

Invasive rats and seabirds after 2,000 years of an unwanted coexistence on Mediterranean islands

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Abstract In the Mediterranean, the survival of endemic long-lived seabirds despite the long-standing introduction of one of the most damaging alien predator, the ship rat (*Rattus rattus*), on most islands constitutes an amazing conservation paradox. A database gathering information on approximately 300 Western Mediterranean islands was analyzed through generalized linear models to identify the factors likely to influence ship rat presence and to account for how ship rat presence and island characteristics may have driven the presence and abundance of seabirds. Our review showed that few Mediterranean islands remain rat-free. At the regional

scale, rat presence was only a limiting factor in the abundance of the smallest seabird, the storm petrel (*Hydrobates pelagicus*), while the distribution and abundance of the three shearwaters were more influenced by island characteristics. We hypothesized that the long-term persistence of these seabirds may have been facilitated by the various biogeographical contexts of Mediterranean islands, likely to provide intra-island refuges.

Keywords Coexistence · Introduced predators · Islands · Mediterranean · Procellariiformes · *Rattus rattus*

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Introduction

For thousands of years, island colonization by humans and intense exploitation of native biotas have triggered catastrophic species extinctions on islands worldwide (Steadman 1995; Alcover et al. 1998; Roberts et al. 2001; Steadman and Martin 2003; Burney and Flannery 2005). As humans keep moving further and faster, they have scattered a large number of species beyond their natural ranges and have been responsible for an unprecedented ecological turnover on islands (Vitousek et al. 1997; Chapin et al. 2000; Rosenzweig 2001). Rats (*Rattus* spp.) have been successfully introduced on more than 80% of the world's major islands and are known to negatively affect island biota, especially birds (Atkinson 1985; Courchamp et al. 2003; Towns et al. 2006; Jones et al. 2008). Evidence of rapid bird extinctions soon after rat arrival has been documented on several islands (e.g., Big South Cape Island in New Zealand, Midway Island in Hawaii, and Lord Howe Island, east of the Australian mainland; Atkinson 1985; Towns et al. 2006). Seabirds in particular are extremely sensitive to rat impact as they have generally evolved in the absence of mammalian predators and thus have not developed any defense mechanisms (Burger and Gochfeld 1994; Blackburn et al. 2004). Consequently, numerous cases of breeding failures, sharp decreases in breeding populations and local extirpations of seabird colonies have coincided with rat introduction on islands (Atkinson 1985; Towns et al. 2006). Most seabird species worldwide are negatively affected by the impact of rats, especially the smallest species and those nesting in burrows or cavities (Imber 1976; Atkinson 1985; Martin et al. 2000; Jones et al. 2008). Therefore, today, rats are identified as a leading cause of extinction risk in 68% of the world's Procellariiform seabirds (e.g., petrels and shearwaters, except albatrosses; Birdlife International 2000).

Except bats, two endemic shrews and an endemic mouse, all terrestrial mammals currently present on Mediterranean islands have been introduced by man and the native mammal fauna found on islands during the Pleistocene has been extinct since the Early Holocene (large mammals), or slightly later (small mammals) (Vigne 1992; Pascal et al. 2006). The Pleistocene mammal fauna was poor and disharmonic. Most species were shrews and vegetarian rodents, and very few if any of these native species were

likely to be potential seabird predators (Vigne 1992; Marra 2005; Gippoliti and Amori 2006). With more than 5,000 islands and islets, the Mediterranean Basin comprises one of the largest groups of islands in the world, with exceptional biodiversity (Delanoë et al. 1996; Médail and Quézel 1997; Myers et al. 2000). This island system has been early and widely colonized by ship rats (*Rattus rattus*) since their spread from the Indian Peninsula (Audouin-Rouzeau and Vigne 1994; Masseti 1995; Vigne and Valladas 1996). The oldest reliable ship rat remains recorded in the north-western Mediterranean islands date back to Roman times (Corsica: 393–151 B.C., Vigne and Valladas 1996; Menorca: 200–100 B.C., Audouin-Rouzeau and Vigne 1994), although older records are possible (Audouin-Rouzeau and Vigne 1994). However, despite the long-standing and widespread rat introduction and human presence on Mediterranean islands, no seabird species extinction has been reported in the Mediterranean Basin since rat introduction (Alcover et al. 1992; Milberg and Tiberger 1993; Vigne et al. 1997; Zotier et al. 1999), although local extirpations have occurred on some islands (Martin et al. 2000; Bourgeois and Vidal 2008). The globally extinct *Puffinus nestori*, formerly restricted to the Balearic Archipelago, vanished during the late Pliocene before humans introduced rats on islands. Among the nine seabird species currently breeding in the Mediterranean islands, the four endemic Procellariiformes have been present since the Pleistocene (Alcover et al. 1992; Zotier et al. 1999). The survival of these endemic long-lived seabirds on Mediterranean islands, despite thousands of years of ship rat presence, constitutes an amazing conservation paradox, since this group of birds is known to be negatively affected by the introduction of alien predators worldwide (Atkinson 1985; Birdlife International 2000; Jones et al. 2008).

The Mediterranean Basin may thus constitute a key site for studying the long-term interactions between introduced rats and seabirds on islands. This paper focuses on three main aims: (1) to identify factors likely to explain ship rat presence on Western Mediterranean islands; (2) to account for how ship rat presence and island characteristics may have driven the presence and abundance of the four Mediterranean Procellariiformes at the scale of the Western Mediterranean Basin, and (3) to review documented data of rat impact on Mediterranean seabird communities.

Methods

Datasets

We focused our study on the Western Mediterranean Basin because it has been more studied than the eastern part. The Western Mediterranean Basin stretches from the Gibraltar Strait (west) to the Adriatic Sea (east), and covers about one-third of the 3,081,880 km² Mediterranean Sea and comprises ca. 700 islands and islets. Although available, data about island characteristics, seabirds, and rats have never been compiled and analyzed on such a wide scale (but see Martin et al. 2000). The data used in this review were collated from published sources (including grey literature), unpublished reports, notes, and personal communication from nature-reserve managers, conservationists, and researchers, who were specifically contacted.

Data on seabird presence and abundance, island characteristics, and ship rat presence were collected for 292 islands (Fig. 1; Appendix 1). Only the most recent and reliable census on breeding seabird populations was used. For each of these islands, five potential explanatory variables for rat presence and seabird presence and abundance were also collected

(Table 1). Because they possess life-history traits likely to make them particularly sensitive to introduced mammal predators (Jones et al. 2008), we focused seabird analyses on the four Mediterranean Procellariiform taxa: the Yelkouan shearwater (*Puffinus yelkouan*) and the Balearic shearwater (*P. mauretanicus*), which are Mediterranean endemic species, and two Mediterranean endemic subspecies, the Mediterranean Cory's shearwater (*Calonectris diomedea diomedea*) and the Mediterranean storm petrel (*Hydrobates pelagicus melitensis*). The Cory's shearwater is the largest species (500–800 g) and its distribution encompasses the entire Mediterranean Basin (57,000–76,000 breeding pairs, Zotier et al. 1999). Its breeding colonies on islands range from small (<20 breeding pairs) to large (e.g., 25,000 breeding pairs on Zembra Island, Tunisia; Isenmann and Moali 2000). The distribution of the Yelkouan shearwater (350–500 g) is sparse and the world population may be limited to only a few thousand breeding pairs (Bourgeois and Vidal 2008). Yelkouan shearwater colonies are generally quite small but can reach up to 1,300–8,600 pairs on Tavolara-Molara islands, Sardinia (G. Spano and N. Baccetti, pers. comm.). The Balearic shearwater (349–416 g) is

Fig. 1 Map of the Western Mediterranean and location of the 292 islands studied

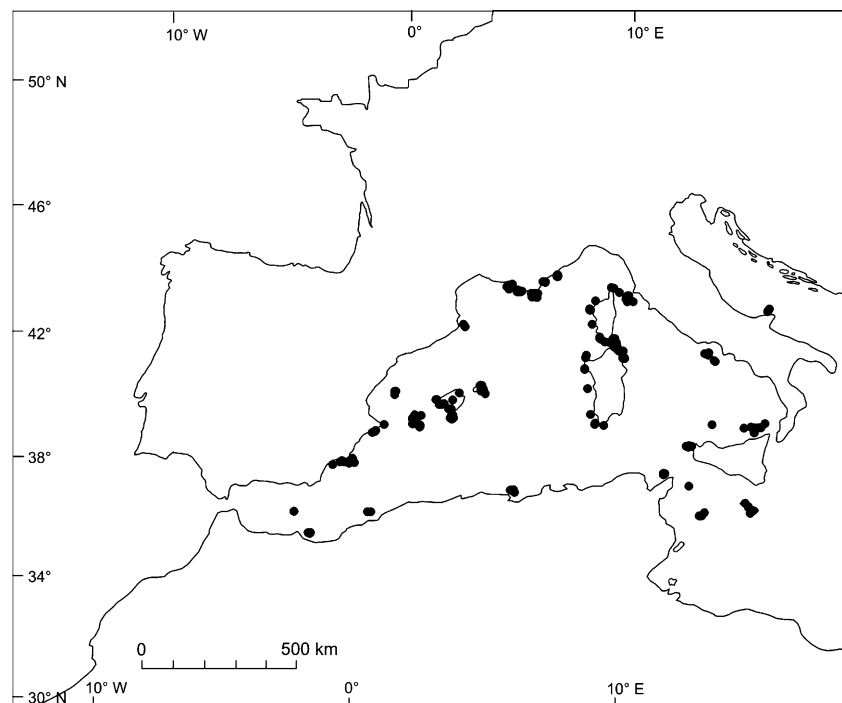


Table 1 Explanatory and response variables with their description and integration in each statistical analysis (Rats = GLM on rat distribution; Seabirds ^D, ^A = GLMs on seabird distribution (D) and abundance (A); Rat impact ^C,

^M = GLMs on rat impact on the breeding success of *Calonectris diomedea* (C) and Kruskal–Wallis ANOVA for *Puffinus mauretanicus* (M)

Parameters	Description	Status	Range	GLMs
<i>Explanatory variables</i>				
Area	Island area (ha)	Continuous	0,021–69,439 ha	Rats and seabirds ^(A, D)
Elevation	Maximum island elevation (m)	Continuous	3–1,445 m	Rats and seabirds ^(A, D)
Rat presence	Ship rat absence or presence on islands	Categorical	0/1	Rats and seabirds ^(A, D)
Distance continent	Minimum distance (m) to continent or land mass (i.e., Sardinia, Corsica, Sicilia)	Continuous	5–245,300 m	Rats
Distance source	Minimum distance (m) to nearest island >5 ha or to continent (whichever is closer)	Continuous	2–70,000 m	Rats
Humans	A: currently uninhabited B: rare/occasional human presence and/or past human presence (in the last 100 years) C: permanent human presence (and presence of tourism)	Categorical		Rats
Dist. near rats	Minimum distance (m) to nearest rat-infested island	Continuous	2–67,000 m	Seabirds ^(A, D)
Substrate	Main island rock substrate: limestone or non-limestone	Categorical		Seabirds ^(A, D)
Geographical region	E: Eastern Mediterranean islands from Gibraltar Strait to French islands W: Western Mediterranean islands from Sardinia to the Maltese archipelago	Categorical		Rat impact ^(C)
Rat impact	Y: ship rat presence and no management action C: local ship rat control A: ship rat absence (with or without eradication)	Categorical		Rat impact ^(C, M)
Year of study	Year when breeding success was monitored	Continuous	1979–2007	Rat impact ^(C)
<i>Response variables</i>				
Seabird abundance	Seabird abundance on islands (i.e., number of breeding pairs)	Continuous	1–25,000 pairs	Seabirds ^(A)
Seabird presence	Seabird absence or presence on islands	Categorical	0/1	Seabirds ^(D)
Breeding success	Shearwater mean breeding success (%)	Continuous	0–100%	Rat impact ^(C, M)

restricted to the Balearic Archipelago (<2,000 breeding pairs; Ruiz and Martí 2004) and usually breeds in small—(<30 breeding pairs) and medium-sized colonies (e.g., 250–300 breeding pairs on main Menorca Island, Balearic Archipelago, R. Triay, pers. comm.). The storm petrel, the smallest species under study (25–29 g), is widely distributed throughout the basin (>15,000 breeding pairs, Zotier et al. 1999) and usually breed in small islands where colonies can sometimes reach thousands of pairs (e.g., 6,550 breeding pairs on Filfla (2 ha), Maltese islands, Borg and Sultana 2002).

Ship rats were considered present on a particular island if mentioned, either continuously or occasionally, and absent if not found despite investigation. When ship rats were eradicated from islands, we used seabird abundance assessed before eradication. Two main island substrates were distinguished (i.e., limestone and non-limestone; Table 1) according to the nature of the dominant substrate. A limestone substrate may provide deeper and more abundant cavities (caves, crevices) than non-limestone substrates (Martin et al. 2000). For rat distribution analysis, we considered continents and islands ≥ 5 ha

as potential sources of permanent rat populations, since 86% of islands ≥ 5 ha housed ship rats in our dataset.

We reviewed studies reporting ship rat impact on Mediterranean Procellariiformes throughout the entire basin by collecting data from published works, unpublished reports, and personal communications. Finally, we collected data on the breeding success of Cory's and Balearic shearwaters in three situations (Table 1): (1) rat-inhabited islands, (2) islands where rats have been controlled within shearwater colonies, and (3) rat-free islands (either absent or eradicated). Unfortunately, for the two other Procellariiform species (storm petrel and Yelkouan shearwater), reliable data on the breeding success were too sparse to be used.

Statistical analysis

In order to highlight factors likely to explain ship rat presence on Western Mediterranean islands, we constructed a generalized linear model (GLM, binomial distribution, LOGIT link function) for a set of 257 islands and islets (see Table 1; Appendix 1). For seabirds, GLMs (binomial distribution, LOGIT link function) were first performed to explore how seabird presence on islands may be influenced by the a priori selected explanatory variables for each seabird species (*P. yelkouan*: $n = 135$ islands; *C. diomedea*: $n = 180$ islands; *P. mauretanicus*: $n = 69$ islands; *H. pelagicus*: $n = 101$ islands; see Table 1; Appendix 1). We performed one model for each seabird species since the four species did not share the same geographical distribution and reliable data on breeding status were not available for each species on all islands. Then, GLMs (normal distribution, IDENTITY link function) were used to evaluate which variables may explain seabird abundance on islands where they breed (*P. yelkouan*: $n = 30$ islands; *C. diomedea*: $n = 79$ islands; *P. mauretanicus*: $n = 13$ islands; *H. pelagicus*: $n = 23$ islands; Table 1). Finally, the effects of rat impact (rat presence, local control, and rat absence), year of study and geographical region on the breeding success of Cory's shearwaters were investigated through GLM analysis (normal distribution, IDENTITY link function). Due to the lack of data on Balearic shearwater breeding success ($n = 13$), we only investigated the effect of rat impact through a non-parametric Kruskal–Wallis ANOVA (Table 1).

All continuous variables (i.e., size, distance, elevation and abundance) were $\log_{10}$ -transformed to

remove right skew distribution and increase normality of their distribution (Sokal and Rohlf 1995; Russell and Clout 2004). Cory's and Balearic shearwater breeding success were arcsin-square-root transformed (Sokal and Rohlf 1995). Before constructing GLMs, we used Spearman rank correlations to identify colinearity between explanatory variables. Even though island area and island elevation were correlated ($r^2 = 0.73$), we kept the two terms in the models since these two factors are known to be potential predictors of seabird presence and abundance (Schramm 1986; Brandt et al. 1995; Muller-Dombois 1999; Lomolino 2000; Sullivan and Wilson 2001; Catry et al. 2003). Furthermore, explanatory value would be lost by arbitrarily dropping one of the variables (Russell and Clout 2004). Models were constructed in order to identify and interpret explanatory variables, not to maximize predictive power (Russell and Clout 2004).

Results

Factors affecting the distribution of ship rats on Mediterranean islands

Ship rats were present on 201 (68.8%) out of the 292 Mediterranean islands for which reliable data were found. The smallest rat-infested islet was 0.021 ha. Rats were found on 36% of islands ≤ 0.5 ha and on 99% of islands ≥ 30 ha (Fig. 2). Ship rat presence was positively related to island area (Table 2; Fig. 2) but negatively related to distance to the nearest potential source of rats (Table 2). Ship rat presence was not related ($P < 0.05$) to elevation, distance to

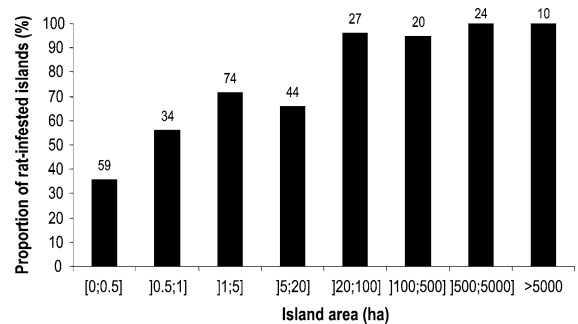


Fig. 2 Proportions of rat-infested islands in relation to island area. The number of islands used for each area interval is indicated (total $n = 292$)

Table 2 Significance of explanatory variables and associated statistic parameters in the rat distribution GLM ($n = 257$; β = estimate; SE = standard error of the estimate)

Parameters	β	SE	Wald statistic	P-value
Intercept	3.57	1.07	11.14	***
Humans (C)	0.58	0.74	0.61	ns
Humans (A)	0.18	0.50	0.13	ns
$\log_{10}$ (area)	2.07	0.36	33.03	***
$\log_{10}$ (distance continent)	-0.17	0.16	1.07	ns
$\log_{10}$ (distance source)	-1.27	0.31	16.74	***
$\log_{10}$ (elevation)	-0.04	0.05	0.01	ns

See Table 1 for more thorough information on explanatory variables

Significance levels: *** ($P < 0.001$); ** ($P < 0.01$); * ($P < 0.05$); ns not significant

continent, or presence and intensity of human activities. There was no evidence of model inadequacy (scaled Pearson $\chi^2 = 219.0$; $df = 250$; $P = 0.08$). In order to clarify the negative relationship between rat presence and distance to the nearest potential source of rats, we performed Mann–Whitney tests to compare, for islands ≤ 5 ha and those > 5 ha, mean distances from the nearest source of rats (i.e., island ≥ 5 ha or continent) between rat-free and rat-infested islets. Small rat-infested islets ≤ 5 ha were significantly closer from the nearest source of rats than small rat-free islets ≤ 5 ha (Mann–Whitney, $Z = 3.5$;

$P < 0.001$; $n_{\text{with rats}} = 74$, $n_{\text{without rats}} = 65$), whereas rat-infested islands > 5 ha were not significantly closer than rat-free islands > 5 ha (Mann–Whitney, $Z = 0.77$; $P = 0.44$; $n_{\text{with rats}} = 101$, $n_{\text{without rats}} = 17$). Finally, 141 (55%) out of 257 islands were ≤ 500 m away from either the nearest island ≥ 5 ha or the continent, among which 118 islands (81%) were ≤ 10 ha (500 m is the maximum-recorded distance ship rats can swim; Russell and Clout 2005). For these 257 islands, the mean distance to the nearest source of rats was 3,654 m (SE = 672 m).

Factors explaining seabird distribution and abundance on Mediterranean islands

Island area was positively related to Yelkouan and Balearic shearwater presence, Yelkouan and Cory's shearwater abundance ($P < 0.05$), and weakly negatively related to storm petrel presence ($P = 0.06$; Tables 3 and 4). Island elevation was positively related to Cory's and Yelkouan shearwater presence and Balearic shearwater and storm petrel abundance. Limestone substrate was positively related to Yelkouan shearwater abundance and storm petrel presence. Rat presence on islands was negatively related to storm petrel abundance, but did not influence either the presence or the abundance of the three shearwaters. Ship rats are present on most islands where the three shearwaters breed (Fig. 3). Distance to the nearest

Table 3 Statistical significance of explanatory variables in GLMs on seabird presence (β = estimate; SE = standard error of the estimate; W = Wald statistic)

Parameters	<i>Calonectris diomedea</i>				<i>Puffinus yelkouan</i>				<i>Puffinus mauretanicus</i>				<i>Hydrobates pelagicus</i>			
	β	SE	W	P-value	β	SE	W	P-value	β	SE	W	P-value	β	SE	W	P-value
Intercept	-4.04	0.99	16.48	***	-8.79	2.23	15.53	***	-3.28	92.73	0.00	ns	-6.86	2.12	10.43	***
$\log_{10}$ (area)	0.29	0.26	1.27	ns	1.14	0.53	4.56	*	0.89	0.39	5.33	*	-0.85	0.45	3.49	0.06
$\log_{10}$ (elevation)	2.35	0.65	12.92	***	4.09	1.47	7.74	**	0.16	0.66	0.06	ns	1.69	1.02	2.74	ns
Substrate (limestone)	0.08	1.19	0.17	ns	0.34	0.36	0.86	ns	1.92	92.72	0.00	ns	1.38	0.38	14.76	***
Rats (presence)	0.19	0.25	0.58	ns	0.14	0.63	0.05	ns	0.35	0.27	1.68	ns	0.31	0.39	0.6	ns
$\log_{10}$ (Dist. near. rats)	0.04	0.26	0.03	ns	-0.27	0.44	0.38	ns	-0.02	0.52	0.06	ns	1.39	0.50	7.59	**
N	179				135				69				100			

See Table 1 for more thorough information on explanatory variables

Significance levels: *** ($P < 0.001$); ** ($P < 0.01$); * ($P < 0.05$); ns not significant

Table 4 Statistical significance of explanatory variables in GLMs on seabird abundance (β = estimate; SE = standard error of the estimate; W = Wald statistic)

Parameters	<i>Calonectris diomedea</i>				<i>Puffinus yelkouan</i>				<i>Puffinus mauretanicus</i>				<i>Hydrobates pelagicus</i>			
	β	SE	W	P-value	β	SE	W	P-value	β	SE	W	P-value	β	SE	W	P-value
Intercept	-0.43	0.43	1.00	ns	-0.85	0.66	1.66	ns	-0.47	1.03	0.21	ns	-2.30	2.90	6.51	*
log ₁₀ (area)	0.43	0.08	29.93	***	0.36	0.14	6.62	*	-0.00	0.00	0.28	ns	-0.19	0.20	0.85	ns
log ₁₀ (elevation)	0.22	0.22	0.99	ns	0.56	0.38	2.28	ns	0.71	0.34	4.39	*	1.25	0.49	6.42	*
Substrate (limestone)	0.09	0.06	0.29	ns	0.28	0.11	6.02	*	^a	^a	^a	^a	0.31	0.19	2.53	ns
Rats (presence)	-0.13	0.10	1.55	ns	0.01	0.29	0.00	ns	0.10	0.24	0.18	ns	-0.44	0.16	7.70	**
log ₁₀ (Dist. Near. Rats)	-0.05	0.10	0.25	ns	0.17	0.15	1.34	ns	0.32	0.39	1.24	ns	0.62	0.25	6.35	*
N	79				30				69				101			

See Table 1 for more thorough information on explanatory variables

Significance levels: *** ($P < 0.001$); ** ($P < 0.01$); * ($P < 0.05$); ns not significant

^a The substrate parameter was not tested for *P. mauretanicus* abundance since it exclusively breeds on limestone islands

source of rats was positively related to storm petrel presence and abundance.

There was no evidence of model inadequacy for Cory's shearwater presence (scaled Pearson $\chi^2 = 194.3$; $df = 174$; $P = 0.86$) and abundance ($\chi^2 = 78.0$; $df = 72$; $P = 0.71$), Yelkouan shearwater presence ($\chi^2 = 131.8$; $df = 129$; $P = 0.58$) and abundance ($\chi^2 = 30.0$; $df = 24$; $P = 0.82$), Balearic shearwater presence ($\chi^2 = 50.6$; $df = 62$; $P = 0.15$) and abundance

(scaled Pearson $\chi^2 = 13.0$; $df = 8$; $P = 0.88$) and storm petrel presence ($\chi^2 = 75.4$; $df = 94$; $P = 0.08$) and abundance ($\chi^2 = 23.0$; $df = 17$; $P = 0.85$).

Evidence of rat impact on Mediterranean Procellariiformes

The presence of rats had a negative effect on the breeding success of Cory's shearwaters ($\beta = -0.25$; SE = 0.03; $W = 55.35$; $P < 0.001$; $n = 219$). The breeding success of Cory's shearwaters was also influenced by the year of study ($\beta = -0.01$; SE = 0.00; $W = 7.67$; $P < 0.01$) and the geographical region ($\beta = 0.06$; SE = 0.06; $W = 7.27$; $P < 0.01$). Breeding success was significantly higher on rat-free islands (rats absent or eradicated) or when rat populations were controlled within shearwater colonies, compared to rat-infested islands where no conservation measure was carried out ($F_{2, 216} = 35.2$; $P < 0.001$; Fig. 4). The breeding success of Cory's shearwaters was not significantly different between rat-controlled and rat-free islands. Balearic shearwater breeding success was not significantly influenced either by rat control or by rat absence ($H_{2, 12} = 1.9$; $P = 0.38$). Chi-square tests for goodness of fit found no evidence of inadequacy for the Cory's shearwater breeding success model (scaled Pearson $\chi^2 = 219.0$; $df = 214$; $P = 0.61$).

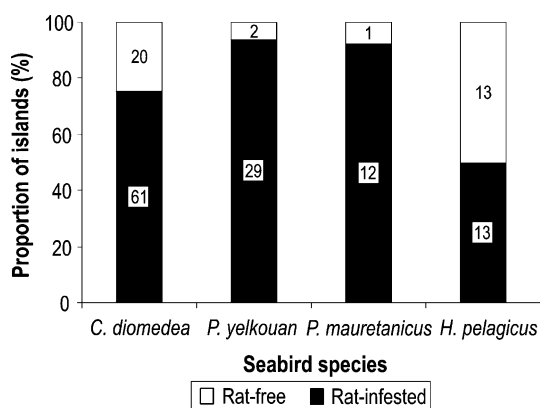


Fig. 3 Proportion of rat-infested and rat-free islands among the islands where the four Procellariiform species (*Calonectris diomedea*, *Puffinus yelkouan*, *P. mauretanicus*, *Hydrobates pelagicus*) are known to breed in the Western Mediterranean. The number of islands used for each species is indicated

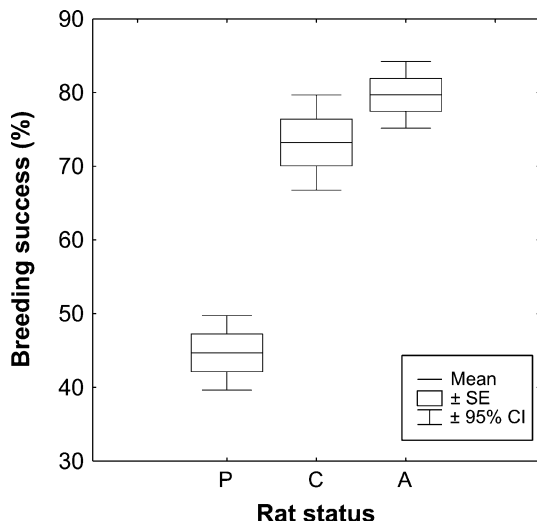


Fig. 4 Influence of rat presence (noted *P*), rat control, and rat absence (absent or eradicated) (noted *C* and *A*, respectively) on the breeding success of the Cory's shearwater on Western Mediterranean islands ($n = 219$). Breeding success is defined as the number of fledged chicks divided by the total number of hatched eggs

Discussion

Ship rat distribution on Mediterranean islands

Today, few Mediterranean islands remain rat-free. Compared to most oceanic archipelagoes, Mediterranean islands generally exhibit a low degree of geographical isolation and can be considered as a group of continental islands, surrounded by the African and Euro-Asiatic landmasses (Greuter 1995). Moreover, most Mediterranean islands are part of wider island systems (e.g., Sardinia, Sicily, Corsica, Balearic), which decreases their isolation from the continent (Sara and Morand 2002). Thus, many Mediterranean islands (mostly small islands) are close enough to each other or to the continent to be reached by rats by natural dispersal (i.e., ≤ 500 m). However, long-standing and intensive human transport and trade activities within the basin have probably largely facilitated the distribution of this commensal and generalist rodent, which has rapidly become established on most Mediterranean islands (Vigne 1992; Audouin-Rouzeau and Vigne 1994; Masseti 1995; Bover and Alcover 2008).

Thus, even though distance to the continent, human presence on islands, and intensity of human activities may have played a significant role in rat dispersal in the past, these factors no longer limit rat presence on Mediterranean islands. Island area and isolation from the nearest potential source of rats were the best explanatory factors in ship rat presence on Mediterranean islands. The larger the island, the more likely it is to be rat-infested. This pattern is consistent with island biogeography theories on island species richness (Lomolino 1982, 1984; Adler and Wilson 1985) as well as on the probability of small mammal species occurring on islands (Adler and Wilson 1985; Russell and Clout 2004). Moreover, this area-related pattern may be related to the highest probability of human colonization on large islands due to highest habitat and resource diversity (Lomolino 2000), and thus to the highest probability of accidental rat introduction. However, in the case of the long-invaded Western Mediterranean island system, 74% of islands ranging from 1 to 5 ha support ship rat populations and many very small islets have also been found to be rat-infested, when close enough to continents or other landmasses. On such very small islets close to a potential source, rats are known to maintain only transient populations (Adler and Wilson 1985; Alcover 1993), facing a higher extinction risk due to founder effect, genetic drift, and inbreeding depression (Heidrick and Kalinowsky 2000; Frankam 2003). Unfortunately, we could not take into account rat population turnover on the smallest islands in this review due to the lack of available data. Distance from the nearest potential rat population source was a limiting factor for rat presence only for the smallest islets and uninhabited islands, whose isolation may limit natural dispersal and human transport links, thereby preventing the external recruitment required for population persistence (e.g., Cheylan 1999).

Ship rat impact on Mediterranean Procellariiformes

Surprisingly, rat presence was not found to be a leading factor explaining the distribution of the four

seabird species at the scale of the entire Western Mediterranean Basin. This pattern is particularly clear for the three shearwater species that virtually breed only on rat-infested islands, sometimes with high rat densities (e.g., Zembra Island, Tunisia, M. Pascal, pers. comm.; Molara Island, Sardinia, G. Spano, pers. comm.; records up to 50 individuals/ha were found in Cabrera Archipelago, Toro Island in Corsica, and Petit Congloué Islet in French Provence; see Alcover 1993 and Cheylan 1999). Only the abundance of the smallest species, the storm petrel, was related to rat presence on islands. Our findings are consistent with those of Jones et al. (2008) in their review on rat impact on seabirds, which points out that seabirds of the Hydrobatidae family (i.e., storm petrels) meet all the criteria for susceptibility to rats. Storm petrels are small-sized seabirds, are burrow or cavity nesters, and have all life stages (i.e., eggs, chicks, adults) likely to be preyed upon. Although rat presence on islands was not a significant component of storm petrel distribution at the scale of the Western Mediterranean, at the archipelago scale, storm petrels only breed on rat-free islands (Massa and Sultana 1990–1991; Martin et al. 2000). This is why it is imperative to consider the scale under study when inferences are made (Lomolino 1999, 2000; Wittaker 2000).

Seabird presence and abundance were mainly related to island's physical characteristics, such as elevation, area, and substrate. Island cliffs may constitute key intra-island refuges for seabird breeding since they may be less covered by vegetation and less accessible to mammal predators (Iguar et al. 2006). On New Island, Falklands, Quillfeldt et al. (2008) showed that thin-billed prions preferred breeding in areas with little vegetation and seemed to avoid areas covered by native tussock grass where ship rat densities were consistently higher. Unlike Cory's shearwaters, which are able to breed in exposed cavities as well as under vegetation without substrate protection (Borg 2000), Yelkouan shearwaters are more selective in their habitat requirements and breeding cavity selection (i.e., selecting deep and winding cavities that may be less accessible to rats; Bourgeois and Vidal 2007; Ruffino et al. 2008). This may explain why Yelkouan shearwaters only rarely breed on small islands, where the probability of finding suitable and safe breeding sites may be lower

than on large islands. Balearic shearwaters breed only on limestone islands, and when breeding on rat-infested islands, breeding sites are generally located in inaccessible sites (i.e., deep limestone caves in high cliffs) where rat densities are low or even nil (Oro et al. 2004). In turn, storm petrels preferentially select safe breeding areas on limestone islands. Moreover, they breed almost exclusively on small islands to avoid human activities, and terrestrial and avian predators on large islands (Erwin et al. 1995; Borg et al. 1992–1994; Oro et al. 2005).

However, at a more local scale, most studies dealing with rat impact on Mediterranean Procellariiformes reported benefits of ship rat absence or rat removal on shearwater productivity (Table 5). Moreover, as confirmed by our GLM analyses, the breeding success of the largest burrowing seabird species, the Cory's shearwater, has frequently been shown to be negatively affected by ship rat impact (e.g., Amengual and Aguilar 1998; Thibault 1995; Igual et al. 2006, 2007; Pascal et al. 2008). From a demographic point of view, population dynamics of Procellariiform seabirds have a low sensitivity to changes in fecundity, while changes in adult survival translate into sharp variations of population growth rates (Cuthbert et al. 2004; Oro et al. 2004; Louzao et al. 2006). This low sensitivity, together with some demographic buffer capacities (e.g., age at recruitment, skip breeding, immigration), could explain how shearwater populations have persisted despite centuries of rat impact. Unfortunately, there are not enough reliable data on Yelkouan and Balearic shearwater breeding success and cases of breeding in rat-free islands to allow rigorous inter-species comparison of shearwater sensitivity to rats. This review failed to find an overall significant difference between the effect of rat absence (either naturally absent or eradicated) and local rat control on the breeding success of the Cory's shearwater. This apparent non-significance may be a result of insufficient data available on the long-term monitoring of Cory's shearwater breeding success after rat eradications, since rat eradication has been proven to enhance long-term ecological benefits compared to local control (Pascal et al. 2008). This also suggested that both rat control and rat eradication may be efficient methods to recover shearwater breeding success. Unfortunately, rat densities and control efforts were

unable to be covered in this review (because of paucity of accurate data), yet these two parameters are expected to determine the magnitude of the increase in shearwater breeding success and thus the success of a rat-removal program (Jouventin et al. 2003; Igual et al. 2006). When rat densities are high, the increase in seabird breeding success after rat removal is expected to be sharper than for colonies where rat densities are low and, similarly, benefits from rat removal should increase with control effort (Igual et al. 2006).

Overall, few studies have been published on rat impact on Mediterranean Procellariiformes (Table 5), especially on the storm petrel, although this species seems to be the most vulnerable to rat impact. This lack of data may be due to the difficulty of taking census, monitoring, and hence evaluating signs of population changes for this cryptic species. In many cases, unfortunately, reports of rat impact on seabirds were circumstantial and equivocal, and sometimes too subjective to allow for clear inferences on the real magnitude of rat impact. Moreover, as predation is a cryptic phenomenon, it is often difficult to make direct observations of predation by rats in the field, especially for burrow-nesting birds (Townes et al. 2006) and to distinguish predation events from the consumption of neglected eggs or carrion provided by natural death (Norman 1975; Towns et al. 2006; Quillfeldt et al. 2008). At present, there is an urgent need to collect more data on the breeding biology of the four Mediterranean burrowing seabirds throughout the Mediterranean basin, to perform long-term studies, and rigorously monitor breeding success of seabirds before and after conservation measures and to routinely quantify rat impact on their productivity with standardized methods.

Conservation implications

Over the past 10 years, eradication of invasive species has become a powerful tool in preventing further extinctions and for restoring native island ecosystems (Veitch and Clout 2002; Towns et al. 2006; Howald et al. 2007). In particular, seabird communities have clearly benefited from the removal of introduced rats from islands worldwide. Indeed, many studies report a significant increase in breeding success of seabirds or new breeder establishment on islands once again

suitable for breeding, following rat eradications (Veitch and Clout 2002; Towns et al. 2006). In the Mediterranean, few eradication attempts have been carried out on islands in the past 20 years, and most of these were restricted to islands <10 ha (L. Ruffino unpublished data). Today, island managers are provided with a variety of powerful methods to eradicate rats and mitigate non-target effects and secondary poisoning events. Moreover, island area may no longer be a limiting factor for rat eradications. Howald et al. (2007) reported 159 successful ship rat eradications worldwide, 14 of them conducted on islands larger than 500 ha. Conservation managers are now also able to remove rats from large and biologically complex islands. They also manage to eradicate rodents that have been introduced on islands for hundreds of years (e.g., *Rattus exulans* on New Zealand islands; Howald et al. 2007). The main challenges for Mediterranean island managers, then, may be to deal with social, ecological, and funding issues. Because most Mediterranean islands are inhabited and closely linked to main islands and continents by human transport and activities, appropriate environmental education and means of preventing reinvasions are required. Furthermore, Mediterranean island systems house non-target vertebrate species with high conservation value that need to be considered when planning eradication programs, but which are expected to benefit from rat removal. As Mediterranean islands are currently under increasing pressure from various human activities, any management operations that would improve seabird population health should be promoted.

Conclusions

The Mediterranean context is particularly intriguing, since the survival of the four Mediterranean Procellariiformes after 2,000 years of ship rat presence on islands seems to go against the current global threat to burrowing seabirds from rat impact (Atkinson 1985; Birdlife International 2000; Jones et al. 2008). Thus, the apparent paradox of long-standing coexistence between rats and seabirds raises some new conservation questions, especially regarding the ability of native island species to “coexist” with introduced rats. Sound understanding of the mechanisms of such

Table 5 Review of ship rat impact on Mediterranean Procellariiformes (C: *Calonectris diomedea*; Y: *Puffinus yelkouan*; M: *Puffinus mauretanicus*; H: *Hydrobates pelagicus*)

Country	Area	Island	Species	Stage affected	Effects on seabird populations	References
Spain	Cabrera, Balearic	Estell Xpat and Estell de s'Esclatasang	C	Eggs and chicks	Major impact: breeding success increased from 0% to 40–42% after rat eradication	Amengual and Aguilar (1998)
		Several islets	H	All stages?	Desertion of colonies after rat colonization in the 1970s	Amengual et al. (2000)
	Balearic	Cabrera and other islets	M	Chicks?	No apparent impact on breeding success at least under a critical threshold value of rat density	Aguilar (2000), Louzao et al. (2006)
			M	Eggs mainly	Medium overall impact. Locally high	Gallo-Orsi (2003)
			M	Eggs mainly	Breeding success increased after rat control	Ruiz and Martí (2004)
Italy	Chafarinas		C	Chicks mainly	Breeding success increased from 27 to 70% and chick mortality decreased from 52 to 11% after rat control	Omata et al. (2002), Igual et al. (2006)
			Y	Eggs mainly	Major breeding failure in certain years	N. Baccetti, personal communication
		Tavolara and Molara	C	Eggs and chicks	Major impact: breeding success increased from 0% to 100% after rat control	Corbi et al. (2005)
	Tuscany	Scola	C	Chicks mainly	Major impact: very low breeding success on rat-infested islands (0%) compared to rat-free islands. Breeding success increased after rat control	Perfetti et al. (2001)
			Y	Chicks mainly	Low breeding success due to rats	Baccetti (1993)
Malta	Malta	Malta	Y	Eggs and chicks	Heavy annual losses of eggs and chicks (between 40% and 100%) mainly due to rats	J. Borg, personal communication
			C	Eggs mainly	Low effect of rat predation compared to egg taking by humans	Borg and Sultana (2000), Borg and Cacha-Zammit (1998)

Table 5 continued

Country	Area	Island	Species	Stage affected	Effects on seabird populations	References
France	Hyères	Port-Cros and Porquerolles	Y	Eggs and chicks	Rat impact fluctuated from year to year	Cheyjan (1985), Vidal (1985)
	Frioul, Marseilles	Pomègues and Ratonneau	C		Breeding success increased from 25% fledged chicks/adult to 65% and 75% after rat control	CEEP-Marseille (unpublished report)
	Lavezzi, Corsica	Lavezzi	C	Chicks mainly	Rats responsible for nearly 85% of breeding failure in certain years	Thibault (1995)
		Lavezzi	C	?	Breeding success increased from 44% to 83% after eradication	Lorvelec and Pascal (2005), Pascal et al. (2006, 2008)
	Northern Corsica	Gargalu and Giraglia	C	?	Breeding success on Gargalu: 3% (with rats), on Giraglia: 73% (without rats)	Thibault et al. (1997)

coexistence is likely to provide important clues to conservation and restoration priorities on other rat-invaded islands worldwide. Here we hypothesize that the long-term persistence of these seabirds at the scale of the Western Mediterranean Basin may have been facilitated by the various biogeographical contexts of Mediterranean islands, providing intra-island refuge areas where interactions with introduced rats may be limited. Rat densities on islands and their fluctuations over time are known to be major factors in seabird vulnerability within breeding sites (e.g., Igual et al. 2006), with seabird productivity increasing when rat densities are low (Quillfeldt et al. 2008). This intriguing coexistence, along with evidence of rat impact on Mediterranean seabirds, also raises new questions on the mechanisms and the intensity by which invasive rats really affect seabirds, and on their ability to drive them to extinction. More work is also needed to clarify the complex relationships linking factors likely to influence rat population densities (i.e., diversity of available resources, presence of other alien predators or competitors on islands), foraging strategy of rats and rat impact on seabird populations. As claimed by Towns et al. (2006), we suggest that the role of rats in seabird population decline should be carefully evaluated relative to that of other factors and caution should be used in attributing any seabird breeding failures, and local or global extinctions to rats. The better we understand both patterns and mechanisms causing decline, the better we can focus our efforts on the most effective measures to mitigate threats.

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Appendix 1

See Table 6.

Table 6 continued

Area	Island/islet	Presence					Area	Island/islet	Presence						
		C	M	Y	H	R			C	M	Y	H	R		
B-Menorca	Pentaleu					1								0	0
	Sa Torre					1 ^a		C-Lavezzi					0		0
	Alcanada					1 ^a							1	0	0
	Sa Porrassa					1 ^a							1	0	0
	Menorca		1	1		1							1	0	0
	Colom			0		1							0	0	1
	Ses Sargentanes					1 ^a							0	0	1
	Bledes			0		1							0	0	1
	L'Aire		0	1		1							0	0	1
	Porros = Sa Nitja			0		0							0	0	1
C-Ajaccio, Sanguinaires C-Bonifacio Strait	Grande de Addaia		0			0							0	0	1
	Binicodrell					0 ^a							0	0	1
	Mezzu Mare					1							0	0	1 ^a
	Petit îlot du Fazzio = Fazzuolo Piccolo		1		0	0							1	0	0
	Grand îlot du Fazzio = Fazzuolo Grande					0							1	0	0
	Saint Antoine					0							0	0	1
	Grain de sable					0							0	0	0
	Grand îlot Bruzzi		0			0							0	0	0
	Senetosa = Scoglio Longu					0							1	0	0
	Piana di Portigliolo					0		C-Palombaggia					0	0	1
C-Calvi C-Cap Corse	Spano		0		0	0						1	0	1	0
	Giraglia		1		1	0						1	0	0	1
	Finocchiarola		0		0	0						0	0	0	1
	Mezzana		0		0	0						1	0	0	1
	Pietricaggiosa		1		0	0						0	0	0	0
	Toro Grande = Grand Toro		1		0							0	0	0	0
	Toro Piccolo = Petit Toro		1		0							0	0	0	0
	1er Rocher du Toro Piccolo		0		0							1	1	0	1
	2e Rocher du Toro Piccolo		0		0							1	1	0	1
	La Folaca		0		0	0						1	1	0	1
La Folachedda		0		0	0						0	0	0	1	

Table 6 continued

Area	Island/islet	Presence					Area	Island/islet	Presence				
		C	M	Y	H	R			C	M	Y	H	R
F-Cannes, Lérins	Rocher NW de la Folachedda	0	0	0	0	1		Petit Langoustier	0	0	0	0	1
	Sainte Marguerite	0	0	0	0	1		Gros Sarranier	0	0	0	0	1
	Saint Honorat	0	0	0	0	1		Petit Sarranier	0	0	0	0	1
	La Tradelière	0	0	0	0	1		Rascas	0	0	0	0	0
	Saint Féréol	0	0	0	0	1		Rousset	0	0	0	0	0
F-Fréjus	Lion de terre	0	0	0	0	1		Deux Frères des Mèdes N	0	0	0	0	0
	Lion de mer	0	0	0	0	1		Deux Frères des Mèdes S	0	0	0	0	0
	D'Or	0	0	0	0	1	F-La Ciotat-Sanary	Verte	0	0	0	0	1
	Les Vieilles	0	0	0	0	1		Bendor	0	0	0	0	1
	Grand Ribaud	0	0	0	0	0		Rousse = Pierreplane	0	0	0	0	1
F-Hyères	Portugais N	0	0	0	0	1		Embiez	0	0	0	0	1
	Petit Ribaud	0	0	0	0	0		Grand Rouveau	0	0	0	0	1
	Redonne	0	0	0	0	0		Petit Rouveau	0	0	0	0	1
	Longue	0	0	0	0	0		Croisette	0	0	0	0	1
	Ratonnière	0	0	0	0	1		Deux Frères N	0	0	0	0	0
F-Marseille, Riou	L'Esterel	0	0	0	0	0	F-Marseille, Frioul	Ratonneau	1	1	0	0	1
	Les Fourmigués de l'Escampobariou	0	0	0	0	0		Pomègues	1	0	0	0	1
	Léoube	0	0	0	0	1		Tiboulen de Ratonneau	1	0	0	0	0
	L'Estagnol S	0	0	0	0	1		Château d'If	0	0	0	0	0
	L'Estagnol N	0	0	0	0	1		Endoume N	0	0	0	0	0
	Endoume S	0	0	0	0	0		Château d'If	0	0	0	0	0
	Maire	1	1	1	1	1		Endoume N	0	0	0	0	0
	Les Cristaux = Christaou	0	0	0	0	0		Endoume S	0	0	0	0	0
	Cap Taillat = Cartaya	0	0	0	0	0	F-Marseille, Riou	Maire	1	1	1	1	1
	Porquerolles	1	1	1	0	1		Tiboulen de Maire	1	0	0	1	1
F-Marseille, Riou	Le Levant	1	1	1	0	1		Pharillons	0	0	0	0	0
	Port-Cros	1	1	1	0	1		Jarron	0	0	0	1	1
	Bagaud	1	1	1	0	1		Jarre	1	1	1	1	1
	Gabinière	0	0	0	0	1		Plane = Calseraigne	1	0	0	1	1
	Petit Langoustier	0	0	0	0	1		Riou	1	1	1	1	1
	Gros Sarranier	0	0	0	0	1		Grand Congloué	1	0	0	1	1

Table 6 continued

Area	Island/islet	Presence					Area	Island/islet	Presence				
		C	M	Y	H	R			C	M	Y	H	R
F-La Ciotat-Sanary	Petit Saranier	0		0	0	1		Petit Congloué	1	0	0	1	1
	Rascas	0		0		0		Empereurs = Impériaux S	0	0	0	1	0
	Rousset	0		0	0	0		Empereurs = Impériaux N	0	0	0		0
	Deux Frères des Mèdes N	0		0	0	0		Moyade	0	0	0	0	1
	Deux Frères des Mèdes S	0		0		0	I-Lazio, Ponziono	Palmarola	1	1	1		1
	Verte	0		0		1		Ventotene	1		1		1
	Bendor	0		0		1		Santo Stefano					1 ^a
	Rousse = Pierreplane	0		0		1		Gavi					1 ^a
	Embiez	0		0		1		Zannone	1		1		1
	Grand Rouveau	0		0		1		Ponza	1		1		1
	Petit Rouveau	0		0		1	I-Tremiti	San Domino	1		1		1
	Croisette	0		0		1		San Nicola			1		1
F-Marseille, Frioul	Deux Frères N	0		0		0		Pianosa					0
	Ratonneau	1		1	0	1		Capraia = Caprara	1				1
	Pomègues	1		0	0	1	I-Tuscany	Giannutri	1		0	0	1
	Tiboulén de Ratonneau	1		0		0		La Scola	1		1		1
	Montecristo			1		1		Rondella		0			1
	Porto Ercole					1 ^a		Mayor = del Barón		0			1
	Capraia			1		1		Perdiguera		0			1
	Pianosa			1		1	S-Cartagena	Las Palomas	1	0		1	1
	Giglio					1		Escombreras	0	0			1
	Palmaiola	1				1	S-Castellón, Columbretes	Columbrete Grande = Colibre	1	0		1	0
	Elba					1		La Ferrera	0	0			0
	Peraïola					1 ^a		La Foradada	1	0			0
M-Alboran Sea	Topi					1		El Bergantin = Carallòt	0	0			0
	Alborán	0	0		0	0	S-Girona, Medes	El Medallot	0	0			0
	Congresso	1			0	1		La Meda Gran	0	0			0
	Rey	0				1		La Meda Petita	0	0			0
Ma-Malta	Isabel II	0				1		Les Feranelles	0	0			0
	Malta	1		1	0	1		Els Tascons grossos	0	0			0
	Gozo	1		1	1	1		El Carall Bernat	0	0			0

Table 6 continued

Area	Island/islet	Presence				Area	Island/islet	Presence			
		C	M	Y	H			C	M	Y	H
S-Agüilas S-Alicante	Fungus	1			0		Els Tascons Petits	0	0		0
	Comino	1		1	0	S-Mazarrón	Cueva de Lobos		0		0
	Cominoto	0		1	0		La Isla		0		1
	Filfla	1			1		Plana		0		1
	El Fraile		0			Sa-Alghero	Foradada	1			1
S-Cabo Nao S-Cabo Palos	Benidorm	0	0		1		Piana de Alghero				1
	Mitjana		0			Sa-Capo Altano	San Pietro		1		1
	L'Olla		0			Sa-Capo Carbonara	Cavoli	0		1	1
	Portichol = Portitxol		0			Sa-Capo del Falcone	Asinara				1
	Hormiga Grande	0	0		1		Piana				1 ^a
Sa-Golfo di Palmas Sa-La Maddalena	Grosa		0		1	Sa-Capo Mannu	Mal di ventre	0		0	0
	El Farallón		0			Sa-Costa Esmeralda	Nibani S				1 ^a
	Sujeto		0				Nibani N				1 ^a
	Ñibani E						Tavolara	0		1	1
	Ñibani W						Topi	0		0	0
	Mortorio	1				Sa-Teulada	Rossa				1
	Camere E	1				Si-Messina, Aeolian	Vulcano				1
	Camere W	1					Lipari				1
	Soffi						Salina				1
	La Vacca	1			0		Alicudi				1
Sa-La Maddalena	Torro						Filicudi				1
	Spargi	1		1			Stromboli				1
	Spargiotto	1		0			Stromcolicchio				1
	Budelli	1		0			Panarea				1
	Razzoli	1		0			Baziluzzo				1
	Santa Maria	1		1	0	Si-Palermo	Ustica	1			1
	Barrettini	1		0		Si-Trapani, Aegadian	Marretimo			1	1
	Corcelli			0			Levanzo				1
	Piana de Corcelli	0		0			Favignana				1
	Stramanari W	0		0		Si-Trapani, Stagnone	Grande = Lunga				1 ^a
	Stramanari E	0		0		Si	Pantellaria	1			1

Table 6 continued

Area	Island/islet	Presence					Area	Island/islet	Presence				
		C	M	Y	H	R			C	M	Y	H	R
Sa-Olbia	Carpa	1		0			Si-Pelagie	Linosa	1				1
	Caprera					1		Lampione	1				0
	Maddalena					1		Lampedusa			1		1
	Figarolo = Figarello	1		1	0		T-Zembra	Zembra	1		0	0	1
	Molarotto	0		0		0		Zembretta	0		0	0	1
	Molara	0		1		1		Lantorcho					0 ^a
	Porri	0		0		0							

^a Islands not used in GLMs for rats but in the relationship between rat presence and island area (Fig. 2)

A: Algerian coast, B: Balearic islands, C: Corsica, F: French coastal islands, I: Italian coastal islands, M: Moroccan coastal islands, S: Spanish coastal islands, Sa: Sardinia, Si: Sicily, T: Tunisian coastal islands

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