

Spatial heterogeneity of mesopredator release within an oceanic island system

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Edited by James H. Brown, University of New Mexico, Albuquerque, NM, and approved November 7, 2007 (received for review August 7, 2007)

Predator–prey communities are ubiquitous in ecology, but introduced predators can drive native species to extinction within island systems, prompting the eradication of such exotics. Ecological theory predicts that elimination of top-introduced predators from islands can lead to the counterintuitive decline of native prey populations through the ecological release of smaller introduced species in a process termed “mesopredator release.” We show, in accordance with mesopredator release theory and counter to conservation goals for a New Zealand island reserve, that initial eradication of cats on Little Barrier Island led to reduced breeding success of Cook’s petrels, which also are vulnerable to predation by a mesopredator, the Pacific rat. The rat’s impact on prey productivity varied with elevation within the island. Rat eradication was followed by a rise in petrel productivity, in support of both ecological theory and practical conservation management goals. It appears that interactions among introduced predators, native prey, and environmental gradients can drive counterintuitive and spatially heterogeneous responses to predator eradications from islands. Location-specific, ecosystem-level understanding is essential for predicting the outcomes of such restoration management techniques.

habitat gradients | introduced predator eradications | island restoration | trophic cascade | Cook’s petrel

Top predators can mediate complex food web processes by influencing the dynamics, including the density, size, productivity, or other life history traits, of prey populations either directly through selective predation (1) or indirectly through top-down regulation of more numerous subpredators (2). Theoretical predictions and observational studies demonstrate that the disappearance of top predators from ecological communities can result in the expansion of smaller predator populations at the expense of primary prey (3, 4). This type of trophic cascade, termed “mesopredator release” (5), was proposed to explain the disappearance of scrub-breeding avifauna in southern California (5, 6) and was demonstrated through correlative studies in other continental food webs (7, 8).

In an application of the mesopredator release hypothesis, Courchamp *et al.* (9) predicted that for closed, oceanic-island ecosystems, where native species are the shared prey of several introduced predators, the ecological release of an introduced mesopredator, after the eradication of an introduced top predator, would increase negative impacts on native prey through higher predation rates by the increased mesopredator population. Theoretical modeling of this scenario, by using an introduced top predator (cat), mesopredator (rat), and endemic prey (bird), demonstrated that when mesopredator release occurred, the decline or extinction of insular native prey species occurred (9, 10). Although both verbal and quantitative models support the counterintuitive idea that an introduced top predator could be beneficial to native prey, there is little empirical evidence of mesopredator release after the eradication of introduced predators from islands. Furthermore, although small insular ecosystems are often modeled as spatially homogeneous habitats, empirical data on habitat selection in small and medium size

oceanic islands are contrary to this assumption (11, 12). Thus, it is poorly understood what role local environmental parameters may play on community-level interactions such as mesopredator release. Data detailing the outcomes of predator–prey interactions and predator eradications are urgently required given the increasing ability of conservation managers to selectively target introduced species within biologically complex island systems where secondary effects of eradications are of major concern (13, 14).

We investigated the impacts of an introduced top predator, the feral cat (*Felis catus*) (2,000–5,000 g), and an introduced mesopredator, the Pacific rat (*Rattus exulans*) (76–145 g), on the breeding success of a small burrowing seabird, the Cook’s petrel (*Pterodroma cookii*) (200 g), on Little Barrier Island, New Zealand. The sequential eradication of cats in 1980, followed by that of Pacific rats in 2004, allowed us to test predictions of the mesopredator release hypothesis by using an insular seabird model across an altitudinal gradient with data collected from two high-altitude and one low-altitude Cook’s petrel study sites. Specifically, we evaluated the predictions of the mesopredator hypothesis that (prediction 1) the removal of the top predator (cat) resulted in a decline in the nesting success of their seabird prey (Cook’s petrel), and (prediction 2) the removal of the mesopredator resulted in an increase of petrel breeding success to a level above that when both introduced predators were present.

Results and Discussion

Data from two high-altitude study sites on Little Barrier Island demonstrate that, from 1972 to 2007, interannual variation in Cook’s petrel breeding success was closely aligned with differences between introduced predator regimes ($F = 35.67$, $df = 2$, $P < 0.001$) (Fig. 1). At these sites, temporal patterns of breeding success were consistent with prediction 1 of the mesopredator release hypothesis, in that the removal of cats resulted in an increase in the predatory impacts of Pacific rats and a decline in the fecundity of the Cook’s petrel (Fig. 1). In the presence of cats and Pacific rats (1972–1979, 6 data years), the breeding success of Cook’s petrel was 0.32 ± 0.03 chicks per burrow. After cat eradication in 1980 (1982–2004, 6 data years), in the presence of Pacific rats as the only introduced predator, petrel breeding success declined ($t = 7.65$, $P = 0.035$) to 0.09 ± 0.04 chicks per burrow. Prediction 2, that the removal of Pacific rats resulted in an increase of Cook’s petrel breeding success to a level above that when both introduced predators were present, also was supported. After the eradication of Pacific rats in 2004 (2005–2007, 3 data years), petrel breeding success increased to 0.59 ± 0.03 chicks per burrow ($t = 4.18$, $P < 0.007$) and also was

Author contributions: M.J.R., M.E.H., and M.N.C. designed research; M.J.R., M.J.I., and R.K.S. performed research; M.J.R. analyzed data; and M.J.R., M.E.H., M.J.I., and M.N.C. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

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that cats were active predators of Cook's petrel and preferred warmer low-altitude habitats on Little Barrier Island (15), suggests that at this site Cook's petrel likely experienced similar or lower breeding success before cat eradication in 1980. Such a scenario is not supportive of prediction 1 of the mesopredator release hypothesis.

A logistic regression model of data from high- and low-altitude study sites (Table 1, model 4), during 2003–2007, indicated site ($\chi^2 = 126.72$, $P < 0.001$), year ($\chi^2 = 126.72$, $P < 0.001$) and the interaction between these two factors ($\chi^2 = 126.72$, $P < 0.001$) to be strong predictors of Cook's petrel breeding success. The statistical patterns in this model resulted from the temporal differences in breeding success at the high-altitude study sites in the years pre- and post-Pacific rat eradication without a corresponding change at the low-altitude site (Fig. 1). Before Pacific rat eradication (2003–2004), the high-altitude study sites showed an average petrel breeding success of 0.05 ± 0.01 chicks per burrow, compared with 0.66 ± 0.04 chicks per burrow at the low-altitude site. Breeding success at high altitude increased immediately to 0.53 ± 0.07 chicks per burrow in the year after Pacific rat eradication (2005) and averaged 0.59 ± 0.03 chicks per burrow from 2005 to 2007 (Fig. 1). During the years when Pacific rats were present, the logistic model (model 4) predicted the probability of breeding success at the high study site to be 0.05 and at the low study site to be 0.64 (Fig. 2). With the eradication of the Pacific rat, these predictions were 0.64 and 0.60 for the high and low sites, respectively (Fig. 2). These values showed close agreement with the observed data (Fig. 1).

Given that we lack observations of a direct link between Pacific rat predation and changes in Cook's petrel breeding success after cat eradication, it is important to consider other explanations for the changes observed in our high-altitude breeding success data. Climatic changes, such as long-term directional changes (16) or short-term fluctuations (i.e., those mediated by the El Niño Southern Oscillation) (17), could have altered the availability of oceanic food resources and impacted Cook's petrel breeding success. However, neither hypothesis is a likely explanation of our results because there is no significant pattern in our reproductive data within the cat and rat predator regime (Spearman rank correlation $P = 0.350$) and a weak trend for the rat regime (Spearman rank correlation $P = 0.056$). In addition, the period of breeding success decline after cat eradication extends over numerous El Niño and La Niña cycles (18), and the neither hypothesis can account for change in Cook's petrel breeding success after rat removal. Although cats preyed on adult and fledgling Cook's petrel outside burrows on Little Barrier Island (15, 19), the decline in breeding success between 1980 and 2004 was a result of the loss of eggs and chicks from within burrows (19). The strongest evidence for the role of the Pacific rat in this decline is the immediate response of Cook's petrel breeding success to rat eradication. Other potential predators of Cook's petrel on Little Barrier Island include the native tuatara (*Sphenodon punctatus*), a terrestrial reptile, and the morepork (*Ninox novaezeelandii*), a small native owl. Because morepork are unable to access Cook's petrel burrows and tuatara maintain only relict populations at lower altitudes, we conclude that the decline of Cook's petrel breeding success at high altitude was caused by Pacific rat predation.

Mechanisms driving spatial heterogeneity of mesopredator release within this study system are intriguing. Climate on Little Barrier Island varies on average by 4°C between warm low-altitude and cool high-altitude habitats (20). The diet of Pacific rats reflected a response to this habitat gradient, with declines in vegetation consumption and increases in invertebrate consumption with increasing altitude (21), a result observed in other studies of this species (22). At high altitude on Little Barrier Island, resource availability or dietary requirements could have driven a shift to predation on Cook's petrel eggs and chicks,

readily available during the period of rapid Pacific rat population growth between December and February (23). Conversely, at low altitudes, the availability of plant foods or different nutritional requirements may have reduced predation on Cook's petrel eggs and chicks.

Despite the feasible role of foraging differences with altitude, it is still puzzling that Pacific rats had such a small impact on Cook's petrel eggs and chicks at low altitudes, yet were so devastating at higher altitudes. Given the spatial and temporal limitations of our low-altitude data, caution should be exercised in concluding that the consistency of low predation rates on Cook's petrel by Pacific rats across all low-altitude habitats, and further studies are required to investigate the role of spatial heterogeneity in predator–prey relationships within insular systems.

Mathematical models have suggested two potential outcomes of mesopredator release after the eradication of introduced top predators from island systems. One predicted outcome is severe mesopredator release (10), a sudden mesopredator population increase resulting in increasing predation rates and the extinction of a native prey population within a short time (5, 9, 10). A second predicted outcome is mild mesopredator release, where the release of the mesopredator results in a reduction of the prey population, but not extinction (10). Our data are consistent with mild mesopredator release as the mechanism driving temporal changes in Cook's petrel breeding success on Little Barrier Island. This study demonstrates that the process can be affected at local scales by more complex habitat-dependent interactions than the simple release of the mesopredator (7) at an island-wide level. Local variation in a trophic cascade such as mesopredator release is unsurprising given that perturbed island ecosystems can operate under the same ecological dynamics as other continental communities (24). However, the process has significant implications for conservation management aimed at island restoration, suggesting that secondary impacts of predator eradications can be location-specific and variable depending, at the island level, on the biology and spatial ecology of introduced predators and native prey and, at a regional level, on the latitude and climate of the islands targeted for management.

This study confirms the importance of ecosystem-level understanding to predict the potential impacts of introduced species management on oceanic islands (13, 24, 25). Encouragingly, such data are increasingly being used in the development of complex solutions for conservation management (14, 26, 27). We suggest that the management of such programs can be aided by research investigating the role of habitat and climatic gradients on the biology of the perturbed systems in question.

Materials and Methods

Study System: Location, Prey, Mesopredator, and Top Predator. Cook's petrel bred in 1- to 5-m-long burrows, with peak egg laying of single eggs in mid-November and hatching in mid- to late December (19). Eggs were left unattended for extended periods (1–3 days) during incubation, and, during chick rearing, which extended for 87 days, chicks were unattended except during adult provisioning (19). Pacific rats (*R. exulans*) were introduced to Little Barrier Island (Hauturu) by Maori settlers ~800 years B.P. and consumed a diet of fruit, seeds, vegetation, invertebrates, vertebrates such as lizards, and the eggs and chicks of small passerines and seabirds (19, 21, 28). Cats (*F. catus*) were introduced to Little Barrier Island in the 1870s and ate a broad diet of insects, rats, and birds (29). Cats were eradicated from Little Barrier Island in 1980 after a 3-year operation involving the use of traps, dogs, and poison (15). As a result of the perceived impacts of the Pacific rat upon Little Barrier Island's flora and fauna, brodifacoum poison was aerially spread across the island in 2004 to eradicate Pacific rats. Posteradication monitoring in 2006 confirmed the absence of all introduced mammals on the island (R. Griffiths, personal communication).

Petrel Surveys. Data on the breeding success of Cook's petrel were collected on Little Barrier Island from 1971 to 2007, including previously published data from ref. 19 and new data from the 2003–2004, 2004–2005, 2005–2006, and

