

Severity of the Effects of Invasive Rats on Seabirds: A Global Review

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Abstract: *Invasive rats are some of the largest contributors to seabird extinction and endangerment worldwide. We conducted a meta-analysis of studies on seabird-rat interactions to examine which seabird phylogenetic, morphological, behavioral, and life history characteristics affect their susceptibility to invasive rats and to identify which rat species have had the largest impact on seabird mortality. We examined 94 manuscripts that demonstrated rat effects on seabirds. All studies combined resulted in 115 independent rat-seabird interactions on 61 islands or island chains with 75 species of seabirds in 10 families affected. Seabirds in the family Hydrobatidae and other small, burrow-nesting seabirds were most affected by invasive rats. Laridae and other large, ground-nesting seabirds were the least vulnerable to rats. Of the 3 species of invasive rats, *Rattus rattus* had the largest mean impact on seabirds followed by *R. norvegicus* and *R. exulans*; nevertheless, these differences were not statistically significant. Our findings should help managers and conservation practitioners prioritize selection of islands for rat eradication based on seabird life history traits, develop testable hypotheses for seabird response to rat eradication, provide justification for rat eradication campaigns, and identify suitable levels of response and prevention measures to rat invasion. Assessment of the effects of rats on seabirds can be improved by data derived from additional experimental studies, with emphasis on understudied seabird families such as Sulidae, Phalacrocoracidae, Spheniscidae, Fregatidae, Pelecanoididae, Phaethontidae, and Diomedidae and evaluation of rat impacts in tropical regions.*

Keywords: eradication, invasive rat, invasive species, seabird, seabird conservation

Revisión de la Severidad Global de los Efectos de Ratas Invasoras sobre Aves Marinas

Resumen: *Las ratas invasoras son uno de los mayores contribuyentes a la extinción y riesgo de extinción de aves marinas en todo el mundo. Realizamos un meta análisis de estudios de interacciones ave marina-ratas para examinar cuales características filogenéticas, morfológicas, conductuales y de historia de vida de las aves marinas afectan su susceptibilidad a las ratas invasoras y para identificar que especies de ratas tienen el mayor impacto sobre la mortalidad de aves marinas. Examinamos 94 manuscritos que demostraron efectos de ratas sobre aves marinas. Todos los estudios combinados resultaron en 115 interacciones rata-ave marina independientes en 61 islas o cadenas de islas con 75 especies de aves marinas en 10 familias afectadas. Aves de la familia Hydrobatidae y otras especies pequeñas que anidan en madrigueras fueron las más afectadas por ratas invasoras. Aves de la familia Laridae y otras especies grandes que anidan sobre el suelo fueron las menos vulnerables a las ratas. De las 3 especies de ratas invasoras, *Rattus rattus* tuvo el mayor impacto promedio sobre aves marinas, seguida por *R. norvegicus* y *R. exulans*, sin embargo, estas diferencias no fueron estadísticamente significativas. Nuestros hallazgos serían de utilidad para que gestores y profesionales de la conservación prioricen la selección de islas para la erradicación de ratas con*

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base en características de la historia de vida de aves marinas, desarrollen hipótesis comprobables sobre la respuesta de aves marinas a la erradicación de ratas, proporcionen justificación para campañas de erradicación de ratas e identifiquen niveles adecuados de medidas de respuesta y prevención de la invasión de ratas. La evaluación de los efectos de ratas sobre aves marinas puede ser mejorada con datos derivados de estudios experimentales adicionales, con énfasis en familias poco estudiadas como Sulidae, Phalacrocoracidae, Spheniscidae, Fregatidae, Pelecanoididae, Phaethodontidae y Diomedidae y la evaluación de los impactos de ratas en regiones tropicales.

Palabras Clave: ave marina, conservación de aves marinas, erradicación, especies invasoras, rata invasora

Introduction

Seabirds play important regulatory roles in marine, intertidal, and terrestrial environments (e.g., Irons et al. 1986; Wootton 1992; Polis & Hurd 1996) because they forage throughout the world's oceans, consume an estimated 7% of ocean primary productivity (Brooke 2004a), and are a food source for other marine and terrestrial predators and humans (Feare 1976; Haynes 1987; Cuthbert 2003). On land and near shore, seabird guano fertilizes terrestrial, intertidal, and subtidal zones, enhancing local primary productivity (Loder et al. 1996; Schmidt et al. 2004; Fukami et al. 2006). Consequently, the conservation of seabirds and their habitats is important for maintaining global biodiversity and key ecosystem services (e.g., Towns et al. 1990; Martin et al. 2000; Atkinson 2002).

Given that seabirds play a substantial role in marine ecosystems, the threatened status of many seabird species is troubling. Of the 328 seabird species currently recognized, 102 are threatened or endangered and 5 are thought to be extinct (IUCN 2006). Invasive species are considered one of the largest terrestrial threats to the persistence of seabird breeding colonies (King 1985). Rats that are commensal with humans (*Rattus exulans*, *R. rattus*, and *R. norvegicus*) are the invasive species with the largest impacts on seabird populations because they occur on over 90% of all island archipelagos (Towns et al. 2006) and throughout all seabird habitats, excluding the highest latitudes. Rats are successful invaders because of their generalist foraging strategy and high adaptability to novel environments. Such strategies allow rats to opportunistically prey on seabirds while supplementing their diets with other island flora and fauna when seabirds are unavailable (Fleet 1972; Major et al. 2007).

Rats prey on seabird eggs, chicks, and adults, and are thought to be responsible for numerous seabird extirpations and population declines (Atkinson 1985). The effects of rats on all age classes of seabirds have helped spur the development of techniques to eradicate invasive rats from islands, which have been applied successfully in 318 campaigns globally and have become a highly effective seabird conservation tool (Howald et al. 2007). Because of the controversial nature of some rat eradication campaigns, however, (Towns et al. 2006), further

investigation of the severity of rat impacts to seabirds and additional data to provide justification for the use of eradication techniques is needed.

We reviewed the literature on invasive rat and seabird interactions and used meta-analytic techniques to determine which characteristics make particular seabird species more or less vulnerable to invasive rat predation. Given limited conservation dollars and the introduction of rats to thousands of islands, prioritization of islands for rat eradication is necessary to maximize return on conservation investment. Rat eradications are currently prioritized with multiple factors in addition to seabird conservation benefits, such as eradication costs, benefits to other flora and fauna, and the probability of reinvasion (Martins et al. 2006; Donlan & Wilcox 2007). Here we systematically identified the characteristics that increase seabird vulnerability to rats. This information can help managers prioritize when, where, and in what order rats should be eradicated to protect breeding seabirds and can direct future research on rat-seabird interactions. We also provide guidelines for the development of testable hypotheses about seabird responses to rat eradication campaigns, identify seabirds with high susceptibility to rat predation, suggest ways to decide on which islands to invest in rat introduction prevention, and consider the response time and magnitude of response needed to respond to a rat invasion should one occur.

The last comprehensive review of rat predation on island avifauna was published over 20 years ago (Atkinson 1985). We updated and expanded on a subset of Atkinson's work by focusing on seabirds and considering this taxon in greater detail. Specifically, we evaluated the morphological, behavioral, and life history characteristics that influence seabird susceptibility to rat invasion; differences in the ability of the three rat species to affect seabirds; influence of rat introduction timing on rat impacts; and gaps in research of rat impacts on seabirds.

Methods

We used electronic search engines, including Biosis Previews from Ovid and the Web of Science, to review scholarly papers. Keywords, such as *rat*, *seabird*,

predation, island, non-native, exotic, invasive, introduced, predator, island nesting, seabird conservation, and eradication were used alone and in various combinations to locate literature on search engines. We searched the libraries of Yale University, Island Conservation, the University of California, Landcare Research (New Zealand), New Zealand Department of Conservation, and the libraries of private individuals for unpublished (gray) literature. References cited in each reviewed paper were examined for relevant sources.

Meta-Analysis

We used meta-analysis to account for variation in the impact level of rats on seabirds among rat-seabird interactions reported in the literature. We investigated nine independent categorical variables separately in the analysis: seabird mean adult weight (small, ≤ 300 g; medium, 301–600 g; large, 601–900 g; extra large, > 900 g), life stage (eggs, chicks, eggs and chicks, adults, chicks and adults, eggs, chicks, and adults), nesting strategy (branches, ground surface, burrows, holes, and crevices), incubation period (≤ 30 days; 31–40 days; 41–50 days; > 50 days), egg mass (≤ 20 g, 21–40 g, 41–80 g, > 80 g), and eggshell thickness (≤ 0.20 mm, 0.21–0.30 mm, 0.31–1.00 mm, > 1.00 mm); time since rat introduction (≤ 300 years; 301–600 years; 601–2000 years; > 2000 years); and rat species (*R. exulans*; *R. rattus*; *R. norvegicus*). Because data on time since rat introduction are often not precise, we subtracted 50 years from obscurely stated times of introduction. For example, for rat introductions stated as before 1700, we used 1650 as the time of introduction. Time since introduction categories were large enough to ensure that these adjustments did not transfer data points from one category to another. To ensure that our selected categories did not affect the outcome of our results, we repeated the time since introduction analysis with continuous rather than categorical variables. Other categorical ranges were selected to ensure results were classified into biologically meaningful ordinations for seabirds.

We used a fixed-effects model in Metawin 2.0 (Rosenberg et al. 2000) to calculate effect sizes and *Q* statistics. We defined a rat-seabird interaction as an impact (positive, negative, or neutral) of introduced rats on seabird individuals or populations. We categorized each interaction based on rat species, time since rat introduction, and seabird characteristics (family, mean adult weight, life stages depredated, nesting type, incubation period, egg mass, and eggshell thickness). Ideally in meta-analysis, effect sizes are calculated based on the data provided in each study and each effect size is weighted by the inverse of its sampling variance ($1/\text{var}$). Nevertheless, measures of effect sizes and variance data were not reported for most ($> 90\%$) of the studies we examined. To take advantage of the ability of meta-analytic techniques to weight effect sizes, we classified all the studies into one of four

methodological groups: (1) isotopic analysis on rats to reveal composition of rat, (2) observation of seabird population decline after rat introduction, (3) experimental manipulation of rats (via rat eradication or control measures), or (4) direct observation of seabird depredation.

If the authors had not already done so, each stated interaction was transformed into a percentage of the local seabird population affected and assigned a categorical weight, which corresponded to the methodology of the study and the impacts observed by the authors (Table 1). Cases that reported percent impact on juvenile age classes or breeding success were not transformed into a percentage of the entire population affected, because population census data did not allow us to reliably scale rat effects to the population level. Instead, the results of juvenile- and breeding-success studies were reported as the proportion of the juvenile population affected and were given lower weights than other studies with numerical quantification of population level impacts. The lower weights helped account for the possibility of rats affecting a higher proportion of the population through adult predation or a lower proportion of the population through no adult predation.

The size of the impact ranged from 0 to 1, where 0 indicated no part of the local seabird population was affected and 1 indicated 100% of the local seabird population was affected. Weights ranged from 1 to 1000 with 1 being the lowest possible weight and 1000 being the highest. Table 1 provides the effects we assigned to studies with

Table 1. Assigned rat effect sizes (as a proportion of the local seabird population affected), their given weights, and the associated justification for studies of rat effects on seabirds that did not numerically quantify rat effects.

Impact proportions	1/weight	Justification
0.01	0.001	coexist with rats
0.05	0.001	minor effects
0.10	0.10	small losses of eggs and chicks
0.50	0.001	breeding success doubled after rat eradication
0.50	0.25	statistically significant, but does not give exact numbers (i.e., breeding numbers significantly lower on islands with rats a Martin et al. [2000])
0.50	0.49	predation observation without other data
0.50	0.49	major in some years; minor in others
0.50	0.49	effects could not be deciphered because of coexistence with introduced cats
0.70	0.10	increase following rat control
0.90	0.10	near extirpation linked to rats
0.99	0.10	100% of 1 or 2, but not all age classes (eggs, chicks, or adults) lost in a year
1.00	0.001	complete extirpation linked to rats

no numerical quantification and the justification for the assigned effect sizes. Studies that merely stated that rats affected seabirds and provided no numeric calculation were given low weights, whereas numerically descriptive studies were given higher weights. For example, studies in which authors reported seabird extirpation were given an impact of 1 and a high weight (1000). A few of the studies reported rat effects on seabirds that could not be quantified due to the presence of invasive cats (*Felis catus*; $n = 6$). Cats also prey on seabirds, leaving the effects from cats and rats difficult to distinguish from each other. Thus, studies with invasive cats were given the lowest possible weight (1) to limit their influence on calculated effect sizes. The assigned weights therefore emphasized studies that had more robust methods. To ensure our weights did not bias our results, we did an unweighted analysis and compared the results with our weighted analysis.

The methodological categories included the following study approaches: direct observations recorded with video cameras; seabird bones in rat middens; remains of seabirds in rat gut contents; rat-chewed eggshells; and seabird carcasses with signs of rat depredation. Studies in which rat effects were “inferred from population decline” generally documented seabird breeding number declines following rat introductions. Stable isotopic analysis studies used rat gut contents to infer rat diet composition. Experimental manipulations usually documented seabird recovery following rat control or eradication measures. In the case of multiple papers citing the same rat-seabird interaction(s) on an island or island chain, experimental manipulations were used preferentially to calculate effect sizes. In the absence of experimental manipulations, we used the most numerically descriptive paper to calculate effect sizes. We categorized single rat-seabird interactions that cited two rat species into two separate interactions for rat analyses.

We selected Glass' delta as our effect size metric, which equals the experimental mean minus control mean, all over the standard deviation of the control group. In our study, controls indicated the absence of rats and resulted in all control means equaling zero (no effect). Variance was substituted with the assigned weights because <10% of studies reported measures of dispersion. We tested for significant effect sizes across all studies and for significant differences in effect size among categories with randomization tests. For each analysis p values (with post hoc Bonferroni corrections) and mean effect size confidence intervals were generated from resampling with 999 randomizations of the data. This procedure, unlike conventional statistics such as chi-square, is robust to non-normal data distributions, which are common in meta-analyses due to small sample sizes and heterogeneity among studies (Rosenberg et al. 2000). Owing to low sample sizes and heterogeneity in studies reviewed, we considered results significant at $\alpha \leq 0.10$.

In addition to looking at overall rat effects across studies, we used Metawin 2.0 to look for significant differences in the magnitude of rat impacts for individual variable categories with a method analogous to analysis of variance (ANOVA). For example, in each variable category, such as the different weight-class categories in the variable seabird weight, the mean effect size, $E+$, of rat impact was calculated. Here, effect sizes indicated the mean proportion of the seabird populations in that category affected and the values ranged from zero to one. Zero indicated 0% of the seabirds in that category were affected by rats and 1 indicated 100% of the seabirds in that category were preyed on by rats (i.e., seabirds were extirpated). Effect size was considered significant if its confidence interval did not include zero (Rosenberg et al. 2000). Bias, also referred to as bootstrap, confidence intervals were used to estimate the range of uncertainty around test statistics. Bias confidence intervals are robust to nonparametric data and are a more conservative estimate of uncertainty than conventional confidence intervals (Efron & Tibshirani 1993).

Analysis of Independent Variables

Independence analyses were performed with Systat 10 (SYSTAT 2000). We used nine independent variables in our analysis; five quantitative (seabird weight, egg mass, eggshell thickness, incubation period, and time since rat introduction) and four categorical (seabird family, nesting strategy, life stage depredated, and rat species). We transformed data on life stage depredated into the percentage of the seabird population each life stage represents by setting the proportion of eggs, chicks, and adults (including all postfledging birds) at 10%, 20%, and 70% of the population, respectively. Although these were crude estimates, when age-class proportions were varied, independence test patterns were consistent. Thus, for independence analyses, we changed life stage to the proportion of seabirds affected. For the remaining three categorical variables, Pearson chi-square statistical analyses were performed to test for independence. We tested for independence of the quantitative variables with pairwise Pearson correlation coefficients with Bonferroni corrected p values. To test for independence between the categorical and quantitative data, we performed ANOVA with post hoc Bonferroni corrections for p values. Results were considered significant at $\alpha \leq 0.10$.

Results

Variable Independence

Owing to low sample sizes, we were unable to perform tests for independence between seabird family and rat species or seabird family and nesting type. Not all variables were independent of each other (see

Supplementary Material). As a result, for some analyses, the mechanisms underlying significant relationships between seabird characteristics and the severity of rat impacts could not be clearly identified. Nevertheless, identification of the seabird characteristics that best predicted rat impacts was possible.

Geographic Distribution and Study Type

Our review confirmed that rats can be successful invaders in most island environments, from wet tropical to subarctic tundra. Rat predation on seabirds was widespread globally; 94 studies demonstrated some impact of introduced rats on seabirds. Together the studies presented 115 independent rat-seabird interactions on 61 islands or island chains for 75 species of seabirds in 10 families (see Supplementary Material; Fig. 1). Seventy-three percent of studies ($n = 69$) cited direct observations of rat predation without effect quantification; 12% ($n = 11$) used experimental manipulation to calculate rat effects; 12% ($n = 11$) inferred rat effects from population decline; and 3% ($n = 3$) used isotopic analysis to infer rat effects. Rats were also shown to extirpate seabird populations directly; our review documented 10 seabird population extirpations following invasive rat introduction (see Supplementary Material).

Seabird Traits

The overall documented impact of rats on seabirds was detrimental across all studies ($E+ = 0.347$, bias CI = 0.2074–0.4884). Seabird phylogeny, morphology, behavior, and life history influenced the impact of rats on seabirds.

Seabird families were not evenly affected by rats (Fig. 2a; $p < 0.01$; $n = 114$). Hydrobatids endured the highest mean population impacts, and albatrosses (Diomedidae), frigatebirds (Fregatidae), and larids experienced the lowest mean population impacts. (Spheniscidae seabirds were excluded from this analysis because there was an insufficient number of studies.) Rats extirpated half the Hydrobatidae seabirds in the studies we examined ($n = 4$ of 8), which suggests rats have higher effects on hydrobatids than all other seabird families. Alcids were also affected strongly, with rats inflicting an 83% mean population impact (Fig. 2a). Many hydrobatids and alcids exhibit burrow- or crevice-nesting strategies (Gaston & Jones 1998; Brooke 2004b), a life-history trait that may explain their high susceptibility to rat predation. Rat species frequent burrows and crevices when foraging, nesting, and caching food (Calhoun 1963; Cheng et al. 2005); thus, burrow- and crevice-nesting seabird species, such as hydrobatids and alcids (Gaston & Jones 1998;

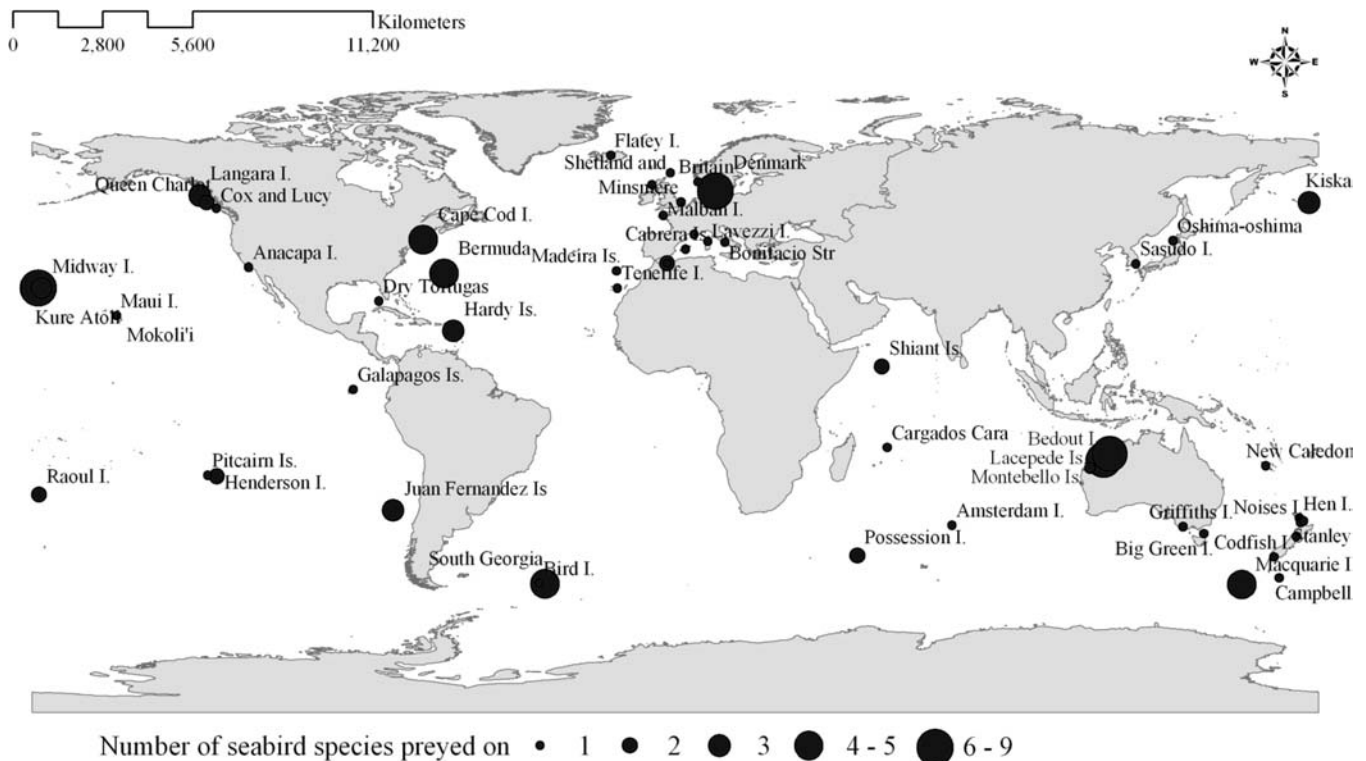


Figure 1. Locations of rat-seabird interactions reviewed for meta-analysis. Dot sizes indicate the number of seabird species affected.

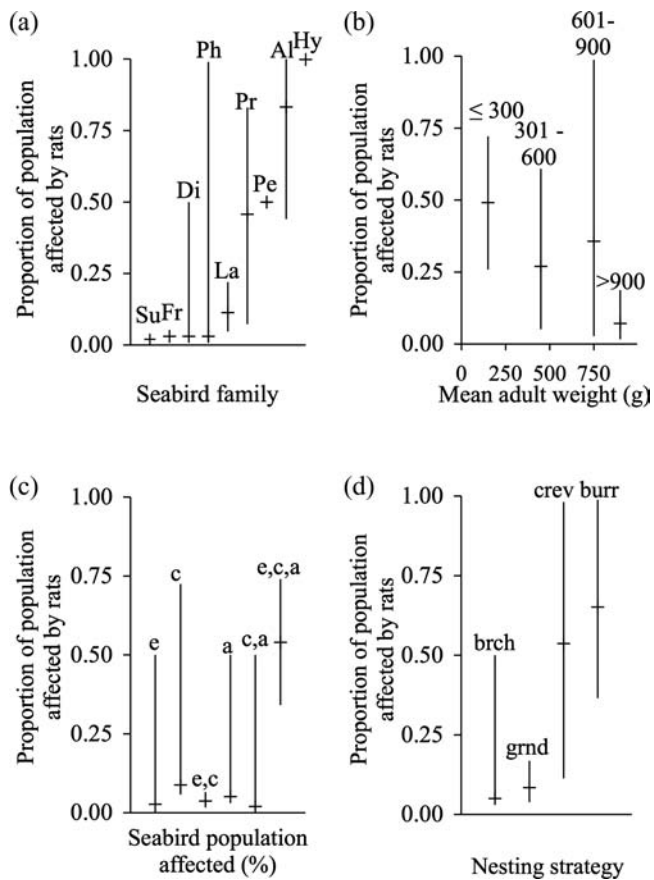


Figure 2. Mean rat effect sizes categorized by seabird (a) family (Su, Sulidae; Fr, Fregatidae; Di, Diomedidae; Ph, Phaethontidae; La, Laridae; Pr, Procellariidae; Pe, Pelecanoididae; Al, Alcidae; Hy, Hydrobatidae), (b) mean adult weight (small, ≤ 300 g; medium, 301–600 g; large, 601–900 g; extra large, >900 g), (c) life stage at which the seabird is depredated (e, eggs; c, chicks; a, adults, and (d) seabird nest type (brch, branch; grnd, ground; crev, crevices; burr, burrows). Horizontal lines are mean effects and vertical lines are bias confidence intervals obtained through the randomization method.

Brooke 2004b), are at higher risk from rat predation than ground nesters (e.g., Laridae, Diomedidae, Spheniscidae, Phaethontidae, and Fregatidae). In addition, hydrobatid and alcid adults often weigh less than most other seabirds in our analysis (Supplementary Material), a factor that could make them easier prey items for invasive rats.

Compared with other seabird families, Pelecanoidids had unusually narrow confidence intervals for average rat effects across the studies we reviewed (Fig. 2a). We believe the small confidence intervals are an artifact of low sample size ($n = 2$) rather than a reflection of biological reality because both studies report the same impact level.

No significant effects of rat impacts on mean adult weight of seabirds were detected (Fig. 2b; $p = 1$; $n = 115$); nevertheless, rats had a 49% population impact level on small seabirds, a value much higher than the 7% impact level on the largest seabirds evaluated. Rats can prey on all life stages of small birds (eggs, chicks, and adults), and even though rat predation did not vary according to the life stage at which the seabird was taken (Fig. 2c; $p = 0.14$; $n = 115$), seabirds that experienced rat predation across all life stages had the highest mean impacts from rats.

Rat predation varied across seabird nesting types (Fig. 2d; $p < 0.05$; $n = 115$). Burrow-nesting seabirds experienced the highest mean impacts from rats and ground nesters experienced comparatively much lower impacts. The difference we observed in rat predation may be due to ground-nesting seabirds being larger (on average) and more adapted to defending themselves and their offspring from native predators (Tinbergen 1967; Lack 1968). Ground nesters are diurnal and actively defend their nests from predation (Kruuk 1964; Tinbergen 1967; Lack 1968), whereas burrow nesters are often nocturnal, which is thought, in addition to their nesting strategy, to be their only antipredator defense (Lack 1968). Therefore, burrow-nesting seabirds may be more vulnerable to nocturnal rat predation than their diurnal, ground-nesting counterparts. Nevertheless, because seabird weight and nesting type are not independent of each other (i.e., it is impossible for large seabirds such as albatrosses to nest in small burrows or crevices), it is unclear whether seabird nesting choice or seabird weight was responsible for the observed lower rat impacts on ground-nesting seabirds.

Seabird incubation period (Fig. 3a; $p = 0.918$; $n = 94$), egg mass (Fig. 3b; $p = 1$; $n = 87$), and eggshell thickness (Fig. 3c; $p = 1$; $n = 39$) did not differentially affect rat predation. Nevertheless, sample sizes were relatively small in these categories, making resolution of differences difficult.

Rat Species and Time since Introduction

We found no difference in predation between rat species and seabird body weight ($\chi^2 = 2.625$, $df = 2$, $p = 0.446$). In fact, the smallest rat, *R. exulans* (adult mass ~ 65 g) preyed on Laysan Albatross (*Phoebastria immutabilis*) adults (mass ~ 2855 g), one of the largest seabirds in our review, supporting the findings that small-mammal predation can result in population-level impacts to large seabirds (Cuthbert & Hilton 2004; Wanless et al. 2007). The three rat species did not differ significantly in the seabirds they preyed on according to nesting type ($\chi^2 = 4.859$, $df = 4$, $p = 0.302$); nevertheless, qualitatively, *R. rattus* preyed mainly on burrow-nesting seabirds (43% of predation events) and *R. norvegicus* and *R. exulans* preyed on burrow nesters and ground nesters equally (Fig. 4). A lack of data for rat predation and seabirds

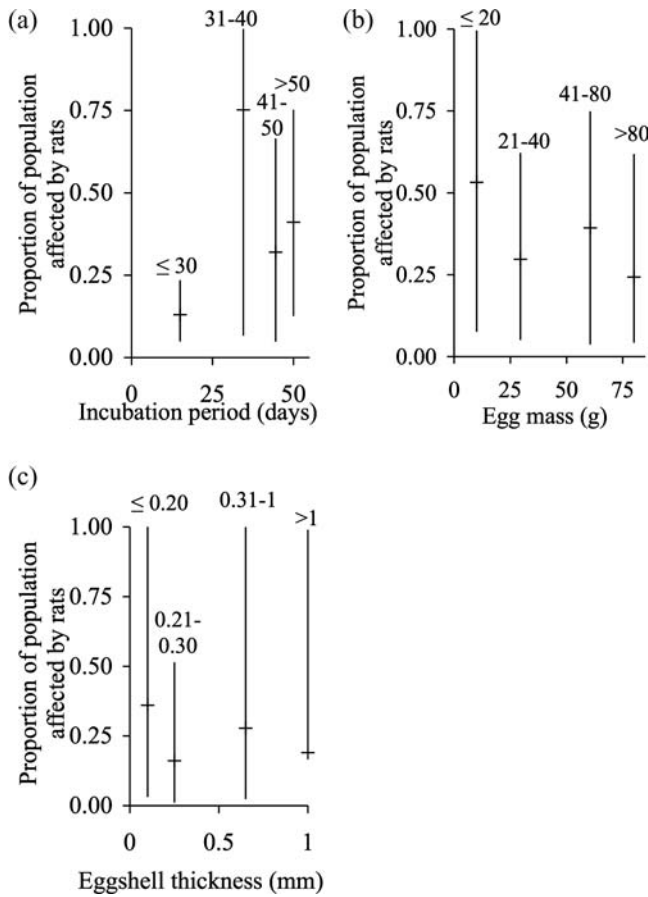


Figure 3. Mean rat effect sizes categorized by seabird (a) incubation period, (b) average egg mass, and (c) eggshell thickness. Horizontal lines are mean effects and vertical lines are bias confidence intervals obtained through the randomization method. Numbers above vertical lines represent the corresponding category used to perform the meta-analysis.

with multiple nesting types left us unable to investigate whether this qualitative trend shows a real preference or whether it is an artifact of the seabird nesting strategies that rats encounter on introduction.

The meta-analysis showed no statistical difference between the 3 rat species in their severity of seabird predation (Fig. 5a; $p = 0.28$; $n = 118$). Nevertheless, *R. rattus* had a much higher mean seabird population impact (48%) than *R. norvegicus* (24%) and *R. exulans* (20%), which suggests biological relevance despite statistical insignificance.

Rat effects were not significantly different for seabirds exposed to rat predation for different lengths of time (Fig. 5b; $p = 1$; $n = 108$), which suggests that time since rat introduction may not be an important factor in driving rat effects on seabirds. When the analysis was repeated

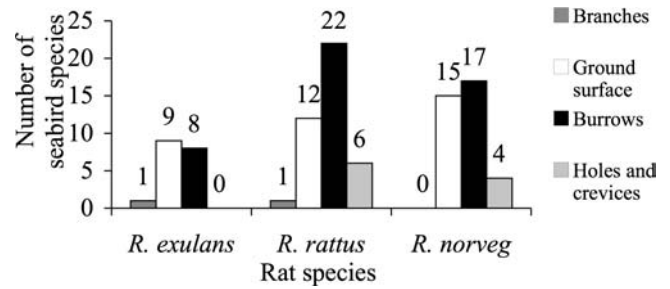


Figure 4. Number of seabird species each rat preyed on categorized by seabird nesting type (norveg, is norvegicus).

with continuous rather than categorical times since introduction, the same results were obtained.

Unweighted Analyses

When all analyses were conducted without our assigned weights, eggshell thickness was the only result that changed qualitatively. Nonqualitative changes (i.e., the pattern remained the same) were found: seabird nest type became statistically nonsignificant ($p = 0.144$), and rat

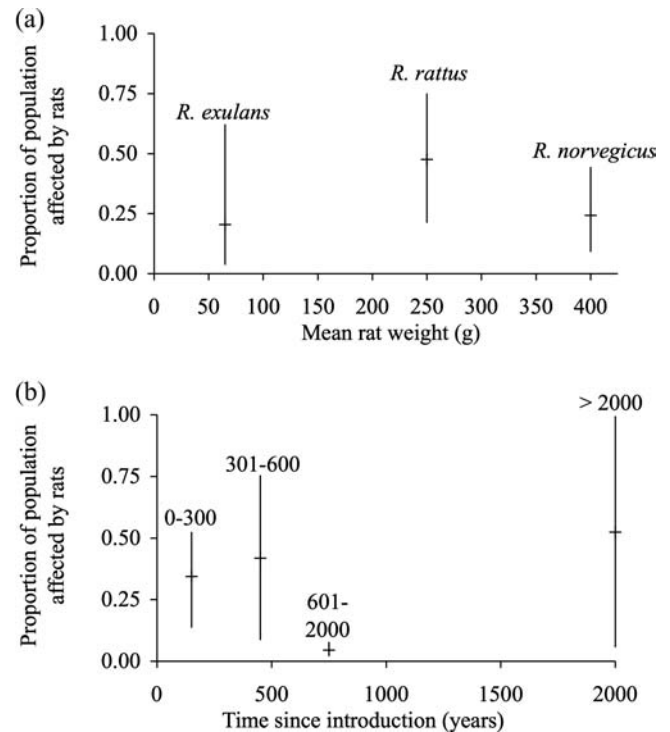


Figure 5. Mean rat effect sizes categorized by (a) mean adult rat weight and (b) time since rat introduction. Horizontal lines are mean effects and vertical lines are bias confidence intervals obtained through the randomization method. Numbers above vertical lines represent the corresponding range of years used to perform meta-analysis.

species effects changed slightly. *R. rattus* still had the highest mean effect size, *R. exulans* the second highest, and *R. norvegicus* the smallest, which suggests that differences between *R. exulans* and *R. norvegicus* are difficult to tease apart.

Fail-Safe Analysis

One potential issue with meta-analysis is publication bias, or the lack of published studies indicating no significant effects. Use of the fail-safe number (Rosenthal 1979), which is the number of studies that would have to show no effect to change the results of meta-analysis from significant to nonsignificant, is one method that addresses publication bias (Rosenberg et al. 2000). Rosenthal (1979) suggests that a fail-safe number needs to be at least $5n + 10$ for one to be confident of results, where n is equal to the number of studies reviewed. We calculated the fail-safe number with Rosenberg's (2005) adaptation of Rosenthal's (1979) method and found that it would take 82,346 studies that show no rat effects to change the overall effect size for the studies we reviewed.

Discussion

Our fail-safe analysis makes us confident that the measured effect sizes of rat impacts to seabirds are significant and cannot be ascribed to sampling bias. In fact, our calculated effect sizes may underestimate actual rat effects because some seabirds are likely extirpated long before rat effects are documented. Considering rat introductions began over 2000 years ago, our review missed cases of undocumented seabird extirpations. Although a few cases reviewed ($n = 10$) indicated that seabirds were extirpated, this number is likely much higher for seabirds unable to coexist with rats for substantial lengths of time. We can examine which seabird species may require immediate conservation action if we consider a lower confidence interval for mean rat effect size of $\geq 20\%$ to be seriously detrimental to seabird populations for seabirds in a particular category. Seabirds that meet this criterion are Hydrobatids and Alcids, those that weigh 300 g or less, those with all life stages taken by rats, those that nest in burrows, and those exposed to *R. rattus*. Seabirds that meet any or all of these categories are in immediate danger of being extirpated (if rats are already present) or are at high risk should rats invade islands on which they breed.

Seabird Traits

Atkinson (1985) suggests that smaller birds that nest in crevices and burrows are the most vulnerable to rat predation. Our findings confirm these predictions. The smallest seabirds had much higher population impacts from rat predation than the largest seabirds (49% and 7% lev-

els of population impact, respectively), whereas burrow and crevice nesters experienced the highest mean rat impacts. Atkinson (1985) also proposes that birds with thicker and heavier eggs and with shorter incubation periods are less vulnerable to predation. In contrast, our results show that neither egg characteristics nor incubation period correlated with rat predation intensity. Nevertheless, the sample sizes we used were low for egg-size analyses, and more data may help distinguish differences between predation intensity and egg size. The lack of a correlation between incubation period and rat impact may suggest that rats can affect equally seabirds that are exposed to long or short stints of predation.

Rat Species and Time since Introduction

The differences in rat mean effect sizes agree with the general hypothesis that *R. rattus* has the highest and *R. exulans* the least potential to devastate avifaunal (including land bird) populations (Atkinson 1985). Excluding land birds, Atkinson (1985) found that *R. norvegicus* preys on more seabird species ($n = 27$) than *R. rattus* ($n = 12$) and *R. exulans* ($n = 12$) and thus suggests that *R. norvegicus* is likely to have the highest impact to seabirds. Nevertheless, when we scaled Atkinson's data to the number of island groups invaded, *R. exulans* appeared to have the highest effects. *R. exulans* depredated 4.0 seabirds per island, whereas *R. norvegicus* and *R. rattus* depredated 1.9 and 1.3 seabirds per island, respectively. Our results showed a different pattern, *R. rattus* preyed on more seabird species (1.8 per island) than *R. norvegicus* (1.6 per island) and *R. exulans* (1.1 per island; Supplementary Material). McDonald et al. (1997) suggest *R. rattus* has a low potential to affect breeding seabirds, but our results suggested the opposite. Seabirds exposed to *R. rattus* predation exhibited at minimum a 21% population-level impact compared with seabirds exposed to *R. norvegicus* or *R. exulans*, which exhibited at minimum a 9% and 4% population-level impact, respectively.

Our data suggest that rat predation effects on seabirds are independent of time since rat introduction. Nevertheless, we had no data for recent introductions (< 87 years ago), which limited detection of a time effect because nearly all seabirds that cannot coexist with rats were excluded from our analyses. For those species or populations of seabirds that do coexist with rats, rat impacts can continue for millennia (Martin et al. 2000). Martin et al. (2000) studied islands in the Mediterranean and found Storm-Petrels (*Hydrobates pelagicus*) are limited to rat-free islands, whereas the least vulnerable seabirds are ground-nesting gulls (*Larus cachinnans* and *L. audouinii*), which supports our findings that rat predation varies according to seabird traits (small burrow nesters were more vulnerable than large ground nesters).

Future Research Directions

No studies noted rat impacts on seabirds from the families Pelecanidae or Phalacrocoracidae, most likely due to a lack of existing data rather than that these seabirds are immune to rat predation. Spheniscidae, Fregatidae, Sulidae, Pelecanoididae, Phaethontidae, and Diomedidae are similarly underrepresented in this review because of the few studies on their interactions with rats ($n = 1, 2, 2, 3,$ and $3,$ respectively). More information on seabirds from understudied families interacting with invasive rats will help prioritization of rat eradications, establishment of appropriate levels of rat introduction prevention measures, and increase efficacy of rat invasion responses.

Few ($n = 11$) researchers used experimental manipulation in their studies as a means to evaluate the extent of rat predation on seabirds. The lack of experimental evidence is partly due to the nocturnal activity and food-caching strategies of rats. Such behaviors make it difficult for researchers to directly quantify rat effects on seabirds because most predation occurs at night and below ground, and often individual seabirds or eggs disappear overnight with no sign of predation. Comparing predation before and after rat control or eradication is the most common method of experimental manipulation, but artificial nest studies also provide a means to quickly quantify rat effects (e.g., Jones et al. 2005). Although proving rat effects can be challenging, the lack of experimental approaches represent a significant gap in our current research. Improving the experimental evidence of rat effects will provide a better basis for eradication campaigns and help prioritize seabird conservation strategies.

Atkinson (1985) postulates that seabirds between the latitudes of 15°N and 20°S are at lower risk from invasive rats because of their coexistence with land crabs. Land crabs prey on seabirds and because seabirds may have evolved defenses against land crab predation, they may be better able to cope with invasive rat predation. Similarly, seabirds on islands with native rat species may be less vulnerable to invasive rats (Atkinson 1985). We could not explore either of these hypotheses because of low sample sizes in the tropical latitudes ($n = 5$) and because no studies documented the presence of native rats.

One important factor we did not consider is the presence of multiple rat species on one island. Only 4 of the 115 interactions we reviewed had more than one rat species present, even though multiple introductions are common (Howald et al. 2007). Multiple rat species may produce combined effects on seabirds that are different from what might be expected of each species individually. Unfortunately, the low number of studies that evaluated the effects of multiple rat species on seabirds left us unable to explore any possible combined effects further. Research on how rat dominance hierarchies affect seabird species would be useful in the context of rat eradication and seabird conservation programs.

Another factor we could not evaluate was the situation in which multiple seabird species are present as food sources for rats. Imber (1978) suggests that islands with multiple seabird species breeding throughout the year may provide a constant source of food for rats, leading to higher rat densities and stronger overall impacts to breeding seabirds. Furthermore, seasonally breeding seabirds that breed when other food sources for rats are scarce (i.e., other seabirds or vegetation) may also be especially vulnerable (Imber 1978). A similar situation could exist for tropical seabird species that have asynchronous breeding periods and thus are susceptible to rat predation year round. Nevertheless, the greater availability of other food sources on tropical islands could potentially reduce the impact of rats on seabirds. We were unable to explore any of these scenarios because of limited sample sizes. The restricted data on multiple interactions point to a limitation of meta-analysis: it may oversimplify multiple interacting factors and thus provide oversimplified results. Although we studied nine variables, it is likely a combination of these and other variables contribute to a specific seabird species' vulnerability to rats. Nevertheless, for prioritizing rat eradications for seabird conservation, prioritizing efforts to prevent or respond to rat introductions, and directing future hypothesis testing on seabird response to rat removal, our findings, although oversimplified, are useful. In fact, evaluating a few variables while recognizing the importance of others may be the only way to make meaningful recommendations to island managers, who often require simple answers for complex problems.

Conclusions

Although the seabird species in our review are not an exhaustive representation of species affected by invasive rats, the emergent pattern is consistent with the generally accepted views of which factors influence the severity of invasive rats' impacts on seabirds (Moors & Atkinson 1984; Atkinson 1985). Small seabirds, those that have all life stages preyed on and those that nest in burrows, are the most susceptible to invasive rat predation. Storm-petrels (Hydrobatidae) fit all these criteria and are particularly defenseless to rat invasions. Although all rats had strong effects on seabirds, *R. rattus* showed the strongest mean effects. Our data on the possible nesting-type preferences of different rat species suggest that a second *Rattus* invasion to an island could result in new seabird species being put at risk.

Islands that are home to populations of *R. rattus* and small seabirds that nest in burrows (e.g., Hydrobatidae, Alcidae, Pelecanoididae, and some Procellariidae) should be given higher priorities in invasive-rat removal programs and are candidates for more intense invasive-rat

prevention and introduction response programs than islands hosting seabirds with lower risk factors. Island habitats with lower potential for seabird population decimation are those with larger ground-nesting seabirds (e.g., Diomedidae, Phaethontidae, and some Laridae) paired with any rat species, but especially *R. exulans* or *R. norvegicus*. Managers should be mindful of both seabird and rat characteristics when devising conservation and invasive-rat prevention strategies and when devising action plans should rat introduction occur. This is especially important because the species most affected by rats (smaller burrow or crevice nesters that are frequently nocturnal) are also the most difficult to census and thus monitor for signs of population changes, potentially leading to an underestimation of the impact of rats after introduction.

We emphasize that although our analysis provides useful factors to consider when prioritizing rat eradications, there are other components to prioritizing eradications. Economics, level of seabird endangerment, population-level impact to seabirds, conservation benefit for other island flora and fauna, and the likelihood of reinvasion are important considerations as well. Potential biotic interactions, including trophic cascades, mesopredator release, and interactions with other invasive species, along with island-specific considerations such as size and human presence should also be considered when prioritizing rat eradications. In short, seabird characteristics that affect seabird vulnerability to rats are just one important component of well-prioritized rat eradication programs.

Rats can affect adult seabirds that are as little as 27 g and as large as 2855 g and seabirds of all phylogenetic, behavioral, morphological, and life history variations. Thus, any current or future rat invasion on an island has the potential to be devastating to seabird populations on local scales and, in the case of a large proportion of a particular seabird species nesting on a single island, on global scales. Future research efforts should focus on experimentally quantifying rat effects, investigating the interaction of seabirds that coexist with native predators, and compiling data for understudied seabird families. Data gathered in these areas of research will assist in prioritizing land-based seabird conservation action, rat eradication, and invasive rat prevention plans.

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Supplementary Material

Variables that are not independent of each other and their significance levels; seabird species reviewed and their morphometric and life history characteristics; and study citations, locations, and assigned effect sizes and weights are available as part of the on-line article from <http://www.blackwell-synergy.com/> (Appendix S1, S2, and S3, respectively). The author is responsible for the content and functionality of these materials.

Literature Cited

- Atkinson, I. A. E. 1985. The spread of commensal species of *Rattus* to oceanic islands and their effect on island avifaunas. Pages 35–81 in P. J. Moors, editor. Conservation of island birds. International Council for Bird Preservation, Cambridge, United Kingdom.
- Atkinson, I. A. E. 2002. Recovery of wildlife and restoration of habitats in New Zealand. *Pacific Conservation Biology* 8:27–35.
- Brooke, M. de L. 2004a. The food consumption of the world's seabirds. *Proceedings of the Royal Society of London Series B-Biological Sciences* 271:S246–S248.
- Brooke, M. de L. 2004b. Albatrosses and petrels across the world. Oxford University Press, New York.
- Calhoun, J. B. 1963. The ecology and sociology of the Norway rat. U.S. Public Health Service Publication 1008:1–288.
- Cheng, J., Z. Xiao, and Z. Zhang. 2005. Seed consumption and caching on seeds of three sympatric tree species by four sympatric rodent species in a subtropical forest, China. *Forest Ecology and Management* 216:331.
- Cuthbert, R. 2003. Sign left by introduced and native predators feeding on Hutton's shearwaters *Puffinus buttoni*. *New Zealand Journal of Zoology* 30:163–170.
- Cuthbert, R., and G. Hilton. 2004. Introduced house mice *Mus musculus*: a significant predator of threatened and endemic birds on Gough Island, South Atlantic Ocean? *Biological Conservation* 117:483–489.
- Donlan, C. J., and C. Wilcox. 2007. Complexities of costing eradications. *Animal Conservation* 10:154–156.
- Efron, B., and R. Tibshirani. 1993. An introduction to the boot strap. Chapman & Hall, New York.
- Feare, C. J. 1976. The exploitation of Sooty Tern eggs in the Seychelles. *Biological Conservation* 10:169–181.
- Fleet, R. R. 1972. Nesting success of the red-tailed tropicbird on Kure Atoll. *Auk* 48:651–659.
- Fukami, T., D. A. Wardle, P. J. Bellingham, C. P. H. Mulder, D. Towns, G. W. Yeates, K. I. Bonner, M. S. Durrett, M. N. Grant-Hoffman, and W. M. Williamson. 2006. Above- and below-ground impacts of introduced predators in seabird-dominated island ecosystems. *Ecology Letters* 9:1299–1307.
- Gaston, A. J., and I. L. Jones. 1998. The auks. Oxford University Press, New York.
- Haynes, A. M. 1987. Human exploitation of seabirds in Jamaica. *Biological Conservation* 41:99–124.
- Howald, G., C. J. Donlan, B. R. Tershy, D. A. Croll, J. Russell, A. Saunders, and M. Clout. 2007. Invasive rodent eradications on islands. *Conservation Biology* 21:1258–1268.
- Imber, M. J. 1978. The effects of rats on breeding success of petrels. Pages 67–71 in P. R. Dingwall, I. A. E. Atkinson, and C. Hay, editors. The ecology and control of rodents in New Zealand nature reserves. Department of Lands and Survey, Wellington.
- Irons, D. B., R. G. Anthony, and J. A. Estes. 1986. Foraging strategies of Glaucous-winged Gulls in a rocky intertidal community. *Ecology* 67:1460–1474.

- IUCN (World Conservation Union). 2006. 2006 IUCN red list of threatened species. IUCN, Gland, Switzerland. Available from www.iucnredlist.org (accessed December 2006).
- Jones, H. P., R. W. Henry, G. R. Howald, B. R. Tershy, and D. A. Croll. 2005. Predation of artificial Xantus's murrelet (*Syntliboramphus hypoleucus scrippsi*) nests before and after black rat (*Rattus rattus*) eradication. *Environmental Conservation* **32**:320–325.
- King, W. 1985. Island birds: will the future repeat the past? Pages 3–16 in P. J. Moors, editor. *Conservation of island birds: case studies for the management of threatened island birds*. International Council for Bird Preservation, Cambridge, United Kingdom.
- Kruuk, H. 1964. Predators and anti-predator behavior of the Black-headed Gull. *Behaviour Supplement* **11**:1–129.
- Lack, D. 1968. *Ecological adaptations for breeding in birds*. Methuen Press, London.
- Loder, T. C., B. Ganning, and J. A. Love. 1996. Ammonia nitrogen dynamics in coastal rockpools affected by gull guano. *Journal of Experimental Marine Biology and Ecology* **196**:113–129.
- Major, H. L., I. L. Jones, M. R. Charette, and A. W. Diamond. 2007. Variations in the diet of introduced Norway rats (*Rattus norvegicus*) inferred using stable isotope analysis. *Journal of Zoology* **271**:463–468.
- Martin, J. L., J. C. Thibault, and V. Bretagnolle. 2000. Black rats, island characteristics, and colonial nesting birds in the Mediterranean: consequences of an ancient introduction. *Conservation Biology* **14**:1452–1466.
- Martins, T. L. F., M. D. L. Brooke, G. M. Hilton, S. Farnsworth, J. Gould, and D. J. Pain. 2006. Costing eradications of alien mammals from islands. *Animal Conservation* **9**:439–444.
- McDonald, R. A., M. R. Hutchings, and J. G. M. Keeling. 1997. The status of ship rats *Rattus rattus* on the Shiant Islands, Outer Hebrides, Scotland *Biological Conservation* **82**: 113–117.
- Moors, P. J., and I. A. E. Atkinson. 1984. Predation on seabirds by introduced animals, and factors affecting its severity. Pages 667–690 in P. J. Moors, editor. *Conservation of island birds: case studies for the management of threatened island birds*. International Council for Bird Preservation, Cambridge, United Kingdom.
- Polis, G. A., and S. D. Hurd. 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *The American Naturalist* **147**:396–423.
- Rosenberg, M. S. 2005. The file drawer problem revisited: a general weighted method for calculating fail safe numbers in meta-analysis. *Evolution* **59**:464–468.
- Rosenberg, M. S., D. C. Adams, and J. Gurevitch. 2000. *MetaWin: statistical software for meta-analysis*. Sinauer Associates, Sunderland, Massachusetts.
- Rosenthal, R. 1979. The “file drawer problem” and tolerance for null results. *Psychological Bulletin* **86**:638–641.
- Schmidt, S., W. C. Dennison, G. J. Moss, and S. G. R. 2004. Nitrogen ecophysiology of Heron Island, a subtropical coral cay of the Great Barrier Reef, Australia. *Functional Plant Biology* **31**:517–528.
- SYSTAT. 2000. SYSTAT for Windows: statistics. Version 10.0. SPSS, Chicago.
- Tinbergen, N. 1967. Adaptive features of the Black-headed Gull *Larus ridibundus*. *Proceedings of the International Ornithological Congress* **14**:43–59.
- Towns, D. R., I. A. E. Atkinson, and C. H. Daugherty. 1990. *Ecological restoration of New Zealand islands: papers presented at conference on ecological restoration of New Zealand islands*. Department of Conservation, Wellington, New Zealand.
- Towns, D. R., I. A. E. Atkinson, and C. H. Daugherty. 2006. Have the harmful effects of introduced rats on islands been exaggerated? *Biological Invasions* **8**:863–891.
- Wanless, R. M., A. Angel, R. J. Cuthbert, G. M. Hilton, and P. G. Ryan. 2007. Can predation by invasive mice drive seabird extinctions? *Biology Letters* **3**:241.
- Wootton, J. T. 1992. Indirect effects, prey susceptibility, and habitat selection: impacts of birds on limpets and algae. *Ecology* **73**:981–991.