



Research Paper

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Alien mammal assemblage effects on burrow occupancy and hatching success of the vulnerable pink-footed shearwater in Chile

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Summary

Alien species are a driver of biodiversity loss, with impacts of different aliens on native species varying considerably. Identifying the contributions of alien species to native species declines could help target management efforts. Globally, seabirds breeding on islands have proven to be highly susceptible to alien species. The breeding colonies of the pink-footed shearwater (*Ardenna creatopus*) are threatened by the negative impacts of alien mammals. We combined breeding monitoring data with a hierarchical model to separate the effects of different alien mammal assemblages on the burrow occupancy and hatching success of the pink-footed shearwater in the Juan Fernández Archipelago, Chile. We show that alien mammals affected the rates of burrow occupancy, but had little effect on hatching success. Rabbits produced the highest negative impacts on burrow occupancy, whereas the effects of other alien mammals were more uncertain. In addition, we found differences in burrow occupancy between islands regardless of their alien mammal assemblages. Managing rabbits will improve the reproductive performance of this shearwater, but research is needed to clarify the mechanisms by which alien mammals affect the shearwaters and to explain why burrow occupancy varies between islands.

Introduction

Alien species are a major cause of biodiversity loss globally (Bellard et al. 2016), and their negative effects are felt strongly in vulnerable island ecosystems (McCreless et al. 2016, Bellard et al. 2017, Russell & Kaiser-Bunbury 2019). Seabirds using those islands as breeding grounds are particularly sensitive to the negative impacts of alien species (Spatz et al. 2017, Holmes et al. 2019). Seabirds are amongst the most threatened vertebrates globally and are the subject of intensive research and conservation efforts worldwide (Croxall et al. 2012, Barbraud 2017, Dias et al. 2019, Rodríguez et al. 2019). Population growth rates in seabirds are generally driven by adult survivorship and juvenile recruitment rates and, as such, processes negatively influencing either of these demographic parameters need to be explicitly considered in the conservation and recovery plans of threatened seabirds (Russell 1999, Sæther & Bakke 2000, Croxall et al. 2012). Seabird juvenile recruitment is negatively affected by the impacts of alien species (Spatz et al. 2017, Dias et al. 2019, Rodríguez et al. 2019), whereas mortality from fisheries by-catch is a major factor affecting adult survival (Anderson et al. 2011, Dias et al. 2019, Rodríguez et al. 2019). Understanding the current trends and factors shaping those two key demographic parameters is fundamental for designing and implementing effective conservation actions to manage seabird populations (Russell 1999, Sæther & Bakke 2000, Jones et al. 2015, Buxton et al. 2016).

The pink-footed shearwater (*Ardenna creatopus*) is a globally threatened species, listed as ‘Vulnerable’ by the International Union for Conservation of Nature (IUCN 2017), and considered as ‘Endangered’ in Chile (<https://clasificacionespecies.mma.gob.cl>) and Canada (Committee on the Status of Endangered Wildlife in Canada 2018). In 2015, the species was added to the Agreement on the Conservation of Albatrosses and Petrels, a binding international treaty created to advance the conservation of threatened procellariiform seabirds (Azócar et al. 2013). Its vulnerable status is attributable to anthropogenic threats, its restricted breeding range (exclusive to Isla Mocha and the Juan Fernández Archipelago in Chile) and a relatively small breeding population size (Brooke 2004, Croxall et al. 2012, IUCN 2017).

Pink-footed shearwaters suffer from fisheries by-catch mortality and the negative impacts of alien mammals (Suazo et al. 2014, Carle et al. 2016, 2019). A wide range of alien mammals are present in the breeding colonies of the pink-footed shearwater (Croxall et al. 2012, Committee on the Status of Endangered Wildlife in Canada 2018). For example, in the Juan Fernández Archipelago, seven species of alien mammals are suspected of interacting with pink-footed



Fig. 1. Geographical location and alien mammal assemblages present in six colonies of the pink-footed shearwater in the Juan Fernández Archipelago.

shearwaters in their colonies (Fig. 1) (Hahn & Römer 2002, Croxall et al. 2012): feral cats and dogs (*Felis catus* and *Canis lupus familiaris*, respectively), southern coati (*Nasua nasua*), rats (*Rattus rattus* and *Rattus norvegicus*), European rabbits (*Oryctolagus cuniculus*) and cattle (*Bos taurus*). Mice (*Mus musculus*) are present on the islands and likely in the colonies. Given that we had only partial information on their presence in the different pink-footed shearwater colonies, we did not include them in the present study. The impacts of these alien mammals on the breeding ecology and reproductive performance of the pink-footed shearwater are poorly understood, despite mammal control and eradication being priorities for the conservation of the species (Hahn & Römer 2002, Croxall et al. 2012). The seven alien mammals may exert a range of negative pressures on breeding shearwaters, from predation (e.g., by cats, coatis and rats) to habitat alteration and competition for burrowing space (e.g., European rabbits and cattle) (Imber et al. 2000, Jones et al. 2016, McCreless et al. 2016, Stolpmann et al. 2019).

In this study, we focused on assessing the effects of different alien mammal assemblages on burrow occupancy by breeding pink-footed shearwater pairs in the Juan Fernández Archipelago (Robinson Crusoe and Santa Clara islands; Fig. 1) and their subsequent hatching success in that breeding burrow, defined as the presence of a chick in the burrow (Dinsmore et al. 2002, Shaffer & Thompson 2007). The presence of different mammal assemblages, and their concurrent management on the two islands, in the various breeding colonies yielded a natural variability that allowed us to investigate the effects of these assemblages on breeding pink-footed shearwaters. In the colonies on Robinson Crusoe Island, seven introduced species were present during the study (Fig. 1; based on Croxall et al. 2012): black and brown rats, European rabbits, southern coati, feral dogs, feral cats and cattle. All of these species were present at all Robinson Crusoe shearwater colonies (Hahn & Römer 2002), with the exception of cows being excluded from Piedra Agujereada (Carle et al. 2016) and cows and coatis being absent from Reserva. On Santa Clara Island (Fig. 1), only rabbits were present at Cerro Alto and Volcán before the 2004 breeding season (95 and 96 burrows monitored while rabbits were present, respectively). No alien mammals were present at Refugio during the whole monitoring period, and none were present at

Cerro Alto and Volcán after the 2003 breeding season when rabbits were eradicated (281 and 598 burrows monitored, respectively). We also assessed trends in burrow occupancy and hatching success as functions of the breeding island and breeding year.

Methods

Study area

The Juan Fernández Archipelago is a volcanic group of islands and islets located c. 660 km off the coast of central Chile (Fig. 1). The three main islands of the archipelago – Robinson Crusoe (48.0 km²), Santa Clara (2.2 km²) and Alejandro Selkirk (49.5 km²) – are characterized by a rugged topography and a subtropical climate (Haberle 2009). Forested areas occur in lowland areas and gullies, whereas the upper elevations are dominated by bush and grasslands, interspersed with unvegetated zones (Stuessy et al. 1998, Bernardello et al. 2006, Haberle 2009). The proximity of the archipelago to the Humboldt Current means that the ocean surrounding the islands is relatively productive, which in turn translates into high terrestrial and marine biodiversity (Hahn et al. 2009). It is not surprising, then, that the Juan Fernández Archipelago is home to important breeding colonies of seabirds and the Juan Fernández fur seal (*Arctocephalus philippii*) (Colwell 1989, Bourne et al. 1992, Hahn et al. 2009). The natural values of the Juan Fernández Archipelago are recognized and protected as a Chilean National Park (www.conaf.cl/parques/parque-nacional-archipelago-juan-fernandez).

The Juan Fernández Archipelago is sparsely populated by humans, with a total population of 926 people in 2017 (https://reportescomunales.bcn.cl/2017/index.php/Juan_Fernandez). The entire population lives in San Juan Bautista on Robinson Crusoe Island (the main township in the islands) and seasonally on Alejandro Selkirk, while Santa Clara Island is uninhabited.

Monitoring of pink-footed shearwater breeding colonies

We monitored a representative sample of breeding burrows in six colonies on two islands in the Juan Fernández Archipelago (Fig. 1 & Table 1): Robinson Crusoe Island (three colonies) and Santa Clara Island (three colonies). The ruggedness of the terrain

Table 1. Characteristics of the six pink-footed shearwater colonies monitored in the Juan Fernández Archipelago. Number of burrows monitored each year and summary statistics of the burrow occupancy and hatching success per year are shown (mean ± standard deviation, and range; excluding missing data for hatching success).

Island	Colony, burrows monitored per year	Burrow occupancy per year, mean ± SD (range)	Hatching success per year, mean ± SD (range)	
Santa Clara	Cerro Alto	0.55 ± 0.11 (0.36–0.69)	0.75 ± 0.20 (0.50–1.00)	
	42 (2002); 53 (2003); 60 (2004); 61 (2005); 41 (2006); 52 (2007); 45 (2008); 22 (2011)			
	Refugio	0.67 ± 0.10 (0.52–0.89)	0.82 ± 0.12 (0.69–0.98)	
	56 (2002); 60 (2003); 60 (2004); 58 (2005); 63 (2006); 77 (2007); 79 (2008); 82 (2009); 91 (2011); 45 (2014); 45 (2015); 44 (2016)			
	Volcán	0.57 ± 0.11 (0.42–0.73)	0.83 ± 0.11 (0.68–0.97)	
	42 (2002); 54 (2003); 57 (2004); 81 (2005); 80 (2006); 84 (2007); 68 (2008); 57 (2009); 45 (2011); 41 (2014); 41 (2015); 44 (2016)			
	Robinson Crusoe	Piedra Agujereada	0.64 ± 0.11 (0.52, 0.72)	0.82 ± 0.11 (0.74–0.90)
		23 (2014); 32 (2015); 32 (2016)		
		Reserva	0.48 ± 0.08 (0.43–0.58)	0.81 ± 0.08 (0.75–0.86)
14 (2005); 14 (2006); 16 (2007)				
	Tierras Blancas	0.61 ± 0.01 (0.60–0.62)	0.76 ± 0.07 (0.75–0.76)	
	42 (2015); 26 (2016)			

and the difficulty of access to the breeding colonies imposed logistical and safety constraints to monitoring the breeding colonies. Moreover, many breeding burrows were located in soft volcanic soil, making them prone to being altered or destroyed by human activity. Therefore, we took care to ensure that our monitoring activities did not disturb or affect the breeding burrows. Our monitoring regime included reproductive samples chosen non-randomly to maximize spatial representativeness within colonies while ensuring accessibility for the researchers and a low risk of disturbance to the breeding burrows. In each colony, we monitored 30–100 burrows each year (Table 1). We excluded from the sample any burrows that were too long for the infrared camera to confirm nest contents (the 3-m-long camera was sufficient to see the back of the majority of burrows). In the smaller colonies on Santa Clara Island, all viable burrows were included.

The breeding burrows were monitored using a miniature camera with infrared illumination through two stages of the annual reproductive season: (1) burrow occupancy – the viable burrow being occupied by a breeding pair with an egg; and (2) hatching success – transitioning from the presence of an egg in a burrow to the presence of a chick. All of the burrows were monitored during the first stage (burrow occupancy), but not all of them were monitored during the second stage (hatching success) within the same reproductive season. Unoccupied burrows were not monitored for hatching success, and we optimized our monitoring efforts by selecting a sample of occupied burrows to be subsequently surveyed for hatching success. Burrow occupancy was determined by two checks during the incubation period between late December and mid-January. Burrows were considered occupied if an egg was seen once or if an adult was seen in the burrow during both checks (it was not always possible to see the egg under the incubating bird). A previous study determined that >99% of burrows with adults observed during both incubation-stage checks contained an egg (Hodum et al. unpublished data). We determined hatching success by checking burrows once during mid- to late February, following the conclusion of the hatching period. Presence of a chick during this check indicated successful hatching,

while absence of a chick indicated failure to hatch. Burrows with no egg or an unattended egg during the hatching check were considered to have failed to hatch a chick. Similarly to other procellariid seabirds, pink-footed shearwaters are not known to re-lay eggs after the first attempt, so failure to hatch indicated reproductive failure for a breeding pair for the entire year.

Three colonies were monitored on Robinson Crusoe Island (see Fig. 1 & Table 1 for further details): (1) Piedra Agujereada had a total of 87 burrows monitored from 2014 to 2016 (total 64 burrows with information on hatching success, 73.6%); (2) Reserva had a total of 44 burrows monitored from 2005 to 2007 (30 burrows with information on hatching success, 68.2%); and (3) Tierras Blancas had 67 burrows monitored from 2015 to 2016 (all burrows with information on hatching success). Another three colonies were monitored on Santa Clara Island (see Fig. 1 & Table 1 for further details): (1) Cerro Alto had a total of 376 burrows monitored from 2002 to 2016 (221 with information on hatching success, 58.8%); (2) Refugio had a total of 760 burrows monitored from 2002 to 2016 (386 burrows without information on hatching success, 50.8%); and (3) Volcán had a total of 694 burrows monitored from 2002 to 2016 (360 burrows with information on hatching success, 51.9%). Note that the number and spatial location of the breeding burrows monitored were not necessarily constant across the whole study period.

The spatial and temporal autocorrelation induced by our monitoring design was accommodated in our modelling framework that accounts for the year- and island-specific effects (see details below). The between- and within-island variation in the presence of alien mammals allowed us to develop and fit a statistical model to evaluate the impacts of different alien mammal assemblages on the burrow occupancy and hatching success of the pink-footed shearwater (Table 2). The presence of each of the seven alien mammals in each of the six pink-footed shearwater colonies was obtained from the literature (Hahn & Römer 2002, Croxall et al. 2012, Carle et al. 2016) and from our personal observations during the fieldwork. The burrow monitoring data are publicly available from FigShare: [10.6084/m9.figshare.12017814](https://doi.org/10.6084/m9.figshare.12017814).

Table 2. Calculation of the probabilities of burrow occupancy and hatching success as a function of the five alien mammal assemblages in the six colonies monitored.

Alien mammal assemblage	Colony (island) and years of monitoring	Probability of burrow occupancy/hatching success
Seven alien mammals present: black and brown rats (<i>Rattus rattus</i> and <i>Rattus norvegicus</i> , respectively), rabbits (<i>Oryctolagus cuniculus</i>), coatis (<i>Nasua nasua</i>), dogs, cats and cows	Tierras Blancas (Robinson Crusoe), 2015–2016	$po_{sp1} = (1 - po_{-rabbit})(1 - po_{-cow})(1 - po_{-coati})(1 - po_{-other})$ $ph_{sp1} = (1 - ph_{-rabbit})(1 - ph_{-cow})(1 - ph_{-coati})(1 - ph_{-other})$
Only rabbits present	Cerro Alto and Volcán (Santa Clara), 2002–2003	$po_{sp2} = (1 - po_{-rabbit})$ $ph_{sp2} = (1 - ph_{-rabbit})$
Cows absent, all other alien mammals present	Piedra Agujereada (Robinson Crusoe), 2014–2016	$po_{sp3} = po_{-cow}$ $ph_{sp3} = ph_{-cow}$
Cows and coatis absent, all other alien mammals present	Reserva (Robinson Crusoe), 2005–2007	$po_{sp4} = po_{-cow} po_{-coati}$ $ph_{sp4} = ph_{-cow} ph_{-coati}$
All alien mammals absent	Refugio (Santa Clara), 2002–2016, and Cerro Alto and Volcán (Santa Clara), 2004–2016	$po_{sp5} = po_{-rabbit} po_{-cow} po_{-coati} po_{-other}$ $ph_{sp5} = ph_{-rabbit} ph_{-cow} ph_{-coati} ph_{-other}$

$p_{-rabbit}$ = the probability of occupancy (po) or hatching success (ph) given rabbits are absent (i.e., the probability of burrow occupancy or hatching success when only rabbits are absent); p_{-cow} = the probability of occupancy (po) or hatching success (ph) given cows are absent (i.e., the probability of burrow occupancy or hatching success when only cows are absent); p_{-coati} = the probability of occupancy (po) or hatching success (ph) given southern coatis are absent (i.e., the probability of burrow occupancy or hatching success when only southern coatis are absent); $p_{-others}$ = the probability of burrow occupancy (po) or hatching success (ph) given alien mammals other than cows, coatis and rabbits are absent, but cows and rabbits are present (i.e., the probability of burrow occupancy or hatching success when cows, coatis and rabbits are absent, but other alien mammals are present).

Statistical analysis

We developed a model to separate the effects of alien species assemblages (Table 2), the island where the monitored burrows were located (Santa Clara or Robinson Crusoe) and the monitoring year. We assumed that these three factors affected the observed burrow occupancy and hatching success independently. This means that the observed burrow occupancy and hatching success in each monitored burrow were assumed to be the outcomes of the combined, but independent, effects of the three factors. This yielded a model whose components can be interpreted as the probabilities of burrow occupancy and hatching success directly attributable to the alien mammal assemblages, the island and the monitoring year alone, regardless of the effects of the other factors. Therefore, to obtain the probability of burrow occupancy and hatching success in any given breeding burrow on any of the two islands, it was necessary to use the three independent probability estimates together and not separately (see model description below).

We modelled the transitions between the two subsequent stages, defining burrow occupancy and hatching success as a function of five alien species assemblages, monitoring year and island through a Bayesian hierarchical model, whereby one stage depends on the state of the previous stage (Hobbs & Hooten 2015, Kéry & Royle 2016):

$$O_{j,z,y} \sim \text{Bernoulli}(po_{j,z,y} V_{j,z,y}), \quad (1)$$

$$po_{j,z,y} = 1 - ((1 - po_z)(1 - po_{sp})(1 - po_y)), \quad (2)$$

$$\text{logit}(po_y) = \beta oy \text{ year}, \quad (3)$$

where $O_{j,z,y} \in \{0, 1\}$ is the occupancy of breeding burrow j of a colony on island z during year y , $V_{j,z,y}$ is the viability of breeding burrow j of a colony on island z during year y , $po_{j,z,y}$ is the probability of occupancy of breeding burrow j of a colony on island z during year y , po_z is the island-specific probability of burrow occupancy (one parameter for each island), po_{sp} is the alien mammal assemblage-specific probability of burrow occupancy (see Table 2 for equations to derive these probabilities), po_y is the year-specific probability of burrow occupancy and βoy is the effect,

on the logit scale, of the monitoring year on po_y . The hatching success was modelled conditional on burrow occupancy (a burrow needs to be occupied for hatching to occur):

$$H_{j,z,y} \sim \text{Bernoulli}(ph_{j,z,y} O_{j,z,y}), \quad (4)$$

$$ph_{j,z,y} = 1 - ((1 - ph_z)(1 - ph_{sp})(1 - ph_y)), \quad (5)$$

$$\text{logit}(ph_y) = \beta hy \text{ year}, \quad (6)$$

where $H_{j,z,y} \in \{0, 1\}$ is the hatching success in burrow j of a colony on island z during year y , $ph_{j,z,y}$ is the probability of hatching success in burrow j of a colony on island z during year y , ph_z is the island-specific probability of hatching success (one parameter for each island), ph_{sp} is alien mammal assemblage-specific probability of hatching success (see Table 2 for equations to derive these probabilities), ph_y is the year-specific probability of hatching success and βhy is the effect, on the logit scale, of the monitoring year on ph_y .

Note that the effect of the monitoring year was measured by equating the first year when any monitoring occurred (2002) to zero, and subsequent years were re-coded accordingly as one (2003), two (2004) and so on. Therefore, the year 2002 provided the baseline for assessing the temporal trends. The year 2002 was also the reference for those colonies for which the first monitoring took place later than 2002. For instance, this means that the first year that Piedra Agujereada was monitored (2014) was re-coded as 12 in our analyses. By following this approach, together with the cross-validation procedure described below, we reduced the potential biases in the modelling induced by the unbalanced sample size corresponding to each year and colony (Table 1). Moreover, we did not estimate year-specific parameters (i.e., one parameter for each year), but instead a trend across years and colonies. This will further minimize any potential effects of the unequal sample sizes.

Our hierarchical model was fitted to the breeding burrow monitoring data using Bayesian Markov chain Monte Carlo methods implemented in the package *NIMBLE* (de Valpine et al. 2017) as interfaced to the R statistical environment (R Development Core Team 2019). Given the imbalance in the monitoring data (different sample sizes for the two islands and the five invasive species

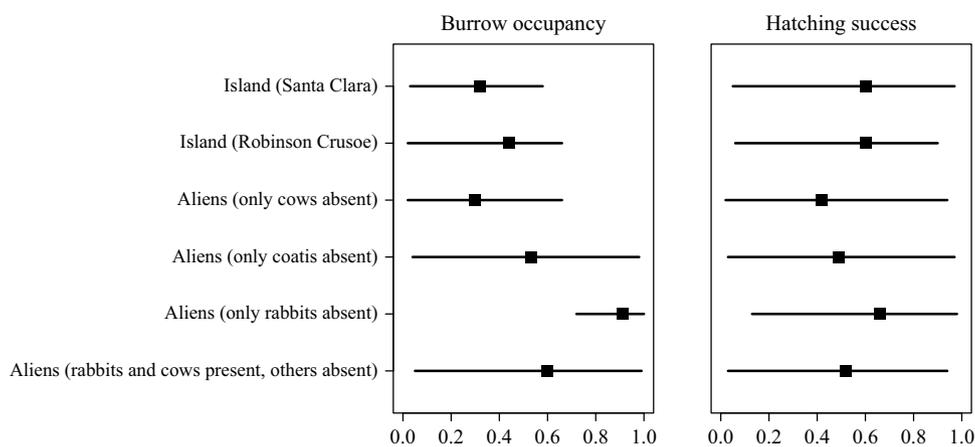


Fig. 2. Posterior estimates (means and 95% credible intervals) of the probabilities of burrow occupancy and hatching success on two islands and with five alien mammal assemblages. See Table 2 for the equations used to estimate these parameters from the monitoring data

assemblages) and the missing hatching success data, we used a 10-fold cross-validation approach to fit and validate the model (Hooten & Hobbs 2015, Roberts et al. 2017, Conn et al. 2018). In each fold, we randomly selected 30 burrow occupancy observations of each alien mammal assemblage (150 observations in total) and randomly assigned 70% of those observations to a within-sample data set (a training data set used to fit the model; 105 observations) and 30% to an out-of-sample data set (a test data set used to validate the model; 45 observations). This procedure produced a total of 150 burrow occupancy observations used in each fold, such that for each alien mammal assemblage there were 21 observations in the within-sample data set and nine observations in the out-of-sample data set.

We ran our Bayesian hierarchical model using one chain with 42 000 iterations and no thinning in each of the 10 folds. We discarded the first 2000 iterations of each fold as burn-in time after visually checking for the appropriate mixing and convergence of the 10 chains (one chain per fold). This procedure produced a total of 400 000 draws of the posterior distribution of all of the parameters in the hierarchical model. We used relatively uninformative Beta priors for all the probability parameters in the hierarchical model $\sim Beta(1,1)$ and an uninformative Normal prior for the effects of the monitoring year, β_{oy} and β_{hy} , $\sim Normal(0, \sigma = 3.16)$. The script for fitting the Bayesian hierarchical model is available in Supplementary Appendix S1 (available online). We assessed the goodness of the fit and the predictive abilities of the hierarchical model by estimating a Bayesian p-value based on the deviance of the model (Hobbs & Hooten 2015, Kéry & Royle 2016, Conn et al. 2018). A Bayesian p-value compares the estimate of a goodness-of-fit test – the deviance in this case – with the test expected value if the model is adequate. Extreme Bayesian p-values (i.e., <0.05 or >0.95) indicate a poor-fitting model (Hooten & Hobbs 2015, Kéry & Royle 2016, Conn et al. 2018).

Results

The percentages of occupied burrows and hatching success were similar across colonies and the two islands when considered collectively (i.e., without accounting for the effects of alien mammals and differences between monitoring years; Table 1). The three colonies on Santa Clara Island had mean burrow occupancy percentages above 50% across monitoring years (Cerro Alto: 55.0%; Refugio: 67.0%; and Volcán: 57.0%). In comparison, the three colonies on Robinson Crusoe Island showed more variability across

monitoring years (Piedra Agujereada: 64.0%; Reserva: 48.0%; and Tierras Blancas: 61.0%). The hatching success in those occupied burrows was relatively high across colonies and, considering the whole study period, was always above 75%. Across years, the mean hatching success of Santa Clara Island’s colonies (Cerro Alto: 75.0%; Refugio: 82.0%; and Volcán: 83.0%) was remarkably similar to the estimates from Robinson Crusoe Island’s colonies (Piedra Agujereada: 82.0%; Reserva: 81.0%; and Tierras Blancas: 76.0%).

Our Bayesian hierarchical model fitted the data (within-sample Bayesian p-value (mean \pm standard error): 0.13 ± 0.08 ; 95% credible interval (CI): 0.03–0.26) and predicted the out-of-sample data adequately (0.34 ± 0.10 ; 95% CI: 0.22–0.48). Nonetheless, the 10-fold 95% CIs for the Bayesian p-value of the within-sample data set also included 0.03, suggesting that in some rare instances the model might not fit the data adequately.

The posterior estimates of the parameters of the model indicated that there were differences in the probability of burrow occupancy, but not in the hatching success. Hatching success was similar across islands and alien mammal assemblages (Fig. 2 & Table 3), with estimates overlapping widely. On the other hand, there were substantial differences in the effects of the same factors on burrow occupancy (Fig. 2 & Table 3). The probability of burrow occupancy was lower in Santa Clara Island than in Robinson Crusoe Island after accounting for the effects of the alien mammal assemblages and the monitoring year (Fig. 2 & Table 3). This result suggests there may be processes other than alien mammal assemblage and year affecting the burrow occupancy of pink-footed shearwaters on Santa Clara Island that do not exist on Robinson Crusoe Island. Both burrow occupancy (monitoring year effect (logit scale), -2.79 ± 2.16 ; 95% CI: -6.54 to 0.18) and hatching success (-1.73 ± 2.00 ; 95% CI: -6.54 to 0.04) showed a negative temporal trend, which suggests that burrow occupancy and hatching success had declined over the monitoring period, regardless of the island and the pressure of invasive mammals. Nonetheless, the posterior 95% CI of the effect of monitoring year marginally overlapped zero, implying that the negative trends were slightly uncertain (Table 3).

The absence of rabbits from pink-footed shearwater colonies resulted in the highest probabilities of burrow occupancy and hatching success compared to the absence of other alien mammals (Fig. 2 & Table 3). The absence of cows, coatis and other alien mammals produced almost identical effects on burrow occupancy and hatching success (Fig. 2 & Table 3). The impacts of alien

Table 3. Posterior estimates of the parameters of the hierarchical model of burrow occupancy and hatching success in six pink-footed shearwater colonies. Note that these estimates show the probabilities independently. In order to obtain the probability of burrow occupancy or hatching success in any given burrow on any of the two islands, it is necessary to use the independent probability estimates together (i.e., the effect of year, the effect of island and the effect of alien mammals).

	Estimated probability of burrow occupancy, mean \pm standard error (95% credible intervals)	Estimated probability of hatching success, mean \pm standard error (95% credible intervals)
Santa Clara Island	0.32 \pm 0.15 (0.03–0.58)	0.60 \pm 0.26 (0.05–0.97)
Robinson Crusoe Island	0.44 \pm 0.18 (0.02–0.66)	0.60 \pm 0.23 (0.06–0.90)
Cows absent	0.30 \pm 0.18 (0.02–0.66)	0.42 \pm 0.27 (0.02–0.94)
Coatis absent	0.53 \pm 0.28 (0.04–0.98)	0.49 \pm 0.28 (0.03–0.97)
Rabbits absent	0.91 \pm 0.08 (0.72–1.00)	0.66 \pm 0.25 (0.13–0.98)
Rabbits and cows present, other alien mammals absent	0.60 \pm 0.29 (0.05–0.99)	0.52 \pm 0.28 (0.03–0.94)
Monitoring year (on the logit scale)	–2.79 \pm 2.16 (–6.54 to 0.18)	–1.73 \pm 2.00 (–6.54 to 0.04)

mammal assemblages on hatching success were more uncertain than they were on burrow occupancy, implying unclear effects of mammal assemblages on the hatching success of the pink-footed shearwater (Fig. 2 & Table 3).

Discussion

Our field monitoring and quantitative modelling revealed that both burrow occupancy and hatching success were similar across six pink-footed shearwater colonies, but these patterns are the product of different underlying mechanisms. The observed variability in burrow occupancy and hatching success was a consequence of the differences in burrow occupancy probabilities rather than in hatching success. Therefore, conservation interventions attempting to improve the reproductive performance of pink-footed shearwaters would better focus on understanding and managing burrow occupancy rather than hatching success. Our results showed that burrow occupancy was determined by the interplay between the impacts of the alien mammal assemblages using the shearwater colonies and other uncertain factors specific to each island. That is, we found differences between the two islands even after controlling for the monitoring year and alien mammal assemblages. Nevertheless, it is important to re-emphasize that our results do not imply that the overall observed burrow occupancy on Santa Clara Island was necessarily lower than on Robinson Crusoe Island, because we modelled the overall burrow occupancy as emerging from the collective effects of the three factors modelled, rather than in isolation.

Our analysis showed that the presence of rabbits had a negative impact on the burrow occupancy of pink-footed shearwaters, whereas the impacts of the other six alien mammals were more uncertain, although they did exist. These findings concur with previous research showing the negative impacts of invasive rabbits on breeding seabirds globally (Imber et al. 2000, Olivera et al. 2010, Brodier et al. 2011, Towns et al. 2016). Interference competition, whereby rabbits monopolize the available habitat and thus exclude breeding shearwaters, is the most likely direct impact of rabbits on pink-footed shearwaters (Ainley & Lewis 1974, Brodier et al. 2011). Rabbits may also affect the burrow occupancy of pink-footed

shearwaters indirectly. For example, rabbit grazing pressure can lead to the severe alteration of plant communities, resulting in seabird burrow damage and breeding habitat loss due to erosion (Bergstrom et al. 2009, Bried et al. 2009).

Interestingly, the uncertain effects of the other six alien mammals, including coatis, rats and cats, on pink-footed shearwater burrow occupancy and hatching success contrasted with the negative effects of alien mammal predators on the reproductive performance of other seabird species reported on other islands (Imber et al. 2000, Jones et al. 2008, 2016, McCreless et al. 2016). Nevertheless, and similarly to our results, the abundance of Mediterranean shearwater species has not been found to be limited by invasive rats (Ruffino et al. 2009). Similarly, rat visitation rates to grey-faced petrel (*Pterodroma gouldi*) nests in New Zealand do not seem to influence hatching success (Stolpmann et al. 2019). It is important to note that we evaluated the negative effects of alien mammal assemblages only on burrow occupancy and hatching success, and it is probable that predatory alien mammals impact other life stages such as chick fledging and/or survival of adults, which we did not assess here. Indeed, there are documented instances of predation on pink-footed shearwater adults and chicks by cats and coatis (Hahn & Römer 2002, Hodum et al. unpublished data). In summary, more information is needed in order to evaluate the hypothesis that only rabbits affect the reproductive ecology of pink-footed shearwaters.

Despite the overall burrow occupancy being similar on Santa Clara and Robinson Crusoe islands (Table 1), our modelling showed that, after accounting for the differences in alien mammal assemblages and temporal trends, burrow occupancy was lower on Santa Clara Island than on Robinson Crusoe Island (Table 2). This result might deserve further research, as it suggests there may be processes affecting the burrow occupancy of pink-footed shearwaters on Santa Clara Island that do not affect the colonies on Robinson Crusoe Island. Potential differences unrelated or indirectly related to alien mammal assemblages that could result in lower occupancy on Santa Clara Island are greater rates of erosion and burrow damage related to loss of native vegetation from intense historical rabbit, sheep and goat herbivory and rockier soil resulting in shorter, perhaps less desirable burrowing habitat.

In addition, we found a negative temporal trend in both burrow occupancy and hatching success, although this trend was marginally uncertain (95% CIs overlapping zero).

The uncertainties reported here require explicit consideration in the conservation management of pink-footed shearwaters (Conroy & Peterson 2013, Groves & Game 2016, Milner-Gulland et al. 2017). Adopting an adaptive monitoring and management approach could help contend with these uncertainties while ensuring that adequate actions are employed to conserve the species (Lindenmayer & Likens 2009, Conroy & Peterson 2013, Salafsky et al. 2016). The continued monitoring of pink-footed shearwater colonies would produce new data that could be used to update our Bayesian hierarchical model, helping narrow the uncertainties in the posterior estimates of our model (Dietze 2017, García-Díaz et al. 2019). It is fundamental to investigate the mechanisms by which alien mammals are producing the negative impacts reported here (e.g., habitat alteration versus competition in the case of rabbits), perhaps framed within the standardised Environmental Impact Classification of Alien Species (Blackburn et al. 2014). This classification system incorporates a standardized set of impact outcomes and mechanisms that can be used to conceptualize and frame hypotheses to explain the processes underlying the reported impacts of the different alien mammals. Moreover, additional research should explore factors not studied here that may be driving the reported differences between islands, as well as the negative temporal trends in both burrow occupancy and hatching success. This research can also be framed within the context of an adaptive monitoring and management programme that updates its methods and objectives with the arrival of new information (Conroy & Peterson 2013, Salafsky et al. 2016).

The conservation of the threatened pink-footed shearwater requires attention to both adult survival rates and juvenile recruitment rates, including burrow occupancy and hatching success, to reach a positive or at least stable population growth rate that will steer the species away from decline (Sæther & Bakke 2000, Croxall et al. 2012). A population viability analysis of the pink-footed shearwater would likely be necessary in order to evaluate the importance of adult survivorship versus recruitment in driving population growth rates, and our model and results can be incorporated into such an analysis (Russell 1999, Sæther & Bakke 2000, Saunders et al. 2018). Managing the presence of alien rabbits in breeding colonies by either eradicating or excluding them would produce higher burrow occupancy rates compared to the current situation. Eradicating rabbits from Robinson Crusoe Island is an important goal to achieve in order to ensure the long-term viability of breeding pink-footed shearwaters (rabbits have already been eradicated on Santa Clara Island and are not currently present in shearwater breeding colonies on Isla Mocha). Due to existing social (gaining local community support) and operational (rugged topography and remoteness) challenges, rabbit eradication on Robinson Crusoe Island is not an immediate prospect (Gregory et al. 2014). In the meantime, other measures can help mitigate the impacts of rabbits on breeding shearwaters. For example, the planned installation in 2020 of a fence to exclude rabbits, cattle, dogs and cats to protect the Piedra Agujereada colony can be an effective interim measure to alleviate the negative effects of these mammals (Carle et al. 2016). In summary, managing rabbits while gathering additional data to fill in knowledge gaps is critical to effectively managing pink-footed shearwater colonies.

More broadly, our findings showcase the crucial role of system-specific information for effectively managing the impacts of alien mammals on seabirds. As demonstrated in our analyses, not all alien mammals affect breeding seabirds equally. Therefore, targeting alien mammals that have been shown to affect seabird populations elsewhere may not be an effective conservation strategy when coping with alien mammals in locations with little or no context-specific information. Alternatively, implementing conservation actions based on pre-existing information and assessing both their efficacy and the impacts of alien mammals using a quantitative approach, drawing on the one described here, will produce new knowledge to support the development of context-specific interventions suited to each situation.

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