

Invasive mammal eradication on islands results in substantial conservation gains

Holly P. Jones^{a,b,1}, Nick D. Holmes^c, Stuart H. M. Butchart^d, Bernie R. Tershy^e, Peter J. Kappes^f, Ilse Corkery^g, Alfonso Aguirre-Muñoz^h, Doug P. Armstrongⁱ, Elsa Bonnaud^j, Andrew A. Burbidge^k, Karl Campbell^l, Franck Courchamp^j, Philip E. Cowan^m, Richard J. Cuthbert^{n,o}, Steve Ebbert^p, Piero Genovesi^{q,r}, Gregg R. Howald^c, Bradford S. Keitt^c, Stephen W. Kress^s, Colin M. Miskelly^t, Steffen Oppelⁿ, Sally Poncet^u, Mark J. Rauzon^v, Gérard Rocamora^{w,x}, James C. Russell^{y,z}, Araceli Samaniego-Herrera^h, Philip J. Seddon^{aa}, Dena R. Spatz^{c,e}, David R. Towns^{bb,cc}, and Donald A. Croll^e

^aDepartment of Biological Sciences, Northern Illinois University, DeKalb, IL 60115; ^bInstitute for the Study of the Environment, Sustainability, and Energy, Northern Illinois University, DeKalb, IL 60115; ^cIsland Conservation, Santa Cruz, CA 95060; ^dBirdLife International, Cambridge CB2 3QZ, United Kingdom; ^eEcology & Evolutionary Biology Department, Institute of Marine Sciences, University of California, Santa Cruz, CA 95060; ^fOregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331; ^gZoology & Ecology, University College Cork, Corcaigh, Ireland; ^hGrupo de Ecología y Conservación de Islas, A.C., Ensenada, C.P. 22800, Baja California, Mexico; ⁱWildlife Ecology Group, Institute of Natural Resources, Massey University, Palmerston North 4474, New Zealand; ^jLaboratory of Ecology Systematics and Evolution, University Paris-Sud, Orsay 91405, France; ^kPrivate address, Floreat, WA 6014, Australia; ^lSchool of Geography, Planning and Environmental Management, The University of Queensland, St Lucia, QLD 4072, Australia; ^mLandcare Research, Lincoln 7608, New Zealand; ⁿCentre for Conservation Science, Royal Society for the Protection of Birds, Cambridge CB2 3QZ, United Kingdom; ^oWildlife Conservation Society, Goroka, Eastern Highlands Province, Papua New Guinea; ^pAlaska National Maritime Wildlife Refuge, US Fish and Wildlife Service, Homer, AK 99603; ^qInstitute for Environmental Protection and Research, I-00144 Rome, Italy; ^rInvasive Species Specialist Group, Species Survival Commission, International Union for the Conservation of Nature, I-00144 Rome, Italy; ^sSeabird Restoration Program, National Audubon Society, Ithaca, NY 14850; ^tTe Papa Tongarewa, Wellington 6011, New Zealand; ^uSouth Georgia Surveys, Beaver Island LandCare, Stanley, FIQQ IZZ, Falkland Islands; ^vGeography Department, Laney College, Oakland, CA 94607; ^wIsland Biodiversity and Conservation Center, University of Seychelles, Anse Royale, Seychelles; ^xIsland Conservation Society, Pointe Larue, Mahé, Seychelles; ^ySchool of Biological Sciences, University of Auckland, Auckland 1142, New Zealand; ^zDepartment of Statistics, University of Auckland, Auckland 1142, New Zealand; ^{aa}Department of Zoology, University of Otago, Dunedin 9016, New Zealand; ^{bb}Science and Capability Group, Department of Conservation, Auckland 1145, New Zealand; and ^{cc}Institute for Applied Ecology, Auckland University of Technology, Auckland 1142, New Zealand

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More than US\$21 billion is spent annually on biodiversity conservation. Despite their importance for preventing or slowing extinctions and preserving biodiversity, conservation interventions are rarely assessed systematically for their global impact. Islands house a disproportionately higher amount of biodiversity compared with mainlands, much of which is highly threatened with extinction. Indeed, island species make up nearly two-thirds of recent extinctions. Islands therefore are critical targets of conservation. We used an extensive literature and database review paired with expert interviews to estimate the global benefits of an increasingly used conservation action to stem biodiversity loss: eradication of invasive mammals on islands. We found 236 native terrestrial insular faunal species (596 populations) that benefitted through positive demographic and/or distributional responses from 251 eradications of invasive mammals on 181 islands. Seven native species (eight populations) were negatively impacted by invasive mammal eradication. Four threatened species had their International Union for the Conservation of Nature (IUCN) Red List extinction-risk categories reduced as a direct result of invasive mammal eradication, and no species moved to a higher extinction-risk category. We predict that 107 highly threatened birds, mammals, and reptiles on the IUCN Red List—6% of all these highly threatened species—likely have benefitted from invasive mammal eradications on islands. Because monitoring of eradication outcomes is sporadic and limited, the impacts of global eradications are likely greater than we report here. Our results highlight the importance of invasive mammal eradication on islands for protecting the world's most imperiled fauna.

conservation | restoration | invasive species | island | eradication

The rate of global species decline and extinction is rapid and likely to increase (1–4), although at least US\$21.5 billion is spent annually worldwide on conservation of biodiversity (5). Improving conservation outcomes has focused largely on high-level increases in efficiency, including the distribution of funding across countries (5), or on identifying the ecoregions, habitats, and species most in need (6). Although great strides have been made in promoting evidence-based conservation (7), systematic evaluations of the effectiveness of different actions taken to protect

biodiversity at the global scale are rare, with the exception of protected areas (8).

Islands occupy ~5.5% of the terrestrial surface area but contain more than 15% of terrestrial species (9), 61% of all recently extinct species, and 37% of all critically endangered species on the International Union of the Conservation of Nature (IUCN) Red List (10). Invasive nonnative mammals (hereafter, “invasive mammals”) are the main cause of animal extinctions on islands and are one of the most important threats to remaining insular biodiversity (10–12). Eradicating invasive mammals from islands is an increasingly common conservation tool and has been attempted on >700 islands (13). However, there has been no

Significance

Global conservation actions to prevent or slow extinctions and protect biodiversity are costly. However, few conservation actions have been evaluated for their efficacy globally, hampering the prioritization of conservation actions. Islands are key areas for biodiversity conservation because they are home to more than 15% of terrestrial species and more than one-third of critically endangered species; nearly two-thirds of recent extinctions were of island species. This research quantifies the benefits to native island fauna of removing invasive mammals from islands. Our results highlight the importance of this conservation measure for protecting the world's most threatened species.

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¹To whom correspondence should be addressed. Email: hjones@niu.edu.

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systematic analysis of the global benefits of mammal eradication to native biodiversity. Here we analyze invasive mammal eradications on islands to quantify (i) demonstrated beneficiaries, i.e., native insular faunal species (defined as mammals, birds, reptiles, amphibians, and invertebrates) for which evidence of positive demographic or distributional responses following invasive mammal eradication are documented; (ii) predicted beneficiaries, i.e., highly threatened terrestrial vertebrate species (defined as mammals, birds, and reptiles listed as critically endangered or endangered on the IUCN Red List, hereafter “highly threatened vertebrates”) predicted to have benefitted from such eradications; and (iii) native insular faunal species demonstrated to have negative demographic or distributional responses following mammal eradication.

Results

The most commonly eradicated taxa included rodents (57%), goats (*Capra hircus*) (11%), and cats (*Felis catus*) (8%). Through a literature search and expert interviews, we found evidence that 236 native terrestrial insular species (596 populations) on these islands were demonstrated beneficiaries of successful mammal eradications, and seven species on six islands showed population-scale negative impacts following mammal eradication.

Benefits included 123 recolonizations of islands by formerly extirpated native species (one mammal, 88 seabird, and 33 landbird populations of 67 species); 40 new colonizations of 34 species; 192 resident populations of 115 species showing a positive population response to eradication; 215 populations of 90 native species that were reintroduced to islands where invasive mammals previously had driven extirpations; three existing resident populations of two species supplemented with individuals derived from captive or wild sources; and 25 populations of 18 species translocated outside their historical ranges for conservation purposes (Table 1 and Table S1).

Although some of the 33 landbird populations that recolonized islands in this analysis may have been present before eradication, their presence is unlikely, because landbirds are some of the best-monitored taxa on islands. By contrast, more than one-third of the seabird populations (37/88) that recolonized islands are hole-, crevice-, or burrow-nesters, which can nest cryptically at low densities and may have had small, undetected colonies before eradication. Some species may have recolonized as the result of increases in metapopulations elsewhere, although evidence indicates that such recolonization is unlikely unless such source populations are within 25 km of the recolonized islands (14), and such immigration would be unlikely if invasive mammals were still present on recolonized islands.

Of the 236 demonstrated beneficiary species, 62 (26%) are threatened with extinction (noted in the IUCN Red List critically endangered, endangered, and vulnerable categories) and 20 (9%) are in the near threatened category. The remainder includes 119 species in the least concern category, one in the data deficient category, and 34 species that are not evaluated. No threatened species qualified for uplisting to a higher extinction-risk category, and four species [island fox (*Urocyon littoralis*), Seychelles magpie robin (*Copsychus sechellarum*), Cook’s petrel (*Pterodroma cookii*),

and black-vented shearwater (*Puffinus opisthomelas*)] qualified for downlisting to a lower category of extinction risk on the Red List after invasive mammal eradication.

Although additional threatened species on other islands may also have benefitted significantly from eradications of invasive species, their populations might not yet have changed sufficiently in distribution, size, or structure to qualify for downlisting to lower categories of extinction risk on the IUCN Red List, or additional remaining threats may prevent their downlisting (15).

Birds were the most frequent beneficiaries of invasive mammal eradications, representing 69% of identified species ($n = 83$ seabird and 79 landbird species). Reptiles represented 18% of all benefitting species; the remaining 13% were distributed across mammals and invertebrates (Table 1). Seabirds, landbirds, and one mammal species were the only groups that newly colonized or recolonized islands without human assistance. Fewer seabird populations ($n = 12$) than landbird ($n = 122$), reptile ($n = 44$), or invertebrate ($n = 29$) populations were reintroduced to restored islands by humans, despite the development of successful techniques for reintroduction (16). Because many mammal eradication programs are aimed explicitly at restoring seabird populations, these data highlight an underused technique in seabird conservation (17).

Mammals, birds, and reptiles are relatively well studied, but responses by other fauna (e.g., amphibians and invertebrates) to both mammal invasion and eradication are poorly understood and underreported. We found little information on invertebrate responses to eradications (35 populations of 20 species), but this lack of information is likely a consequence of limited monitoring, because invertebrate species and associated communities on islands can respond dramatically to the removal of invasive mammals (18–20).

Although most studies documented benefits to native fauna, eradication projects can have negative impacts. Short-term negative impacts are distinct from the long-term population-level impacts on native species that were the focus of our analysis. For example, birds may consume toxicant bait intended for invasive mammals, and scavengers may ingest toxicants and suffer secondary poisoning (21, 22). In most cases, these negative impacts are transitory, because the eradication operation ceases when invasive mammals no longer pose a threat, and long-term benefits then accrue. For example, following the mortality of 320 glaucous-winged gulls (*Larus glaucescens*) that scavenged rat carcasses or consumed bait after rat eradication on Hawadax Island, Alaska, both nest and population counts increased by an order of magnitude or more within a year after the eradication (23). Short-term nontarget mortality risks will vary depending on eradication methods (e.g., toxicants, hunting) and must be planned for, potentially mitigated, and ultimately balanced against the longer-term population-scale benefits expected from the absence of invasive mammals. We found only eight populations that experienced population-level negative impacts from which the species did not recover by 3–17 y after eradication, and four of these populations are expected to make full recoveries with more time (Table S2). The documentation and sharing of short- and long-term negative

Table 1. Numbers of species with demonstrated benefits from invasive mammal eradications

Animal	Resident population recovery	Unassisted colonization	Unassisted recolonization	Reintroduction	Conservation introduction
Invertebrate	5 (5)	0	0	16 (29)	1 (1)
Landbird	35 (50)	12 (12)	16 (33)	36 (122)	11 (17)
Seabird	41 (73)	22 (28)	50 (89)	9 (12)	0
Mammal	3 (11)	0	1 (1)	7 (7)	4 (5)
Reptile	31 (55)	0	0	22 (44)	2 (2)

Numbers of populations are shown in parentheses.

impacts is key to avoiding or minimizing such impacts and identifying potentially untenable impacts for future eradication planning.

We restricted our review to studies demonstrating the responses of individual species to invasive mammal eradications, because few studies consider ecosystem-scale impacts (24, but see 25–27), despite evidence that these ecosystem-scale impacts do occur. This lack of ecosystem-scale data underscores the oft-repeated point that it is important to view eradications within a whole-ecosystem context (28). Indirect negative side effects from eradication projects may arise and need to be accounted for in future eradications on other islands. Invasive mammal eradications also can benefit other invasive species. For example, invasive plants may recover from herbivory, and invasive birds may recover from predation (29). Eradications also can generate complex indirect effects characterized as ecological regime shifts. Ecological regime shifts are difficult to classify as positive or negative and will be best assessed overall against management goals and values.

Information on native species' responses to mammal eradication was rare; only 22 studies of 63 species documented specific responses to eradications, and very few of those studies contained quantitative information on population responses (trends in size or abundance, reproductive success, or other demographic parameters). This lack of data underscores a sizeable gap in monitoring efforts following eradication. Long-term monitoring programs will be key to establish conservation gains and improve the efficacy of posteradication conservation measures. When recovery was quantified, several significant conservation outcomes were documented. For example, the Scripps's murrelet (*Synthliboramphus scrippsi*) population on Anacapa Island, Channel Islands, CA had a threefold increase in hatching success and a 14% increase in the number of nests per year following black rat (*Rattus rattus*) eradication (30).

Documented beneficiaries of invasive mammal eradications are likely underreported because of a lack of monitoring. To estimate the potential benefit of eradications to highly threatened terrestrial vertebrates on the IUCN Red List, we enumerated the islands where these species have documented evidence of breeding since 1990 and where invasive mammals have been eradicated. We predicted that these species benefitted from invasive mammal removal. A total of 107 highly threatened predicted beneficiary species (229 populations) were identified (Table 2 and Table S3), representing 6% of all 1,852 highly threatened terrestrial vertebrate species globally (31) and 12% of all 860 highly threatened insular terrestrial vertebrates (32). Unlike mammal and bird species, which have all been assessed for the IUCN Red List, reptiles are incompletely assessed (31) so the predicted reptile beneficiaries ($n = 30$ species) quantified here are an underestimate. Among seabirds, 47% of the world's critically endangered species and 74% of the endangered species potentially benefitted from eradication (Table 2), a result that reflects their being obligate island-breeders and commonly maintaining metapopulations across multiple islands. Only 19% ($n = 21$) of these predicted beneficiaries were also identified as demonstrated beneficiaries; this result likely reflects

insufficient monitoring following eradications rather than lack of benefit. Sufficient commitment to monitoring is key to documenting and learning from conservation interventions.

We divided the number of islands (with highly threatened vertebrates) that experienced eradication ($n = 134$) by the total number of islands with the potential to benefit from eradication (those with human populations of 1,000 or less; $n = 804$) and found that 17% of islands globally were exposed to the potential benefits of eradication. There were 110 highly threatened vertebrate populations with predicted beneficiaries on 71 islands with no remaining invasive vertebrates posteradication. The other 49 islands (with 83 threatened populations) that experienced eradication had one to nine invasive mammal species still present (Table S4), and 14 islands had unknown invasive mammal presence. The majority of islands (35/39, 90%) with one or two remaining invasive mammal species supported introduced rodents (Table S4). This result underscores the potential for many more threatened species to benefit from further mammal eradication efforts. Human population size on islands also was positively correlated with the number of invasive mammal species that remained on islands ($R^2 = 0.64$; $df = 101$; $P < 0.001$), a relationship we expect for all islands globally. Given the sizeable human population on the islands with the greatest number of invasive mammals and the difficulties associated with eradication on islands with human populations (33), current technological and social capacity may not be sufficient to eradicate invasive mammals from those islands in a socially and economically acceptable manner. The threatened species found only on such large, complex, and/or human-inhabited islands may require additional conservation strategies, such as creating invasive mammal-free refuges on some subset of the island (34) or assisted introduction or reintroduction of the threatened species to suitable islands where no invasive mammals exist.

Significant additional benefits likely accrue to other, lesser-known, endemic taxa (35), i.e., nonthreatened vertebrates, invertebrates, and plants. Further, we excluded several countries where few invasive mammal eradications have occurred (e.g., 36, 37), although there are documented responses in other countries that are worth noting. For example, rat eradication was undertaken on Great Bird Island, an islet off Antigua in the Lesser Antilles, which houses the only population of world's rarest snake, the critically endangered Antigua racer (*Alsophis antiguae*) (36). The outcome has been highly successful, with the Antigua racer population increasing 20-fold on four islands (38). Following rat eradication on Langara Island in Canada, the population of ancient murrelets (*Synthliboramphus antiquus*) was estimated to double, and Cassin's auklets (*Ptychoramphus aleuticus*) recolonized the island (37). Our analysis did not include invasive plant, bird, reptile, or invertebrate eradications, making our results a conservative estimate of eradication benefits.

Including both demonstrated and predicted beneficiaries, 786 populations of 321 native insular species were documented or predicted to benefit from mammal eradication on 261 islands globally (Fig. 1), highlighting the importance of invasive mammal eradication on islands as a conservation tool. Future research

Table 2. Numbers of highly threatened insular vertebrate species and numbers of populations predicted to have benefitted from invasive species eradications

Animal	Critically endangered species	Critically endangered populations	Endangered species	Endangered populations
Landbird	9 (9)	15	27 (18)	77
Seabird	8 (47)	14	23 (74)	56
Mammal	5 (5)	6	5 (3)	6
Reptile	13 (12)	24	17 (10)	31

The percent of all highly threatened insular species is shown in parentheses.

should assess the impacts of invasive mammal eradications on ecosystem services delivered by native biodiversity and the social, cultural, and economic benefits to humans. Overall, continued investment in invasive mammal eradication on islands offers a unique opportunity to stem the loss of biodiversity, help achieve global conservation commitments [such as the Aichi Targets of improving biodiversity by protecting ecosystems, species, and genetic diversity and reducing pressures on biodiversity (39)], restore the integrity of insular ecosystems (27, 40), and contribute to sustainable development (41).

Methods

Demonstrated Beneficiaries. We identified all islands with successful mammal eradications using the Database of Island Invasive Species Eradication (DIISE) (13) and limited this analysis to the eight countries that have the most eradications: New Zealand, Australia, Ecuador, Seychelles, the United States, the United Kingdom, France, and Mexico. These countries (including their overseas territories) represent 82% of global invasive mammal eradications (724 of 877 mammal eradications across 532 of 658 islands). In the DIISE (13), every individual island from which an invasive mammal population was completely and intentionally removed is considered an independent eradication. We selected eradication events that were classified having good or satisfactory data quality (verified by a primary reference reporting the event or by documentation in a peer-reviewed summary paper). We excluded events classified as restricted range (i.e., eradication only took place on part of the island), in which re-invasion had occurred [as these events may reflect undiagnosed operational failure (42)], and eradication events for only domestic animal populations (which typically are fenced and dependent on human support).

We searched the Web of Science for published literature on recovery of, restoration of, or negative impacts to species with targeted key word searches: [island name] AND eradication; [island name] AND restoration; [island name] AND translocation (Table S5). We also conducted a broader search with the keywords [eradication OR removal] AND [recovery OR response OR “negative impacts” OR decline OR “population reduction”] AND [island]. We did not find any information when searching for neutral responses by adding OR neutral OR “neutral response” OR “no response” to the above search string; that result is unsurprising because the lack of reporting nonsignificant results is well documented in the literature (43, 44). Moreover, one cannot assume that the absence of impact on a species is neutral because of potential time lags in species’ responses. For example, many species are monitored over the very short term after an eradication project, but population responses may take much longer than a few months or a year to emerge. Such delays in population response often occur for long-lived philopatric species such as seabirds (17). Therefore we did not enumerate neutral responses. We searched specifically for vertebrate species but also documented invertebrate responses when our searches produced information about them. We did not include plant responses because monitoring of plants is rarer, and their responses have been reviewed elsewhere (45). This approach may not have generated an exhaustive list of published data on species’ responses to mammal eradication, so from August 2012 to April 2014 we searched published databases (Table S5) to supplement our dataset and used expert interviews to check its accuracy and completeness. We recorded the year(s) in which the responses were recorded to capture events that occurred after mammal eradication. We excluded translocations that failed to establish breeding populations if this information was available.

We classified benefits into five categories: (i) a species’ increased population size or reproductive success (hereafter, “resident population recovery”); (ii) a species naturally recolonized an island after being extirpated (hereafter, “recolonization”); (iii) a species colonized an island for the first time (hereafter, “unassisted colonization”); (iv) a species was reintroduced to an island where the species historically bred; and/or (v) a species was translocated to an island outside the species’ historical range (hereafter, “conservation introduction”).

Two categories of negative impacts are of interest in reference to eradication projects: (i) short-term nontarget mortality, in which a species is expected to suffer some mortality as a result of mammal eradication, but the loss of individuals does not have an impact at a population scale, and (ii) population reduction, in which a population of a given species is negatively impacted by eradication mechanisms such as toxicant impacts, change in habitat availability, or reduction in prey base. For the purposes of our analyses, we focused on population reduction to provide consistency against demonstrated beneficiaries with population-level increases. We used the Genus/species (rather than Genus/species/subspecies) name

when analyzing subspecies on the IUCN Red List categories and as our taxonomic unit of interest when reporting species number.

Using the datasets underpinning the Red List Index (1, 46), extracted from Hoffmann et al. (15) and updated to 2014 (*sensu* 3), we identified species for which the response to the eradication of invasive mammals in any of the above five categories was sufficiently large to move the species to a lower or higher category of extinction risk on the IUCN Red List. Using these sources and methods, we were able to exclude Red List recategorizations driven by other conservation actions, improved knowledge, revised taxonomy, or other reasons.

For predicted and demonstrated beneficiaries, we identified both the species and island for each response and defined a population as one species on a single island (hereafter, “populations”). A single island could have multiple species that responded to eradication efforts, and a single species could have responded to mammal eradication on multiple islands. These distinctions mean that many more populations than species responded to eradication efforts, and the number of species that responded to eradications was much larger than the total number of islands with eradications in our analyses. An island with multiple populations could have both predicted and demonstrated beneficiaries; for mapping purposes, we identified such islands as “both.”

Predicted Beneficiaries. We extracted breeding populations of critically endangered or endangered landbirds, seabirds, reptiles, and mammals from the Threatened Island Biodiversity database (32). We used populations classified as confirmed, probable, or potential breeders since 1990, with those classified as potential breeders limited to confirmed or probable breeding prior to 1990 (32, 47). Data excluded sea turtles and marine mammals and were accessed November 24, 2014 and updated in January 2016. We assumed that each highly threatened taxon could benefit from any mammal species eradication, whether through direct relationships [e.g., predation between cats and rodents and landbirds (48, 49)] or indirect relationships [e.g., degradation of seabird habitat by herbivores (50, 51)]. We divided the total number of predicted beneficiaries by the number of globally known highly threatened insular species to obtain the percent of insular species predicted to have benefitted from mammal eradication. We did not calculate the percent of all native fauna that were demonstrated beneficiaries of mammal eradication because a full list of native insular fauna at the global scale was not available. We also noted from the database estimated human population size, if invasive mammals were estimated to be absent from the island, and, if not, how many and which invasive mammal species remained on each island (32, 47). Approximate human population size reflects available census data in government reports and websites up to 2012 for each island. Inherent in these datasets is uncertainty linked to the absence of information. Invasive mammal presence reflects species classified as confirmed or suspected (which we considered present) or absent on the island and is based on data from literature searches, online databases, and input from experts (32). We excluded from analyses the islands for which no data regarding invasive mammal(s) (11 islands) or human population size (18 islands) were available.

To estimate the number of islands with species that had the potential to benefit from eradication, we summed the number of islands from the Threatened Island Biodiversity database that support breeding populations of highly threatened birds, mammals, and reptiles and with zero or <1,000 human inhabitants, regardless of whether the island had an eradication ($n = 804$ islands). We used a human population of <1,000 as a generalized threshold for assessing the potential for undertaking eradication of all major invasive mammals (cats, rodents, ungulates), given that human population size is considered a key limiting factor for implementing eradications. Our parameters are approximately reflective of successful eradications done to date and those currently being planned (13, 52). We consider this approach appropriate to the scale of the analyses we undertook. Ultimately the feasibility of conducting an eradication is evaluated by experts assessing the environmental, social, and technical circumstances at an island scale. We used a similar calculation for the number of highly threatened vertebrate species ($n = 860$ species) on those islands to calculate the proportion of species with potential to benefit from eradication that actually did benefit.

We used Pearson’s product moment correlation to relate the number of invasive mammals remaining on islands that had experienced successful mammal eradications to the size of the human population on those islands. We could perform this analysis only for islands from the predicted beneficiaries dataset, because this was the only database with detailed information on remaining invasive mammals and human population size.

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