



Drivers of Seabird Population Recovery on New Zealand Islands after Predator Eradication

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Abstract: *Eradication of introduced mammalian predators from islands has become increasingly common, with over 800 successful projects around the world. Historically, introduced predators extirpated or reduced the size of many seabird populations, changing the dynamics of entire island ecosystems. Although the primary outcome of many eradication projects is the restoration of affected seabird populations, natural population responses are rarely documented and mechanisms are poorly understood. We used a generic model of seabird colony growth to identify key predictor variables relevant to recovery or recolonization. We used generalized linear mixed models to test the importance of these variables in driving seabird population responses after predator eradication on islands around New Zealand. The most influential variable affecting recolonization of seabirds around New Zealand was the distance to a source population, with few cases of recolonization without a source population ≤ 25 km away. Colony growth was most affected by metapopulation status; there was little colony growth in species with a declining status. These characteristics may facilitate the prioritization of newly predator-free islands for active management. Although we found some evidence documenting natural recovery, generally this topic was understudied. Our results suggest that in order to guide management strategies, more effort should be allocated to monitoring wildlife response after eradication.*

Keywords: population dynamics, predator eradication, recolonization, recovery, restoration, seabirds

Conductores de la Recuperación de Poblaciones de Aves Marinas en Islas de Nueva Zelanda después de la Erradicación de Depredadores

Resumen: *La erradicación de mamíferos depredadores introducidos en las islas se ha vuelto cada vez más común, con más de 800 proyectos exitosos en todo el mundo. Históricamente, los depredadores introducidos extirparon o redujeron el tamaño de muchas poblaciones de aves marinas, cambiando las dinámicas de ecosistemas isleños completos. Aunque el principal resultado de muchos proyectos de erradicación es la restauración de las poblaciones afectadas de aves marinas, las respuestas de las poblaciones naturales se documentan raramente y los mecanismos son poco entendidos. Usamos un modelo genérico de crecimiento de la colonia de aves marinas para identificar a las variables clave relevantes anticipadoras para la recuperación o recolonización. Usamos modelos mixtos lineales generalizados para probar la importancia de estas variables en la conducción de las respuestas de las poblaciones después de la erradicación de depredadores en islas alrededor de Nueva Zelanda. La variable más influyente que afecta a la recolonización de las aves marinas alrededor de Nueva Zelanda fue la distancia a la población fuente, con pocos casos de recolonización sin una población fuente a ≤ 25 km. El crecimiento de la colonia se vio más afectado por el estado de la metapoblación; hubo poco crecimiento en la colonia de especies con un estado declinante. Estas características pueden facilitar la priorización de islas nuevamente libres de depredadores para un manejo activo. Aunque encontramos algunas evidencias documentando la recuperación natural, en general este tema fue pobremente estudiado. Nuestros resultados sugieren que para guiar estrategias de manejo, se debe asignar más esfuerzo al monitoreo de la respuesta de la fauna silvestre después de la erradicación.*

Palabras Clave: aves marinas, dinámica de poblaciones, erradicación de depredadores, recolonización, recuperación, restauración

Introduction

Introduced predators have been implicated in two-thirds of animal species extinctions on islands (Atkinson 1985, 1989; Jones et al. 2008). In contrast, recent progress with island restoration has made it one of the most successful collaborative global conservation initiatives (Howald et al. 2007). To date, 25 species of non-native predators have been removed from over 800 islands around the world (Donlan & Wilcox 2008; Bellingham et al. 2010; Keitt et al. 2011). These successes show no sign of slowing, as eradication of introduced predators on increasingly larger islands with more complex terrain becomes feasible (Howald et al. 2007; Lavios et al. 2007; Veitch et al. 2011a).

After eradication, restoration of affected populations of native fauna can be active, where dispersal of wildlife is deliberately manipulated through techniques such as translocation or social attraction (Jones & Kress 2012), or passive, where populations of native animals are left to grow or recolonize naturally (Scott et al. 2001). Seabird populations are particularly vulnerable to the impacts of introduced predators (Moors & Atkinson 1984) and may not recolonize or recover passively due to species-specific social (Nocera et al. 2006) or life-history constraints (Doherty et al. 2004). Considering these unique traits, active restoration can help reestablish populations. However, passive restoration is far more widely used due to financial and logistical constraints associated with management on isolated oceanic islands. Although eradications have become more efficient and cost-effective, costs remain high on remote offshore islands (Martins et al. 2006; Ewen & Armstrong 2007; Aguirre-Munoz et al. 2008). There is currently no published research-based prioritization scheme to identify sites which will benefit most from passive or active restoration after predator eradication.

Seabirds have low reproductive output (Wooller et al. 1992), exhibit natal and breeding site philopatry (Greenwood 1980), and are unable to adapt their behavior to avoid predation by non-native predators (Wanless et al. 2007). Thus, populations are often extirpated or severely reduced on islands after predators are introduced (Townes et al. 2006; Rauzon 2007). When predators are eradicated, the same life-history traits that render seabirds vulnerable to predation can make population recovery slow or nonexistent. Seabirds in island ecosystems often act as bottom-up ecosystem engineers by delivering marine-derived nutrients in their guano and, for burrow-nesting species, causing physical disturbance to soils through nest construction (Sanchez-Pinero & Polis 2000; Bancroft et al. 2005; Ellis 2005). When seabirds are eliminated from islands, nutrients are no longer imported, changing ecosystem processes (Croll et al. 2005).

Thus, seabird population recovery after eradication, although slow and complex, is generally essential for the recovery of island ecosystem functioning.

The New Zealand archipelago represents a rich source of information on predator eradication. New Zealand fauna evolved in the absence of mammalian predators; thus, the introduction of mammals by humans had disproportionately large impacts (Diamond 1990). With the arrival of humans, 577 of 735 islands around New Zealand were invaded by non-native mammals and most seabirds were extirpated from the mainland (Townes & Ballantine 1993; Parkes & Murphy 2003; Tennyson & Martinson 2006). However, more offshore islands have been cleared of predators around New Zealand than any other country (over 15% of invaded islands), including a range of eradication projects completed >25 (Dunlevy et al. 2011; Island Conservation 2011).

Despite a significant and ongoing investment in predator eradications in New Zealand, largely to benefit seabird populations, little research has been conducted to determine patterns of seabird recolonization and recovery after eradication. The few studies that followed natural population responses of seabirds after predator removal had variable results (Gaze 2000; Veitch et al. 2011b). There is, accordingly, little understanding of the factors that may facilitate passive seabird recovery. Thus, a comprehensive review of posteradication seabird population responses and the development of an overarching conceptual model to identify key factors in recovery would be useful for guiding management and monitoring and could also be used to develop a framework for island conservation investment strategies.

Therefore, we outlined a conceptual model of the ecological and demographic factors influencing seabird colony growth and recolonization after predator eradication; tested empirically, with collated data from posteradication surveys, which island and species characteristics most influenced seabird recovery; and developed recommendations for passive restoration monitoring, particularly with regard to its potential to prioritize active management and improve models of population growth.

Methods

For the purpose of this review, we define *islands* as sites surrounded by water and terrestrial sanctuaries surrounded by predator-proof fences. *Population recovery* refers to a local increase in the number of individuals at a colony after predator removal, as opposed to an increase in the metapopulation. *Recolonization* refers to a species of seabird recorded breeding on an island after not having been recorded there within a decade prior to eradication.

Conceptual Model Overview

With few exceptions, pelagic seabirds breed in colonies on oceanic islands. Separation between breeding sites due to water barriers means that island populations can be considered metapopulations (Oro 2003; Oro et al. 2011). However, behavioral mechanisms associated with coloniality (e.g., philopatry and social attraction) mean that population dynamics are characterized by traits that may not conform to more straightforward metapopulation processes (Matthiopoulos et al. 2005). Furthermore, seabirds have low annual reproductive output, fecundity is low, and intermittent breeding is common (Warham 1990; Cubaynes et al. 2011). Thus, any model of population recovery and recolonization at a newly predator-free site must incorporate both slow intrinsic rates of population increase and seabirds' unique behaviorally driven metapopulation dynamics (Johst & Brandl 1997).

We developed a generic seabird colony growth model by combining standard matrix population models (Croxall & Rothery 1991; Caswell 2001) and a model of metapopulation processes on the basis of diffusion, range expansion, and reinvasion (Supporting Information) (Lubina & Simon 1988; Sinclair et al. 2006). We considered the potential effects of release from the impacts of introduced predators on each parameter in the generic model (Table 1).

Posteradication Population Recovery

Any increase in intrinsic population growth after predator eradication depends largely on the magnitude of predation effects on adult and prebreeder survival and breeding success, which will in turn affect the size, distribution, and age structure of a remnant seabird population (Supporting Information). Any positive response in demographic rates after predator eradication is often dictated by the relative sizes of the introduced predators and their seabird prey (Table 1) (Jones et al. 2008). Towns et al. (2011) categorize introduced predators into large predators, such as cats, that consume seabirds of all age classes and small predators, such as rats, that commonly consume only eggs and chicks. Large predators can kill and hoard more seabirds than they consume at one time (Short et al. 2002). Large predators depress adult and prebreeder survival, and because many seabirds are obligately biparental, this translates into a decrease in breeding success. When large predators are eradicated from a colony, adult survival often increases (Keitt & Tershy 2003; Nogales et al. 2004), resulting in relatively rapid population increase due to the high sensitivity of population growth rates to changes in adult survival (Lavers et al. 2010). Small predators are more likely to influence breeding success (Towns et al. 2006; Jones et al. 2008). Thus, when small predators are eradicated, reproductive success often increases (Pascal et al. 2008), which

has variable effects on colony growth (Finkelstein et al. 2010). When both large and small predators are present at a colony, interactions can be complex. If large (super) predators are eradicated before small (meso) predators, mesopredator release may occur (e.g., cats eradicated before rats and mice lead to inflated numbers and activity of rats and mice [Russell et al. 2009]), which may be followed by increased predation on seabirds. This increase in predation can lead to more dramatic responses in reproductive success should the mesopredators be subsequently eradicated (Courchamp et al. 1999; Rayner et al. 2007).

An increase in intrinsic population growth after predator eradication will also depend on species-specific characteristics, such as age at first breeding and the number of eggs laid per breeding attempt, that will influence the rate at which potential new recruits are created. For many seabird species, age at first breeding is over 5 years and only 1 or 2 eggs are laid (Warham 1990), resulting in long generation times and a subsequent lag between predator eradication and population growth. Thus, any response in intrinsic population growth is also related to time since predator eradication (Table 1). Seabirds have other unique, species-specific traits that will likely play a role in recovery after eradication, such as natal philopatry (Milot et al. 2008), intermittent breeding (Cubaynes et al. 2011), and a disproportionately high number and influence of prebreeders and immature birds on population dynamics (Oro et al. 2006).

At higher population densities, intrinsic population growth is likely to be limited by negative density dependence (Pontier et al. 2008; Moller et al. 2009). The number of available nest sites may be limited due to competition between or within species, resulting in emigration or reduced breeding success (Table 1). If colonies are dense, removal of predators (or other sources of mortality, such as harvesting) may result in a decrease in breeding success and a net negative effect on colony growth (Moller et al. 2009). Conversely, if colonies are sparse, populations may be influenced by Allee effects and positive density dependence (Stephens et al. 1999). Removal of predators from a moderate-sized colony, where social attraction encourages prospecting individuals to settle, may lead to increased growth (Kildaw et al. 2005). However, it is currently unknown when net positive density effects become negative; thresholds are likely to be both species and site-specific.

Extrinsic or metapopulation processes are particularly important for local recolonization of breeding populations extirpated by predators. When a space becomes free of predators, the number of immature birds that prospect is likely to depend on the distance to a source population and the number of immature birds in a metapopulation (Supporting Information). The probability of an immature bird locating and prospecting a new site is greater at shorter distances to the natal colony and

Table 1. Predictor variables that will hinder or facilitate colony growth after predator eradication drawn from parameters of generic population growth models.

<i>Population growth model</i>			
<i>Process*</i>	<i>Symbol</i>	<i>Description</i>	<i>Variable</i>
Intrinsic	S^A	annual survival rates of adults (A)	type of predator eradicated
	S_{I-1}^{Pr}	and prebreeding birds (Pr)	
	S_{AFR}^I	survival of immature birds to age at first return (AFR)	environmental stochasticity
	P^{ret}	philopatry	unknown
	AFR	age at first return	time since eradication, species-specific mean
	$Skip$	proportion of breeding-age birds not breeding	environmental stochasticity, species-specific mean
	BS	breeding success	size of predator eradicated, species-specific mean availability of high-quality habitat (i.e., size of conspecific and heterospecific populations)
Extrinsic	$N_p t$	number of prospectors	status of species' metapopulation
	Ds	distance to a source population	distance to source population
	H	habitat quality	amount of anthropogenic habitat alteration
	C	intra- and interspecific social cues	conspecific population size before eradication and number of other species breeding on the island

* Intrinsic or site-specific processes and extrinsic or metapopulation processes are outlined in Supporting Information.

when more immature prospectors are available in an increasing or stable metapopulation (Table 1) (Vuilleumier et al. 2007). Recruitment to a newly predator-free space is mediated by habitat quality and social cues (Crespin et al. 2006; Wilcox et al. 2006). If an island has been altered by anthropogenic disturbance (e.g., cleared for farming), recruitment may be less likely (Table 1). Arguably, the most influential factors affecting recruitment in seabirds, however, are density-mediated social attraction, habitat copying, and competition for nest sites (Doligez et al. 2003; Parejo et al. 2006; Schippers et al. 2011). Thus, the population sizes of con- or heterospecifics immediately following predator eradication will either encourage (social attraction) or impede (competition) recruitment (Table 1).

Data Collation

We collated information on pre- and posteradication seabird populations around New Zealand from published and unpublished literature and interviews with island researchers. We scored seabird responses as a binary recovery or recolonization or no observed recovery or recolonization and developed a statistical model to test the relative effects of a set of key recovery factors identified in the conceptual model outlined above.

We constructed an updated list (final search, July 2012) of predator eradication projects on New Zealand islands based on Clout and Russell (2006), Towns et al. (2006), Bellingham et al. (2010), and Keitt et al. (2011). We then searched for information about seabird population status pre- and posteradication in Google Scholar and Web of Science. We searched for each island name and *seabird** or *bird** as keywords. We also reviewed New Zealand

ecological journals *Notornis* and *Tane* and conference proceedings from Veitch and Clout (2002) and Veitch et al. (2011a). If no published information on a particular project was available, we contacted research personnel working on the island and asked the following questions: Is there any evidence (anecdotal, observational, or census data) of seabirds of any species recolonizing or increasing in relative abundance on the island after predator removal? Were there any species that were expected to recolonize or recover (i.e., they bred on the island historically or are known to prospect there), but never did? Are there any rock stacks, islets, or islands within approximately 10 km of the island with populations of seabird. If so, of what species are these populations?

To be included in further analyses, relative abundance of seabirds had to have increased, decreased, or remained unchanged at the colony site (too few studies documented changes in seabird reproductive success or survival after eradication); successful predator eradication had to have been >3 years ago; and there had to have been no active restoration of seabirds. Furthermore, because of insufficient data on some taxa, from this point forward only species that lay one egg per year are considered.

Deriving Predictor Variables

We included factors as predictor variables that we identified as likely to affect intrinsic population growth, recruitment, or both, when developing the conceptual model (Table 1): island characteristics, species characteristics, and available data. Island characteristics were

Table 2. Predictor variables included in models of seabird response (defined as either recolonization or colony recovery) after eradication of introduced predators.

<i>Variable</i>	<i>Type</i>	<i>Scoring or category</i>	<i>Description</i>	<i>Source</i>
Response	Bi ^a	0	no observed population recovery or recolonization	this study
		1	observed population growth or recolonization after eradication	
Relative predator size ^b	Cat ^c	large predator	cats, possums, stoats, pigs (superpredators)	this study
		small predator	rats and mice (mesopredators)	
		large and small predators	both predators eradicated at the same time	
		mesopredator release	large predators removed before small	
Years since predator eradication ^d	Con ^e		year from eradication to survey	this study
Years predators present on island ^f	Con		not enough data	Veitch & Clout 2002
Age at first breeding ^d	Con		only available for a few species, others approximated based on family and mass	Marchant & Higgins 1990
Population size at eradication ^b	Con	1	none	this study
		2	rare (25 or fewer burrows or breeding pairs)	
		3	small (25–100 burrows or breeding pairs)	
		4	medium (100–1000 burrows or breeding pairs)	
		5	large (1000 + burrows or breeding pairs)	
Interspecific competition or facilitation ^d	Con		number of other burrow-nesting species breeding on the island	this study
Habitat modification ^d	Cat	1	none recorded	this study
		2	burned historically	
		3	occupied by Maori (archeological evidence)	
		4	stock grazing or mining	
		5	farmed	
		6	occupied by Maori and farmed by Europeans	
Distance to source population ^d	Con		kilometers	Google Earth 6.2.2
New Zealand population status ^d	Cat	D	decreasing metapopulation	(Miskelly et al. 2008)
		I	increasing metapopulation	(IUCN 2012)
		S	stable metapopulation	
Available data ^f	Cat	1	anecdotal	this study
		2	observation of increase in relative abundance	
		3	increase direct counts of birds or burrows	

^aBinomial variable.^bUsed in colony recovery analysis only.^cCategorical variable.^dUsed in both recolonization and colony recovery analyses.^eContinuous variable.^fExcluded from further analysis.

relative size of predators eradicated, time between seabird surveys and eradication, number of years predators were present on an island, the degree of habitat modification, distance to a source population, num-

ber of other seabird species breeding at the time of eradication. Although island size has the potential to affect seabird communities, that is, smaller islands tend to have greater diversity of species per unit area

(Estades 2001), we did not include it in our models because it was correlated with habitat modification and number of other breeding seabird species. Species characteristics were age at first reproduction, population size at the time of predator eradication, and population status in New Zealand. We also used available data as a variable to control for different types of seabird data (anecdotal, observational, and quantitative) collected before and after eradication (details in Table 2).

Statistical Analyses

For each seabird species on each island, we scored evidence of recolonization or population recovery as 1 and a lack of evidence as 0 (Table 2). We found no evidence of negative responses. To assess whether recovery predictor variables (Tables 1 and 2) explained seabird population responses on different islands, 17 a priori candidate generalized linear mixed models (GLMMs) were considered in a model selection framework. Models had binomial error structure, log links, and Laplace approximations. We accounted for random variation between islands and species by including these as random variables in GLMMs. Interaction terms were not included because mixed models would be overparameterized (i.e., too many parameters and insufficient data points within each category) and thus cause nonconvergence (Ginzburg & Jensen 2004). To ensure that resulting parameter estimates would be comparable, we standardized the data by subtracting the mean and dividing by 2 standard deviations (Schielzeth 2010). Statistical tests were run in R version 2.14.2 with the library lme4 (R Development Core Team 2010).

We ranked candidate models with Akaike's information criterion (AIC) corrected for small sample sizes and overdispersion (QAIC_c) (Burnham & Anderson 2002). The QAIC_c weights (w_i) were used to evaluate model likelihoods. When the best supported model received a weight of less than 0.9, we used model averaging 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).

We carried out 3 separate analyses, the first with all seabird responses (recolonization and colony population increase) aggregated. This analysis revealed that the predictor variable 'data type' had low weight; thus, its effects were considered weak and it was removed from further analysis. The other 2 analyses separated recolonization and colony population increase as response variables. Different predictor variables were used for each analysis depending on biological relevance (Table 2).

Results

We identified 92 islands from around New Zealand from which all non-native predators had been eradicated between 1936 and 2011 (Supporting Information). From this larger data set, we classified 132 seabird responses (evidence of recolonization or population growth or no evidence) from 48 islands with predators eradicated. However, after screening results, data included responses of 103 seabird populations on 41 islands. Of these responses, 49 involved population recovery and 54 involved recolonization.

When all seabird responses (recolonization and colony growth) were combined into one analysis, the model that received the most weight included only distance to a source population as a predictor (Supporting Information). Model weights were <0.5 for top models in all analyses (Supporting Information); thus, model selection exclusively was used to draw inference from our data set.

Population Growth

For models explaining colony growth, parameter estimates that received the highest summed Akaike weights included colony size before eradication and metapopulation status (Table 3). Colonies with a smaller size pre-eradication were more likely to show detectible growth in size following eradication than larger colonies. Little colony growth was observed in large populations after predator eradication; colony growth was most likely in populations with 25–100 individuals (Fig. 1). Seabird colony growth after eradication was also more likely in species with increasing or stable metapopulations (Fig. 1).

Recolonization

When recolonization events were the focal posteradication response, time since predator eradication, distance to a source population, and the number of similar species breeding on the island received considerable summed Akaike weight (>0.9, Table 3). Parameter estimates and standard errors bounded zero for time since eradication, indicating this effect was weak (Table 3). Recolonization was negatively related to the distance to a source population. When the nearest source population was ≥ 25 km, the proportion of observed recolonization events fell below 50% (Fig. 2). Recolonization was positively related to the number of other species breeding on an island (Fig. 3a). The number of successful recolonization events was greater on islands with ≥ 2 other breeding species. Because we suspected the relationship between recolonization and the number of other breeding species may have been related to island size (Estades 2001) and habitat (i.e., habitat copying; Parejo et al. 2006), we corrected

Table 3. Summed Akaike weights (w), weighted parameter estimates (wPE), and unconditional standard errors ($SE\mu$) calculated from all candidate models describing population recovery and recolonization probability of seabirds around New Zealand after predator eradication.

Parameter ^a	w	wPE	$SE\mu$	95% CI
Colony growth				
intercept	1.000	1.82	1.63	3.20
number of other spp. breeding	0.093	-0.02	0.07	0.14
age at first breeding	0.190	-0.04	0.16	0.31
population size	0.654	-0.61 ^a	0.55	1.07
years since eradication	0.194	-0.12	0.24	0.48
small predators	^b			
mesopredator release	0.102	0.29	0.57	1.12
large predators	0.102	-0.11	0.29	0.57
large and small predators	0.102	1.56	379.93	744.66
distance to source	0.261	-0.22	0.37	0.73
habitat modification	0.095	0.00	0.01	0.01
decreasing metapopulation	^b			
increasing metapopulation	0.740	1.57 ^a	1.37	2.69
stable metapopulation	0.740	1.35 ^a	1.31	2.58
Recolonization				
intercept	1.000	-2.94	8.69	17.04
number of other spp. breeding	0.941	13.28 ^a	7.77	15.23
age at first breeding	0.126	-0.12	0.16	0.32
years since eradication	0.931	-2.70	5.27	10.32
distance to source	0.956	-7.58 ^a	3.99	7.82
habitat modification	0.074	-0.01	0.10	0.19
decreasing metapopulation	^b			
increasing metapopulation	0.370	-0.97	9.70	19.01
stable metapopulation	0.370	1.35	8.79	17.23

^aWeighted estimates with strong effects (i.e., SEs that did not bound zero).

^bReference categories.

for these factors post hoc. When number of species was corrected for island area ($[1 + \text{number of species}]/\text{island area}$), we detected no difference in the number of successful recolonization events (Fig. 3b). When the number

of species was corrected for habitat modification ($= [1 + \text{number of species}]/[\text{habitat modification category}]$; Table 2), standard error did not overlap (Fig. 3c), indicating that recolonization was more likely on islands with more seabird species in less modified habitat.

Discussion

The number of successful island eradication projects has increased rapidly in the past few decades, with hundreds of islands around the world cleared of introduced predators. Many of these eradication projects aim to benefit affected seabird populations; however, this is the first wide-ranging review of seabird population responses after predator removal and of the crucial factors that may impede or facilitate this recovery. Although the available data were relatively sparse, our analyses allowed us to identify trends in seabird population responses to predator eradication that will be valuable in planning restoration interventions and subsequent monitoring.

Recolonization by an extirpated species depends largely on extrinsic factors, that is, the newly predator-free site must be prospected and colonized by new recruits. **Two factors had strong effects on the likelihood of recolonization: distance to a source population and local diversity of other seabirds.** More recolonizations were observed on islands with a source population within 25 km. Seabirds are less likely to set up new colonies near the edge of a metapopulation (Schipper et al. 2009). For example, in a marked metapopulation of Audouin's Gull (*Ichthyophaga audouinii*), recruitment probability decreased exponentially with distance from a source population (Oro & Pradel 1999). The low probability of recolonization events at a large distance from source

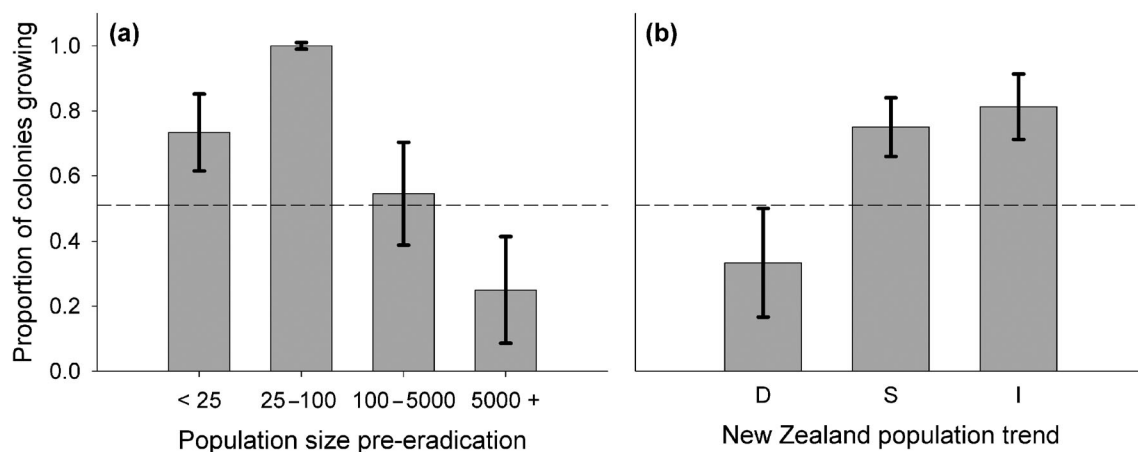


Figure 1. Relationship between proportion of colonies ($\pm SE$) at which subsequent increases in abundance were recorded in New Zealand and (a) size of existing seabird colonies at the time of predator eradication and (b) species' metapopulation trend (D, decreasing; S, stable; I, increasing; dashed line, null proportion of recorded colonies increasing in abundance of 0.5).

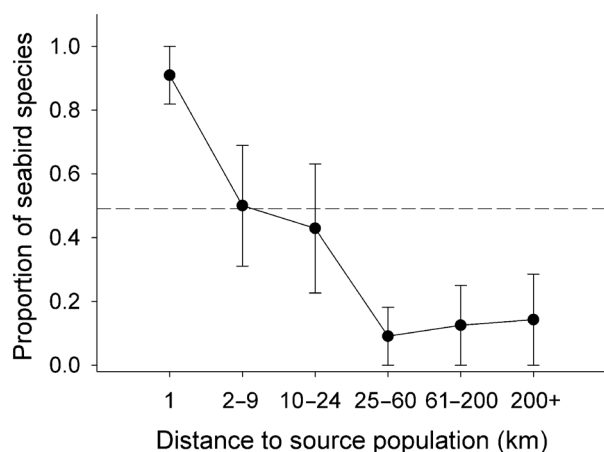


Figure 2. Relationship between proportion of seabird species that recolonized islands in New Zealand after predator eradication and distance from source populations (dashed line, null proportion of recorded colonies increasing in abundance of 0.5).

populations suggests strong metapopulation connectivity among nearby populations of New Zealand seabirds. Furthermore, recolonizations were observed on islands with a greater diversity of seabird species with less habitat modification. The most likely ecological explanation for this result is the “heterospecific habitat copying hypothesis” (Wagner et al. 2000), whereby when choosing their breeding site animals key into the presence and performance of heterospecifics with similar ecological needs, as demonstrated in numerous colonial bird species (Parejo et al. 2005; Parejo et al. 2006; Buxton & Jones 2012). Thus, new recruits of an extirpated species may be using the presence of other ecologically similar species on an island as a cue to safe breeding habitat and nearby feeding grounds.

An increase in the relative size of a remnant colony of seabirds after predator eradication is a much more complex process, involving a combination of intrinsic population dynamics and extrinsic factors. The main complication is that any colony remaining after eradication may be highly disrupted, with altered demographic rates and habitat use. This could result in an unstable age structure and habitat copying into suboptimal areas, that is, an evolutionary trap (Cushing & Saleem 1982; Igual et al. 2007). Furthermore, if a colony was decreasing in size at a fast enough rate before eradication, the removal of predators may only slow the rate of decline rather than reverse the trend (Moller 2006). Our results suggest that the likelihood of detectable colony growth after eradication is negatively related to pre-eradication population size. There were fewer cases of colony growth in very large populations (> 5000 individuals; Fig. 2), which may indicate negative density dependence (i.e., limited resources near carrying capacity resulting in little popula-

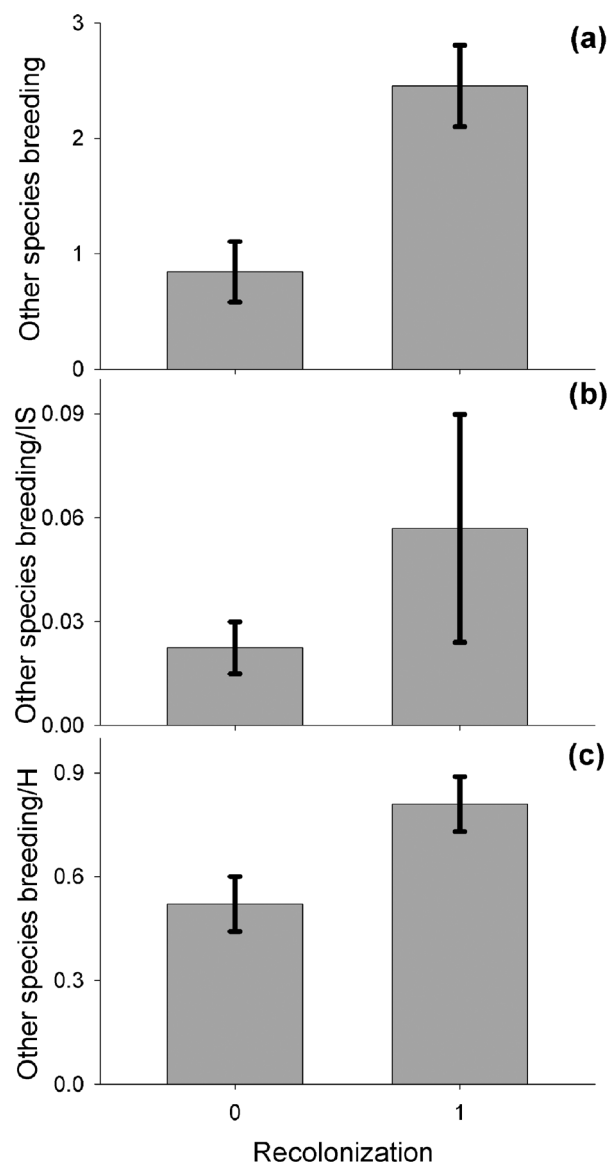


Figure 3. Relationships between observed recolonization by previously occurring seabird species following introduced predator eradication and (a) number of ecologically similar seabird species breeding on an island; (b) number of breeding species corrected for island size (IS); and (c) number of breeding species corrected for habitat quality (H).

tion growth at a large population size; Moller et al. 2009), that predators were swamped and having a relatively insignificant effect (Lyver et al. 2000), or that it is difficult to detect growth reliably when a population is large to begin with. However, we also found few cases of colony growth in very small colonies (<25 individuals; Fig. 2), which may indicate positive density dependence (e.g., Allee effects and weak social attraction) is preventing growth at small population sizes (Stephens et al. 1999; Doligez et al. 2003). Our results suggest that mid-sized

seabird populations could have a higher probability of recovery under a passive posteradication management scheme. Colony growth after eradication was also more likely in species with an increasing or stable metapopulation. This suggests that metapopulation status could indicate the potential for a colony to grow. If the metapopulation is declining due to extrinsic pressures, the newly predator-free colony is also likely to be vulnerable to decline because of the same pressures. In addition, a declining metapopulation would provide fewer immature birds to prospect and recruit to the newly predator free space. The former situation is perhaps less likely, as classic metapopulation theory stresses the variability and high turnover of local populations (Hanski 1998; Oro 2003). We found that a small number of species with declining metapopulations recovered locally after predator eradication (Fig. 2). Thus, although a low probability of passive restoration is expected for species in decline, local dynamics may override the metapopulation's trend to some degree.

In this study, age at first breeding had no effect on colony growth. This result was unexpected, considering seabird species with earlier ages at first breeding would be expected to have a higher per capita growth rate (Aubry et al. 2009) and hence have greater potential to grow after predator eradication. There are numerous reasons for the lack of a detectable effect of this variable. For example, we may not have included a large enough range of ages at first breeding, which is unlikely because species from Common Diving Petrels (*Pelecanoides urinatrix*) (average first breeding, 2 years) to Sooty Shearwaters (*Puffinus griseus*) (average first breeding 7 years) were included. Also, age at first breeding is highly variable, depending on environmental conditions and density dependence (Votier et al. 2008) and thus may not be a reliable predictor of recovery. Furthermore, intrinsic factors, such as age at first breeding may be swamped by immigration. Indeed, none of the variables that affect intrinsic population dynamics exclusively (age at first breeding, time since predator removal, type of predator removed; Table 1) were identified as being important, suggesting they may be less important than extrinsic forces and dispersal dynamics when seabird populations are recovering after disturbance.

In attempting to identify the ecological factors that influence colony growth and recolonization of seabirds after eradication of introduced predators, we found many understudied parameters. Density dependence and habitat limitation (Kokko et al. 2004; Moller 2006), intermittent breeding (Cubaynes et al. 2011), annual survival rates of different age classes (Votier et al. 2008), natal philopatry (Steiner & Gaston 2005), and the relative importance of prospecting and recruitment (Becker & Bradley 2007) are likely to play fundamental roles in colony recovery, but are poorly understood for many species, notably procellariiforms. Furthermore, reliable estimates of popula-

tion parameters (e.g., demographic rates) are unavailable before and after eradication for most species in New Zealand and globally. Thus, although the most plausible (and available) factors influencing posteradication recovery were included in our models, they are not exhaustive, and much unaccounted variance is likely to remain.

In reviewing seabird recovery posteradication in New Zealand, the lack of posteradication monitoring studies is also of concern. Monitoring data existed for only 34% of species breeding on predator-eradicated islands, and these were mostly procellariiforms. Furthermore, only 3.6% of species with pre-eradication count data had posteradication count data, suggesting that it is not possible to compare pre- and posteradication counts reliably. Without robust outcome monitoring, it is impossible to evaluate the effectiveness of expensive predator eradication programs in restoring seabird breeding populations or as part of wider coastal ecosystem recovery projects.

Our results indicated that natural posteradication recovery of seabird populations was more likely on islands less than 25 km from source populations, with higher numbers of similar seabird species, with mid-sized populations at the time of eradication, and in species with a stable or increasing metapopulation. We suggest that managers prioritize passive restoration on islands and for species that meet these criteria. If sites do not meet these specifications, active management techniques should instead be implemented. If uncertainty about passive restoration is to be reduced, monitoring and modeling seabird recovery will be essential steps for island management decision making.

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Supporting Information

A generic model of seabird colony growth (Appendix S1), a list of islands in New Zealand with all non-native predators removed (Appendix S2), and a summary of top 5 candidate models investigating the effects of a range of key environmental variables on the probability of detecting a seabird population response (Appendix S3) are available on-line. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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