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FEATURE PAPER

Seabird population changes following mammal eradications on islands

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island restoration; invasive mammals; eradication; population growth rate; lambda; species recovery; natal philopatry; seabirds.

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Abstract

Seabirds are among the most threatened groups of birds, and predation by invasive mammals is one of the most acute threats at their island breeding stations. Island restoration projects increasingly involve the eradication of invasive non-native mammals, with benefits for seabirds and other island fauna. To date, demonstrated benefits of invasive mammal eradication include increased seabird nesting success and enhanced adult survival. However, the recovery dynamics of seabird populations have not been documented. Drawing on data from across the world, we assemble population growth rates (λ) of 181 seabird populations of 69 species following successful eradication projects. After successful eradication, the median growth rate was 1.119 and populations with positive growth ($\lambda > 1$; $n = 151$) greatly outnumbered those in decline ($\lambda < 1$; $n = 23$, and seven showed no population change). Population growth was faster (1) at newly established colonies compared to those already established, (2) in the first few years after eradication, (3) among gulls and terns compared to other seabird groups, and (4) when several invasive mammals were eradicated together in the course of the restoration project. The first two points suggest immigration is important for colony growth, the third point reflects the relative lack of philopatry among gulls and terns while the fourth reinforces current best practise, the removal of all invasive mammals where feasible.

Introduction

Although islands occupy only *c.* 5% of terrestrial surface area, 37% of all critically endangered bird species on the IUCN Red List inhabit islands (Ricketts *et al.*, 2005; Tershy *et al.*, 2015). Moreover, 88% of the 140 bird species that have gone extinct since 1500 were endemic to islands (Butchart, Stattersfield & Brooks, 2006). Invasive non-native mammals (hereafter, invasive mammals) are the main cause of animal extinctions on islands and one of the most important threats to remaining insular biodiversity (Medina *et al.*, 2011; Tershy *et al.*, 2015; Bellard, Cassey & Blackburn, 2016). Eradicating invasive mammals from islands is an increasingly common conservation tool, with more than 1200 projects undertaken worldwide (DIISE, 2015). Successful projects have delivered such benefits as positive demographic and distributional changes in a wide variety of taxa (Jones *et al.*, 2016), as well as wider ecosystem enhancement (Mulder *et al.*, 2011).

Amongst the potential beneficiaries of such eradication projects are many of the world's seabirds. Seabirds are one of the most threatened of all bird groups (Croxall *et al.*, 2012), due to a combination of impacts at breeding locations from invasive species, especially on oceanic islands, and at-sea threats. The latter arise mainly from interactions with fisheries, changes in prey stocks and pollution (Derraik, 2002; Jones

et al., 2008; Croxall *et al.*, 2012; Zydelis, Small & French, 2013; Frederiksen *et al.*, 2014; Clarke, Sato & Small, 2014).

There is increasing evidence that control or eradication of invasive mammals can benefit seabird populations on islands where they nest. For example, following eradication, breeding success can be enhanced either via an increase in hatching success and/or an increase in fledging success (Cooper *et al.*, 1995; Towns & Broome, 2003; Rayner *et al.*, 2007) while adult survival may also improve (Keitt & Tershy, 2003; Williams, Byrd & Konyukhov, 2003). Islands, abandoned by certain species, can be recolonized (Ratcliffe *et al.*, 2010; Buxton *et al.*, 2014), although this is not assured (Miskelly & Taylor, 2004). There is also the possibility that hitherto-unoccupied islands are colonized. However, few studies have established that changes in seabird breeding and survival parameters actually lead to long-term population increases (Lavers, Wilcox & Donlan, 2010). Such increases are, arguably, the metric by which the success of invasive mammal eradication efforts for seabird conservation should be judged (Gerber, DeMaster & Roberts, 2000).

Evaluating the impact of invasive mammal eradication on seabird population trajectories on islands presents challenges. This is partly due to the life-history characteristics of seabirds, where several years elapse between fledging and the onset of breeding (e.g. over 10 years in the case of some albatross species, Diomedeidae). This means that, if an eradication programme enhances seabird breeding success, there will be a substantial lag before the enhanced breeding success leads to higher recruitment to and growth of the breeding population. This delay in population growth would be reduced were there substantial immigration. However, many seabird species are commonly assumed to be strongly philopatric, returning to their natal site to breed, and restricting immigration to enhance recruitment at other sites (Warham, 1990; Coulson, 2002).

Not only have the slow life-histories of seabirds contributed to the paucity of robust post-eradication seabird monitoring programmes (Buxton *et al.*, 2014), but also the necessary timescale for adequate monitoring, ideally at least 10 years, is often beyond the remit of funding agencies. This is especially true when the monitoring may need to be undertaken on remote, logistically demanding, and correspondingly costly islands. However, such monitoring, on a biological timescale compatible with seabird life history, is essential if the value of eradication programmes to seabird populations is to be demonstrated to funders – who often fund eradications specifically in the hope of conserving seabirds (Kappes & Jones, 2014). Moreover, monitoring is a key component of adaptive island management, where the mechanisms of recovery can inform future conservation initiatives (Buxton *et al.*, 2016).

While detailed long-term seabird monitoring certainly poses challenges, it does offer advantages for measuring the success of island restoration projects. Because seabird biology is well known, population changes can arguably be more fully understood than can changes in the populations of other, poorly researched taxa. In addition, the fact that seabirds often have a well-defined and largely synchronous breeding season, particularly on higher latitude islands, means only a single, suitably timed visit is required each year. Finally, conspicuous vertebrates, like seabirds, can represent umbrella species whose improved status, achieved via island restoration, promotes benefits to other lesser known taxa (Aslan *et al.*, 2015).

The initial aim of our study was therefore to bring together for the first time the scattered global data on seabird population changes after successful invasive mammal eradications. We then proceeded to examine what factors may influence rates of population recovery.

Seabird recovery could potentially be influenced by intrinsic factors affecting population growth, such as seabird species or taxonomic group. It could also be influenced by such extrinsic factors as whether the mammal eradicated was a predator of adult seabirds (e.g. feral cat *Felis catus*) or young seabirds (e.g. rat *Rattus* spp.). Another potential influence is the size and proximity of neighbouring colonies. We hypothesized that immigration would be more extensive (Buxton *et al.*, 2014), and therefore colony growth immediately after an eradication project would be more rapid, closer to larger colonies. This could influence decisions about future eradication projects.

Given the delayed maturity of seabirds, any population growth immediately after eradication is likely largely due to immigration. Only after the passage of several years, namely the number of years elapsing between an eradication project and age at first breeding, will higher recruitment of the chicks reared after the eradication contribute to growth. Where possible, we therefore compared on-island population growth in the years between eradication if there was a colony already present, or colonization if a new colony was established post-eradication, and the species' age of first breeding, and subsequently.

Materials and methods

Data collation

The DIISE database provides information on islands where vertebrate eradications have been undertaken, the mammal or other species eradicated, whether or not the project was successful, and contact details for those involved. We used this database as a starting point to identify original sources describing which mammal eradications were successful (defined as a failure of targeted attempts to detect the mammal concerned 2 years after eradication), and subsequently collated data (from publications, technical documents and direct contact with practitioners) on seabird population growth rates from as many of these islands as possible. We excluded islands where reinvasion subsequently occurred and negative seabird impact continued, but did include islands where these incursions were stopped in a timely manner and thus not expected to impact potential seabird benefit. We ignored instances where it was extremely unlikely that the eradicated mammal would have had any influence on the seabird (e.g. mice at a king penguin *Aptenodytes patagonicus* colony). To the best of our knowledge, none of the seabird colonies were

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established by translocation and only one, that of Monteiro's storm-petrel *Hydrobates monteiro* on Praia, witnessed a conservation intervention, namely provision of extra nest-boxes, that might have influenced population change after invasive eradication. With one exception, the growth of the wedge-tailed shearwater *Puffinus pacificus* colony at Kaena Point, Oahu, Hawaii (VanderWerf *et al.*, 2014), the data come from relatively small islands (<300 km^2), and not 'inland islands' protected by predator-proof fences.

While some data allowing population growth calculation were obtained from published literature, a large proportion was obtained via correspondence with researchers involved in the project. The data sources are detailed in the supplementary material. This data acquisition phase lasted from mid-2014 to the end of 2015. If published data were relatively recent, up to 2010 or a more recent date, we did not attempt to collect further census data from correspondents.

To be included in further analysis, seabird populations, more precisely the number of adult breeding pairs, had to be censused at the time of eradication, or at the time of recolonization, and at least once more after eradication or recolonization. Proxy estimates of breeding population, for example, number of chicks raised, were not used since the ratio of chicks raised to pairs breeding is likely to be different before and after an eradication. For eradications of cats and ungulates that required extended campaigns, in some cases, we do not utilize the final year of eradication, but rather the year in which the vast majority of animals were removed as 'year zero' for calculating lambda, because this year heralded a sufficient reduction in threat to offer the prospect of seabird benefit. Likewise, for rat eradications, we considered the year in which operations were completed to remove invasive rodents as year zero, rather than any subsequent year when confirmation of the success of the eradication became available. Where more than one invasive was removed over an extended period (e.g. Motouhora), we used the year the last invasive was removed to conservatively determine 'year zero'. In general, the data period covered 5–20 years. In the circumstance where (re-)colonization occurred some years after eradication, population growth was calculated from the year colonization was recorded, not from the year of eradication.

Calculations of growth rate

To calculate the annual rate of population change (λ – lambda) of a species at a colony, we proceeded as follows. If there were only two censuses (e.g. at the time of eradication and x years later), then lambda was considered constant and was the x^{th} root of the proportional population change between the two censuses. If there were three or more censuses, the gradient of the linear regression through those points plotted on a semi-log scale was calculated; then the anti-log of the gradient yielded lambda, again assumed constant over the period in question. Where the data allowed, three separate values of lambda were calculated: (1) for the period between eradication and age of first breeding (AFB; i.e. the period when immigration is presumed responsible for any increase in population); (2) for the years after AFB (when increased breeding success at the colony could have contributed to enhanced recruitment, in addition to any immigration); and (3) over the entire data period for the species at the colony. For each species appearing in the dataset, we identified AFB from standard sources (Cramp, 1983–1985; Marchant & Higgins, 1990; Del Hoyo, Elliott & Sargatal, 1992–1996; Brooke, 2004).

Ideally, to control for ongoing regional population changes among the seabirds of interest, we would compare lambda values at three types of colony, those where eradication of the target species had been successful, those where invasive mammals persisted, either because no project was undertaken or because non-target species remained, and those which had never hosted invasive mammals (Jones, 2010). Since the data did not allow such a control, we used region as a random factor in the analyses (see Statistical analyses), on the assumption that populations of seabirds of different species in the same region would be showing similar population trajectories in the absence of conservation interventions.

Drivers of recovery

Eradication projects were divided into groups based on the species eradicated, namely predator of adult seabirds (cat or mongoose *Herpestes* sp.), chick/egg predator (rat or mouse), browser/grazer (goat *Capra hircus* or rabbit *Oryctolagus cuniculus*) or multiguild (both a browser and a predator eradicated and/or pigs *Sus scrofa* eradicated). We were unable to source enough data to analyse whether any invasive mammals remaining after eradication significantly affected seabird recovery. In particular, we cannot exclude the possibility that house mice *Mus musculus*, known to have seabird impacts (Wanless *et al.*, 2007), might have remained.

For every island, we collected data on the size of the seabird colony, if any, at the time of eradication and the date of colonization (in relation to the eradication date) if it was re-colonized. Since the proximity and size of a nearby colony could influence the likelihood of immigration, a key element of correspondence was the search for information about the nearest neighbouring colony of a seabird breeding on an island from which mammals were eradicated. We sought, mainly from correspondents, information about the size of the neighbouring colony and its distance from the restored island.

The species were assigned to one of four broad groups with somewhat different life histories – albatrosses and petrels (Procellariiformes), suliforms and tropicbirds, gulls/terns (Laridae), and auks (Alcidae). We also obtained further intrinsic data on individual species, namely AFB (see above), mass (from Handbook of Birds of the World Alive: www.hbw.com) and IUCN threat status (www.birdlife.org). The spreadsheet we used in the analysis is provided as Supplementary Material.

Statistical analyses

All statistical tests were run in R version 3.2.2 (R Core Team, 2015). To assess whether λ differed before and after each species' AFB, we fitted linear mixed models. We

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included after AFB as a binary dummy variable, with before AFB set as a reference class. To examine whether λ differed more before and after AFB in a recolonizing population versus one where a colony was already present, we included the presence of a colony at the time of eradication and the interaction between presence of a colony and the binary after AFB variable. To account for variation between islands, metapopulations, and seabird species, we included island nested within region and species as random variables. We use 95% confidence intervals around parameter estimates that do not overlap 0 to indicate that covariates have a strong effect on λ.

To assess whether predictor variables influence the overall seabird population growth rate after eradication (λ: column O, supplementary data table), we used an information theoretic approach. We examined three separate sets of linear mixed effects models: 1) including all λ values; 2) λ values where a colony was present at the time of eradication; and 3) λ values from sites where birds recolonized after eradication. Each global model included island nested within region and species as random variables and the following fixed effects: the type of predator eradicated, seabird mass (which might affect life history and thus the species' potential for population growth), taxonomic group, IUCN status (also possibly correlated with potential for population growth), age at first breeding, the size of the colony (if any) on the restored island, the distance to the nearest neighbouring colony, the size of that colony, and the interaction between the latter. We included only one interaction term, because too many cause mixed models to become overparameterized (i.e. too many parameters and insufficient data points within each category) and thus cause non-convergence (Ginzburg & Jensen, 2004). To ensure resulting parameter estimates would be comparable, we standardized the data by subtracting the mean and dividing by the standard deviation (Schielzeth, 2010). All categorical covariates (type of invasive mammal eradicated, seabird taxonomic group, IUCN status) were transformed into binary dummy variables with one set as a reference class of zero. Our dataset contained only 10 species classified as threatened or near-threatened on the IUCN Red List, and so IUCN status was considered a binary variable with 'least concern' set to 1 and near-threatened, vulnerable, and endangered set to 0 (i.e. as a reference class; Hardy, 1993). To assess collinearity among fixed effects, we computed a Spearman's correlation matrix. We omitted one of each covariate randomly when correlations (r) were >0.5 (suliforms/tropicbirds dummy variable was removed, as it was positively correlated with mass, $r = 0.74$). We considered all possible combinations of variables in a model selection framework using the *dredge* function in the *MuMIn* package (Bartoń, 2013).

We ranked candidate models with Akaike's Information Criterion (AIC) corrected for small sample sizes (AICc) (Burnham & Anderson, 2002). The AICc weights were used to evaluate model likelihoods. We model averaged all models with ΔAICc < 10 to generate parameter estimates, unconditional standard errors, and 95% confidence intervals, which were used with parameter likelihoods to estimate the effect size for each predictor variable (Johnson & Omland, 2004).

Results

The dataset included information from 61 islands spread across all the world's major oceans and at a range of latitudes (cool temperate, subtropical and tropical) from 49°S (Kerguelen Islands) to 52°N (Hawadax Island, Alaska). We were able to calculate population growth rates of 181 populations of 69 seabird species: 28 petrels, 13 suliforms and tropicbirds, 20 gulls and terns, and eight auks. The species were mostly widespread in distribution and classified as least concern ($n = 59$), with four near-threatened, five vulnerable and one endangered (Polynesian storm-petrel *Nesofregatta fuliginosa*). The distribution of λ values across all populations is shown in Fig. 1, where the median value is

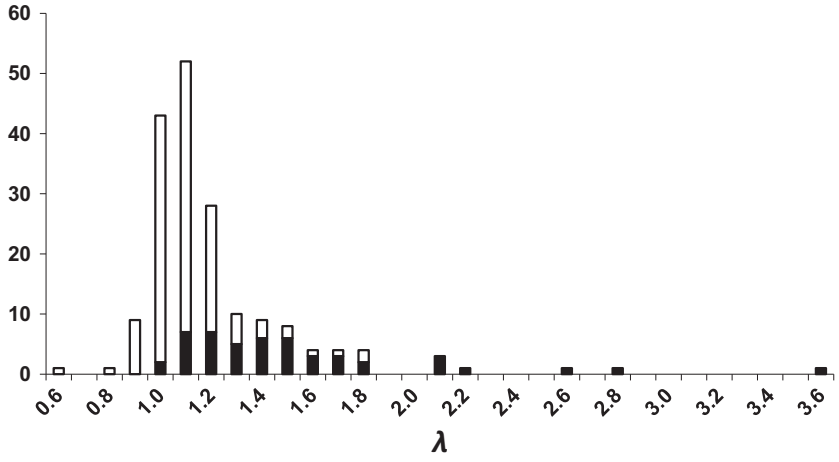

Figure 1 Frequency distribution of 181 population growth rate (λ) estimates. An estimate plotted as 1.4, for example, represents growth rates between 1.350 and 1.449. Open portions of the columns represent populations where a colony was already present at eradication, filled portions where a colony grew after post-eradication colonization.

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1.119, the inter-quartile range 1.034–1.252, and the overall range 0.628–3.567. The three largest values (>2.5) all derive from newly established tern colonies (Suppl. Material). Following successful eradication, populations with positive growth ($\lambda > 1$; $n = 151$) greatly outnumbered those in decline ($\lambda < 1$; $n = 23$), with seven showing no detectable change. Lambda values were higher at islands where a colony established shortly after eradication than at those where a colony was already present (Fig. 1: Colony establishes, mean $\lambda = 1.514 \pm$ SE 0.071 ($n = 48$); Colony already present, mean $\lambda = 1.098 \pm 0.013$ ($n = 153$); Students t-test, $t = 5.59$, $P << 0.001$).

Population growth in the years immediately after eradication and before the species' AFB was somewhat greater than population growth after AFB (Before, mean $\lambda = 1.227 \pm$ SE 0.047 ($n = 70$); After, mean $\lambda = 1.132 \pm 0.040$ ($n = 23$); Students t-test, $t = 1.26$, $P = 0.071$). The same was true if the comparison was across the 21 species/islands where we had paired data for population growth before and after AFB (Before, mean $\lambda = 1.271 \pm$ SE 0.108; After, mean $\lambda = 1.135 \pm 0.044$ ($n = 21$); Paired t-test, $t = 1.14$, $P = 0.267$). When we accounted for the presence of a colony at the time of eradication, we observed a higher λ immediately after eradication and a lower λ after each species' AFB (parameter estimate 97.5% CIs for λ post-AFB: −0.82 to −0.07). Moreover, there was a significant interaction between λ after AFB and the presence of a colony at eradication (parameter estimate 97.5% CIs: 0.002–0.82), where the decrease in λ after AFB was greater on islands where there was no colony present at the time of eradication versus those where a colony was present (Table 1, Fig. 2).

In the absence of a significant signal of change in population growth rate with time since eradication, to determine which factors were driving seabird population recovery, we modelled overall growth rate (calculated across the maximum data period available) against biologically relevant explanatory variables. Using colony on the restored island as a continuous variable we found that the eradication of multiple species was followed by faster population growth (Fig. 3), and that populations of gulls and terns grew faster than those of other seabird groups (Table 2, Fig. 4).

Using the presence or absence of a colony on a restored island as a binary variable, we found the most important variable to be the presence or absence of a colony at the time of eradication (Table 3). Population growth was slower where a colony was already present, in accord with the results shown in Table 1. More rapid growth still occurred where there were multi-species eradications and among populations of gulls/terns.

Table 1 Model of population growth rate (λ) before and after age of first breeding (AFB) according to whether a colony was present at the time of eradication

$n = 96$	Parameter estimate	2.5% CI	97.5% CI
(Intercept)	1.814	1.642	1.985
λ pre-AFB		n/a[a]	
λ post-AFB	−0.443	−0.816	−0.069
Colony present at eradication	−0.699	−0.892	−0.507
λ post-AFB*Colony present at eradication	0.410	0.002	0.821

[a]Reference category.

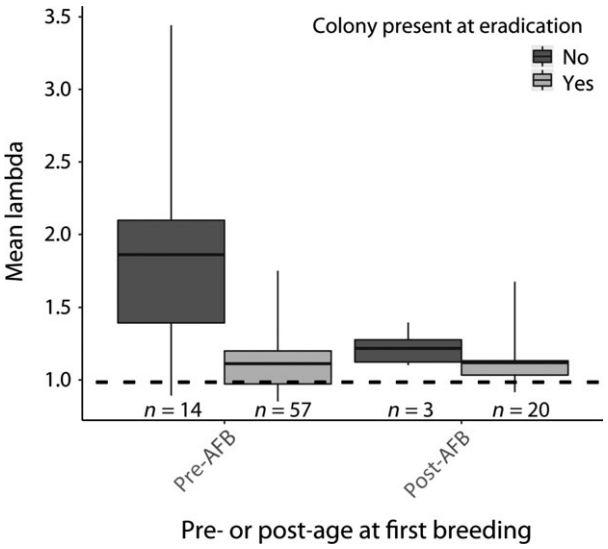

Figure 2 Population growth (λ) according to whether a colony was or was not present at eradication. Lambda was lower after age at first breeding (AFB) on islands without colonies present at the time of eradication but did not change when a colony was already present at eradication (see text). In each whisker plot, the central black bar is the mean, the box is the inter-quartile range, and the whiskers are the 98 percentile ranges. The horizontal dashed line shows a λ value of 1, indicating no population change.

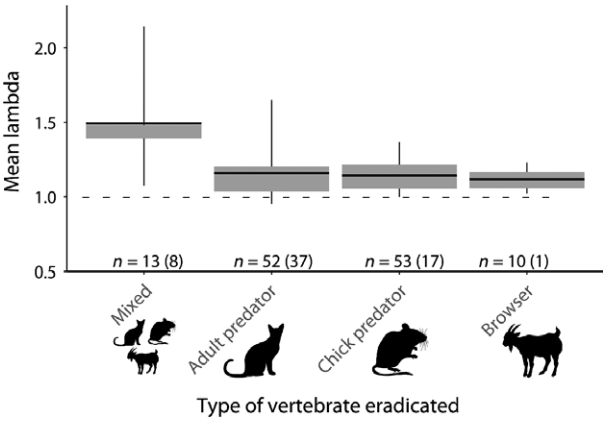

Figure 3 Population growth (λ) according to the types of mammals eradicated. Raw sample sizes outwith brackets, sample sizes used in models within brackets. In each whisker plot, the central black bar is the mean, the box is the inter-quartile range, and the whiskers are the 98 percentile ranges. The horizontal dashed line shows a λ value of 1, indicating no population change.

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Table 2 (a) Top five ranked candidate models of overall population growth rate (λ) of seabirds after eradication, where population (if any) at eradicated colony is treated as a continuous variable (n = 63). (b) Summed Akaike weights (w), weighted parameter estimates (wPE), unconditional standard errors (SEμ), and 95% confidence intervals (CI) calculated from candidate models with ΔAICc <10

(a) Model	k	AICc	ΔAICc	Akaike weight
Mixed predators eradicated	6	−9.97	0.00	0.44
Gulls/terns + Mixed predators eradicated	7	−.47	2.51	0.12
Browser eradicated + Mixed predators eradicated	7	−5.40	4.57	0.04
Auks + Mixed predators eradicated	7	−5.37	4.60	0.04
Null	5	−5.37	4.60	0.04

(b) Covariate	w	wPE ± SEμ	2.5 CI	97.5 CI
(Intercept)	NA	1.15 ± 0.04	1.07	1.24
Mixed predators eradicated*	0.88	0.32 ± 0.08	0.16	0.48
Gulls/terns*	0.22	0.11 ± 0.06	0	0.22
Browser eradicated	0.08	0.01 ± 0.16	−0.31	0.33
Auks	0.07	−0.09 ± 0.08	−0.25	0.07
Mass	0.07	−0.05 ± 0.03	−0.1	0
Least concern IUCN	0.04	0.02 ± 0.08	−0.15	0.19
Chick predators eradicated	0.04	−0.03 ± 0.09	−0.21	0.15
Petrels	0.03	0.01 ± 0.07	−0.13	0.15
Size of source pop	0.02	−0.04 ± 0.02	−0.08	0
AFB	0.02	0.03 ± 0.03	−0.02	0.09
Numbers of birds at eradication	0.02	−0.03 ± 0.02	−0.07	0
Distance to source pop	0.01	−0.01 ± 0.03	−0.08	0.05

Asterisks indicate parameter estimates with 95% confidence intervals that do not overlap 0.

We then separated population growth data into cases of recolonization and recovery (where a colony was present at the time of eradication). Although there were too few data (n = 18 and 46, respectively) to draw any robust conclusions, there was some evidence that distance to and size of a source population resulted in a higher lambda after recolonization (Table 4). Population growth of a colony already present at eradication was faster in populations of gulls and terns.

Discussion

Our results constitute the most comprehensive compilation to date of the response of seabird populations to invasive mammal eradications. In the great majority (83 percent) of cases, seabird populations grew following eradication, which can only strengthen the case for undertaking further eradications to benefit seabirds and to aid wider island restoration where seabirds have major roles in supporting terrestrial ecosystem function (Mulder *et al.*, 2011).

The median λ of 1.119 and inter-quartile range of 1.034–1.252 are broadly similar to the λ recorded from expanding

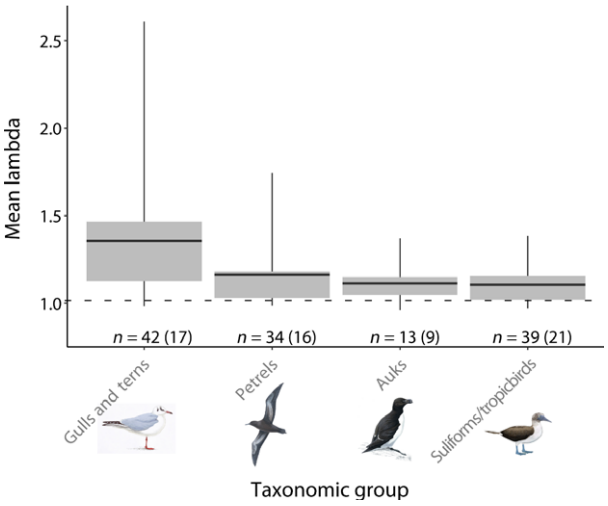

Figure 4 Population growth (λ) according to seabird group. Raw sample sizes outwith brackets, sample sizes used in models within brackets. In each whisker plot, the central black bar is the mean, the box is the inter-quartile range, and the whiskers are the 98 percentile ranges. The horizontal dashed line shows a λ value of 1, indicating no population change. Bird images © Mike Langman (rspb-images.com).

seabird populations, for example, the northern fulmar *Fulmarus glacialis* and northern gannet *Morus bassanus* populations of the North Atlantic in the 20th century (Lloyd, Tasker & Partridge, 1991; Mitchell *et al.*, 2004). The highest values of λ (Fig. 1), particularly those above 1.4, which is the highest growth rate recorded among populations of threatened birds (Green & Hirons, 1991), are almost certainly the result of immigration. These high values are more common among newly established colonies, where immigration inevitably plays a role in their formation, and probably continues to do so for at least some time thereafter. For example, the highest value plotted in Fig. 1, 3.56, refers to the growth of a sooty tern *Onychoprion fuscatus* colony on Rabbit Island off Antigua, in the Caribbean, in the 3 years after rat eradication.

A high proportion of the data came from personal correspondence and 'grey' literature (Suppl. Material). Partly this is because detailed long-term monitoring has not been a consistently high priority following eradications, an omission highlighted by other authors (Buxton *et al.*, 2014; Kappes & Jones, 2014). While monitoring of seabird populations on islands following predator eradications has been infrequent, that of nearby islands with and without invasive mammals has been virtually non-existent in most parts of the world. This effectively precludes rigorously addressing the counterfactual, namely what would have happened to the seabirds on the restored island without the conservation intervention of eradication. However, the fact that most seabird populations increased following eradication strongly points to the population-level benefits of such endeavours, particularly in the light of the global declines and threatened nature of many seabird populations.

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Table 3 (a) Top five ranked candidate models of overall population growth rate (λ) of seabirds after eradication, where population (if any) at eradicated colony is treated as a binary variable ($n = 71$). (b) Summed Akaike weights (w), weighted parameter estimates (wPE), unconditional standard errors (SEμ), and 95% confidence intervals (CI) calculated from candidate models with ΔAICc <10

(a) Model	d.f.	AICc	ΔAICc	Akaike Weight
Mixed predators eradicated + Birds present or absent at eradication	7	−23.47	0.00	0.36
Birds present or absent at eradication	6	−22.96	0.51	0.28
Gulls/terns + Birds present or absent at eradication	7	−19.13	4.34	0.04
Gulls/terns + Mixed predators eradicated + Birds present or absent at eradication	8	−19.04	4.43	0.04
Mixed predators eradicated	6	−18.44	5.03	0.03

(b)	w	wPE ± SEμ	2.5 CI	97.5 CI
(Intercept)	NA	1.2 ± 0.04	1.13	1.27
Birds present or absent at eradication*	0.95	−0.11 ± 0.03	−0.16	−0.05
Mixed predators eradicated*	0.56	0.21 ± 0.08	0.05	0.37
Gulls/terns	0.10	0.08 ± 0.05	−0.02	0.19
Browser eradicated	0.05	−0.01 ± 0.1	−0.2	0.18
Auks	0.04	−0.04 ± 0.07	−0.17	0.09
Least concern IUCN	0.03	0.03 ± 0.06	−0.09	0.16
Petrels	0.03	−0.03 ± 0.05	−0.13	0.07
Chick predators eradicated	0.03	−0.01 ± 0.06	−0.12	0.11
Mass	0.02	−0.03 ± 0.02	−0.08	0.02
AFB	0.01	0.02 ± 0.02	−0.03	0.06
Distance to source pop	0.01	−0.01 ± 0.03	−0.07	0.04
Size of source pop	0.01	−0.01 ± 0.02	−0.05	0.03

Asterisks indicate parameter estimates with 95% confidence intervals that do not overlap 0.

We did not detect any signal of increased rates of population growth after each species' age of first breeding, the point at which enhanced recruitment of philopatric young breeders could plausibly increase population growth rate. On the contrary, population growth in the years immediately after eradication was, if anything, higher than later. This suggests a considerable role for immigration in determining the trajectory of seabird populations after eradication. This unexpected result can be illuminated by a thought experiment. Growth in the early years is likely overwhelmingly due to immigration. Subsequent growth, following the age of first breeding, could be driven by immigration alone, or by some combination of continuing immigration and/or enhanced recruitment. If it was due to immigration alone, particularly if it was due to the settlement of a constant number of immigrants, then, counter-intuitively, growth rate might decline over time as the immigrants become a smaller fraction of the breeding population. In the longer term, perhaps longer than several seabird generations, and therefore longer than most datasets available to us,

Table 4 (a) Top five ranked candidate models of population growth rate (λ) of seabirds after eradication, where data were separated into cases of recolonization (top, $n = 18$) and recovery (lower, where a colony was present at eradication bottom, $n = 46$). (b) Summed Akaike weights (w), weighted parameter estimates (wPE), unconditional standard errors (SEμ), and 95% confidence intervals (CI) calculated from candidate models with ΔAICc <10

Recolonization

(a) Model	d.f.	AICc	ΔAICc	Akaike Weight
Size of source pop	5	14.14	0.00	0.50
Size of source pop + Distance to source pop	6	17.07	2.93	0.11
Mixed predators eradicated + Size of source pop	6	17.34	3.20	0.10
(Null)	4	17.41	3.26	0.10
Chick predators eradicated + Size of source pop	6	19.66	5.51	0.03

(b)	w	wPE ± SEμ	2.5 CI	97.5 CI
(Intercept)	NA	2.33 ± 0.69	0.87	3.79
Size of source pop	0.83	6.81 ± 4.09	−2.05	15.68
Distance to source pop	0.17	−0.39 ± 0.2	−0.82	0.03
Mixed predators eradicated	0.13	0.29 ± 0.13	0	0.57
Chick predators eradicated	0.05	−0.12 ± 0.23	−0.63	0.38
Gulls/terns	0.03	−0.08 ± 0.14	−0.39	0.23
Petrels	0.03	0.03 ± 0.17	−0.32	0.38
AFB	0.02	0.06 ± 0.05	−0.06	0.18
Mass	0.01	0.04 ± 0.09	−0.15	0.23

Recovery

(a) Model	d.f.	AICc	ΔAICc	Akaike Weight
Null	5	−40.51	0.00	0.41
Gulls/terns	6	−39.51	1.00	0.25
Mixed predators eradicated	6	−36.23	4.28	0.05
Browser eradicated	6	−35.12	5.39	0.03
Mass	6	−35.00	5.51	0.03

(b)	w	wPE ± SEμ	2.5 CI	97.5 CI
(Intercept)	NA	1.11 ± 0.03	1.05	1.17
Gulls/terns*	0.38	0.11 ± 0.04	0.02	0.2
Mixed predators eradicated	0.08	−0.09 ± 0.13	−0.36	0.17
Browser eradicated	0.05	0.05 ± 0.09	−0.14	0.23
Auks	0.03	−0.04 ± 0.05	−0.14	0.05
Chick predators eradicated	0.03	0.04 ± 0.04	−0.04	0.13
Least concern IUCN	0.03	−0.04 ± 0.06	−0.17	0.08
Mass	0.03	−0.03 ± 0.02	−0.08	0.01
Petrels	0.03	0.02 ± 0.06	−0.09	0.13
Numbers of birds at eradication	0.02	−0.02 ± 0.01	−0.05	0.01
AFB	0.02	−0.03 ± 0.02	−0.08	0.02
Size of source pop	0.02	−0.02 ± 0.02	−0.06	0.01
Distance to source pop	0.01	0 ± 0.02	−0.04	0.04

Asterisk indicates parameter estimate with 95% confidence intervals that does not overlap 0.

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immigration rates might change as, for example, density dependence influenced immigration.

Another means by which rapid population growth immediately after eradication could arise would be a reduction in the age of first breeding. There is no information on this possibility and we note that it would tend to generate a more-or-less abrupt population increase, rather than the steady population growth generally observed.

Our analyses (Tables 1 and 3) suggest that population growth after eradication was fastest on islands without a prior colony. This too reinforces the importance of immigration. A fixed number of immigrants will generate higher λ values in a small new colony than a larger established colony.

The very fact that a colony was newly established could indicate the favourable status of the species' regional population, a factor which itself could contribute to the higher λ of newly established colonies. However, this result does not exclude the possibility that the increase in the overall number of birds might be greater at larger, established colonies than at new and necessarily small colonies.

The results also emphasize that seabirds are perhaps less philopatric to their natal sites than is widely accepted (Weimerskirch, 2002; Brooke, 2004; Friesen, 2015). Further suggesting a lack of philopatry are observations of seabirds of several species and taxonomic groups arriving to colonize and breed on newly restored islands shortly after project completion (Bell, 1998; Ratcliffe *et al.*, 2010; Rocamora & Henriette, 2015). For some species, there could be a pool of immature prospecting birds ready to take advantage of newly created 'safe havens'.

Unsurprisingly, we found a consistent pattern of faster population growth among terns and gulls than among other seabird groups. The known mobility of tern colonies and relative lack of philopatry for both groups contributes to this result (Jones & Kress, 2012). For example, three species of tern *Sterna* spp. were quickly attracted to Eastern Egg Rock, Maine, following gull control and the use of acoustic playback and decoys (Kress, 1983). In contrast to the mobility of terns is the apparent reluctance of auks to establish new colonies, at least without the use of social attraction techniques (Parker *et al.*, 2007).

Given that Buxton *et al.* (2014) reported post-eradication recolonization was more likely close (<25 km) to established colonies, we anticipated that population growth rate would be influenced by the size and proximity of neighbouring colonies. We similarly found that population growth after recolonization was faster if there was a large source population nearby. Moreover, the growth rate of the population of the one single-island endemic (depending on taxonomy) in our dataset, Gould's petrel *Pterodroma leucoptera leucoptera* where immigration could be excluded, was a modest 1.035 (Supporting Information Table S1). However, we had too few data to draw any robust conclusions.

While our results neither support nor reject using neighbouring colonies as a criterion for the selection of islands for future eradications, the fact that multispecies eradications were followed by faster population growth argues for eradicating multiple invasive mammals in a single operation wherever possible. Such multiple operations are becoming increasingly feasible (Russell, 2011), and may have the additional advantage of reducing the chance of such effects as competitor or mesopredator release (Courchamp, Langlais & Sugihara, 1999; Caut *et al.*, 2007; Dilley *et al.*, 2016). The possibility of such outcomes should be evaluated on a case-by-case basis (see Helmstedt *et al.*, 2016), ideally with eradication planning considering responses in a whole-ecosystem context (Zavaleta, Hobbs & Mooney, 2001).

Predators have been eradicated from islands for decades now, with the goal of protecting biodiversity, often specifically seabirds. However, post-eradication monitoring of seabirds is sporadic and the impacts of eradication on seabirds have never before been collated. Our study provides a strong confirmation that invasive mammal eradication is usually followed by growth of seabird populations. This finding is critical for the many funders and practitioners who fund and implement eradication operations specifically to enhance seabird populations. An important contributor to that growth is immigration – a surprising finding given that most seabirds are considered philopatric. Further work and, crucially, more systematic monitoring for at least 10 years, and preferably longer, after eradication are needed to identify the factors which influence the rate of immigration. We encourage eradication practitioners and funders to consider building the cost of long-term post-eradication monitoring into project budgets in order to more accurately quantify the impacts of eradication on seabirds. The extra cost will be small compared to the overall budget, yet such information will be critical for prioritizing future eradication efforts.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Islands where mammal eradications were completed and subsequent seabird population growth rate calculated.

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