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CONTRIBUTED PAPERS

Recovery of insular seabird populations years after rodent eradication

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Abstract

Seabirds have been particularly affected by invasive non-native species, which has led to the implementation of numerous eradication campaigns for the conservation of these keystone and highly vulnerable species. Although the benefits of eradication of invasive non-native species for seabird conservation have been demonstrated, the recovery kinetics of different seabird populations on islands after eradication remains poorly evaluated. We conducted long-term monitoring of the number of breeding pairs of seven seabird species on a small atoll, Surprise Island, New Caledonia (southwestern tropical Pacific). Marine avifauna of the island were surveyed yearly 4 years before to 4 years after rodent eradication (conducted in 2005), and we conducted multiple one-time surveys from ~10 years before and ~15 years after eradication. We sought to determine how different seabird species responded to the eradication of invasive rodents in an insular environment. Three species responded positively (two- to 10-fold increase in population size) to eradication with differences in lag time and sensitivity. The number of breeding pairs increased (effect sizes = 0.49–0.95 and 0.35–0.52) for two species over 4 years post-eradication due to immigration. One species had a longer (at least 5 years) response time than all others; breeding pairs increased for over 10 years after eradication. Long-term sampling was necessary to observe the responses of the seabird populations on the island because of the delayed response of a species to eradication not visible in the first years after eradication. Our results confirmed the positive effects of eradication of invasive non-native species on seabirds and emphasize the importance of mid- and long-term pre- and post-eradication surveys to decipher the mechanisms of seabird recovery and confirm the benefits of eradication for conservation purposes.

KEYWORDS

birds, invasive species, mammals, Oceania, population dynamics, restoration, threatened species

Resumen

Las especies invasoras no nativas han afectado en lo particular a las aves marinas, lo que ha derivado en la implementación de numerosas campañas de eliminación para conservar estas especies importantes y muy vulnerables. Aunque se han demostrado los beneficios de la eliminación de especies invasoras no nativas para la conservación de las aves marinas, se conoce poco sobre la cinética de la recuperación de las diferentes poblaciones insulares después de la eliminación. Realizamos un monitoreo a largo plazo del número de parejas reproductoras de siete especies de aves marinas en Isla Surprise, Nueva Caledonia, un atolón pequeño en el suroeste del Pacífico tropical. Censamos anualmente la

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avifauna marina de la isla cuatro años antes y cuatro años después de la eliminación de roedores (realizada en 2005) y realizamos varios censos únicos de ~10 años antes y ~15 años después de la eliminación. Buscamos determinar cómo las diferentes especies de aves marinas respondían a la eliminación de los roedores invasores en un ambiente insular. Tres especies respondieron positivamente (un incremento poblacional de 2 a 10 veces mayor) a la eliminación con diferencias en el tiempo de desfase y en la sensibilidad. El número de parejas reproductoras incrementó (tamaños eficientes = 0.49 a 0.95 y 0.35 a 0.52) para dos especies cuatro años después de la eliminación debido a la inmigración. Una especie tuvo un tiempo de respuesta más largo (al menos cinco años) que las demás; las parejas reproductoras incrementaron más de diez años después de la eliminación. El muestreo a largo plazo fue necesario para observar las respuestas de las poblaciones de aves marinas en la isla porque una especie tuvo una respuesta retardada que no fue visible en los primeros años después de la eliminación. Nuestros resultados confirmaron los efectos positivos que tiene la eliminación de especies invasoras no nativas sobre las aves marinas y recalca la importancia de los censos a mediano y largo plazo antes y después de la eliminación para identificar los mecanismos de la recuperación poblacional y confirmar los beneficios con fines de conservación que tiene este método.

Recuperación de las poblaciones de aves marinas insulares años después de la eliminación de roedores

PALABRAS CLAVE

aves, dinámicas poblacionales, especie amenazada, especie invasora, mamíferos, Oceanía, restauración

INTRODUCTION

The deleterious effects of invasive non-native species have been documented for many components of the biosphere. When successfully established, they erode biodiversity (Bellard et al., 2016), disrupt ecosystem functioning and services (Kumschick et al., 2015), favor the emergence of infectious diseases (Ogden et al., 2019), and negatively affect human economies at multiple scales (Diagne et al., 2021). Despite growing awareness, the number of transported and introduced species keeps increasing worldwide (Seebens et al., 2017), favored by globalization and global changes (Essl et al., 2020; Levine & D'Antonio, 2003). Because the spread of invasive non-native species contributes to the global biodiversity crisis (Pyšek et al., 2020), mitigating their ecological impacts represents a key scientific and management challenge for the coming decades.

Islands are hotspots of invasive non-native species establishment and impacts (Dawson et al., 2017) due to their particularly high endemic species richness (Kier et al., 2009) and their great vulnerability to invasions (Bellard et al., 2017; McCreless et al., 2016). Isolation (MacArthur & Wilson, 2001), small surface areas, lack of ecological redundancy (i.e., simplified trophic networks), and naiveté of some island species to introduced predators or competitors all contribute to this vulnerability (Heavener et al., 2014). Consequently, the global decline of insular biodiversity is disproportionately faster and more substantial compared with continental biodiversity (Tershy et al., 2015), with invasive non-native species as the main driver (Bellard et al., 2016).

The most important driver of insular extinctions is introduced mammals, among which are cats, rodents, and goats (Courchamp et al., 2003; Doherty et al., 2016; Jones et al., 2016).

Scientists have paid particular attention to invasive rodents, such as Norway rats (*Rattus norvegicus*), black rats (*R. rattus*), Pacific rats (*R. exulans*), and house mice (*Mus musculus*), because of their wide distribution ranges, opportunistic omnivorous diet, and commensal habits (Harris, 2009; Jones et al., 2008).

Island avifauna is especially vulnerable to invasive rodents (Ruffino et al., 2015). Invasive rodents have direct and indirect negative effects on insular bird species, from predation at all stages of the birds' lifecycle to competition for resources (Caut et al., 2008; Duron et al., 2017; Matsui et al., 2010). Because birds are key engineers of island ecosystems (through pollination, seed dispersal, and nutrient deposition), their decline can have catastrophic impacts on island ecosystems through multi-trophic cascading effects (Fukami et al., 2006; Graham et al., 2018; Towns et al., 2009). Among island birds, seabirds are one of the most endangered species groups and have experienced a sharp decline in abundance over the past few decades (Croxall et al., 2012; Paleczny et al., 2015). However, seabirds share unique ecological characteristics and are essential for the functioning and stability of marine and terrestrial ecosystems (Duda, Glew, et al., 2020; Duda, Robertson, et al., 2020; Graham et al., 2018).

Invasive non-native species, climate change, and bycatch are the top three threats to seabirds in terms of overall impacts, number of species affected, and estimated total number of individual birds potentially affected (Dias et al., 2019). Eradicating invasive non-native species—and more specifically invasive mammals—from islands is often considered the most efficient conservation action to preserve biodiversity, and successful eradication campaigns have already been conducted on more than 900 islands worldwide (Jones et al., 2016; Database of Island Invasive Species Eradications (DIISE) 2018,

Spatz et al., 2022). Past examples show that eradications can lead to a partial recovery of ecosystem functions and preinvasion populations in some native species, although the positive effects on bird population dynamics are not always significant (Harper & Bunbury, 2015; Rodríguez et al., 2019). Among the different taxa, seabird populations benefit the most from mammal eradication; 73 populations have recovered (Jones et al., 2016). However, only a few studies have provided comprehensive feedback on seabird dynamics following rodent eradications on islands incorporating the pre- and posteradication dynamics of multiple seabird populations of an insular ecosystem over a long period (e.g., Brooke et al., 2018; Le Corre et al., 2015). This lack of research limits understanding of the different mechanisms behind posteradication dynamics.

To confirm the benefits of invasive non-native species management, we conducted long-term monitoring of seabird populations on Surprise Island, New Caledonia (southwestern tropical Pacific) 10 years before and 15 years after a rodent eradication program.

Our main objective, 16 years after rodent eradication, was to quantify the response of the breeding seabird populations on Surprise Island. We examined which seabird species increased (or not) in the number of breeding pairs after eradication and the rate and extent of this increase.

METHODS

Study site

Surprise Island (18°28'55"S/163°05'12"E) is in the d'Entrecasteaux Reefs, 200 km north of the main island of New Caledonia in the southwestern tropical Pacific. D'Entrecasteaux Reefs are made up of five islands—Huon, Le Leizour, Fabre, Cayes W, and Surprise—and 13 species of breeding seabirds were recorded there from 2002 to 2018 (Robinet et al., 1997) (Appendix S1). Surprise Island is an isolated and uninhabited island of 24 ha and a maximum elevation of 9 m above sea level. Vegetative cover is composed of two main assemblages: a central open patch known as the Plain, covered with bare ground and herbaceous plant species (e.g., Gramineae, Amaranthaceae, Compositae, and Portulacaceae) and a peripheral crown of woody vegetation dominated by *Argusia argentea*, *Scaevola sericea*, and *Pisonia grandis* (Figure 1). Nine species of seabirds have historically nested regularly on the island: brown booby (*Sula leucogaster*), red-footed booby (*Sula sula*), masked booby (*Sula dactylatra*), black noddy (*Anous minutus*), brown noddy (*Anous stolidus*), great frigatebird (*Fregata minor*), lesser frigatebird (*Fregata ariel*), wedge-tailed shearwater (*Ardenna pacifica*), and bridled tern (*Onychoprion anaethetus*). Since 2014, Surprise Island has been included in the Mer de Corail' Natural Park (Martin & Lecren, 2014), which resulted in the prohibition of entering or engaging in any activity related to hunting and fishing on the islet. Moreover, local anthropogenic pressure is particularly low in terms of fishing efforts (e.g., Allain et al., 2016) and there is limited plastic pollution (Berr et al., 2020).

Two non-native rodents—the black rat and house mouse—were accidentally introduced during guano mining in the late 19th and early 20th centuries or during the installation of an automatic weather station in 1965. Studies conducted prior to eradication, as well as initial results immediately following rodent eradication on Surprise, highlight the detrimental effects of these non-native rodents on the island's ecosystem. For rats, direct observations revealed predation on seabird eggs and chicks, and diet analysis confirmed seabird consumption (Caut et al., 2008). The direct effect of mice was less studied, but there was an overlap in diet between the two rodent species, and removal of the rats could have led to a release of the mice and thus created further negative impacts of mice on the island's ecosystem (see Caut et al., 2009 for more details). Given these negative impacts, both rodents were eradicated in 2005 and successful rodent eradication was confirmed in 2006 (Caut et al., 2009), a notable result given the high probability of failure attributed to rodent eradications in tropical atolls (Holmes et al., 2015; Keitt et al., 2015). In addition, no release of introduced plant species or invertebrates was detected on Surprise after eradication, which might have been expected given the change in ecosystem functioning induced by rodent eradication (Caut et al., 2009; Courchamp et al., 2011).

Core survey data collection

We conducted standardized pre- and posteradication sampling, which we refer to as the core survey, every year from November to December from 2002 to 2009. The core survey, therefore, included 4 years pre- (2002–2005) and 4 years posteradication (2006–2009). Numbers of seabird breeding pairs were estimated for each species with line transects designed for the multitrophic survey of the eradication program. Ten parallel transect lines, 230–420 m long, were set up across the island and spaced 50 m apart to avoid counting the same birds several times (Figure 1). Transect orientation was assessed using a compass and it covered the whole island. Seabirds were counted in 10-m-wide sections (5 m each side of the transect lines) by observers walking along transect lines. Counts were conducted every 10 m, thereby covering successive 100-m² transect sections. For each 100-m² section, the number of seabirds were counted and the status (adult, juvenile, and chick) of individuals and vegetation type were noted. Four main types of vegetation covered the transects: two arborescent (*Pisonia grandis* or *Argusia argentea*), one shrub (*Scaevola sericea*), and the Plain.

Species sampled

We focused our core survey on brown booby, red-footed booby, masked booby, black noddy, brown noddy, great frigatebird, and lesser frigatebird. Data were combined for both species of noddies and both species of frigatebirds due to the imperfect taxonomic distinction made by the different observers. For logistical reasons, the time spent surveying was short, the



FIGURE 1 Surprise Island, d'Entrecasteaux Reefs, New Caledonia. Types of vegetation patches and the topography, anthropogenic modifications, and survey transect start markers are shown (black crosses) for 2005.

number of observers was limited, and burrow scopes could not be used; thus, we did not count shearwaters and removed this species from the analyses. Bridled terns, which were likely extirpated by rats prior to our core surveys, were also removed.

Great and lesser frigatebirds, red-footed boobies, and black noddies nests were mostly found in shrubs or trees. Great frigatebirds were also observed nesting on the ground on herbaceous vegetation in open areas, similarly to brown boobies. Masked boobies nested at the top of the beach, either on the sand, on coral debris, or in the grass of the upper beach vegetation ridge. Brown noddies laid eggs in habitats similar to the latter or in small bushes, often in near the beach, but also on the flat part of the island.

The three species of boobies and noddies breed all year round in the d'Entrecasteaux area, and frigatebirds breed during the winter (June–November), and their breeding appears more synchronized than boobies and noddies (Robinet et al., 1997). Survey protocols were approved by the French Ministry of Agriculture (R-45GRETA-F1-04).

Number of breeding pairs

During each survey, the collection number of breeding pairs of each nesting species was recorded. This number was recorded as

the number of “active” nests (i.e., nests on which either adults, eggs, or chicks were observed). In remote, dense island seabird colonies, this method is used to lower the risk of underestimation when a large proportion of adult breeders fly above the island when observers approach (Le Corre et al., 2015; Robinet et al., 1997). Another possibility to estimate the total amount of breeding birds is to use correcting factors that account for breeding failure at each stage (i.e., a juvenile is weighted by its survival chance at this stage; the chance of survival for a juvenile is higher than for a chick or an egg). To be consistent with previous studies (e.g., Robinet et al., 1997) and to confirm the possibility of using correcting factors, results using this method are in Appendices S8–S10.

Effect of eradication on seabird density

To examine the effect of rodent eradication on the seabird populations during our core survey, we applied a generalized linear mixed-effect model (GLMM) with a negative binomial distribution and used the Bayesian approach in the brms R package (Bürkner, 2017; R Core Team 2021). We investigated the species-specific effect of the eradication on the number of breeding pairs per 100-m² section by using two fixed effects: species of the breeding pairs counted and the number of years

after eradication. We added two random factors to the models: location of the section on the transect (section) and vegetation of the transect section (habitat). Because we assumed that species respond differently to eradication, we implemented a model incorporating an interaction between species and the effect of the number of years after eradication:

$$\text{number of breeding pairs per } 100 - m^2 \text{ section}_{i,t} \sim \mu + \text{species}_i + \beta_{\text{eradication}_i} \times t + (1|\text{section}) + (1|\text{habitat}) + \epsilon_{i,t}, \quad (1)$$

where species is a factor with five levels (*i*: brown booby, frigatebirds, masked booby, noddies, or red-footed booby), *t* is an integer representing the year after eradication (*t* = 0 for surveys from 2002 to 2005, *t* = 1 for 2006, *t* = 2 for 2007, *t* = 3 for 2008, and *t* = 4 for 2009), and $\beta_{\text{eradication}_i}$ is the linear coefficient representing the effect of the year after eradication considering the focal species. Section is a factor with values from 1 to 42 (1, close to the west beach, and 42, close to the east beach), and habitat is a factor with one of five habitat types (*Argusia argentea*, *Pisonia grandis*, Plain, *Scaevola sericea*, and not specified).

We tested whether rodent eradication influenced seabird community densities by examining whether the 95% confidence interval (CI) of $\beta_{\text{eradication}_i}$ did not include 0. The residuals of all the GLMMs were verified using the DHARMa R package (Hartig, 2019). The conditional effects of $\beta_{\text{eradication}_i}$ were plotted using the conditional_effect() function of the R package brms. We compared the 95% highest posterior density interval (HPDI) of the estimated marginal means of linear trends (EMMLT) among the different species in the year after eradication in the emmeans R package (Lenth, 2022).

Extrapolated total number of seabird breeding pairs on the island

Following Robinet et al. (1997), we estimated the total number of breeding pairs of each species (*i*) on Surprise Island each year (*t*) with the following proportional formula:

$$\text{abundance total}_{i,t} = \text{abundance transect}_{i,t} \times \frac{\text{total surface of Surprise covered with vegetation}}{\text{Transect surface}_t}, \quad (2)$$

where the number of pairs of species *i* was counted in year *t* with our transect method and corrected by the surface covered in the transect in year *t*. Because the transects were designed to cover a large part of the island across all the habitats (Figure 1), they were considered representative of the total surface coverage. The surface of Surprise Island covered with vegetation was equal to 204,000 m² at the time of the core study. This extrapolation was done to compare our core survey with the extended surveys (see below).

Extended surveys data collection

We also compiled data from extended seabird surveys conducted on Surprise Island 10 years before and 12 years after our core survey (Table 1). Data from the two surveys before eradication conducted in December 1995 and December 1996 were taken from Robinet et al. (1997). These two surveys used a similar method to our core survey by extrapolating the total number of breeding pairs from transect count data. Robinet et al. (1997) used five transects, and the number of breeding pairs was estimated by converting the number of nests, chicks, and juveniles to the number of breeding pairs via conversion factors (as we did in Appendix S8-S10).

Five other posteradication surveys were conducted in March and October 2017, July 2019, and February and July 2021. The October 2017 survey was conducted in a way similar to the core survey. Because reopening of the line transects became impossible following the classification of Surprise Island as a wilderness area, numbers of breeding pairs were exhaustively counted during subsequent surveys. Because boobies and noddies breed throughout the year and the number of breeding pairs was measured as the number of active nests, we did not expect too much bias in the number of pairs counted induced by the difference in dates between the extended and core surveys. Therefore, we kept in our analyses all extended surveys. When two surveys took place in the same year, we kept only the maximum number of breeding pairs observed between the different surveys. For frigatebirds, which have a more finite breeding season (June–November), we retained only the October 2017 survey, which was the closest in the season to the core survey and corresponded primarily to juvenile breeding.

RESULTS

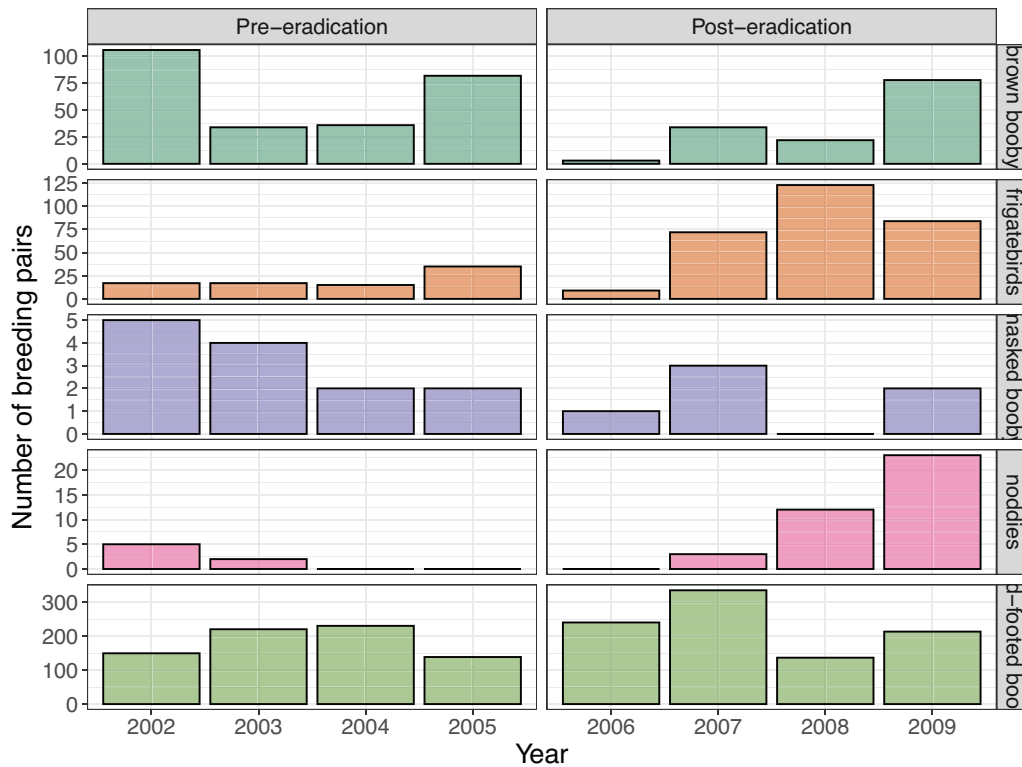
Overview of the core survey data 2002–2009

Considering seabirds counted along the 10 transects during eight surveys, divided into four before and four after eradication, Surprise Island was dominated by boobies and specifically red-footed boobies (Figure 2). Specifically, red-footed boobies were the most abundant species over these 8 years; there were a minimum of 137 breeding pairs counted along the 10 transects and an average of 209 breeding pairs (SD 67). Brown booby and frigatebirds were the second most abundant species with, respectively, a mean of 50 breeding pairs (35) and 47 (42). Before eradication, the maximum number of breeding pairs of frigatebirds was 35, but it reached 123 after eradication. Noddies, with a mean of 6 (8), and masked booby, with a mean of 2 (2), were the less abundant species. As for frigatebirds, noddies showed a much higher maximum number of breeding pairs after eradication: five in the before eradication versus 23 after eradication.

According to our core survey, frigatebirds, red-footed boobies, and noddies occurred mainly on trees and shrubs, whereas brown and masked boobies were in the Plain (Appendix S2).

TABLE 1 Overview of the different surveys used to build the seabird long-term monitoring on Surprise Island.

Year	Month	Type of data	Survey	Invasive rodent presence	Reference
1995	November—	total number of breeding pairs extrapolated from a count on five transects	extended	yes	Robinet et al. (1997)
1996	December				
2002		total number of breeding pairs extrapolated from a count on 10 transects	core		
2003					
2004		number of breeding pairs per 100-m ² transect section along the 10 transects			
2005					
2006				no	
2007					
2008					
2009					
2017	March	total number of breeding pairs extrapolated from a count on 10 transects	extended		
2017	October	total number of breeding pairs with an exhaustive count			
2019	July				
2021	February				
2021	July				

**FIGURE 2** Annual number of breeding pairs for five seabirds surveyed on Surprise Island from 2002 to 2009 along 10 transects. Graphs on the left show results of four surveys conducted before rodent eradication from (2002 through 2005) and the graphs on the right show results of four surveys conducted after the rodent eradication (2006 through 2009).

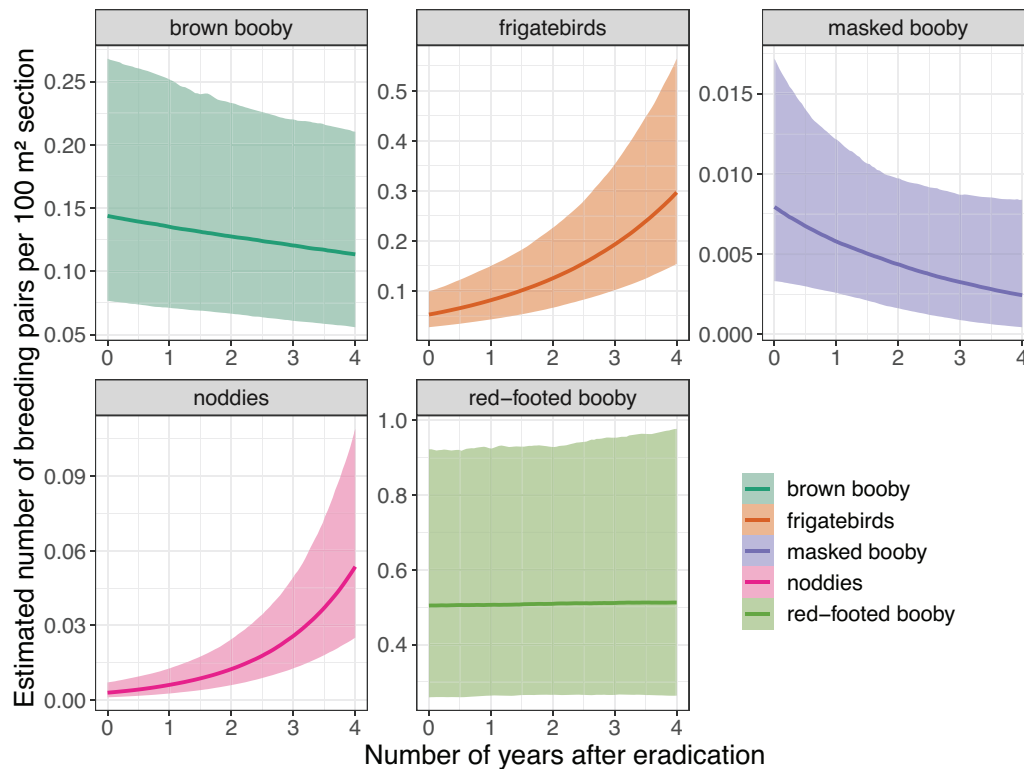


FIGURE 3 Effect of rodent eradication on the number of seabird breeding pairs (covered on axis label) on Surprise Island during transect sampling from 2002 to 2009 (dotted lines, estimated marginal means; shading, 95% CI from the generalized linear mixed model). The y-axis is different for each species.

Response of seabird species to eradication

Regarding the response of each species or group of species, the GLMMs (95% CI Bayesian $R^2 = 0.097\text{--}0.14$) showed that the eradication influenced the number of seabird breeding pairs counted in the transect sections during the 4 years following the eradication: $\beta_{\text{eradication, frigatebirds}} = 0.24\text{--}0.64$ and $\beta_{\text{eradication, noddies}} = 0.40\text{--}1.07$ (Appendices S3–S7). Among the species and group of species, only frigatebirds and noddies showed an early positive response to eradication (Figure 3). Furthermore, the strength of their response was equivalent, 95% HPDI of EMMLT = 0.49–0.95 for noddies and 95% HPDI of EMMLT = 0.35–0.52 for frigatebirds. The three species of the genus *Sula* showed no early response to eradication: 95% HPDI of EMMLT = -0.061 to 0.063 for the red-footed boobies, 95% HPDI of EMMLT = -0.68 to 0.077 for the masked boobies, and 95% HPDI of EMMLT = -0.15 to 0.015 for the brown boobies.

Extended surveys and assessment of long-term population dynamics

Looking at the total number of breeding pairs on the island (extrapolated for the 1995 and 1996 extended surveys and for the 2002–2009 core survey data), the rapid responses of noddies and frigatebirds in the years following eradication were confirmed by the recent surveys (Figure 4). Noddies showed

the strongest response with a 10-fold increase in total abundance from before eradication (400 breeding pairs extrapolated in December 1995) to the latest surveys (5346 breeding pairs in 2021). For frigatebirds, 1586 breeding pairs were found in October 2017, which corresponded to a six-fold increase compared with the level before eradication (398 pairs in December 1996). However, the number of frigatebird pairs increased less strongly after 2009 than the number of noddy pairs. For example, the number of frigatebirds breeding pairs extrapolated was 707 in 2008 and 484 in 2009. Unlike frigatebirds and noddies, no change in the abundance of red-footed booby was detected in the 4 years following the eradication, although the inclusion of the extended surveys revealed an increase in the total breeding population counted of red-footed booby, which reached 4698 pairs in 2017, 5548 in 2019, and finally 3256 in 2021. Before eradication, the extrapolated number of red-footed booby pairs never exceeded 2883. By contrast, brown booby and masked booby still showed no long-term positive response to the eradication.

DISCUSSION

General seabird population trends

Rodent eradication on Surprise Island benefited several seabird populations. The number of breeding pairs of noddies and

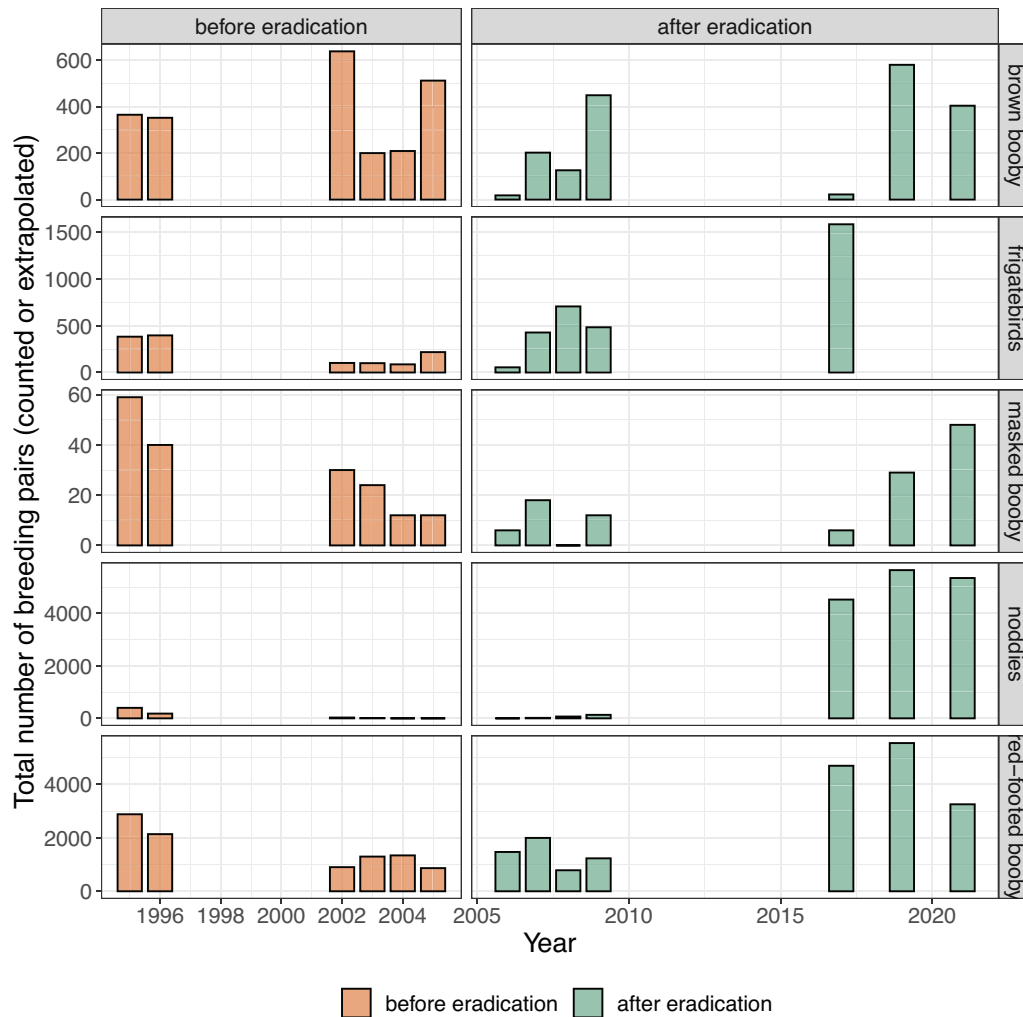


FIGURE 4 Dynamics of seabird breeding pair populations from 1995 to 2021 on Surprise Island before (orange) and after (blue) rodent eradication. Three data sources were combined: transect surveys performed by Robinet et al. (1997) from 1995 to 1996, our core surveys from 2002 to 2009, and our recent surveys from 2017 to 2021. The maximum number of pairs observed per year for each species is shown for every species except frigatebirds. Due to their synchronous phenology, only the October 2017 survey was retained for frigatebirds. The total number of breeding pairs was extrapolated for all the surveys before 2017 and counted thereafter.

frigatebirds increased rapidly after the removal of the two invasive rodents, and breeding pairs of red-footed boobies also increased but more slowly. Assessment of these trends was only possible because of the long duration of the surveys, which spanned over 20 years and began before eradication, allowing the establishment of robust population trends prior to eradication and the observation of changes in population dynamics that would not be visible immediately after eradication.

Our core survey showed an increase in the density of breeding pairs since eradication in 2005, but only for frigatebirds and noddies. This early and substantial increase in the number of breeding pairs supports the positive effect of rodent eradication on frigatebirds and noddies, regardless of vegetation changes on Surprise. The five more recent extended surveys not only strongly confirmed these trends, but also demonstrated the subsequent increase in red-footed boobies. Since 2007, the number of breeding pairs of frigatebirds was much higher than

observed before eradication. The increase in the number of nesting pairs of noddies has been confirmed since 2017, and the species has become one of the most abundant on Surprise. The recent increase in red-footed booby breeding pairs (observed since 2017) suggests mainly a higher breeding success for this species (Le Corre et al., 2015). In addition, even if most seabird species show philopatric trends, because Surprise Island is now rodent free, seabird individuals from nearby islands could be attracted to Surprise. In contrast, masked booby and brown booby populations have not yet increased. This difference in species responses led to a seabird community shift from a booby-dominated community to a more diverse community with frigatebirds and noddies in larger proportions.

Similar changes in an equivalent seabird community have already been documented after rodent eradication in a long-term monitoring program. Le Corre et al. (2015) found that modeling the combination of two mechanisms, increase in

breeding success and immigration of new breeding pairs, could be responsible for the increase in the number of breeding pairs of red-footed boobies only 6 years after eradication. The delayed response of red-footed booby and the mechanisms explaining their increase seem consistent with the posteradication dynamics we found on Surprise. Other studies showed positive trends in other seabird populations following the eradication of rodents (Barbraud et al., 2021; Brooke et al., 2018), with positive responses occurring around 10 years after eradication. These results show that following rodent eradication, the response time of the seabird populations could be particularly long, mainly because these species exhibit delayed sexual maturity and are long-lived (among other factors). Consequently, our results confirm the positive effects of eradication on seabird populations within a decade and show that positive trends can be observed within 4 years of rodent eradication for some species. We have thus shown that the benefits of eradications can be seen and quantified quickly for seabird populations.

The absence of a control island means we could not definitively validate the causal link between the rodent eradication and the increase in frigatebirds, noddies, and red-footed booby populations. However, we found no clear relationships between the seabird community dynamics and fluctuations in climate (temperature, precipitation, and winds) or inshore and offshore primary productivity (Appendix S11). In addition, there is no documented evidence of growing seabird populations on nearby archipelagos (e.g., islets in the Great Barrier Reef [Woodworth et al., 2021]), although the closest neighboring islands (d'Entrecasteaux Reefs, Chesterfield Archipelago) are too poorly studied to accurately assess long-term trends.

Seabird species-specific responses to rodent eradication that outweigh habitat change

Because positive responses from frigatebirds and noddies were visible 4 years after eradication, it can be assumed that the increase in breeding pairs in the early posteradication phase may be primarily due to the settlement of source populations from other atolls to d'Entrecasteaux Reefs, some located 20–60 km from Surprise (Robinet et al., 1997). This increase may be due to the disappearance of rodent signals or an increase in the amount of nesting sites available (Courchamp et al., 2003; Watari et al., 2011). However, according to our results, these early increases are not due to a change in vegetation but rather to an increase in the density of breeding pairs in the same habitat type.

For frigatebirds, predation by rodents, whether on adults, chicks, or eggs, is not well known (Jones et al., 2008). However, such predation is rather unlikely given the strong nest-defensive behavior of frigatebirds (Atkinson, 1984; Jones et al., 2008), so we did not expect a strong predation release effect (especially on adults). In addition, frigatebirds generally lay only one egg per clutch, take care of their offspring for a very long time, and reach sexual maturity after at least 7 years (Nelson, 1976). Therefore, they generally exhibit a slow life history, and increases in breeding success or adult survival cannot result in a rapid breeding population increase. However, even though frigate-

birds are highly philopatric species, they are also very mobile, even during breeding (Dearborn et al., 2003; Weimerskirch et al., 2017). Thus, the gradual increase in the early posteradication stage of these species on Surprise Island is more likely due to the immigration of new seabirds from the closest atolls of the d'Entrecasteaux Reefs rather than additional survival chances in the existing population. The small increase in the number of frigatebird breeding pairs seems to confirm the small or no effect of predation release. In contrast, noddies are small species (between 100 and 200 g for an adult) and thus more vulnerable to predation by rodents, especially their eggs and juveniles. Furthermore, noddies reach sexual maturity faster (e.g., 3 years for black noddies [Gauger, 1999]). In addition to the immigration effect (also coming from the atolls of the d'Entrecasteaux Reefs), a significant effect of predation release could be a reason for their very large increase since 2006 which, unlike the frigatebirds, continued after 2009.

Red-footed boobies showed a more delayed increase in the number of breeding pairs. Like frigatebirds, boobies are large birds (more than 1 kg for adults), and predation by rodents is also not much documented for these species, but a predation release effect was already documented on a small island by Le Corre et al. (2015). We hypothesize that the gradual change in vegetation following rodent eradication progressively increased the amount of habitat available to red-footed boobies, and, combined with a light predation release effect, this led to a delayed increase in their numbers. Since the 2005 eradication, we observed a strong variability of the shrub cover between years mainly due to the fluctuation of rainfall and extreme climatic events (e.g., cyclones) from 1 year to another and a gradual closure of the Plain to shrubs. The reasons for this closure are not known, but we assume that a cascade effect induced by the eradication of rodents could be the cause (Watari et al., 2011). According to Le Corre et al. (2015), a later immigration of other individuals from the atolls of the d'Entrecasteaux Reefs could also have influenced the large increase in the number of breeding pairs on Surprise.

We assumed that brown boobies would respond positively to eradication because they nest on the ground and are, therefore, more susceptible to disturbances and predation by rodents, as are red-footed boobies. However, they are less sensitive to predation because of their biological characteristics (Jones et al., 2008). In addition, the closure of the Plain made brown booby's nesting place much smaller and less suitable, which could partially explain their lack of numerical response.

The lack of response from masked boobies is less surprising because, on the one hand, their distribution was limited to beaches, which could have protected them in part from predation and modification of vegetation by rodents. On the other hand, other studies show that masked boobies coexist and have even recolonized islands where rats are present (e.g., Bolton et al., 2011).

Although we focused only on boobies, frigatebirds, and noddies in our study, we have noticed recent signals of possible recolonization of bridled terns on Surprise. We observed two breeding pairs in 2021; thus, they could be one of the other species benefiting from rodent eradication on Surprise Island.

Throughout our study, we did not differentiate the effects of the two rodent species. Both species have negative effects on seabirds (Shiels et al., 2014), and studies prior to rodent eradication focused more on the rat because there were more of them and evidence of their predation on seabirds was greater (Caut et al., 2008 and 2009). However, considering that mice can have a strong negative effect on seabirds, directly or indirectly, and eradication of rats without eradication of mice could lead to a massive increase of the mouse population due to competition release (Caut et al., 2007), eradication of mice in addition to rats was necessary. Thus, the benefits of eradication observed on surprise cannot be attributed to the removal of only one or the other rodent species but to the combination of both.

Phenology as a buffer to seabird response dynamics

In contrast to species that breed all year round in the d'Entrecasteaux area, frigatebirds are winter breeders. Because we included only one recent extended survey for frigatebirds (October 2017), our results should be interpreted with caution. A shift in the phenology of the breeding pairs following eradication could be also an explanation for the increasing number of breeding pairs during our core survey. The core survey took place from November through December, a time that corresponds to the end of the breeding season for frigatebirds. Consequently, a shift in breeding time could induce a deferment of peak breeding; thus, the number of pairs present during this season would be more important than before eradication. However, the October 2017 survey showed a population of 1586 breeding pairs versus a population of 220 in 2005, and it seems unlikely that such an increase was due only to a change in phenology. Such effects are not expected for the other species, because of their year-round phenology (absence of a phenological peak); however, strong interannual variations should be considered. This is particularly the case for red-footed boobies, which showed strong variability in the number of breeding pairs between 2017 and 2021. Because of this high variability, continuing to monitor this species would be prudent, especially to confirm the observed increase.

Conservation perspectives

The benefits of eradicating invasive rodents are not restricted to seabird communities; it also benefits other groups of organisms. On Surprise Island, an increase in skink and some invertebrates was also documented (Watari et al., 2011). Elsewhere, some direct and indirect effects of invasive rodents have also been reported on insect communities (St Clair, 2011, Holthuijzen et al. 2021), intertidal communities (Kurle, 2021), and even island-adjacent coral-reef ecosystems (Benkwitt et al., 2021) and nearshore ecosystems (Rankin & Jones, 2021).

To improve understanding of island species responses to invasive non-native species eradications, three key elements must be considered. First, monitoring communities before erad-

ication is necessary not only to highlight the negative effects of invasive non-native species, but also to understand ecosystem functioning, through at least main species interactions, and prevent, as much as possible, unexpected cascading effects following eradication (e.g., increased abundance of other invasive species in response to reduced predation [Caut et al., 2009]). The monitoring of communities before eradication is also necessary to establish a baseline and produce better quantification of eradication effects. Second, the first few years after eradication appear to be extremely informative for predicting the longer-term effects; these early trends were confirmed in longer-term community-wide analyses. Although post-eradication surveys may occur less frequently, regularly scheduled surveys over the long-term are particularly important to track and evaluate ecosystem and species responses to rodent eradication. Finally, long-term monitoring is essential to consider the main responses of the island community to eradication because, as we have shown, these responses are complex, occur over multiple time scales and periods, and are species-specific. Ideally, similar ecosystems that have not been negatively affected by invasive non-native species or are unmanaged should be studied in parallel to better assess the changes induced by conservation actions (e.g., before-after control-impact protocol [Caut et al., 2009]). Last but not least, this should improve understanding of insular ecosystem ecology and promote conservation funding.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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