooth texture). Open squares, islands with no rats; filled squares, islands with rats.

legged Gull) or in interaction with other variables (Mediterranean Shearwater, Storm Petrel) (Table 3). The abundance of the Mediterranean Shearwater and the Storm Pe-

Table 3. Result of general linear model analysis of the effect of the explanatory variables on the distribution and the abundance of colonial birds on all islands studied in the western Mediterranean for the four colonial nesting bird species widespread in the area.*

Species	Variables and their interactions					
	archipelago (p)	area (p)	substrate (p)	rats (p)	rats × area (p)	rats × substrate × area (p)
Cory's Shearwater	n.s.	<0.001	n.s.	<0.01	n.s.	n.s.
Mediterranean Shearwater	<0.05	—	<0.05	—	<0.01	n.s.
Storm Petrel	<0.001	—	—	—	n.s.	<0.01
Yellow-legged Gull	<0.001	<0.001	n.s.	n.s.	n.s.	n.s.

*Only variables or interactions with significant effects are shown; n.s., nonsignificant; —, variables that cannot be tested alone because of significant interactions with other variables.

rel was affected significantly by rock substrate, either directly or in interaction with the presence of rats and island area. Rats had a significant effect on the abundance of Cory's Shearwaters (directly), Mediterranean Shearwaters (in interaction with island area), and Storm Petrels (in interaction with rock substrate and island area).

The abundance of all species except the Storm Petrel increased with island area (Fig. 5). The abundance of Storm Petrels was highest on small, rat-free islands with a limestone substrate, and when rats were present this species bred only on islands with a limestone substrate (Fig. 5). On the larger islands, the abundance of the Mediterranean Shearwater increased with island area irrespective of the presence of rats. Its abundance was higher on islands with a limestone substrate. Storm Petrels were missing from most small islands without rats, in contrast to Cory's Shearwaters, which were more

abundant on larger islands but were negatively affected by rats on the smaller islands. The abundance of the Yellow-legged Gull was highest on the larger islands.

Discussion

Presence of Rats and the Distribution of Colonial Nesting Birds

Our results identified three colonial species that were negatively affected by the presence of rats: two seabirds, the Storm Petrel and the Cory's Shearwater, and one aerial insect feeder, the Pallid Swift. These species breed in cavities or under rocks. The Storm Petrel and, to a lesser extent, the Pallid Swift are restricted to rat-free is-

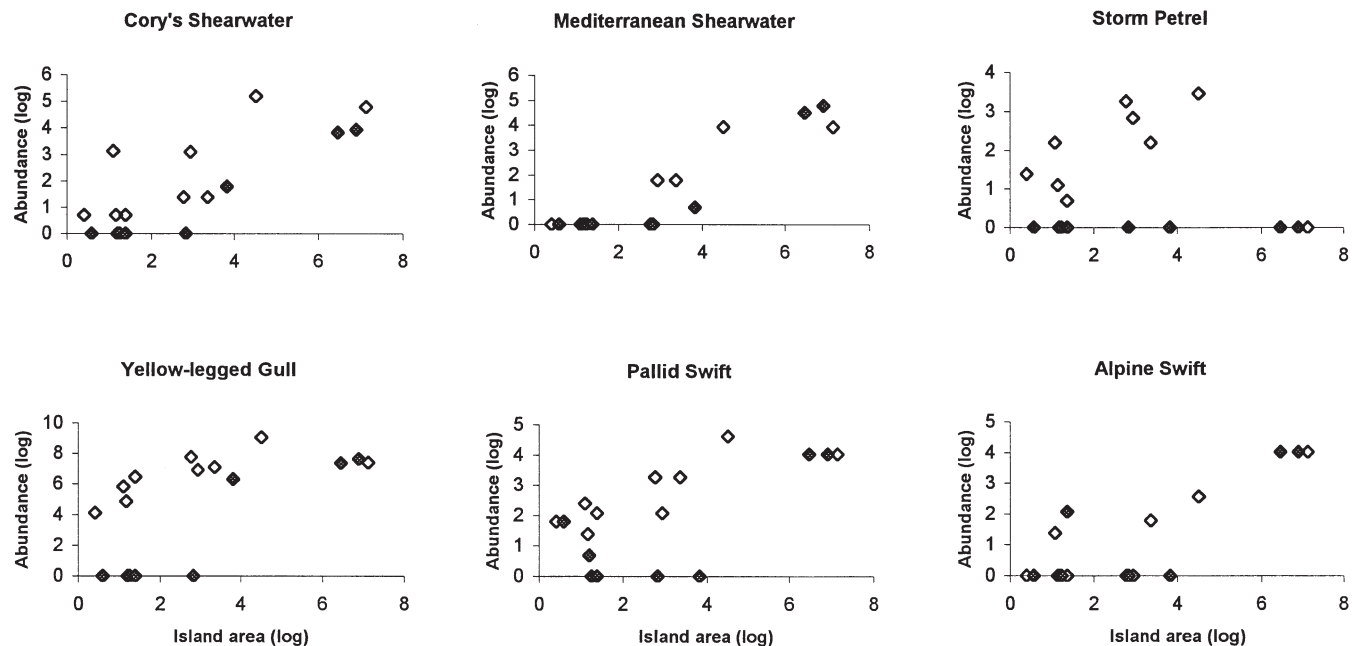


Figure 4. Variation in nesting-bird species abundance in relation to island area and presence of rats on the Provence Islands. Open diamonds, islands with a limestone rock substrate (smooth texture); filled diamonds, islands with a neutral or acidic rock substrate (coarse texture).

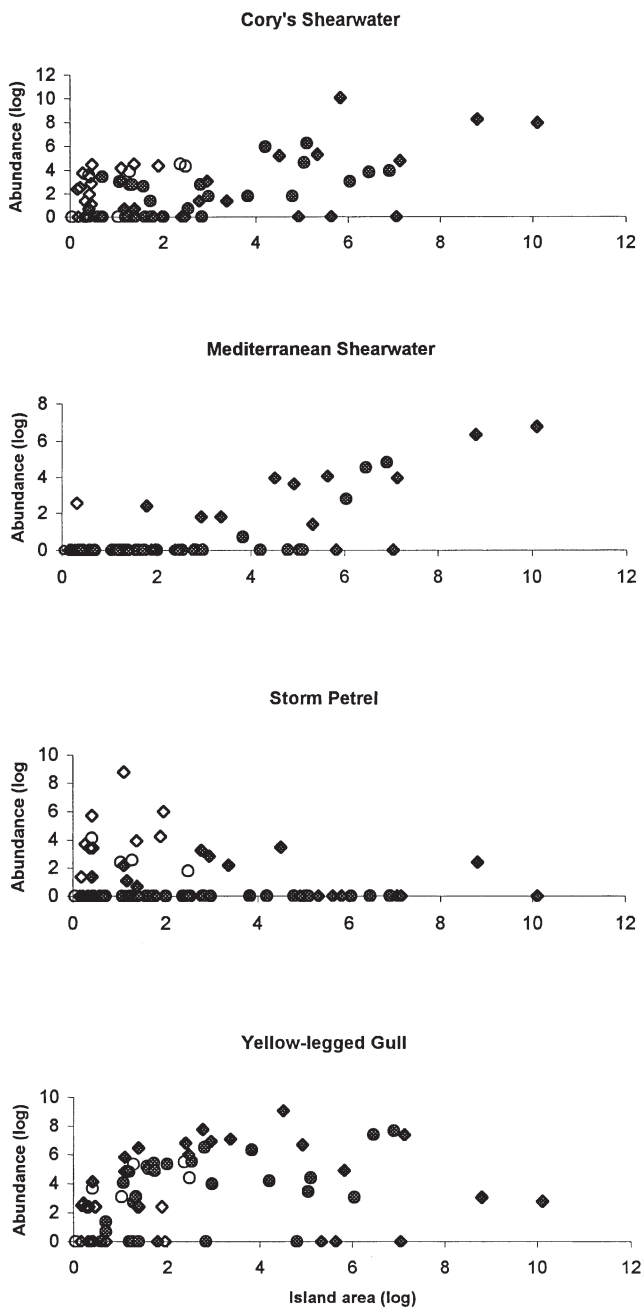


Figure 5. Variation in nesting-bird species abundance in relation to island area, presence of rats, and rock substrate in the western Mediterranean islands for the four widespread colonial species. Open circles, islands with no rats and acidic or neutral rock substrate; filled circles, islands with rats and acidic or neutral rock substrate; open diamonds, islands with no rats and a limestone rock substrate; filled diamonds, islands with rats and a limestone rock substrate.

lands or to islands with limestone substrate when rats are present (Figs. 2, 4, & 5). Cory's Shearwater was affected negatively by rats mainly on the smaller islands, where it is more common in the absence of rats (Figs. 2, 3,

& 5). For two of these three species (Pallid Swift and Cory's Shearwater), direct and experimental evidence of rat effects exists. Of the 24 islands in the Bonifacio channel studied by Penloup et al. (1997), the 7 rat-free islands had on average 48 pairs of Pallid Swifts per island, whereas the 17 rat-infested islands had only an average of 2 pairs.

Black rats were accidentally introduced on a rat-free islet, Toro (Cerbicale Archipelago, Bonifacio Channel, Corsica), between 1986 and 1989. In 1990 rat densities were estimated at 50 individuals per hectare (Granjon et al. 1992). These rats were eradicated in 1991 (Thibault 1992). The Pallid Swift population had dropped from 200 pairs before rats arrived to fewer than 30–40 pairs in 1994, in the only survey that took place after rat colonization and subsequent eradication (Penloup et al. 1997; Appendix 1). During the same period, the number of pairs in the adjacent Pallid Swift colony on a rat-free islet, Vacca, remained stable at 115 pairs (G. Gory, D. Brunstein, and V. Bretagnolle, unpublished data). Penloup et al. (1997) also studied predation of artificial nests placed in sites mimicking Pallid Swift nests on rat-infested and rat-free islands. On rat-infested islands, only the least accessible nests survived (20–40%), whereas accessible nests suffered a 100% loss. On rat-free islands, over 80% of the nests in both categories survived the experiment. Photographic evidence obtained by five automatic cameras, checked twice a day and moved to a new location every second or third day, confirmed that predation in sites mimicking Pallid Swift nests in rocky areas was essentially due to rats (53 pictures out of 60 pictures, the remaining seven nests being predated by Ravens [*Corvus corax*]; Penloup et al. 1997).

Thibault (1995) monitored a monospecific colony of Cory's Shearwater, situated on 66-ha Lavezzi Island and consisting of between 255 to 400 breeding pairs, to assess the effect of rats on its reproductive success. Direct evidence of chick predation by rats was found every year during the 19 years of monitoring. Rat numbers fluctuated annually, and the breeding success of the Shearwaters, measured each year between 1979 and 1997 in four of the six subcolonies, was consistently lower in years of high rat abundance (Appendix 2). In 1989, 1992, and 1993, rats were experimentally eliminated from one to three of the subcolonies of Cory's Shearwater (Daycard & Thibault 1990; Thibault 1995), and in 1994 rats were eradicated from all subcolonies. In years of partial rat eradication, subcolonies from which rats had been eradicated had significantly higher breeding success than subcolonies that had rats (Appendix 2; 1989, $\chi^2 = 6.80$, $p = 0.009$; 1992, $\chi^2 = 6.06$, $p = 0.014$; 1993, $\chi^2 = 10.02$, $p = 0.001$). In 1994, when rat eradication took place in all subcolonies, breeding success was higher than in any of the other years ($\chi^2 = 11.66$, $p = 0.001$).

There is no direct evidence of rats affecting Storm Petrels. Such evidence, however, does exist for closely related species from the same family (Hydrobatidae), (e.g., in the genera *Pelagodroma* and *Oceanodroma*; review in Burger & Gochfeld 1994).

Effects of Bird Species Body Size and Rat Density

A study of petrel predation by rats suggests that species of weight similar to or smaller than that of rats (in our case Storm Petrel and swifts) are most vulnerable (Imber 1975; Moors & Atkinson 1984). For larger Procellariiformes, in which chicks are rapidly emancipated by adults (Mediterranean and Cory's Shearwaters; Thibault et al. 1997; Zotier 1997), rats can limit reproductive success only during certain years at high rat density (Vidal 1985; Mayol 1986; Thibault 1995; Zotier 1997; Appendix 2). On medium-sized or larger islands, fluctuation in rat density led to irregular predation with limited effect on population dynamics (i.e., positive annual growth rate may occur; Thibault et al. 1996; Appendix 2). Conversely, on smaller islands, rat densities are higher and generally do not fluctuate (Cheylan 1986a; Granjon 1987; Granjon et al. 1992). Constant predation on chicks depresses colony size on these islands. Population persistence may result more from immigration than from local recruitment. This is suggested, for example, for the Cory's Shearwater on Lavezzi Islands by the capture, on small islets where rats are abundant, of breeding birds banded as chicks on the larger nearby island (J.-C.T., unpublished data).

We did not detect significant effects of rats on the Mediterranean Shearwater or Yellow-legged Gull, at least with regard to distribution, although both seemed to have higher abundance on rat-infested islands with a limestone substrate (Figs. 5 & 4, respectively). There is, however, evidence in several studies of predation on Mediterranean Shearwater nests (review in Zotier 1997). This lack of rat effects may be related to the need of the Mediterranean Shearwater, contrary to the other Procellariiforms studied here, to breed in the vicinity of its food resources. This may imply regular shifts of its colonies in response to shifts in the distribution of food (R. Zotier, personal communication), a strategy employed by the Shag (Guyot & Thibault 1996). Such shifts would be likely to mask long-term effects of rats.

Rats apparently do not affect the larger non-Procellariiformes such as gulls or Eleonora's Falcon. We attribute this to longer parental care (for Shags; van Tets 1965) and to the placement of nests in open microhabitats less exposed to rat predation (photographic evidence in Penloup et al. 1997). Rats negatively affect the smallest non-Procellariiformes (Pallid Swift). No effect was observed for Common and Alpine Swifts, which select better-protected nesting sites such as holes in buildings (Common Swift) and deep, vertical cracks in cliffs (Alpine Swift).

Effects of Island Area and Rock Substrate

In many studies, island area has been a dominant variable explaining species distribution and abundance. Ours

is no exception. The total number of nesting sites probably increases with area for most species, whereas rat densities are known to decrease with area on the islands we studied (Cheylan 1988).

One of the prominent and unexpected results of our study was demonstration that among islands with rats the abundance of several colonial nesting species was higher on the islands with smooth limestone rock substrate, especially in the three species most sensitive to the presence of rats. On limestone islands the higher availability of appropriate nesting sites (cavities and caves) and the smoother texture of limestone rock results in a higher number of sites safe from rat predation than on islands with coarse-rock substrate. This is illustrated by the presence of Storm Petrels on rat-infested limestone islands such as Gozo in the Maltese Islands (Borg & Sultana 1992-1994) and Marettimo, Sicily (approximately 1000 pairs; Massa & Sultana 1990-1991), where large numbers of birds breed in inaccessible caves. On islands with acidic or neutral substrate, rock surface is coarse and even subvertical rock faces can be climbed by rats (Penloup et al. 1997; J.-C.T., personal observation).

We speculate that the restriction of Storm Petrels to smaller islands in some archipelagoes (Figs. 2 & 5) may not be due entirely to the systematic presence of rats on larger islands. Competition for nest sites with larger Procellariiformes (Cory's and Mediterranean Shearwaters) may also limit numbers on larger islands even in the absence of rats. Toro Island, Sardinia, for example, with an area of >15 ha and no rats, has 500-1000 pairs of Cory's Shearwater but only 50-100 pairs of Storm Petrel localized to a few areas in walls and small crags, (J.-C.T., personal observation). On Foradada Island, Sardinia, approximately 300 pairs of Storm Petrels breed in caves unsuitable to shearwaters (R. Paddeu, personal communication; see also Ramos et al. 1997; Zotier et al. 1999).

Changes in Bird Distributions Due to Rats and Potential for Active Management

Despite the evidence of rat effects on colonial birds, there is no suggestion that rats caused the extinction of colonial bird species at the scale of the entire Mediterranean basin (Alcover et al. 1992; Vigne et al. 1997). *Puffinus nestori*, restricted to the Balearic islands during the Pliocene (Alcover 1989), disappeared before rats colonized the islands. Others species (Procellariidae, Sulidae, and Alcidae) might have been extirpated during the Holocene either by hunting or by alien predators (Mourer-Chauviré & Antunes 1991; Tyrnberg 1998; Zotier et al. 1999).

Conversely, at a more local scale, historical and archeozoological data show that rats caused extinction, for example, for the Storm Petrel on Hyères Island and

on Levant Island during the twentieth century (Guyot et al. 1985). Recent habitat perturbation has probably amplified the phenomenon as in the decline of the Storm Petrel on Plane Island, Marseille, France, after an increase in Yellow-legged Gulls modified the vegetation favorably to rats (Vidal 1997; Zotier 1997).

On the whole, however, the variety of island size or island substrate has probably helped maintain small populations of rat-sensitive species in most archipelagoes and explains why archeozoology suggests stability in species numbers (Vigne et al. 1997). But qualitative stability does not preclude major temporal shifts in species abundance, and our results suggest that several colonial species are less abundant on rat-infested islands than would be expected in the absence of rats. They also suggest that this effect can be mediated both by island area and by rock substrate. It has been shown in various parts of the world that eliminating rats from islands is possible (e.g., Taylor & Thomas 1989, 1993; Chapuis et al. 1994; Siorat & Pascal 1995; Kaiser et al. 1997). Such attempts in the Mediterranean would be especially meaningful on small or medium-sized islands, where we have shown that the effects of rats are highest. The chances of successful rat control are greatest on these islands. This should reverse the demographic deficit of the larger bird species that still breed on these islands and allow local (re)colonization by the smaller, rat-sensitive species. This can significantly increase both their local and regional population sizes and widen their distribution. The effect of such actions would be most dramatic on islands with coarse-rock substrate where rat-safe breeding sites are rare. Such programs, together with carefully planned measures preventing rats from (re)colonizing rat-free islands, in a sea sailed by millions of professional and recreational boats each year, should be a priority in the management of colonial birds in the Mediterranean.

Acknowledgments

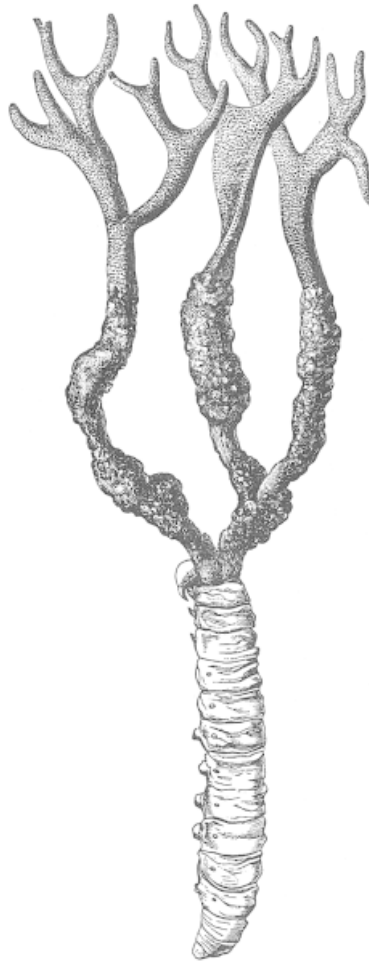
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Appendix 1

Distribution and abundance of colonial birds for 72 islands in the western Mediterranean, ranked according to decreasing area within each archipelago, with information on black rat presence (a, absent; p, present), area, and island rock substrate.^a

Archipelago/island	CDIO	PYEL	HPEL	PARI	FELE	LCAC	LAUD	AAPU	APAL	AMEL	CLIV	Black rat	Area (ha)	Substrate
Cabrera Archipelago, Spain ^b														
Cabrera	0	0	0	20	3	0	0	55	0	0	0	p	1154.00	limestone
Illa des Conills	0	36	0	10	4	800	200	5	0	0	0	p	137.00	limestone
Na Redona	0	0	0	10	0	400	0	0	0	0	0	p	10.76	limestone
Na Plana	77	0	70	10	0	10	0	5	0	0	0	a	5.62	limestone
L'Illa imperial	0	0	0	10	8	10	0	0	0	0	0	p	3.05	limestone
Na Pobra	92	0	50	10	0	10	0	5	0	0	0	a	2.94	limestone
Estell Xapat	89	0	0	5	5	10	0	0	0	0	0	a*	0.60	limestone
Estell de ss	2	0	0	0	1	10	0	0	0	0	0	a	0.58	limestone
Estell d'en Terra	17	0	0	0	0	10	0	0	0	0	0	a	0.57	limestone
Illa de ses Bledes	30	0	30	0	0	0	0	0	0	0	0	a	0.53	limestone
Estell des Coll	6	0	0	0	3	0	0	0	0	0	0	a	0.51	limestone
L'Espunya	0	0	30	0	1	0	0	0	0	0	0	a	0.44	limestone
Illa de ses Rates	3	0	0	0	0	10	0	0	0	0	0	a	0.39	limestone
Illa des Fonoll	0	12	0	0	0	0	180	0	0	0	0	a*	0.37	limestone
Na Foradada	43	0	40	5	4	10	0	0	0	0	0	a	0.31	limestone
Estell d'en Fora	10	0	0	5	2	0	0	0	0	0	0	a	0.17	limestone
Riou Archipelago, Provence ^c														
Riou	180	50	31	0	0	8520	0	0	100	12	0	p	90.00	limestone
Maire	3	5	8	0	0	1196	0	0	25	5	0	p	28.00	limestone
Jarre	21	5	16	0	0	1000	0	0	7	0	0	p	18.00	limestone
Plane	3	0	25	0	0	2338	0	0	25	0	0	p	15.00	limestone
Jarron	1	0	1	0	0	650	0	0	7	0	0	p	3.00	limestone
Tiboulen de Maire	1	0	2	0	0	130	0	0	3	0	0	p	2.20	limestone
Grand Conglué	22	0	8	0	0	339	0	0	10	3	0	p	2.00	limestone
Petit Conglué	1	0	3	0	0	60	0	0	5	0	0	p	0.50	limestone
Les Impériaux	0	0	3	0	0	11	0	0	0	0	0	a	0.20	limestone
Hyères Island, Provence ^c														
Porquerolles	120	50	0	0	0	1620	0	55	55	55	0	p	1254.00	schist
Le Levant	50	120	0	0	0	2100	0	0	55	55	0	p	996.00	granite
Port-Cros	45	90	0	0	0	1600	0	0	55	55	0	p	640.00	granite
Bagaud	5	1	0	0	0	545	0	0	0	0	0	p	45.00	granite
Grand Ribaud	0	0	0	0	0	0	0	0	0	0	0	p	16.00	gneiss
La Gabinière	0	0	0	0	0	0	0	0	0	7	0	p	3.00	gneiss
Gros Sarranié	0	0	0	0	0	0	0	0	1	0	0	p	2.30	gneiss
Petit Langoustier	0	0	0	0	0	0	0	0	0	0	0	p	2.50	gneiss
Petit Sarranié	0	0	0	0	0	0	0	0	5	0	0	p	0.80	gneiss
Zembra Island, Tunisia ^d														
Zembra Island	22500	0	0	10	0	135	10	550	0	0	0	p	340.00	limestone
Zembretta Island	0	0	0	1	0	900	0	0	0	0	0	p	10.00	limestone
Lantorcho	0	0	0	0	0	0	0	0	0	20	0	a	1.00	limestone
Maltese Island ^e														
Malta	2750	850	0	0	0	15	0	0	0	0	0	p	24500.00	limestone
Gozo	3750	560	10	0	0	20	0	0	0	0	0	p	6700.00	limestone

continued

Appendix 1 (continued)

Archipelago/island	CDIO	PYEL	HPEL	PARI	FELE	LCAC	LAUD	AAPU	APAL	AMEL	CLIV	Black rat	Area (ha)	Substrate
Kemmuna	0	55	0	0	0	0	0	0	0	0	0	p	280.00	limestone
Kemmunett	0	10	0	0	0	0	0	0	0	0	0	p	5.00	limestone
Filfla	65	0	6500	0	0	125	0	0	0	0	0	a	2.00	limestone
Bonifacio Strait ^f														
Spargi	20	15	0	0	0	20	0	0	10	0	0	p	420.00	granite
Santa Maria	200	3	0	0	0	0	0	0	0	0	0	p	205.00	schist
Budelli	500	0	0	0	0	80	0	0	0	0	0	p	164.00	granite
Razzoli	100	0	0	0	0	30	40	0	15	0	0	p	154.00	granite
Cavallo	5	0	0	0	0	0	0	0	3	0	0	p	120.00	granite
Lavezzi	370	0	0	30	0	65	0	0	3	0	0	p	66.00	granite
Piana de Cerbiciale	5	0	0	0	0	51	10	0	0	0	0	p	18.50	gneiss
Forana	15	0	0	18	0	670	0	0	0	0	5	p	15.50	granite
Corcelli	1	0	0	160	0	250	0	0	0	0	0	p	11.60	granite
Spargiotto	75	0	5	0	0	80	0	0	35	0	0	a	11.00	granite
Barrettini	90	0	0	7	0	240	0	0	35	0	0	a	9.70	granite
Piana de Cavallo	0	0	0	30	0	208	0	0	0	0	0	p	6.40	granite
Piana di Corcelli	0	0	0	0	0	130	0	0	0	0	5	p	4.70	granite
Pietricaggiosa	3	0	0	60	0	217	0	0	0	0	0	p	4.60	granite
Maestro Maria	0	0	0	0	0	147	0	0	0	0	0	p	4.00	gneiss
Ratino	13	0	0	15	0	175	0	0	0	0	0	p	3.80	granite
Islet A	15	0	0	75	0	21	7	0	3	0	7	p	2.80	granite
Islet B	15	0	0	100	0	14	0	0	0	0	10	p	2.60	granite
Toro NR ^g	48	0	12	10	0	205	0	0	200	0	0	a	2.60	granite
Porraggia	0	0	0	30	0	121	0	0	42	0	20	a	2.30	granite
San Bainsu	20	0	0	1	0	57	0	0	1	0	3	p	1.90	granite
Sperduto	0	0	10	5	0	21	0	0	20	0	10	a	1.80	granite
Carpa	30	0	0	0	0	3	0	0	0	0	0	p	1.00	granite
Stramarina w	0	0	0	0	0	1	0	0	0	0	0	p	1.00	granite
Stramarina e	0	0	0	0	0	1	0	0	0	0	0	p	1.00	granite
Vacca	36	0	60	10	0	38	0	0	115	0	0	a	0.50	granite
Petit Fazzio	12	0	0	0	0	13	0	0	0	0	0	a	0.24	limestone
Islet L	0	0	0	0	0	0	0	0	3	0	0	a	0.05	granite
Benidorm, Spain ^b														
Benidorm	0	0	400	0	0	0	0	0	0	0	0	a	6.00	limestone
Foradada, Sardinia ⁱ														
Foradada	0	0	300	0	0	0	0	0	0	0	0	a	0.50	limestone

^aCDIO, Calonectris diomedea; PYEL, Puffinus yelkouan; HPEL, Hydrobates pelagicus; LCAC, Larus cachinnans; APAL, Apus pallidus; AMEL, Apus melba; AAPU, Apus apus; FELE, Falco eleonorae; PARI, Phalacrocorax aristotelis; LAUD, Larus audouinii; CLIV, Columba livia. Asterisk (*) designates two islands without rats when birds were surveyed by Alcover et al. (1993) and where signs of rats have been subsequently reported (Anonymous 1998).
^bPurroy (1977); Tomás et al. (1991); Alcover et al. (1993); Jaume & Suárez (1993); Muñoz (1995).
^cCheyllan (1984); Vidal (1986); Cheyllan (1986b); Zotier (1997); Zotier & Vidal (1999).
^dGauthier (1981); Anonymous (1986).
^eSultana & Gauci (1982); Borg & Sultana (1992-1994).
^fBonifacio straits: Thibault et al. (1987); Bretagnolle & Thibault (1990); Rabouam et al. (1995); Pentloup et al. (1997); C. Rabouam, J.-F. Seguin, & J.-C. Thibault, unpublished data.
^gToroNR, Toro before colonization by black rats.
^hMinguez (1994).
ⁱR. Padden, personal communication.

Appendix 2

Comparison of breeding success of Cory's Shearwater in four subcolonies of Lavezzi Island during 1979–1997 (Thibault 1995 and Thibault, unpublished data).

Year	Subcolony ^a				Overall
	1	3	5	8	
	0.80 (25)	0.81 (11)	0.75 (44)	0.39 (31)	0.67 (111)
1980	0.83 (23)	0.78 (9)	0.76 (46)	0.19 (26)	0.63 (104)
1981	0.82 (22)	0.70 (10)	0.57 (47)	0.80 (30)	0.70 (109)
1982	0.45 (20)	0.10 (10)	0.49 (47)	0 (25)	0.32 (102)
1983	0.73 (26)	0.50 (10)	0.51 (49)	0.18 (27)	0.48 (112)
1984	0.90 (21)	0.70 (10)	0.52 (42)	0.06 (18)	0.54 (91)
1985	0.48 (21)	0.70 (10)	0.71 (45)	0.05 (21)	0.51 (97)
1986	0.23 (22)	0 (10)	0.02 (40)	0.06 (16)	0.08 (88)
1987	0.64 (25)	0.08 (13)	0.04 (44)	0.05 (20)	0.20 (102)
1988	0.63 (27)	0 (14)	0.42 (45)	0.12 (25)	0.35 (111)
1989	0.48 (25)	0.15 (13)	0.24 (42)	0.85 ^b (27)	0.44 (107)
1990	0.85 (27)	0.33 (12)	0.46 (39)	0 (22)	0.45 (100)
1991	0.65 (29)	0.69 (13)	0.62 (42)	0.19 (21)	0.55 (105)
1992	0.40 (30)	0.50 (11)	0.70 ^b (44)	0.08 (26)	0.46 (111)
1993	0.87 ^b (30)	0.50 ^b (12)	0.65 ^b (48)	0.05 (22)	0.57 (112)
1994	0.83 ^b (36)	0.92 ^b (13)	0.84 ^b (37)	0.54 ^b (26)	0.78 (126)
1995	0.66 (38)	0.73 (15)	0.52 (42)	0.30 (27)	0.54 (122)
1996	0.54 (33)	0.64 (11)	0.53 (45)	0.82 (22)	0.60 (111)
1997	0.48 (33)	0.91 (11)	0.42 (36)	0.54 (24)	0.54 (117)

^aEach cell indicates breeding success (mean number of birds fledged per breeding attempt) and sample size (in parentheses).

^bRats eradicated.

