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A Consideration of Mesopredator Release and New Zealand's Predator Free Plan: A Literature Review

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A Consideration of Mesopredator Release and New Zealand's Predator Free Plan:
A Literature Review

by
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Abstract

Invasive mammalian predators are responsible for the loss of biodiversity and species extinctions worldwide: New Zealand is no exception. To protect native species, lethal eradication has become the primary means to control or remove invasive mammalian predators. These control attempts can indirectly affect non-target species through trophic interactions. Eliminating the apex predator can result in a release of lesser predators that can consequently continue causing damage, i.e., suppressing, the native prey population. This ecological interaction among trophic guilds is termed “mesopredator release.” The research outlined in the present work provides a review of the concepts underlying mesopredator release, depicts how New Zealand is a suitable environment for such a release to occur, and the modifications that need to be made to lethal eradication plans make these more successful.

Introduction

Invasion of ecosystems by introduced species is one of the leading global causes of loss of biodiversity. In New Zealand in particular, introduced mammalian predators are actively reducing the population size of the 16 species of flightless birds that inhabit the North and South islands of New Zealand, as well as negatively affecting other native species (King, 2001). Predation by the introduced black rat (*Rattus rattus*) and stoat (*Mustela erminea*) pose the greatest risk to the native fauna (Innes 1990, Murphy & Bradfield 1992). Other introduced predators include the common brushtail possum (*Trichosurus vulpecula*) native to Australia and the feral cat (*Felis catus*). Damage by invasive species to the New Zealand native fauna has been extensively researched over the past few decades; including damage to bat (Scrimgeour et al. 2012), bird (Bond et al. 2019), lizard (Monks et al. 2019), and fish populations (O'Donnell et al. 2017).

Total eradication of introduced mammal species on select New Zealand offshore islands has proven effective in improving island native species populations and providing a safe haven to which to transfer endangered species. The Bay of Plenty region off the North Island (ca. 37°37'51"S, 176°43'02"E) hosts 18 offshore islands that have been cleared of all exotic predators and now act as protective havens for native flora and fauna (Predator-Free [no date]). With these accomplishments in mind, New Zealand has announced an initiative to be entirely predator free by 2050. The New Zealand Department of Conservation has received an initial budget of US \$ 28 million and will annually receive US \$ 7 million to fund the project (Predator Free 2016). Plans for removal of invasive species include lethal control as the primary technique. For instance, Compound 1080 (sodium fluoroacetate), a metabolic poison that does not occur naturally, is a popular and effective choice because it can be spread from the air, only targets mammals, does not bio-accumulate in soils or water, and is cost effective (NZEPA 2017).

Lethal control has been assumed to be beneficial to the biodiversity of the native flora and fauna, as observed in the eradication of exotic predators in the Bay of Plenty Region. However, these islands are closed systems of reduced area that allow for a more comprehensive distribution and implementation of lethal eradication methods over a short period of time (Bombaci et al. 2018). Attempting lethal eradication on a larger scale across the entire country will take several decades and introduces compromises to the efficacy of the technique.

In environments affected by multiple species of long-established invasive predators, typical eradication techniques such as poisoning may not be effective in recovering the native ecosystem (Zavaleta *et al.* 2001, Hare *et al.* 2019). The food web is a delicate balance between predators and prey, and manipulation of an apex predator population can result in disruption or alteration of established trophic cascades (Tompkins & Veltaman 2006). The removal of an apex predator species can, for example, result in the release of populations of a trophically lesser predator species. This trophic cascade is known as ‘mesopredator release’ and paradoxically can result in native species being more negatively impacted (Rayner *et al.* 2007).

Understanding potential and unexpected consequences of lethal eradication is important when attempting a large scale eradication plan such as that proposed for New Zealand (Anonymous 2000). The measure of success in a conservation project should include both absence of the invasive species *and* recovery of target populations (Caut *et al.* 2008). The questions driving the present research are: 1) What is ‘mesopredator release’? 2) What concepts underlying mesopredator release play a role in New Zealand’s lethal eradication of invasive mammalian predators? 3) How can the concept of mesopredator release be used to inform future lethal eradication plans? My purpose is not to provide a complete review of all the literature pertaining to the topic but to frame the concept of mesopredator release and assess the potential consequences of New Zealand’s decision to lethally eradicate exotic predators.

Methods

A review of literature on the parameters of mesopredator release and its correlation with lethal eradication in New Zealand was conducted using various search engines. Key words in the searches included: mesopredator release AND New Zealand, mesopredator release AND top-down effect, mesopredator release AND feral cats, mesopredator release AND island populations, mesopredator release AND productivity. Prior to the initial search, references also were collected and reviewed from pertinent peer-reviewed articles. Resources in this thesis are from domains of Conservation Biology, Ecology, and Environmental Science.

Literature Review

Mesopredator Release

Several decades ago in the ecological field, researchers began to observe the power predators wielded over food webs, specifically: how other species were released from population control after the removal of a trophically higher predator from the ecosystem (Pacala & Roughgarden 1984). The term ‘Mesopredator Release’ was used by Soulé and colleagues (1988) to describe the process whereby in the absence of large and dominant predators, smaller predators underwent population explosions. This release in turn could result in the local extinction of endangered prey species (Soulé *et al.* 1988). Mesopredator release can be defined as the expansion in density, expansion in distribution, or change in behavior, of a trophically mid-rank predator, due to a decline in the density or distribution of an apex predator, often at the expense of the primary prey (Brashares *et al.* 2010, Prugh *et al.* 2009, Rayner *et al.* 2007).

A mesopredator is defined as a mid-rank predator in the food web, independent of its size or taxonomy, within the framework of its ecosystem. An ecosystems specific food web can contain several mesopredators (Prugh *et al.* 2009). Importantly, a species’ role in the food chain is

dictated by the specific ecosystem they inhabit. For example, the domestic cat (*Felis catus*) is a mesopredator in urban environments where it is preyed upon by coyotes, but is the apex predator in many oceanic island ecosystems (Duffy & Capece 2012). An apex predator suppresses the population of mesopredators, effectively regulating the impact these predators have on smaller prey species (Ritchie & Johnson 2009).

Trophic Control: Top-Down and Bottom-Up Effect

There are two hypotheses that explain the population dynamics of an ecosystem: top-down control, and bottom-up control. Top-down control regulates via predation and bottom-up control regulates by prey and resource availability (Leibold *et al.* 1997). In systems with the potential for mesopredator release, the food web is regulated by top-down control. In the elimination of top-down control, two species from the same trophic level compete for the same resources in the absence of an apex predator (Elmhagen & Rushton 2007). A mathematical model can be used to create a two-species competition model, with the assumption that one species is competitively superior to the other. The model demonstrates that removal of one species will result in the release of the other species at the same trophic level. For example, if the superior competitor is under control, the inferior, uncontrolled, competitor may dramatically increase in numbers. If a sudden increase in predator population numbers exceeds the sustainability of the prey, damage to the prey population can be substantial. In addition, the model demonstrates that if both superior and inferior competitors were under control, the inferior competitor would still increase. Competitor release is particularly damaging for prey species when the inferior competitor has a higher affinity for the shared prey (Caut *et al.* 2007).

Predicting Mesopredator Responses

Intraguild predation is the function of mesopredator suppression by apex predators, defined as the “killing and eating of species that use similar, often limiting, resources and are thus potential competitors” (Polis *et al.* 1989, Prugh *et al.* 2009). As a result, an apex predator may kill for two reasons: a) food; or b) elimination of competition. Population pressure applied by the apex predator results in both behavioral and habitat changes in the mesopredator (Ritchie & Johnson 2009). Consequently, there are two factors that influence the strength of mesopredator release: a) species diversity; and b) the productivity of the system (Brashares *et al.* 2010). In low productivity ecological systems, it is predicted that the apex predator could potentially become extinct and mesopredators become limited by prey availability (Prugh *et al.* 2009). In more and highly productive systems, it is predicted that the apex predator would thrive due to the high availability of resources and the stability of the mesopredator population. If the apex predator is removed from a highly productive system, the result will be a strong mesopredator release. For example, when a red fox, *Vulpes vulpes* (mesopredator) population was observed in response to a decline in population numbers of wolves, *Canis lupus* (apex predator), it was found that the greatest mesopredator release occurred in areas of high productivity (Elmhagen & Rushton, 2007). In areas of high productivity, top-down control is therefore increasingly important in regulating mesopredator outbreaks. It is important to note that when both top-down and bottom-up control is relaxed, there is potential for an explosion of mesopredator growth (Prugh *et al.* 2009).

In areas of high species diversity that host complex trophic webs, removal of an apex predator will have limited effects. In contrast, in areas of low species diversity, removal of an apex

predator can potentially result in very strong mesopredator release; this is most commonly observed in island ecosystems (Rayner *et al.* 2007).

Island Specific Mesopredator Release

The strongest mesopredator effect will occur in areas of low species diversity, islands are particularly susceptible and can experience an amplification of negative effects on primary prey species. Mesopredator release on an island can be examined mathematically using a three-species model: prey-mesopredator-apex predator. This model can be contextualized using a population of bird (prey), rat (mesopredator), and feral cat (apex predator). The model uses a set of variables to represent population (B [ird], R [at], C [at]), intrinsic growth rate (r_b, r_r, r_c), predation rate of the apex predator on the prey (μ_b) and on the mesopredator (μ_r), the predation rate of the mesopredator on the prey (η_b) and on other food items (η_s), carrying capacity K_b , and non-avian food (S). The model assumes that the apex predator preys on both the mesopredator and the prey. Equations one, two, and three, represent the standard relationships among the three species on a given island.

$$[1] \quad \frac{dB}{dt} = r_b B \left(1 - \frac{B}{K_b}\right) - \frac{B}{S+B} \eta_b R - \frac{B}{B+R} \mu_b C$$

$$[2] \quad \frac{dR}{dt} = r_r R \left(1 - \frac{\eta_b \eta_s R}{\eta_b S + \eta_s B}\right) - \frac{R}{B+R} \mu_r C$$

$$[3] \quad \frac{dC}{dt} = r_c C \left(1 - \frac{\mu_b \mu_r C}{\mu_r B + \mu_b R}\right)$$

Using these equations, it can be concluded that: a) the rat population alone is capable of eradicating the bird population but the cat is not; and b) when both cat and rat populations are present, the cat protects the bird population by controlling or eradicating the rat population. When a control effort is applied to the rat population (λ_r) and to the cat population (λ_c), the models change:

$$[4] \quad \frac{dB}{dt} = r_b B \left(1 - \frac{B}{K_b}\right) - \frac{B}{S+B} \eta_b R - \frac{B}{B+R} \mu_b C$$

$$[5] \quad \frac{dR}{dt} = r_r R \left(1 - \frac{\eta_b \eta_s R}{\eta_b S + \eta_s B}\right) - \frac{R}{B+R} \mu_r C - \lambda_r R$$

$$[6] \quad \frac{dC}{dt} = r_c C \left(1 - \frac{\mu_b \mu_r C}{\mu_r B + \mu_b R}\right) - \lambda_c C$$

Models three, four, and five, demonstrate that with high enough control, cat populations can be eradicated. This in turn results in prey disappearing if the rat population is not under sufficient control from predation. The models also demonstrate that when there is limited control on the cat population, the prey will not go extinct if the rat population is under strong enough population constraint. This supports the theory that the presence of the apex predator can indirectly protect a shared prey source from the mesopredator (Courchamp *et al.* 1999). Although rats prey on birds less than cats do, a sudden release of the rat population could cause an increase in pressure on

prey (Newman & McFadden 1990). This model demonstrates the need for careful control of apex predators in island ecosystems.

Mesopredator Release in New Zealand

Linear and Triangular Interactions to Predict Cascading Effects in New Zealand

To understand interactions among predators, mesopredators, and prey, in New Zealand, a triangular structure must be used. Triangular interactions results in shared predation on the same prey species, in this case birds in New Zealand. For mesopredator release to be detected, the mesopredator must exceed and replace the predation of the apex predator (Prugh *et al.* 2009). Mesopredators tend to be more efficient predators than apex predators, and in New Zealand's case, there are numerous mesopredators at the same trophic level. Feral cats and stoats are carnivorous and opportunistic hunters while possum, rat, and mouse, are omnivores. As omnivores, the mesopredators can maintain increased pressure on the prey species even when prey population is low (Courchamp *et al.* 1999).

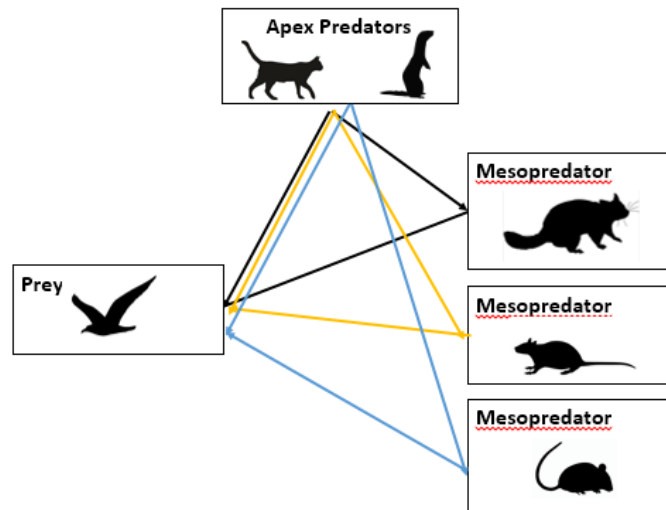


Figure 1. Triangular interactions on mainland New Zealand. Apex predators are (left to right) feral cat (*Felis catus*) and stoat (*Mustela erminea*). Mesopredators are (top to bottom), common brushtail possum (*Trichosurus vulpecula*) native to Australia, and rats (*Rattus rattus*) and mice (*Mus musculus*) native to Eurasia. Not shown are similar triangular interactions among mesopredators and prey.

Figure 1 demonstrates the multiple triangular interactions within the trophic structure of a potential trophic web in New Zealand. It may take a substantial loss of prey to initiate a signal of mesopredator release. For example, when a stoat population was removed from central north New Zealand, there lacked evidence of a strong mesopredator release of mice or rats (Ruscoe *et al.* 2011). This result suggests that the rat and mouse population may have increased, but were unable to carry out predation at levels equivalent to those of the apex predator, causing the mesopredator release to go unnoticed. With additional prey species under a regime of population monitoring, e.g., lizards and insects, cascading mesopredator effects could potentially be detected sooner (Prugh *et al.* 2009). In contrast, there may be only one triangle formation

representing interaction between species on islands or in areas of low species diversity. For example, on Little Barrier Island, centered ca. 36°12'06"S, 175°04'52"E, in the Hauraki Gulf off the north coast of the North Island of New Zealand, there is a single triangle describing the relationships among cat, rat, and bird. (Rayner *et al.* 2007).

New Zealand Island Mesopredator Release

On several islands off the coast of New Zealand, the consequences of eradication of apex predators have been made obvious. On Little Barrier Island, Rayner and colleagues (2007) used the invasive cat (predator) and rat (mesopredator) population to test the effect of mesopredator release on the native Cook's petrel (*Pterodroma cookii*) population over a 32 year span. In the presence of both cat and rat populations, a baseline number for chicks per burrow was recorded. It was found that upon cat eradication, the increased rat population caused a decrease in the number of chicks per burrow, demonstrating that eradication of the apex predator was detrimental to the native prey species (Rayner *et al.* 2007).

It is not unusual to find that removing feral cats from island ecosystems is potentially detrimental to prey species. In another study, on Stewart Island (centered ca. 47°00'28"S, 167°52'36"E, off the south coast of the South Island) the effects of feral cats on the native kakapo parrot (*Strigops habroptilus*) population were observed. Of the 118 feline scat samples collected, only 5.1% contained remains of kakapo, whereas 93% contained rat remains. The ratio of kakapo to rat found in the scat suggest that removing the feral cat population could increase damage to the kakapo population. This evidence was supported by the island mesopredator mathematical model that suggested that eradication of cats and limited control of rats would result in a decline in the numbers of kakapo (Courchamp *et al.* 1999).

A previous study by Fitzgerald *et al.* (1991) also had determined that feral cat eradication may not be the most effective approach for preserving bird species in island populations. On Raoul Island, centered ca. 29°16'02"S, 177°55'30"W 1000 km northeast of New Zealand, rats and cats live together sharing a varied avian prey base. Together, they have caused devastation to the seabird population. After trapping and testing stool samples of the feral cats, it was observed that the cat population does not kill a significant number of birds but rather that their diet was primarily composed of rats. It was determined that the removal of cats from the island would result in an increase in the rat population and continued devastation to the seabird population (Fitzgerald *et al.* 1991). Eradication of the rat population would however likely lead to a shift in the cats' prey base, to seabirds, so the results of that study should be viewed with caution.

Cats are not the only predator capable of causing a mesopredator release. It has been found in many New Zealand islands that the eradication of rats can cause a release of mice, *Mus musculus*. Mouse populations tend to be smaller than rat populations, but there is evidence of them greatly expanding their numbers in the absence of rats. Removal of rats can cause a mesopredator release of mice because rats both outcompete and prey upon mice (Caut *et al.* 2007). In some cases, mouse populations were undetectable until a rat population had been eradicated. This has been the case on several New Zealand islands, including Quail Island (centered at 43°37'41"S, 172°41'25.5"E, in Charteris Bay, on the east coast of the South Island), where mice have overcome two eradication campaigns (Bowie *et al.* 2018). In addition, it was found that the stronger the control of rats, the larger became the final population of mice (Caut *et al.* 2007).

New Zealand Mainland Mesopredator Release

There has been limited research on mesopredator release on the mainland of New Zealand and limited research on how trophic cascades are affected by the eradication of its constituent species. Stoats and feral cats share the title of apex predator in the New Zealand ecosystem; however, with a larger body size, feral cats tend to be the dominant predator. In a study on stoat behavior in response to the presence of feral cats, it was found that stoats altered their foraging behavior in response to perceived competition, avoiding areas of potential high risk. This suggests that these two apex predators do not overlap their habitat, an important factor in potential competitor release. If the feral cat was eradicated, the stoat could fill the niche left open due to reduced competition. Depending on the prey type, this could have detrimental effects on native populations (Garvey *et al.* 2015).

In addition, there has been research carried out on the central North Island on the effect of removing a stoat population from a controlled environment. The investigators found that there was not a significant increase in rat population after the removal of stoats. At the time of the experiment, the environment was in a period of low productivity due to it not being a masting year, when trees produce large number of fruit (Ruscoe *et al.* 2011). During masting years, rat and mice populations increase due to food availability (Jones *et al.* 1998, Tompkins & Veltaman 2006). The low productivity, consistent with the models, resulted in lack of observation of a mesopredator release. However, during the same year, possum populations were experimentally removed and rat populations increased. In the region of the experiment, the latter two species share 55% prey type and do not prey on each other. This is evidence of the possum population outcompeting the rat population for shared food sources. The rat population increase was exacerbated by it being a non-masting year (Ruscoe *et al.* 2011).

Mesopredator Release Effect Informing Lethal Eradication

Considerations before Lethal Eradication is Implemented

Although lethal eradication can often be successful at eliminating a target species, the removal of the target species is not the only measure of success. The measure of success in a conservation project should include the absence of the invasive species *and* the recovery of target populations (Caut *et al.* 2008). It has been demonstrated that mesopredator release is a complex and potentially dangerous in its effect on native prey species. If lethal eradication is to be the primary conservation tool, there should be distinct phases of pre- and post-eradication.

In the pre-eradication phase, the target location should first have a detailed outline characterized describing the relationships among distinct trophic levels in the ecosystem (Caut *et al.* 2007). Specifically, the evaluation should first include a qualitative assessment of the trophic interactions between both native and exotic species. Secondly, the evaluation should include an assessment of the functional roles of exotic species in the ecosystem (Zavaleta *et al.* 2001). An example would be outlining the current impact of rats on local bird populations. This latter evaluation could result in insights on the damage that may occur in the chance of a mesopredator release (Caut *et al.* 2008). By performing a pre-eradication assessment, a plan could be created to strategically target populations simultaneously or in a stepwise fashion. For example, Fitzgerald *et al.* (1991) showed that, on Raoul Island, eradication of cats would result in an

increase in the rat population with detrimental effects on the bird population. However, eradication of rats, the cats' preferred prey base, would merely cause a shift in prey base onto seabirds. A sequential or careful combined eradication program might achieve more beneficial results without detrimental effects on seabird populations.

The benefit of pre-eradication planning was supported in a study on Macquarie Island, an Australian island located between New Zealand and the Antarctic, centered ca. 54°37'21"S, 158°52'07"E. Here, researchers performed qualitative modelling of the ecosystem to account for potential consequences of invasive species removal involving rabbits, rats, and mice. Based on the modelling results, it was determined that equal targeting of all three non-native pest species would be most effective, but that eradication of the mouse population had a high level of uncertainty (Raymond *et al.* 2011). With this plan established, a more effective and comprehensive eradication period could ensue.

In addition, it is important to consider the most effective lethal eradication technique for the target species. In a Costa Rican study, it was found that mosquito (genus *Wyeomyia*) population size doubled due to an evolved resistance to a pesticide that is eradicating their top predator, damselfly larvae (*Mecistogaster modesta*). Though both invertebrate populations were targeted for eradication, the resistance allowed a mesopredator release of *W. abebela* (Weathered *et al.* 2019). The results stress the importance in understanding how specific eradication techniques affect targeted species in order to avoid an unintentional mesopredator release. With these types of comprehensive plans, mesopredator release and other consequences of lethal eradication can be limited or predicted.

In the post-eradication phase, there should be a reevaluation of the timing and method of lethal eradication. This post-eradication phase could yield valuable insights into the effectiveness of the plan. For example, in one New Zealand study, it was found that the simultaneous removal of rabbits and cats maximized the native bird success. The authors also determined if one species had to be targeted first, rabbits should take initial priority (Zavaleta *et al.* 2001). In other studies, it has been suggested if all the invasive species cannot all be targeted simultaneously, it is best to target the trophically most inferior invasive predator first (Caut *et al.* 2008). It is important to accurately assess trophic interactions because models that replicate release from top-down control recognize highly specific control as an optimum choice to avoid accidental by-kill. However, it does increase the risk for release of competitors from the same trophic level.

Conclusion

New Zealand's intensive plan for lethal eradication calls for a pause to evaluate the high potential for mesopredator release and negative consequences on native species. Lethal eradication of apex predators has been determined to be responsible for the release of lesser predator populations. Through mathematical modeling of varying ecosystems and ecological scenarios, it has been found that mesopredator release can be more detrimental to the prey population than the prior removal of apex predators. Island populations of indigenous species are particularly at risk because of their low species diversity and limited geographic range; New Zealand and its offshore islands are no exception. The current lethal eradication planning prior to implementation in New Zealand is simple, with success of operation based solely on kill rates of targeted species rather than improvement in the prey species population. By implementing a pre-

eradication plan that characterizes the ecosystem of interest and looks for trophic level interactions, New Zealand could provide substantially more protection to their species of interest. New Zealand is under pressure to quickly and efficiently eliminate invasive mammalian predators, but if a change is not made to the process of lethal eradication, the country could see native species go extinct in their attempt to provide relief.

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