



Introduced predators and nest competitors shape distribution and breeding performance of seabirds: feral pigeons as a new threat

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Abstract Petrels are particularly sensitive to predation by introduced species. Many populations have reduced their breeding ranges, currently mainly occupying predator-free sites. Breeding range reduction leads to interspecific competition for nesting sites, which can be detrimental to petrels. Here, we evaluate how the presence of introduced mammals (cats *Felis catus* and rats *Rattus* spp.) and potential competitors for nest sites (Cory's shearwaters *Calonectris borealis* and feral rock pigeons *Columba livia*) shape the distribution, breeding density, and breeding performance of Bulwer's petrel *Bulweria bulwerii* on Tenerife, the largest and most densely human populated of the Canary Islands. We estimated nest density, assessed the role of nest location and physical characteristics of nests on breeding success, and determined

causes of breeding failure by introduced predators and competitors. Nest density was higher in predator-free colonies on marine rocks. Cat presence was the best predictor of nest density, but it was not correlated with either presence or abundance of competitors. Breeding success varied between years and colonies but was not related to nest characteristics. Pigeon competition for nests was the most frequent cause of breeding failure (7.3%), followed by rat predation (6.3%). We also compared petrel and pigeon nest cavities and found considerable overlap in the physical size of nest sites. Our study provides insights into an overlooked impact of the invasive rock pigeon: nest competition with small seabirds. We encourage more research on the effects of pigeons on nest density, as well as disease and pathogen transmission, and vegetation changes within seabird colonies.

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Introduction

Seabirds and, particularly, petrels (order Procellariiformes) occur in vast ocean areas, but their breeding colonies are usually restricted to islands that are markedly limited in area in comparison with their large pelagic feeding grounds (Brooke 2018). The reduced breeding range is thought to be a consequence of

predation. Predation pressure is generally lower on islands than on the mainland, although humans have introduced many predators worldwide (Mulder et al. 2011). Petrels are in decline mainly due to predation by introduced species on their breeding grounds, being one of the most endangered avian groups (Rodríguez et al. 2019; Dias et al. 2019). So, invasive species drive petrel local extinctions and restrict breeding petrel distribution to predator-free sites, such as islets or sea cliffs (Spatz et al. 2014, 2017).

The breeding density of birds is usually limited by the availability of nesting sites and, for cavity-nesting bird species, cavities are a limited resource (Newton 1994). Many seabirds, especially petrels, nest underground, and share nesting grounds with other species. Under these circumstances, sympatric species fiercely compete for favourable nesting sites, with the smaller species usually defeated (Cory's shearwater *Calonectris borealis* vs. Bulwer's petrel *Bulweria bulwerii*, Macaronesian shearwater *Puffinus baroli*, and band-rumped storm-petrel *Hydrobates castro*; Ramos et al. 1997; Wedge-tailed shearwater *Ardenna pacifica* vs. Tahiti petrel *Pseudobulweria rostrata*; Villard et al. 2006; Streaked shearwater *Calonectris leucomelas* vs. *H. castro* and Swinhoe's storm-petrel *Hydrobates monorhis*; Sato et al. 2010; Bonin petrel *Pterodroma hypoleuca* and *A. pacifica* vs. Tristram's storm-petrel *Hydrobates tristami*; McClelland et al. 2008), although differences in microhabitat or nest site characteristics can partially alleviate interspecific competition (Sullivan and Wilson 2001; Bourgeois and Vidal 2007; Troy et al. 2016).

Our knowledge on interspecific interactions between petrels and other non-petrel native species is limited. Evidence suggests that competition for nesting holes has little effect on petrels under natural conditions, i.e. without cumulative effects of other anthropogenic threats (Rodríguez et al. 2019). However, when native species abundance increases as a result of human actions, such as provision of supplementary food or nesting habitat, interspecific competition can be detrimental for threatened petrel populations, e.g. the nest competition of white-tailed tropicbird *Phaethon lepturus* hampered the recovery of the endangered Bermuda petrel *Pterodroma cahow* (Madeiros et al. 2012). Future research on interspecific interactions must be further intensified and focused on identifying problematic species for endangered petrels, because this

basic information is still unavailable for many of them (Rodríguez et al. 2019).

In the Canary Islands, seven procellariiform species breed currently (Bulwer's petrel *B. bulwerii*, Cory's shearwater *C. borealis*, Manx shearwater *Puffinus puffinus*, Macaronesian shearwater *P. baroli*, European storm-petrel *Hydrobates pelagicus*, band-rumped storm-petrel *H. castro* and white-faced storm-petrel *Pelagodroma marina*). All of them are threatened with declining small populations, except Cory's shearwater (Lorenzo 2007). Small-sized species show small and patchily distributed breeding colonies, mainly located on predator-free islets and marine rocks which are difficult to access (Lorenzo 2007). Due to the limited surface of these breeding areas, competition between birds for nest sites may be intense as in other nearby locations (Ramos et al. 1997; Bried and Bourgeois 2005).

The rock pigeon *Columba livia* is an invasive species introduced worldwide (CABI 2008), which has been eradicated from the Galápagos Islands to protect its unique biodiversity applying the "precautionary principle" (Phillips et al. 2012). This species, native to Europe and the Canary Islands (geographically closer to Africa than mainland Europe), has suffered a genetic introgression with domestic pigeons during the last few centuries (Johnston and Janiga 1995; Lorenzo 2007; Giunchi et al. 2020). Thanks to its high reproductive rates and behavioural plasticity, feral rock pigeons can become pests (Johnston and Janiga 1995). The negative ecological impacts of feral rock pigeon populations include transmission of infectious diseases and pathogens (Foronda et al. 2004; Burt et al. 2018; Mori et al. 2019), changes in chemical soil properties by means of the acidity of its excrement (Spennemann and Watson 2017), and competition with native species for resources such as food or nesting sites (Forero et al. 1996; Hernández-Brito et al. 2014). Despite its impacts, field studies focusing on their role as nest competitors are few (e.g. Forero et al. 1996; Hernández-Brito et al. 2014; this study).

Here, we assess the role of feral rock pigeons on the nesting density and breeding performance of a small seabird, Bulwer's petrel, on a densely human-populated island of the Canary Islands. To compare the impact of pigeons with that of introduced predators and other nest competitors, we also evaluated the presence of cats *Felis catus* and rats *Rattus* spp., and the abundance of native Cory's shearwaters.

During 2017–2020, we (1) estimated Bulwer's petrel nest density in colonies, (2) assessed the impact of nest location and physical characteristics of nests on breeding success, and (3) quantified causes of breeding failure as a result of introduced predators and native competitors. We hypothesized that at sites where invasive species occur, i.e. cats and rats, nest density and breeding success would be lower than at sites free of introduced predators. Given that the potential nest competitors studied here, i.e. pigeons and shearwaters, are benefited by the absence of introduced predators, i.e. cats and rats, we hypothesized that nest competition could lead to breeding failure at predator-free sites. We also compared physical characteristics of nest cavities used by petrels and pigeons to assess nesting niche segregation. We predict that some overlap occurs between the nesting niches of these two species.

Materials and methods

Study area and species

The study was conducted on Tenerife, the largest and the highest (2034 km² and 3718 m above sea level—a.s.l.) of the Canary Islands (Fig. S1). The coastline (342 km) is predominantly rocky with boulder shores, cliffs up to 400 m high, and small marine rocks on the north coast. The climate is subtropical and oceanic. Oceanographic conditions in this archipelago are influenced by northeast trade winds and marine upwelling that occurs off the north-west African coast. In 2019, the local human population was approximately 949,000 inhabitants, but as the island's economy is highly dependent upon the tourism, each year several millions of visitors are received (Instituto Canario de Estadística, www.gobiernodecanarias.org/istac/).

Bulwer's petrel is a small pelagic procellariiform (75–130 g), with a disjointed pan-oceanic distribution in tropical and subtropical waters of the Pacific, Indian, and Atlantic Oceans. Canarian Bulwer's petrels visit breeding grounds from April to September and nest mainly in small crevices, caves, and holes under rocks, usually close to the sea, where they lay a single egg per breeding attempt in late May-early June (Hernández et al. 1990; Martín and Lorenzo

2001). Chicks fledge mainly during the second fortnight of September (Martín and Lorenzo 2001).

Cory's shearwater is the largest (700–800 g) and most abundant procellariiform species in the Canary Islands (Lorenzo 2007). It is distributed extensively on the island under 1000 m a.s.l. and is well known to compete for nests with Bulwer's petrels on other nearby colonies (Ramos et al. 1997; Bried and Bourgeois 2005). Cory's shearwaters visit their breeding colonies from March to November. Single-egg clutches are laid in early June and chicks fledge from late October to early November (Martín and Lorenzo 2001).

In the Canaries, the feral rock pigeon is abundant and distributed widely in rural and urban environments, but especially in coastal sectors (Lorenzo 2007). This sedentary and medium-sized bird (230–370 g) uses holes and crevices on sea cliffs and marine rocks as roosting and breeding sites (Lorenzo 2007). Rock pigeon clutch size is 1–2 eggs and pairs can make several breeding attempts per breeding season. Its breeding period is concentrated in spring and summer, but pigeons can breed throughout the year (Martín and Lorenzo 2001). Nowadays in Tenerife, most rock pigeons seen in the wild resemble birds of domestic origin (*authors' pers. obs.*). Studies conducted on Tenerife indicate that feral rock pigeons could be vectors of pathogens for the endemic pigeons, Bolle's pigeon *Columba bollii* and the white-tailed laurel pigeon *Columba junoniae* (Foronda et al. 2004; Abreu-Acosta et al. 2009).

Two species of rats (black rat *Rattus rattus* and brown rat *R. norvegicus*) and feral domestic cats *Felis catus* have been introduced in Tenerife since fifteenth century (Nogales et al. 2006). Rats and cats are widely distributed on the main island, but they are absent on the marine rocks (Nogales et al. 2006; *authors' pers. obs.*). Introduced mammals intensively depredate eggs, chicks, and adults, which lead to seabird population declines worldwide (Spatz et al. 2017).

Nesting density, nest characteristics and breeding performance

During the 2017–2020 breeding seasons (June-early September), we visited all known Bulwer's petrel nesting sites (Hernández et al. 1990; Lorenzo 2007). Other sites with the potential to accommodate

colonies (apparently free of introduced predators and with suitable holes) were also visited. We visited 43 sites, spending a total of 218 h/observer of effective prospecting (Fig. S1; Table S1). During daylight hours, we counted the number of Bulwer's petrel and Cory's shearwater nests in places accessible on foot using a hand-held flashlight to inspect holes and crevices. We also recorded the presence or absence of feral rock pigeons, rats, and feral cats according to field signs (individuals, feathers, nests, prey remains, or droppings). Studied site edges, including those without petrels, were delineated and plotted using landscape features in aerial photographs, maps, and a geographic information system (*Qgis* v3.14.16). Four inaccessible sites were inspected using a thermal monocular Helion XP50 (Pulsar, Lithuania) from vantage points (80–130 m) to estimate the number of nests according to attendance behaviour of adults. Bulwer's petrel and feral rock pigeon nests from five petrel colonies were described with nine variables (Table 1).

We assessed breeding success of 209 breeding attempts (2018, $n = 71$; 2019, $n = 70$; 2020, $n = 68$) in five colonies, four of them located on marine rocks (without introduced predators) and one on a coastal cliff (Fig. S1). Each nest was visited at least twice: to confirm incubation in late June or early July and to record the presence or absence of a full-grown chick in late August or early September. We assumed that nestlings observed during the second visit would fledge successfully.

To identify causes of breeding failure, the nest and its surroundings were inspected, paying special attention to the presence of unhatched eggs, eggshells,

dead chicks, droppings, and signs of introduced predators. Pigeon nests at sites (e.g. crevices, caves, holes, or burrows) previously used by petrels for nesting, i.e. in the previous breeding season or early in the same breeding season, were considered breeding failures.

Statistical analysis

To assess the role of the colony location (main island vs. marine rock), presence of predators (cats and rats), and nest competitors (pigeons and Cory's shearwaters) on the density of Bulwer's petrel nests, we ran Linear Models (LMs). We did not include year as a response variable as nest density is relatively consistent among years and we had just a density estimate to many colonies. Given our limited sample size (43 sites), we compared LMs including just a single predictor. Then, we ranked the models according to its AICc value (the lower AICc, the better the model), including a null model containing just the intercept.

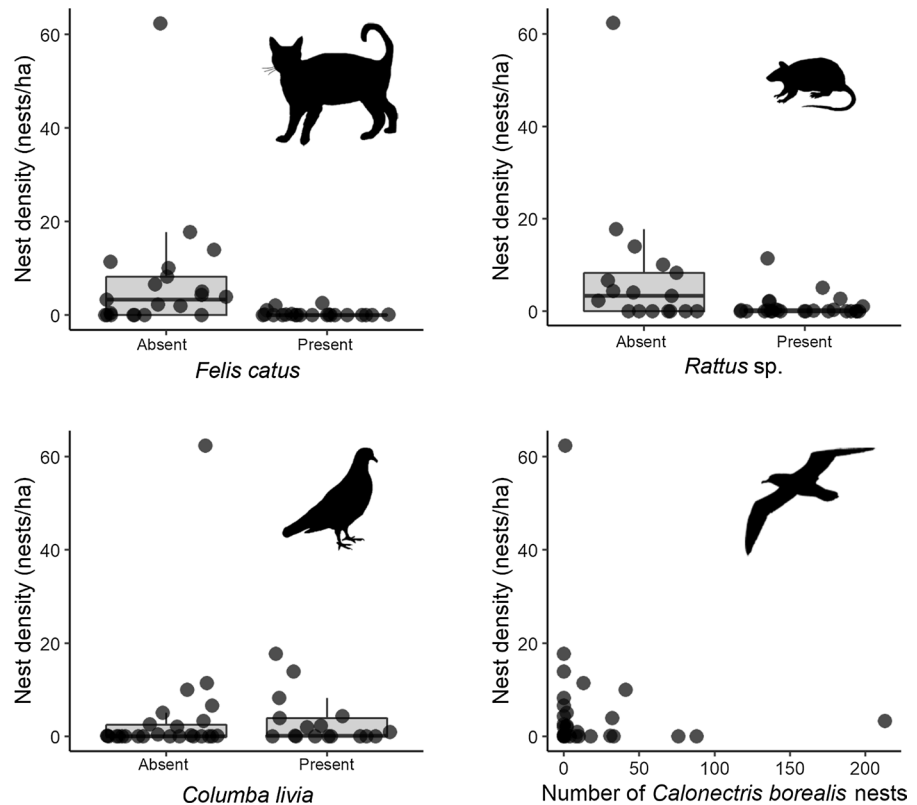
To test for potential differences in breeding success (0 = failure; 1 = success) among colonies and years, we ran Generalized Linear Mixed Models (GLMMs) with family binomial (link = logit). We included nest identity as a random factor, given that the same nests were studied each breeding season, and year and colony as predictors. We ranked competitive models according to AICc.

To assess potential relationships between breeding success (0 = failure; 1 = success) and nest features, we ran GLMMs with family binomial (link = logit). We included nest identity as a random factor and used seven variables describing nests (height, width, depth, chamber height, vertical difference height,

Table 1 Variables used to describe nests of Bulwer's petrels *Bulweria bulwerii* and feral rock pigeons *Columba livia* on Tenerife, Canary Islands

Variable	Description
Nest type	Proportion of nest cavity sides bounded by rock: all rock, rock crevice; soil bed, soil crevice; and all soil, burrow
Entrance height	Minimum height of the nest entrance (cm)
Entrance width	Minimum width of the nest entrance (cm)
Depth	Maximum length from entrance to the nesting chamber (cm)
Chamber height	Height of the nesting chamber (cm)
Difference in heights	Difference in height from the entrance and the nesting chamber (cm)
Entrance curvature	In degrees (0–90°), curve between the entrance and the chamber
Slope	In degrees (0–180°), angle measured in a 1 m radii from the nest entrance considering vertical up as 0°
Nest material	Absent (0), Present (1)

Fig. 2 Box-and-whisker plots of the nesting density of Bulwer's petrels *Bulweria bulwerii* according to the presence of introduced predators (cats *Felis catus* and rats *Rattus* sp.) and competitors (feral rock pigeons *Columba livia* and Cory's shearwaters *Calonectris borealis*) on Tenerife, Canary Islands. Dots have been jittered for a better visualization. The line within boxes indicates the median, the bottom and top of the box represent the first and third quartiles, and the whiskers extend 1.5 times the interquartile range



Bulwer's petrel and feral rock pigeon nest characteristics

A considerable overlap in features describing Bulwer's petrel and pigeon nests was observed according to the Principal Component Analysis, indicating both species share part of their nesting niches (Fig. 3; Table S4). PC1 retained 33.5% of the variation and was highly correlated with entrance height (-0.89), chamber height (-0.74), depth (-0.65), and entrance width (-0.54). PC2 retained 16% of the variation and was highly correlated with difference in heights (-0.71), entrance curvature (-0.52), and entrance width (-0.51) (Table S4). Five out of the seven variables describing the petrel and pigeon nests reached significant differences (Table S5, Fig. S2). Petrel nests had smaller entrances (i.e. lower height and width) and smaller nesting chambers (i.e. height). Petrel nest entrances were more curved than those of pigeon nests, and slopes were steeper in pigeon nests. Depth and vertical difference in height between entrance and nest chambers were similar in the two species' nests (Table S5, Fig. S2).

Discussion

Our results support our hypotheses and indicate that the main factor shaping breeding distribution of small procellariiforms, such as Bulwer's petrel, is the presence of invasive mammals (Spatz et al. 2014, 2017). In addition, nest competition with feral rock pigeons was the main identified cause of breeding failure of Bulwer's petrels, highlighting an overlooked impact of this species (which can become a pest or invasive species depending on its native or introduced range) on small seabirds. This was supported by the overlap in the nesting niches of both species. Contrary to our predictions, our data do not provide any evidence for impacts of Cory's shearwaters on Bulwer's petrel nesting density or breeding success.

Rats and cats have been present in the Canary Islands for several centuries (Nogales et al. 2006). So, these predators have shaped the current breeding distribution of Bulwer's petrels, mainly relegating them to isolated predator-free marine rocks on which dense colonies form (Hernández et al. 1990). At predator-free sites, such as the Desertas Islands,

Table 2 Results of the LMs and GLMMs explaining nest density and breeding success of Bulwer’s petrel *Bulweria bulwerii* on Tenerife, Canary Islands, during 2018–2020 breeding seasons. See main text for details

Predictor	df	AICc	ΔAICc
<i>Nest density</i>			
Presence of <i>Felis catus</i>	3	320.66	0.00
Presence of <i>Rattus</i> sp.	3	321.06	0.40
Colony location (main island or marine rock)	3	321.70	1.04
Null model	2	323.89	3.24
Presence of <i>Columba livia</i>	3	326.13	5.47
Abundance of <i>Calonectris borealis</i>	3	326.13	5.47
<i>Breeding success vs. colony and year</i>			
Colony * Year	16	279.33	0
Colony + Year	8	280.98	1.65
Colony	6	281.81	2.48
Null model	2	285.46	6.13
Year	4	285.74	6.41
<i>Breeding success vs. nest traits</i>			
Null model	2	285.46	0
Difference in heights	3	286.21	0.75
Chamber height	3	286.87	1.41
Slope	3	287.07	1.61
Entrance curvature	3	287.19	1.73
Entrance height	3	287.43	1.97
Entrance width	3	287.51	2.05
Depth	3	287.51	2.05

Table 3 Causes of breeding failure of Bulwer’s petrel *Bulweria bulwerii* breeding attempts on Tenerife, Canary Islands, during 2018–2020 breeding seasons

Causes of breeding failure (<i>n</i> = 96)	<i>n</i> (%)
Unknown	72 (75.0)
Nest competition with pigeons	7 (7.3)
Predation by rats	6 (6.3)
Abandoned egg	4 (4.2)
Dead chick	4 (4.2)
Broken egg	2 (2.1)
Chick falling from nest site	1 (1.0)

Madeira, breeding success ranges between 60 and 75% (Nunes and Vicente 1998), but in rat-invaded colonies on the Bonin Islands, Japan, marked die-off of breeding adults by predation can occur (Kawakami et al. 2010). As a whole, breeding success in Tenerife

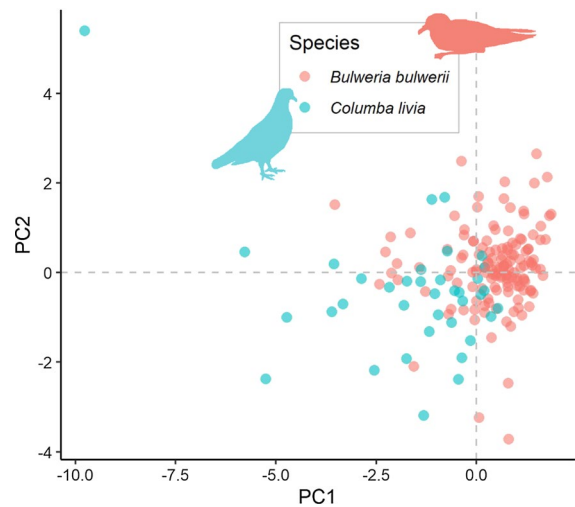


Fig. 3 Scores on the second principal component axis (PC2) plotted against those on the first principal component axis (PC1) from a PCA carried out on seven continuous variables describing Bulwer’s petrel *Bulweria bulwerii* (red) and feral rock pigeon *Columba livia* (blue) nests on Tenerife, Canary Islands, during 2018–2020 breeding seasons

is low (54.1% of laid eggs produced a fledgling), but we observed strong spatiotemporal variation. No fledglings were produced during two consecutive seasons on a coastal locality on the main island (#14 in Table S1) where invasive rats were present. By contrast, in the predator-free sites more than 50% of the breeding attempts produced a fledgling (Table S2).

Nest competition with feral rock pigeons was the main identified cause of breeding failure of Bulwer’s petrels. A minimum of 7.3% of Bulwer’s petrel breeding attempts failed due to interactions with pigeons. In those cases, we confirmed that pigeons occupied petrel nests causing breeding failure (signified by the presence of unattended eggs or dead chicks) or disruption to the petrel’s use of the nest sites. Similar to small petrels, feral rock pigeons also benefit from nesting and roosting on predator-free marine rocks to avoid predation (*authors’ pers. obs.*). Other agonistic interactions may occur between nesting or roosting pigeons and breeding petrels. Aggressive interactions might disrupt petrel nest attendance and transmit pathogens and diseases, leading finally to petrel breeding failure (Forero et al. 1996; Foronda et al. 2004; Hernández-Brito et al. 2014).

Although we failed to detect a clear relationship between petrel nest density and pigeon competition,

systematic breeding failure mediated by pigeon competition for nest sites might deflate petrel nesting density to a point of local extinction. Field observations support this reasoning. First, the highest nesting density of petrels was recorded on the small rock La Coronela (#25 in Table S1), where no feral rock pigeons were present. Second, on Roque La Playa (#33 in Table S1), we found only six petrel nests in the same area where a minimum of 18 nests were counted in August–September 1983 (E. Hernández, *com. pers.*). Furthermore, we confirmed the presence of seven pigeon nests, three of them at sites previously used by petrels (E. Hernández, *com. pers.*). Third, we could not detect petrels on two predator-free rocks representing a potentially large extension to apparent suitable nesting habitat (#30 and #31 in Table S1). These rocks held at least four Cory's shearwater breeding pairs and a large number of breeding and roosting pigeons (>110 pigeons counted at dusk). Unfortunately, no previous estimates of petrel abundance were available for these rocks. A plausible explanation for the absence of petrels is the interspecific competition with increasing number of pigeons. In support, qualitative comparisons between old and current photographs show marked loss of vegetation in recent decades. The Canary spurge *Euphorbia canariensis* population has declined from nine large plants to only one small plant (Fig. S3), which is probably related to the acidity and accumulation of pigeon excrement (Spennemann and Watson 2017; Fig. S4).

Pigeon population size increases primarily around human-modified areas (e.g. livestock farms, cereal silos, garbage dumps, dunghills, and urban centres) (Giunchi et al. 2012). Therefore, petrel breeding colonies closer to these sites are more susceptible to pigeon nest competition. At a global scale, the breeding distribution of Bulwer's petrels, but also other endangered small petrel species, greatly overlaps with the range of native and introduced pigeons. Therefore, nest competition between them may occur, particularly in proximity to human-transformed landscapes. Despite the information gap on nest competition nest between feral rock pigeons and seabirds in scientific journals, our results are not the only evidence. We have compiled evidence of pigeon nest competition with at least 15 species across the world (Table 4). More studies are required to understand in greater detail the role of pigeons on seabird nest density,

transmission of diseases and pathogens to seabirds, and vegetation changes at seabird colonies.

Conservation implications

The Canary Bulwer's petrel faces several human-related threats on land, i.e. predation by introduced mammal predators (Hernández et al. 1990), collisions with electricity transmission wires (Gómez-Catasús et al. 2021), road casualties (Tejera et al. 2018), habitat destruction and attraction to artificial night lights (Rodríguez et al. 2012). These threats mainly occur on the main human-inhabited islands. Owing to this fact, the bulk of the breeding pairs are currently restricted to geographically small secure breeding sites (mostly marine rocks). We highlight an overlooked threat to these petrel sanctuaries: pigeon competition for nesting sites. To minimize such interspecific competition as a matter of urgency, artificial nest boxes should be installed in the main petrel sanctuaries (marine rocks) with high densities of pigeons. Artificial nests must be designed to exclude pigeons and larger Procellariiformes, i.e. Cory's shearwater, by designing them with long and narrow entrances. This action would facilitate long-term monitoring of population and breeding success, and would help to improve the conservation status of Bulwer's petrel by providing secure nest sites. This action has successfully increased the annual productivity of other endangered petrel species (Bolton et al. 2004). Given that rock pigeons can easily become a pest (CABI 2008), we also advocate their culling in some petrel colonies to avoid unnatural high densities (Giunchi et al. 2012). Of course, other small petrels (e.g. Macaronesian shearwater *Puffinus baroli* and band-rumped storm-petrel *Hydrobates castro*) and endemic species (i.e. land snails, lizards and plants) living in those marine rocks might also benefit from feral rock pigeon removal or control. On the main island colonies, control of invasive mammals is the most urgently required intervention, but additional actions to reduce artificial light attraction, and wire and vehicle collisions should be also considered.

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Table 4 Evidence of seabird competition for nest sites with rock pigeon *Columba livia*

Seabird species	Location	Rock pigeon range	Observations	Source
Bulwer's petrel <i>Bulweria bulwerii</i> , Monteiro's storm-petrel <i>Hydrobates monteiroi</i>	Vila Islet, Santa Maria, and Praia Islet, Graciosa, Azores	Native	One instance of a Bulwer's petrel nest taken over by feral rock pigeons on Vila Islet. The former owner had settled in a neighbouring cavity and the nest was re-occupied by a prospecting adult/sub-adult the night following pigeon nest removal. Also a case in a Monteiro's storm-petrel nest on Praia Islet. The nest contained a half-grown Monteiro's storm-petrel chick in early August and pigeon feathers inside the nest in early September. Chick may have fledged or been killed or ousted by the pigeons	Joël Bried <i>pers. comm.</i>
Macaronesian shearwater <i>Puffinus baroli</i> , band-rumped storm-petrel <i>Hydrobates castro</i>	Azores	Native	We have the feeling that rock pigeons may interfere with the breeding of small Procellariiformes in rock cliffs. However, the areas are impossible to access, so there are no data available	Jaime Ramos <i>pers. comm.</i>
European storm-petrel <i>Hydrobates pelagicus</i>	Goulien and Biarritz, France	Native	Interactions between pigeons and storm-petrels explain population reductions in small colonies	Cadiou et al. (2004)
European storm-petrel <i>Hydrobates pelagicus</i>	Terreros Islet, Almería, Spain	Native	Given that there are few available caves and crevices for storm-petrel nests on the islet, the recent islet colonization by pigeons (2012) could be a threat to the small storm-petrel breeding population (around 10 pairs). The pigeon population is nine breeding pairs and camera traps have demonstrated that pigeons visit storm-petrels nest sites	Sergio Eguía <i>pers. comm.</i> , Eguía and Pérez Morales (2020)
Yelkouan shearwater <i>Puffinus yelkouan</i>	Malta	Native	Pigeons and shearwaters share several nest crevices/caves. Pigeons displace shearwaters in a few nests monitored for several years in two colonies. One out of 11 shearwater nest sites was occupied by pigeons in a cave at Majjistral colony in 2021. One out of 10 shearwater nest sites was occupied by pigeons on St Paul's Island in 2020. A shearwater re-occupied the nest site in the following breeding season, but the attempt failed (broken egg) and pigeons were nesting in its place	Martin Austad <i>pers. comm.</i>
Wedge-tailed shearwater <i>Ardenna pacifica</i>	Mokulua Nui, Oahu, Hawaii	Introduced	Images of the pigeon chicks in the shearwater nest and observations of territorial and aggressive behaviours of pigeons chasing away adult shearwaters from their nests	Brooke Friswold <i>pers. comm.</i>

Table 4 (continued)

Seabird species	Location	Rock pigeon range	Observations	Source
White-tailed tropicbird <i>Phaethon lepturus</i>	Bermuda	Introduced	The tropicbirds nest only over late spring to early autumn in natural erosion cavities in the limestone cliffs. The pigeons tend to move into nesting spaces when they depart soiling the nests and infusing them with mites. The Department of Environment and Natural Resources actively controls the feral rock pigeons to prevent this as much as possible. Major storm activity resulting in nesting habitat destruction increases competition for nest sites which can be further compounded by the pigeons' year-long presence using surviving nest sites	Patrick Talbot <i>pers. comm.</i> , Dowson and Madeiros (2009)
Red-tailed Tropicbird <i>Phaethon rubricauda</i> , white tern <i>Gygis alba</i>	Oahu, Hawaii	Introduced	There are no quantitative data showing reduced nest success, but both species avoid sites that are used for roosting or nesting by pigeons. The tropicbirds nest in small caves and on ledges on rocky cliffs along the coast. There are several suitable areas with caves that are used for nesting by pigeons, and the tropicbirds have never used those areas even though they nest close by. There are many caves so there may not be much competition, but the tropicbirds avoid those areas. Terns nest in trees in urban areas where pigeons are abundant, and they have abandoned several large trees that have become roosting sites for pigeons or where human garbage has attracted a large number of pigeons	Eric VanderWerf <i>pers. comm.</i>
Bridled tern <i>Onychoprion anaethetus</i>	Penguin Island, Australia	Introduced	At least 22 nests were occupied by pigeons in one study plot of 97 tern pairs, but pigeon occupation rate was higher on the cliffs than under the <i>Rhagodita</i> sp. bushes and artificial nest boxes	Aurélie Labbé <i>pers. comm.</i>
Grey ternlet <i>Anous albivitta</i>	Lord Howe Island, Australia	Introduced	Cliff nesting grey ternlets, attempting to find sites inaccessible to black rats, were nesting in large sea caves but commonly out-competed by feral rock pigeons. No quantitative data, but Lord Howe Board staff ran a programme of shooting during the ternlets non-breeding season up until 2015. While the success of the rodent eradication has yet to be confirmed, the ternlets returned to non-sea cave rock cavities in 2020, reducing the conflict with pigeons	Nicholas Carille <i>pers. comm.</i>

Table 4 (continued)

Seabird species	Location	Rock pigeon range	Observations	Source
Pigeon guillemot <i>Cepphus columba</i>	Puget Sound, Washington, USA	Introduced	Pigeons bred in guillemot nest boxes positioned under a dock to increase the size of the existing guillemot colony. Nest provisioning programme terminated due to pigeon interference. They are the same size, so no way to exclude them from nest boxes	George Divoky <i>pers. comm.</i>
Black guillemot <i>Cepphus grylle</i>	Bangor, Northern Ireland	Native	Pigeons compete with guillemots for artificial nest boxes	Katherine Booth Jones <i>pers. comm.</i>

This is a non-exhaustive list of seabirds compiled by means of a post in the 11 section of the World Seabird Union website (<https://www.seabirds.net/forum/topic/367/feral-pigeons-columba-livia-and-seabirds/>), social networks (Twitter; https://twitter.com/Atram_Rguez/status/139710938024445426), and as result of an email to 67 global seabird researchers

skills of Iván Méndez, Juan Curbelo, Moisés de León, Héctor Manuel Figueroa, Adrián Borges, José María Benítez, and Eligio Benítez as skippers, we landed in all rocks and inaccessible coastal sectors. This study was coordinated by the Canarian regional SEO/BirdLife’s office. Our special thanks to its staff, Juan Antonio Lorenzo and Elena Ramos. We thank Chloe Carothers-Liske for improving the English grammar. We also thank Benjamin Metzger and James Crymble of BirdLife Malta and those colleagues included in Table 4 for sharing their observations on nesting competition between seabirds and pigeons. Two anonymous reviewers improved an earlier version.

Author contributions BR and AR designed the study. BR, FS, JMM, ES, and AR collected field data. AR analyzed the data. YA managed and coordinated the research project. BR and AR drafted the manuscript and all authors commented and approved the final version of the manuscript.

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Data availability All data are included in the article and its supplementary information files.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All procedures in this study were approved by insular and regional governments. Permits to conduct fieldwork were granted by Cabildo de Tenerife (Permit Numbers: AFF82/17, AFF94/18, and AFF142/19) and Gobierno de Canarias (permit numbers: 2017/10464 and 2018/6842).

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