

Bird demographic responses to predator removal programs

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Abstract Invasive predators pose a significant risk to bird populations worldwide. Humans have a long history of removing predators from ecosystems; current island restoration actions typically focus on the removal of invasive predators, such as non-native rodents, from seabird breeding islands. While not overly abundant, the results of predator removal studies provide valuable information on the demographic response of birds, and can assist conservation practitioners with prioritizing invasive predator removal projects. We review such studies focusing on observed demographic responses of bird populations to predator removal campaigns and whether ecological factors are useful in predicting those responses. From the 800+ predator removal programs identified, a small fraction ($n = 112$) reported

demographic responses of bird populations. Change in productivity was the most commonly reported response, which on average increased by 25.3% (2.5 SE) with predator removal. The best supported model for predicting the change in productivity from predator removal incorporated bird body mass, egg mass, predator type, nest type and an interaction term for body mass and nest type (AIC_c weight = 0.457). The predicted percent increase in productivity resulting from hypothetical predator removal ranged from 16.9 to 63.0% (mean = 45.0, 5.6 SE), and was lowest for large, surface nesting birds such as albatrosses. The predicted increase in productivity resulting from predator removal alone was insufficient to reverse the predicted population decline for 30–67% of bird species considered, suggesting that in many cases, removal of predators must be performed in combination with other conservation actions in order to ensure a stable or increasing population.

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Introduction

The threats leading to population declines in birds are many and varied, including bycatch in fisheries, habitat destruction, and pollution (Birdlife International 2008). Non-native predators pose a significant risk to

many bird populations, and are currently ranked as the third most significant threat to birds according to the International Union for the Conservation of Nature (Birdlife International 2008). Rats (*Rattus* spp.), feral cats (*Felis catus*), and mustelids are cosmopolitan predators of bird populations, particularly on islands (Atkinson 1989; Jones et al. 2008; Nogales et al. 2004). There is a long history of humans controlling both native and non-native predators to protect birds or simply to increase their numbers for human benefit (e.g., coyote (*Canis latrans*) control programs to increase Bobwhite Quail (*Colinus virginianus*) populations for recreational hunting) (Guthery and Beasom 1977). Studies that follow bird responses to such predator control programs can provide valuable information and guidance with prioritization and planning, since many bird conservation programs today involve the eradication or control of non-native predators at breeding colonies (Aguirre-Muñoz et al. 2008; Harding et al. 2001; Howald et al. 2009).

Conservation prioritization efforts typically target species that are most endangered or areas where restoration efforts appear most effective or feasible (Brooke et al. 2007; Martins et al. 2006). More recently, the return on investment approach has been advocated as a tool to maximize conservation benefits, such as habitat protection or increases in the number of breeding seabirds (Donlan and Heneman 2007; Murdoch et al. 2007; Naidoo et al. 2006). This approach requires the ability to predict both the cost and benefit of conservation interventions. However, while bird responses to non-native predator removal have been studied, the demonstrated benefits of those removal campaigns have not been systematically reviewed (but see Beauchamp et al. 1996; Côté and Sutherland 1997 for a limited review of terrestrial birds). Controlling non-native predators has not led to population recovery for some bird populations (Beauchamp et al. 1996; Carter et al. 1992), while other populations have dramatically increased in numbers following predator removal (Donlan et al. 2007; Keitt and Tershy 2003; Rayner et al. 2007). Thus, identifying life-history characteristics or other factors that can be used to help predict benefits to bird populations from invasive predator control would provide value to conservation planners and practitioners.

Here we present a literature review on the demographic responses of birds resulting from predator removal programs. We focus on invasive predator

removal programs, but also include native predator control programs because of the overall dearth of published studies. The objectives of our analysis were to (1) provide an overall estimate of the known changes in bird productivity as a result of predator removal programs, (2) determine what factors (bird body mass, egg mass, nest type, or predator type) can be used to predict predator removal benefits, (3) assess the demographic contribution of past predator removals to bird population recovery, and (4) explore how much invasive predator removal campaigns are likely to contribute to population recovery for some bird species currently at risk.

Materials and methods

Predator removal and bird productivity

We collated studies reporting on bird demographic responses resulting from the control or removal of predators from the published and grey literature. All studies were included in the overall summary of the benefits of the removal of predators. For statistical analyses, however, we used a subset that included those studies reporting the results of removing a single predator or in a few cases a single predator-type (i.e., two species of invasive rat). We chose to exclude studies involving the removal of more than one predator from statistical analysis since the bird's demographic response could not be attributed to a particular predator. In a few multiple-predator studies, authors identified one predator as being responsible for most or all of the bird mortality, and thus those studies were included in the analysis. Lastly, studies reporting demographic benefits for groups of birds only (e.g., ducks) were excluded since bird body mass (an explanatory variable in our model; details below) could not be determined.

Factors influencing predator removal benefits for birds

Bird productivity estimates pre- and post-predator removal were compared, with the difference between the two values assumed to be the result of predator removal. We used generalized linear models to explore whether bird nest type (i.e., surface, not surface), bird body mass, egg mass, or predator type

(rodent, non-rodent) were important factors in determining the observed effect of predation on birds. Due to the small sample size on non-rodent removal studies and the severity of invasive rodent predation, we chose to group predators as rodent or non-rodent (Atkinson 1985; Jones et al. 2008). Because the response variable, productivity, is a proportion, values were logit-transformed (Crawley 2007). Since only four explanatory variables were considered, all possible model combinations were run. The best performing model were selected based on Akaike's Information Criterion (AIC; Burnham and Anderson 2002). We conducted analyses in the statistical program R and SPSS and adopted a α -level of 0.05 (R version 2.7.0, R Foundation for Statistical Computing; SPSS 16 for Mac, SPSS Inc., Chicago).

Predator removals and bird population recovery

Demographic population models were developed for two distinct data sets. The first data set included species with complete demographic data (i.e., breeding success, juvenile survival, and adult survival) and empirical data on the demographic response of removing predators. We estimate the change in the population growth rate (λ) following predator removal. The second data set included bird species with complete demographic data and known predator impacts, but no predator removal program had been initiated. Here, we predict the change in population growth rate from a hypothetical predator removal. In cases where multiple studies yielded contrasting demographic parameter estimates, we used information from the longest-term or most recent studies rather than averaging data across all studies.

For both datasets, we developed a stochastic, stage-structured, population-projection matrix for each bird population. We chose a 20-year time interval because it is most relevant from a management perspective and allowed us to overlook density-dependent processes associated with long-term projections for most species (Morris and Doak 2002). The model consisted of two stage-classes (juveniles and adults), and only females were included (i.e., productivity was multiplied by 0.5 assuming a 1:1 sex ratio). The model was written in Matlab (version 7.5.0, MathWorks Inc.).

We evaluated the effect of predator removal on bird population dynamics in two phases. First, using the stage-based matrix and published population

parameters, we obtained a baseline or pre-removal population growth rate. Second, we incorporated the change in productivity as a result of predator removal (in the case of the first data set; see "Appendix 1"). In cases where a predator removal program had not yet been initiated, we estimated the demographic response as a result of predator removal using the general linear model described above. The predicted response in productivity as a result of a hypothetical removal was adjusted for bird body mass, egg mass, nest type, and predator type. The new demographic model then generated a post-removal population growth rate. We then scored the estimated demographic benefits from predator removal with respect to its contribution to reversing population decline ($\lambda \geq 1.00$).

Results

Predator removal and bird productivity

A review of the literature yielded 112 studies that examined the change in productivity of 87 bird species as a result of the control or removal of predators ("Appendix 1"). Average study duration was 6.0 years, with 4.8 years of data prior to control/removal efforts and 3.8 following (total range of study years: 1–38). Eleven studies examined the effects of predators on adult or juvenile survival ("Appendix 1") and one study reported on the removal of a domesticated herbivore, *Ovis aries* (Norman 1970). These studies were excluded from statistical analysis due to small sample size. The mean change in productivity for all studies following predator removal was +25.3% (2.5 SE). All but 12 studies reported a positive response in productivity. Overall, predator type (rodent or non-rodent) did not have a significant effect on changes in bird productivity following predator removal ($P = 0.085$; Table 1). However, when predator types were treated on an individual basis, the observed change in bird productivity as a result of predator removal was significantly less following the removal of avian predators compared to rats (Fig. 1; $P = 0.011$) and stoats ($P = 0.019$). Percent change in productivity ranged from –82 to 6,150%; four studies reported zero productivity prior to and increased productivity following predator removal (range 0.455–0.625; "Appendix 1").

Table 1 Top five models examining the effects of removing single predators on bird productivity ($n = 33$)

Model	AIC _c	ΔAIC _c	W
$\beta_o + \beta_{\text{nest}} + \beta_{\text{mass}} + \beta_{\text{predator}} + \beta_{\text{egg}}$ (main effects) ^{a,b}	42.649	0.000	0.457
$\beta_o + \beta_{\text{nest}} + \beta_{\text{mass}} + \beta_{\text{predator}} + \beta_{\text{egg}} + \beta_{\text{mass}} \times \beta_{\text{nest}}$	43.943	1.294	0.239
$\beta_o + \beta_{\text{nest}} + \beta_{\text{mass}} + \beta_{\text{egg}} + \beta_{\text{mass}} \times \beta_{\text{nest}}$	46.423	3.774	0.069
$\beta_o + \beta_{\text{nest}}$	47.619	4.970	0.038
β_o (null model)	47.947	5.298	0.032

Bird body mass, egg mass, nest type (surface and not surface), and an interaction between body mass and nest type made up the best performing model. ΔAIC is the difference between AIC values for each model and the lowest AIC value. A lower AIC value indicates a better fitting model; W is the model's Akaike weight, the relative probability that the model is the best fit to the data tested. β_{nest} = bird nest type (surface or not surface), β_{mass} = bird body mass, β_{predator} = predator type (mammal or bird), β_{egg} = fresh egg mass

^a Model coefficients: intercept = 1.6106, nest type = 0.9222, body mass = -0.0010, egg mass = 0.0100, predator type = -0.9264

^b P -value: nest type = 0.024, body mass = 0.031, egg mass = 0.050, predator type = 0.085

Factors influencing predator removal benefits for birds

Twenty-six studies included the removal of a single predator and estimates of changes in bird productivity (some studies provided data for multiple bird species, total $n = 33$). The best performing model (main effects) based on AIC_c values included bird body

mass, egg mass, nest type, and predator type (Table 1). The second model (which includes an interaction term for bird body mass and nest type) performed nearly as well ($\Delta\text{AIC}_c < 2.0$; Burnham and Anderson 2002) therefore model averaging was applied. The averaged model was used to estimate the effects of hypothetical predator removal.

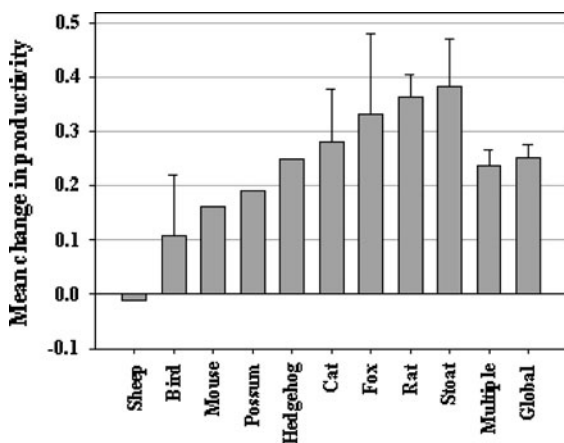


Fig. 1 Mean change (\pm SE) in bird productivity following the removal or eradication of predators ($n = 111$). Sample sizes differ: sheep *Ovis aries* (1), birds *Cassidix mexicanus prosopidicola*, *Corvus brachyrhynchos*, *C. corone*, *C. corax*, *Larus canus*, *L. n. scopulinus*, *L. argentatus* (5), deer mouse *Peromyscus maniculatus* (1), brushtail possum *Trichosurus vulpecula* (1), hedgehog *Erinaceus europaeus* (1), cat *Felis catus* (6), fox *Alopex lagopus*, *Vulpes fulva* (2), rat *Rattus rattus*, *R. norvegicus*, *R. exulans* (18), stoat *Mustela erminea* (3), and multiple predators (73). Multiple predator removal studies included native and non-native predators. Global value includes all studies

Predator removals and bird population recovery

Complete demographic data were available for 24 bird species, including data on productivity before and after predator removal. Percent change in lambda before and after predator removal ranged from -12.3 to +36.7%, with an overall mean of 11.3% (2.3 SE; Table 2). Of the 24 species assessed, three had a positive population growth rate prior to predator removal, while 17 had positive population growth rates following ($\lambda \geq 1$, Table 2).

Complete demographic data were available for an additional 12 bird species that currently suffer from predation by introduced predators, but currently lack a control/eradication campaign (Table 3). Prior to adjusting the demographic parameters to account for hypothetical predator removal, nine of the 12 species were predicted to be in decline (baseline $\lambda < 1.00$, Table 3). The predicted increase in productivity resulting from hypothetical predator removal ranged from 16.9 to 63.0% (mean = 45.0%, 5.6 SE) and was lowest for large, surface nesting birds (Table 3). Hypothetical predator removal resulted in a positive population growth rate for three of the nine species in

Table 2 Projected population growth rates (λ) for birds pre- and post-predator removal based on the empirically estimated demographic rates provided in "Appendix 1"

Species	Predator	λ -pre	λ -post	% Change	Source(s)
Cory's Shearwater <i>Calonectris diomedea</i>	Black rat <i>Rattus rattus</i>	0.898 (0.003)	0.954 (0.003)	5.8	Amengual and Aguilar (1998) and Jenouvrier et al. (2008)
Sooty Shearwater <i>Puffinus griseus</i>	Weka <i>Gallirallus australis</i> & black rat	0.954 (0.003)	1.053 (0.013)	9.9	Clucas et al. (2008), Harper (2007) and Jones (2002)
Red-tailed Tropicbird <i>Phaethon rubricauda</i>	Polynesian rat <i>Rattus exulans</i>	0.882 (0.009)	0.896 (0.010)	1.5	Fleet (1972) and Schreiber et al. (2001)
Black Brandt <i>Branita bernicla</i>	Arctic fox <i>Alopex lagopus</i>	0.916 (0.016)	0.935 (0.010)	2.0	Anthony et al. (1991), Ward et al. (1997) and Ward et al. (2004)
Mallard <i>Anas platyrhynchos</i>	Many, primarily red fox <i>Vulpes vulpes</i>	0.954 (0.003)	1.083 (0.004)	26.0	Drilling et al. (2002) and LaGrange et al. (1995)
Blue-winged Teal <i>Anas discors</i>	Many, primarily striped skunk <i>Mephitis mephitis</i>	0.863 (0.011)	1.092 (0.015)	20.9	LaGrange et al. (1995) and Rohwer et al. (2002)
Blue Duck <i>Hymenolaimus malacorhynchos</i>	Stoat <i>Mustela erminea</i>	0.821 (0.004)	1.188 ^a (0.004)	36.7	Whitehead et al. (2008)
American Coot <i>Fulica americana</i>	Many, primarily red fox	0.937 (0.003)	1.019 (0.003)	7.8	Brisbin and Mowbray (2002) and Garretson et al. (1996)
Ring-necked Pheasant <i>Phasianus colchicus</i>	Many, primarily striped skunk	0.894 (0.012)	1.013 (0.0150)	11.7	Chessness et al. (1968) and Leif (1994)
Ruffed Grouse <i>Bonasa umbellus</i>	Many, primarily Great Horned Owl <i>Bubo virginianus</i>	1.069 (0.003)	1.191 (0.004)	16.2	Bump et al. (1947) and Small et al. (1991)
Southern Dunlin <i>Calidris alpina schinzii</i>	Many, primarily red fox	0.986 (0.003)	1.030 (0.003)	4.4	Pauliny et al. (2008)
Snowy Plover <i>Charadrius alexandrinus</i>	Red fox and feral cat <i>Felis catus</i>	0.977 (0.022)	1.088 (0.016)	10.2	Neuman et al. (2004) and Paton (1994)
Piping Plover <i>C. melodus</i>	Many, primarily red fox	0.852 (0.012)	0.967 (0.013)	19.8	Larson et al. (2002) and Melvin et al. (1992)
Golden Plover <i>Pluvialis apricaria</i>	Carrion Crow <i>Corvus corone</i> and Common Gull <i>Larus canus</i>	0.987 (0.014)	0.864 (0.020)	-14.2	Parr (1993) and Piersma et al. (2005)
Lapwing <i>Vanellus vanellus</i>	Red fox and Carrion Crow	0.998 (0.003)	1.036 (0.003)	2.3	Bolton et al. (2007) and Peach et al. (1994)
Greater Sandhill Crane <i>Grus canadensis tabida</i>	Many, primarily coyote <i>Canis latrans</i>	0.811 (0.008)	1.036 (0.003)	3.7	Ellis et al. (2000), Littlefield (2003) and Tacha et al. (1992)
Bridled Tern <i>Onychoprion anaethetus</i>	Black rat	0.811 (0.008)	1.008 (0.013)	19.5	Haney et al. (1999) and Lorgelec and Pascal (2005)
Least Tern <i>Sternula antillarum</i>	Many, primarily red fox	0.943 (0.003)	1.135 (0.002)	19.2	Massey et al. (1992) and Minsky (1980)
Western × Glaucous-winged Gull <i>Larus occidentalis</i> × <i>glaucescens</i>	Many, primarily gulls	0.845 (0.003)	0.914 (0.003)	6.9	Good (2002) and Spear et al. (1987)

Table 2 continued

Species	Predator	λ -pre	λ -post	% Change	Source(s)
Chatham Island Pigeon <i>Hemiphaga novaeseelandiae</i>	Many, including Harrier <i>Circus approximans</i>	1.119 (0.013)	1.104 (0.015)	-1.4	Flux et al. (2001)
New Zealand Wattlebird <i>Callaeas cinerea</i>	Many, including black rat	0.982 (0.004)	1.228 ^a (0.003)	24.5	Basse et al. (2003)
Stitchbird <i>Notiomystis cincta</i>	Polynesian and Norway rat <i>R. norvegicus</i>	0.853 (0.004)	0.905 ^a (0.005)	5.2	Empson and Miskelly (1999)
Rarotonga Monarch <i>Pomarea dimidiata</i>	Many, primarily black rat	0.971 (0.009)	1.110 (0.012)	12.5	Robertson et al. (1994) and Robertson and Saul (2007)
Yellow-headed Blackbird <i>Xanthocephalus xanthocephalus</i>	Many, primarily red fox	0.990 (0.004)	0.998 (0.004)	0.8	Garretson et al. (1996) and Tvedt and Crawford (1995)

^a Best case scenario using juvenile and adult survival rates from intensively managed sites

decline. The mean increase in population growth rate was 3.6% (0.9 SE, range: 0.2–9.8%).

Discussion

The results of our literature review highlight that for the majority of bird species studied, the removal of predators has resulted in increased productivity and survival. In only a few instances was bird productivity or survival lower following predator removal (Empson and Miskelly 1999; Flux et al. 2001; Norman 1970; Powlesland et al. 1999). Due to the paucity of studies involving the removal of a single native predator ($n = 2$), it was not possible to determine whether native or non-native predators have a greater impact on bird demography. However, the increases in bird productivity following the removal of a native mouse and fox were some of the lowest reported, 16.2 and 18.3%, respectively (Fig. 1; Anthony et al. 1991; Millus et al. 2007).

Rodents, especially rats (*Rattus* spp.), are notorious bird predators (Atkinson 1985; Jones et al. 2003). Even the small Polynesian rat (*R. exulans*) and house mouse (*Mus musculus*) are known to cause significant mortality of albatrosses and petrels more than 50× their size (Cuthbert and Hilton 2004; Wanless et al. 2007; Woodward 1972). Jones et al. (2008) reported significant impacts of rats, especially the black rat *Rattus rattus*, on small burrowing seabirds. While the results of our analysis showed that rats and stoats are more effective bird-predators than other bird species, overall, the removal of predators (rodent vs. non-rodent) was not well supported by our model ($P = 0.085$; Table 1). The inability to detect an effect in this analysis is likely due to the inclusion of a vast array of predators ($n = 61$). In the case of the non-rodent group, predators varied greatly in size and ability from small crabs *Coenobita* spp. to coyote (Littlefield 2003; Schaffner 1991). In addition, a number of studies reported predation by small mammals or birds which could not be excluded with fences or otherwise removed from the treatment area (Lokemoen et al. 1987; Mayer and Ryan 1991; Parr 1993). Thus, the change in bird productivity included in our model may not have resulted from the removal of the target predator species.

The type and location of a bird's nest has been shown to influence predation rates (Burger and

Table 3 Model results for a hypothetical predator eradication for species/locations where little or no predator control currently exists

Species	Bodymass (g) ^a	Egg mass (g) ^a	Nest type	Predator type	Parameters		% increase in F_a^b	λ		Source	
					P_a	S_j		S_a	Baseline		Post-eradication
Tristan Albatross <i>Diomedea dabbenena</i>	7,050	449	S	R	0.33	0.81 ^c	0.91	21.4	0.948 (0.003)	0.955 (0.003)	Wanless et al. (2009)
Northern Royal Albatross <i>Diomedea e. sandfordi</i>	6,577	416	S	NR	0.19	0.93	0.95	24.2	0.973 (0.002)	0.980 (0.002)	Robertson (1998) and Taylor (2000)
Laysan Albatross <i>Diomedea immutabilis</i>	3,310	218	S	R	0.56	0.92	0.93	35.4	1.017 (0.003)	1.048 (0.003)	Fisher (1975) and Ludwig et al. (1998)
Sooty Albatross <i>Phoebastria fusca</i>	3,250	207	S	R	0.58	0.88	0.90	33.5	0.952 (0.001)	0.976 (0.001)	Weimerskirch and Jouventin (1998)
Westland Petrel <i>Procellaria westlandica</i>	1,294	138	NS	NR	0.62	0.64 ^d	0.96	62.7	1.041 (0.001)	1.081 (0.001)	Waugh et al. (2006)
Manx Shearwater <i>Puffinus puffinus</i>	487	57	NS	R	0.56	0.44 ^d	0.85	63.0	0.966 (0.005)	1.034 (0.005)	Appleton et al. (2006) and Mavor et al. (2006)
European Storm-petrel <i>Hydrobates pelagicus</i>	28	7	NS	R	0.65	0.82	0.83	62.2	0.935 (0.002)	1.007 (0.002)	Minguez and Oro (2003) and Oro et al. (2005)
Brown Pelican <i>Pelecanus o. californicus</i>	4,000	110	S	NR	1.09	0.30 ^d	0.88 ^e	16.9	1.001 (0.005)	1.012 (0.005)	Anderson et al. (1996) and Shields (2002)
Yellow-eyed Penguin <i>Megabyptes antipodes</i>	5,140	242	S	NR	1.36	0.59	0.90	19.3	0.959 (0.002)	0.964 (0.002)	Marchant and Higgins (1990), Ratz et al. (2004) and Richdale (1957)
African Penguin <i>Spheniscus demersus</i>	2,836	106	S	R	0.47	0.32 ^d	0.91	39.1	0.976 (0.001)	0.988 (0.002)	Crawford et al. (1999) and Mclean (1985)
Akepa <i>Loxops coccineus</i>	12	1.5	NS	NR	0.48	0.31	0.77	61.3	0.843 (0.002)	0.889 (0.001)	Freed et al. (2008)
Hawaii Creeper <i>Oreomystis mana</i>	14	1.4	NS	R	1.70	0.31 ^d	0.78	61.2	0.939 (0.004)	1.038 (0.004)	Lepson and Woodworth (2002)

P_a productivity (mean number of fledged chicks per pair per year), S_j annual juvenile survival, S_a annual adult survival, λ population growth rate (SE), S surface, NS not surface, R rodent, NR not rodent

^a From Brooke (2004), del Hoyo et al. (1992), Marchant and Higgins (1990) and Schönwetter (1967)

^b Predicted demographic benefit based on the coefficients from the best-supported eradication effects model (see Table 1)

^c Juvenile survival estimated from Wandering Albatross *Diomedea exulans* (Wanless et al. 2009)

^d First year survival only

^e Estimate based on small sample size and survival for 180 days post-release, extrapolated to annual rate (Anderson et al. 1996)

Gochfield 1991; Igual et al. 2007; Moors and Atkinson 1984). Typically, birds nesting on or near the ground or in burrows are especially vulnerable to predation due to ease of access to nests (Atkinson 1985). Thus seabirds and other surface nesting birds would presumably experience the largest increase in productivity following predator removal compared to tree dwelling species which can avoid some predators (e.g., foxes). Our results provide further support for this idea with nest type (surface vs. not surface) a significant factor in our model ($P = 0.024$; Table 1).

Bird body mass and egg mass are also known to influence predation rates with smaller birds and smaller, thin-shelled eggs typically suffering increased predation (DeGraaf and Maier 1996; Haskell 1995; Imber 1975; Jones et al. 2008; Roper 1992). However, Blight et al. (1999) and Jones et al. (2008) found that egg mass, eggshell thickness, and predator gape did not differentially affect predation by rodents. Our results suggest bird body mass ($P = 0.030$) is a reliable predictor of predator removal benefits (Table 1) and provides limited support for egg mass ($P = 0.058$; Table 1).

The ability of the model to predict the benefits of predator removal prior to an eradication event varied across species. In the case of the California Brown Pelican *Pelecanus occidentalis californicus*, the predicted 16.9% increase in productivity following hypothetical predator removal is above the range of values reported for feral cat predation (Anderson et al. 1989; Table 3) However, for Tristan Albatross (*Diomedea dabbenena*), the predicted increase in productivity resulting from predator removal is 21.4%, which is comparable to the reported mortality by Cuthbert and Hilton (2004) who suggest that 15–39% of chicks die as a result of mouse predation each year. Like any set of models, discrepancies do and will exist for a suite of reasons. First, biases in reporting may influence the dataset since studies reporting a null effect can be difficult to publish (Csada et al. 1996). Only 15 of the 112 studies presented report no significant increase (or decrease) in fecundity following predator removal (“Appendix 1”; Bolton et al. 2007; Clark et al. 1995; Dion et al. 1999; Flux et al. 2001; Garretson et al. 1996; Harper 2007; Kauhala 2004; Powlesland et al. 2003; Rohwer et al. 1997). Second, there may be unusual or idiosyncratic circumstances that are not anticipated by the model. For example, on Gough Island, the mice predating Tristan

Albatross have developed large body size compared to populations elsewhere (mean 27.2 g compared to 9–25 g; Jones et al. 2003) and on the Falkland Islands, the tiny Thin-billed Prion (*Pachyptila belcheri*; 145 g) manages to coexist with mice, cats, and black rats (Quillfeldt et al. 2008). Finally, our ability to accurately predict the outcome of conservation actions, and thus prioritize management, is limited by the availability and quality of published data. Despite more than 800 successful invasive mammal eradications worldwide (Donlan and Wilcox 2008), less than 20% of studies directly quantified the benefits to birds. Inclusion of additional quantitative studies examining the demographic response of birds (especially those >1,500 g) following predator removal would increase the ability to predict conservation benefits *a priori*.

From the data available, removing invasive predators often reverses a negative population growth rate. Seventeen of the 24 bird species predicted to be in decline in Table 2 had estimated lambdas greater than one following invasive predator removal. Further, three of the nine declining species in Table 3 showed a positive population growth rate following hypothetical invasive predator eradication. For those bird species that predator eradication does not reverse population decline, predator removal is likely to result in cost-effective increases in lambda relative to other conservation actions (Wilcox and Donlan 2007, 2009). Like any threatened species program, multiple conservation strategies will often be necessary to ensure recovery of threatened populations.

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Appendix 1

See Table 4.

Table 4 Summary of published studies reporting the demographic response of birds to the control or eradication of predators (including multi-predator studies)

Family	Species	Body mass (g) ^a	Egg mass (g) ^b	Nest type	Predator(s)	Par Eradication		S_j	S_a	Source(s)
						Pre	Post			
Procellariidae	Blue Petrel <i>Halobaena caerulea</i>	197	42	NS	Feral cat <i>Felis catus</i>	P_a 0.24	0.64			Cooper et al. (1995)
	White-chinned Petrel <i>Procellaria aequinoctialis</i>	1,335	134	NS	Feral cat	P_a 0.55	0.86			van Rensburg and Bester (1988)
Cory's Shearwater <i>Calonectris diomedea</i>		840	99	NS	Feral cat	P_a 0.36	0.22			Cooper et al. (1995)
					Norway rat <i>Rattus norvegicus</i> , black rat <i>R. rattus</i>	P_a 0.48	0.69			Jouventin et al. (2003)
					Black rat	P_a 0.43	0.86	0.88	0.92	Mougin et al. (2000) and Towns et al. (2006)
					Black rat	P_a 0.47	0.85			Lorvelec and Pascal (2005)
					Black rat	P_a 0.48	0.89			Igual et al. (2006)
					House mouse <i>Mus musculus</i> , rabbit <i>Oryctolagus cuniculus</i>	P_a 0.41	0.55			Zino et al. (2008)
					Black rat	P_a 0.33	0.49			Thibault (1995)
					Black rat	P_a 0.18	0.67			Amengual and Aguilar (1998)
	Sooty Shearwater <i>Puffinus griseus</i>	803	95	NS	Weka <i>Gallirallus australis</i> , black rat	P_a 0.83	0.77	0.85	0.95	Clucas et al. (2008), Harper (2007) and Jones (2002)
	Short-tailed Shearwater <i>Puffinus tenuirostris</i>	619	89	NS	Sheep <i>Ovis aries</i>	P_a 0.51	0.50			Norman (1970)
	Black-vented Shearwater <i>Puffinus opisthomelas</i>	405	52	NS	Feral cat	A_m 0.16	0.01			Keitt and Tershy (2003) and Keitt et al. (2002)
	Audubon's Shearwater <i>Puffinus l'herminieri</i>	163	29	NS	Black rat	P_a 0.45	0.86			Pascal et al. (2008)
	Little Shearwater <i>Puffinus assimilis</i>	156	32	NS	Black rat	P_a 0.00	0.75			Pascal et al. (2004)
	Galapagos Petrel <i>Pterodroma phaeopygia</i>	408	56	NS	Polynesian rat <i>Rattus exulans</i>	P_a 0.24	0.62			Pierce (2002)
	Zino's Petrel <i>Pterodroma madeira</i>	204	37	NS	Black rat, feral cat	P_a 0.30	0.72			Cruz and Cruz (1987)
					Black rat, feral cat	P_a 0.08	0.51			Zino et al. (2001)

Table 4 continued

Family	Species	Body mass (g) ^a	Egg mass (g) ^b	Nest type	Predator(s)	Par	Eradication		S _j	S _a	Source(s)
							Pre	Post			
Phaethontidae	Great-winged Petrel <i>Pterodroma macroptera</i>	587	81	NS	Feral cat	P _a	0.16	0.64			Cooper et al. (1995)
	Grey-faced Petrel <i>Pterodroma n. gouldi</i>	668	80	NS	Feral cat	P _a	0.08	0.54			van Rensburg and Bester (1988)
	Pycroft's Petrel <i>Pterodroma pycrofti</i>	146	32	NS	Norway rat ^c	P _a	0.13	0.37			Imber et al. (2000)
	Cook's Petrel <i>Pterodroma cookii</i>	179	41	NS	Polynesian rat	P _a	0.33	0.60			Pierce (2002)
	Bonin Petrel <i>Pterodroma hypoleuca</i>	176	39	NS	Polynesian rat, feral cat ^d	P _a	0.49	0.75			Imber et al. (2003)
	Salvin's Prion <i>Pachyptila vittata salvini</i>	162	35	NS	Black rat, house mouse ^e	P _a	0.47	0.82			Seto and Conant (1996)
	Red-tailed Tropicbird <i>Phaethon rubricauda</i>	624	77	S	Feral cat	P _a	0.47	0.66			van Rensburg and Bester (1988)
	White-tailed Tropicbird <i>Phaethon lepturus</i>	334	43	S	Polynesian rat	P _a	0.20	0.26	0.47	0.85	Fleet (1972), Schreiber and Schreiber (1993) and Schreiber et al. (2001)
	Black Brant <i>Branta b. nigricans</i>	1,230	100	S	Many, primarily black rat	P _a	0.30	0.42			Schaffner (1991)
	Mallard Anas <i>Anas platyrhynchos</i>	1,029	52	S	Arctic fox <i>Alopex lagopus</i>	P _a	0.64	0.82	0.23	0.84	Anthony et al. (1991) and Ward et al. (1997, 2004)
Anatidae	Blue-winged Teal <i>Anas discors</i>	387	28	S	Many, primarily red fox <i>Vulpes vulpes</i>	P _a	0.36	0.57	0.61	0.55	Drilling et al. (2002) and Pearse and Ratti (2004)
	Northern Shoveller <i>Anas clypeata</i>	613	38	S	Many, primarily red fox	P _a	0.63	0.93			Duebber and Lokemoen (1980)
	Blue Duck <i>Hymenolaimus malacorhynchos</i>	775	62	S	Many, primarily striped skunk <i>Mephitis mephitis</i>	P _a	0.14	0.39			LaGrange et al. (1995)
					Many, primarily striped skunk	P _a	0.14	0.30	0.38 ^f	0.55	Rohwer et al. (2002) and LaGrange et al. (1995)
				Many, primarily red fox	P _a	0.23	0.63			Sargeant et al. (1974)	
				Many, primarily stoat <i>Mustela erminea</i>	P _a	0.10	0.54			Whitehead et al. (2008)	
					S _j	0.00	0.49				

Table 4 continued

Family	Species	Body mass (g) ^a	Egg mass (g) ^b	Nest type	Predator(s)	Par	Eradication		S _j	S _a	Source(s)
							Pre	Post			
Ducks ^g					Many, primarily striped skunk	S _j	0.81	0.69			Balsler et al. (1968)
Ducks ^g					Striped skunk, Franklin's ground squirrel	P _a	0.24	0.68			
Ducks ^g					<i>Spermophilus franklinii</i>	P _a	0.03	0.15			Greenwood (1986)
Ducks ^g					Many, primarily red fox	P _a	0.17	0.54			Lokemoen and Woodward (1993)
Ducks ^g					Many, primarily striped skunk	P _a	0.06	0.14			Sargeant et al. (1995)
Ducks ^g					Many, primarily red fox	P _a	0.60	0.89			Duebber and Kantrund (1974)
Ducks ^g					Many, primarily feral cat	P _a	0.25	0.07			Meckstroth and Miles (2005)
Ducks ^g					Many, primarily feral cat	P _a	0.06	0.81			Greenwood et al. (1990)
Ducks ^g					Many, primarily striped skunk	P _a	0.30	0.58			Lokemoen et al. (1982)
Ducks ^g					Many, primarily red fox	P _a	0.08	0.60			Lokemoen et al. (1987)
Ducks ^g					Many, primarily raccoon dog <i>Nyctereutes procyonoides</i>	P _a	0.62	0.61			Kauhala (2004)
Ducks ^g					Many, primarily striped skunk	P _a	0.10	0.33			Doty and Rondeau (1987)
Ducks ^g					Many, primarily raccoon <i>Procyon lotor</i>	P _a	0.20	0.54			Rohwer et al. (1997)
Ducks ^g					Many, primarily red fox	P _a	0.26	0.55			Garretson et al. (1996)
Ducks ^g					Many, primarily striped skunk	P _a	0.29	0.53			Chodachek and Chamberlain (2006)
Ducks ^g					American Crow <i>Corvus brachyrhynchos</i>	P _a	0.07	0.12			Clark et al. (1995)
Ducks ^g					Many, primarily red fox	P _a	0.20	0.50			Sargeant et al. (1974)
Ducks ^g	Grouse <i>Pedioecetes phasianellus</i>										

Table 4 continued

Family	Species	Body mass (g) ^a	Egg mass (g) ^b	Nest type	Predator(s)	Par	Eradication		S _j	S _a	Source(s)
							Pre	Post			
Rallidae	American Coot <i>Fulica americana</i>	638	29	S	Many, primarily raccoon	P _a	0.67	0.86	0.44	0.49	Garretson et al. (1996) and Brisbin and Mowbray (2002)
Phasianidae	Purple Swamphen <i>Porphyrio porphyrio</i>	950	32.3	S	Rabbit, Australasian Harrier <i>Circus approximans</i>	P _a	0.76	0.19			Haselmayer and Jamieson (2002)
	Malleefowl <i>Leipoa ocellata</i>	2,000	168	S	Red fox	S _j	0.12	0.40			Priddel and Wheeler (1997)
	Ring-necked Pheasant <i>Phasianus colchicus</i>	1,109	33	S	Many, primarily striped skunk	P _a	0.22	0.32	0.61	0.51	Chessness et al. (1968) and Leif (1994)
	Ruffed Grouse <i>Bonasa umbellus</i>	572	20	S	Many, primarily Great Horned Owl <i>Bubo virginianus</i>	P _a	0.38	0.68	0.14	0.34	Edminster (1939) and Rusch et al. (2000)
Recurvirostridae	Weka <i>Gallinulus australis greyi</i>	760	34	S	Many, primarily feral cat	P _a	0.06	0.38			Bramley (1996)
	Gray Partridge <i>Perdix perdix</i>	390	18	S	Red fox <i>Vulpes vulpes</i>	P _a	0.33	0.40			Tapper et al. (1996)
	Tetraonids [§]				Many, primarily red fox	P _a	0.59	0.77			Marcstrom et al. (1988)
	Black Stilt <i>Himantopus novaezelandiae</i>	223	40	S	Many, primarily feral cat	P _a	0.19	0.33			Keedwell et al. (2002)
Charadriidae	Killdeer <i>Charadrius vociferus</i>	97	17	S	Many, primarily ferret	P _a	0.01	0.11			Pierce (1986)
					Many, primarily feral cat	P _a	0.29	0.53			Reed (1998)
					Many, including deer mice <i>Peromyscus maniculatus</i>	P _a	0.33	0.14			Mabee and Estelle (2000)
	Snowy Plover <i>Charadrius alexandrinus</i>	42	8	S	Many, primarily gulls (<i>Larus</i> spp.) Red fox, feral cat	P _a	0.26	0.62	0.38	0.73	Nol and Brooks (1982) Neuman et al. (2004) and Paton (1994)
Piping Plover <i>Charadrius melodus</i>		55	10	S	Many, including deer mice Many, primarily coyote <i>Canis latrans</i>	P _a	0.54	0.57			Mabee and Estelle (2000)
					Many, primarily red fox	P _a	0.17	0.90	0.48	0.74	Larson et al. (2002) and Melvin et al. (1992)

Table 4 continued

Family	Species	Body mass (g) ^a	Egg mass (g) ^b	Nest type	Predator(s)	Par	Eradication		S _j	S _a	Source(s)
							Pre	Post			
					Many, including deer mice	P _a	0.75	0.60			Mabee and Estelle (2000)
					Many, primarily red fox	P _a	0.25	0.92			Rimmer and Deblinger (1990)
					Many, primarily mink <i>Mustela vison</i>	P _a	0.33	0.51			Mayer and Ryan (1991)
					Many, primarily mink	P _a	0.34	0.62			Kruse et al. (2001)
					Many, primarily coyote	P _a	0.28	0.93			Smith et al. (1993)
					Many, primarily coyote	P _a	0.45	0.91			Murphy et al. (2003)
					Many, primarily red fox	P _a	0.25	0.42			Larson et al. (2002)
	Golden Plover <i>Pluvialis apricaria</i>	215	27	S	Carrion Crow <i>Corvus corone</i> , Common Gull <i>Larus canus</i>	P _a	0.47	0.09 ^b	0.71	0.82	Parr (1993) and Piersma et al. (2005)
	Lapwing <i>Vanellus vanellus</i>	234	23	S	Red fox and Carrion Crow	P _a	0.26	0.34	0.60	0.75	Bolton et al. (2007) and Peach et al. (1994)
	Redshank <i>Tringa totanus</i>	159	20	S	Many, primarily red fox	P _a	0.66	0.39			Isaksson et al. (2007)
	New Zealand Dotterel <i>Charadrius obscurus</i>	153	23	S	Many, primarily red fox	P _a	0.38	0.92			Isaksson et al. (2007)
					Many, primarily feral cat	P _a	0.47	0.80			Dowding (1997)
	Banded Dotterel <i>Charadrius bicinctus</i>	60	9	S	Many, primarily feral cat	S _a	0.83	0.82			Dowding (1997)
					Many, primarily feral cat	P _a	0.51	0.78			Norbury and Barlow (1998)
	Chatham Island Oystercatcher <i>Haematopus chathamensis</i>	600	46	S	Many, primarily feral cat	P _a	0.78	0.46			Norbury and Heyward (2008)
					Many, primarily feral cat	P _a	0.35	0.64	0.81	0.94	Moore (2009)
	Shorebirds [§]				Many, primarily feral cat	S _a	0.94	0.98			Moore (2009)
	Southern Dunlin <i>Calidris alpina schinzii</i>	55	9.4	S	Hedgehog <i>Erinaceus europaeus</i>	P _a	0.68	0.93			Jackson (2001)
	Greater Sandhill Crane <i>Grus canadensis tabida</i>	5,571	161	S	Many, primarily red fox		0.40	0.65	0.33 ^f	0.77	Pauliny et al. (2008) and Warmock and Gill (1996)
					Many, primarily coyote	P _a	0.42	0.55	0.80	0.87	Ellis et al. (2000), Littlefield (2003) and Tacha et al. (1992)

Table 4 continued

Family	Species	Body mass (g) ^a	Egg mass (g) ^b	Nest type	Predator(s)	Par	Eradication		S _a	Source(s)	
							P _a	Post			
Sternidae	Bridled Tern <i>Onychoprion anaethetus</i>	100	20	S	Black rat	P _a	0.00 ⁱ	0.53	0.78	0.83	Haney et al. (1999) and Lorvelec and Pascal (2005)
	Sooty Tern <i>Onychoprion fuscatus</i>	180	35	S	Black rat, feral cat	A _m	0.23	0.02			Rodriguez et al. (2006)
	Brown Noddy <i>Anous stolidus</i>	200	37	S	Black rat	P _a	0.05	0.77			Pascal et al. (2004)
	Least Tern <i>Sterna antillarum</i>	42	7	S	Many, primarily red fox	P _a	0.35	0.99	0.54	0.88	Massey et al. (1992) and Rimmer and Deblinger (1992)
Common Tern <i>Sterna hirundo</i>		125	21.0	S	Ring-billed <i>Larus n. scopolinus</i> and Herring Gull <i>L. argentatus</i>	P _a	0.19	0.67			Minsky (1980)
	Western x Glaucous-winged Gull <i>L. occidentalis</i> × <i>glaucescens</i>	951	94.6	S	Many, primarily gulls	P _a	0.01	0.11	0.55 ^f	0.84	Good (2002) and Spear et al. (1987)
	Xantus's Murrelet <i>Synthliboramphus hypoleucus</i>	168	37	NS	Black rat	P _a	0.48	0.93			Whitworth et al. (2005)
Columbidae	Chatham Island Pigeon <i>Hemiphaga n. chathamensis</i>	800	40	NS	Deer mouse Many, including Harrier <i>Circus approximans</i>	P _a	0.63	0.80			Millus et al. (2007)
	New Zealand Wood Pigeon <i>Hemiphaga novaeseelandiae</i>	600	30	NS	Black rat, brushtail possum <i>Trichosurus vulpecula</i>	P _a	0.66	0.58	0.85 ^f	0.96	Flux et al. (2001)
	White-winged Dove <i>Zenaidura asiatica</i>	153	8	NS	Brushtail possum Many, primarily black rat Many, primarily Great-tailed Grackle <i>Cassidix mexicanus prosopidicola</i>	P _a	0.00	0.52			Innes et al. (2004)
						P _a	0.25	0.75			Powlesland et al. (2003)
						P _a	0.00	0.46			Clout et al. (1995)
						P _a	0.38	0.50			Blankinship (1966)

Table 4 continued

Family	Species	Body mass (g) ^a	Egg mass (g) ^b	Nest type	Predator(s)	Par		S _j	S _a	Source(s)	
						Pre	Post				
Psittacidae	New Zealand Kaka <i>Nestor meridionalis</i>	429	21	NS	Brush-tail possum, black rat	P _a	0.33	0.50		Powlesland et al. (2003)	
							S _j ¹	0.60	0.50		Powlesland et al. (2003)
Icteridae	Glossy Black-cockatoo <i>Calyptorhynchus lathami</i>					A _m	0.12	0.06		Powlesland et al. (2003)	
		430	26	NS	Stoat, brush-tail possum	P _a	0.19	0.84		Moorehouse et al. (2003)	
							P _a	0.23	0.42		Garnett et al. (1999)
		65	5	NS	Many, primarily raccoon	P _a	0.61	0.63	0.43 ^f	0.67	Garnett et al. (1999) and Twardt and Crawford (1995)
Emberizidae	Red-winged Blackbird <i>Agelaius phoeniceus</i>	53	4	NS	Many, primarily raccoon	P _a	0.62	0.64		Garnett et al. (1999)	
						P _a	0.15	0.25		Dion et al. (1999)	
Cotingidae	Bellbird <i>Anthornis melanura</i>	36	3	NS	Stoat	P _a	0.16	0.66		Kelly et al. (2005)	
						A _m ^k	0.10	0.02		Powlesland et al. (1999)	
Petroicidae	New Zealand Robin <i>Petroica australis longipes</i>	35	3	NS	Brush-tail possum, black rat	P _a	0.21	0.70		Powlesland et al. (1999)	
						P _a	0.42	0.57		Empson and Miskelly (1999)	
Callaeidae	Yellowhead <i>Mohoua ochrocephala</i>	28	2	NS	Stoat	S _d ¹	0.88	0.54		Empson and Miskelly (1999)	
						P _a	0.65	0.86		O'Donnell et al. (1996)	
		230	19	NS	Many, including brush-tail possum and black rat	P _a	0.13	0.42	0.79	0.85	Innes et al. (1999)
						P _a	0.05	0.62			Basse et al. (2003)
Monarchidae	Stitchbird <i>Notiomystis cincta</i>	35	3	NS	Polynesian and Norway rats	P _a	0.77	0.87		Empson and Miskelly (1999)	
						S _j ¹	0.87	0.88			
						S _d ¹	0.79	0.91			
Monarchidae	Rarotonga Monarch <i>Pomarea dimidiata</i>	22	2	NS	Many, primarily black rat	P _a	0.26	0.62	0.79	0.84	Robertson et al. (1994) and Robertson and Saul (2007)
								0.33 ± 0.02	0.59 ± 0.02		

Table 4 continued

Family	Species	Body mass (g) ^a	Egg mass (g) ^b	Nest type	Predator(s)	Par	Eradication		S_j	S_a	Source(s)
							Pre	Post			
Mean \pm SE (single predator studies only)											
							0.33 \pm 0.04	0.64 \pm 0.04			

Results of models examining the effect of predator control or eradication on bird population trajectories are presented. S Surface, NS not surface, Par demographic parameter affected by predator removal, P_a productivity (mean number of fledged chicks per pair per year), S_j annual juvenile survival, S_a annual adult survival, A_m adult mortality (proportion of population predated)

^a Mean mass of males and females combined (Dunin 1993)

^b From Marchant and Higgins (1990), Schönwetter (1967), and Thomson et al. (1998)

^c Rabbits also present on the island, however, only affected petrel breeding in 1 year (Imber et al. 2000)

^d *Pterodroma cookii* productivity most affected by rats predated eggs and chicks: deteriorated seriously after extermination of feral cats from Hauturu, but improved significantly after eradication of rats from Whenua Hou (Imber et al. 2003)

^e Control program initiated for rats only. Mice were found in traps, but no mouse predation was recorded (Seto and Conant 1996)

^f First year survival only

^g Individual species not identified in this study

^h Removal of gulls and crows likely lead to increased predation by foxes which were not controlled (Parr 1993)

ⁱ Only 1 year of monitoring data available prior to the eradication

^j Proportion of fledglings alive after 2 months of leaving the nest

^k 1996 data excluded because the use of fine particle bait lead to 43% incidental mortality of North Island Robins

^l Survival from September to December only (Empson and Miskelly 1999)

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