



## Good predators: the roles of weka (*Gallirallus australis*) in New Zealand's past and present ecosystems

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**Abstract:** There is increasing interest in restoring native predators in order to regulate ecosystems and maintain biodiversity, but predator reintroductions are still controversial for complex social and ecological reasons. Few studies have examined predator restoration on islands or in ecosanctuaries, where highly endemic faunas have typically undergone precipitous declines and extinctions due to novel invasive predators, and translocations are used to restore species. Currently in New Zealand, discussions regarding predators typically focus on introduced mammalian pests, and the importance of native predators is frequently overlooked. We present a case study of the mesopredatory New Zealand weka (*Gallirallus australis*), a threatened flightless rail that provokes controversy among restoration practitioners due to concerns that it may decrease populations of other threatened species. We (1) review studies of weka diet and impacts on native and exotic fauna; (2) contrast prehistoric and contemporary predation webs focused on weka; and (3) consider the role of biocultural approaches in the management and restoration of socio-ecological systems with weka. Weka are opportunistic omnivores that can include vertebrates in their diet, and on small islands where weka can reach high densities there is some evidence that they may limit some prey populations. However, very few manipulative experimental studies measuring effects of weka on native species have been carried out, and such studies would be extremely valuable. Weka also consume invasive rodents and, if they obtain a sufficiently high density, may provide benefits in ecosanctuaries by limiting invasive mice populations. Māori historically harvested weka, and such harvest may now valuably limit weka numbers at certain island or ecosanctuary sites, perhaps replacing the effect of extinct avian competitors and apex predators. How weka and other native predators should be managed on islands depends on the value placed on ecosystem restoration, species-focused conservation, or biocultural enrichment.

**Keywords:** avian predator, biocultural restoration, ecosystem restoration, island conservation, mesopredator, prehistoric predation

### Introduction

“New Zealand's avifauna did not evolve in the absence of predators but only in the absence of mammalian predators.” Holdaway (1989).

Predators, which we define for this paper as terrestrial vertebrate species that prey on other terrestrial vertebrates (including their eggs), play a crucial role in regulating ecosystems and maintaining biodiversity. Apex predators, which we define as predators that are not killed by other species as adults, occupy the top trophic position in a community and can indirectly affect plant diversity and abundance by mediating the density and behaviour of herbivore populations (Ripple et al. 2014). They also suppress populations of smaller predators (mesopredators, which differ from apex predators in that they are killed by other predators as adults), thereby moderating predation on smaller prey species (Ritchie & Johnson 2009). Both apex and mesopredators may help regulate disease and

buffer ecosystems against invasion (Ritchie et al. 2012), so the decline or loss of predator populations can have far-reaching consequences for ecosystem processes and function (Estes et al. 2011).

Although the important role of predators in ecosystems is now widely acknowledged, restoring predator populations is still controversial, because predators can have deleterious impacts on other valued species (Ritchie et al. 2012). Weka (*Gallirallus australis*) are a textbook example of this conflict, being a threatened species that sometimes preys on other threatened species. As the impacts of predators are highly context-dependent, ecologists have limited ability to forecast their effects on ecosystems (Ritchie et al. 2012; Alston et al. 2019). In addition, the majority of research and discussion around reintroducing and managing terrestrial predators within a conservation framework has focussed on continents (Ripple et al. 2014; Wallach et al. 2015; Stier et al. 2016; Alston et al. 2019). However, island ecosystems like New Zealand present

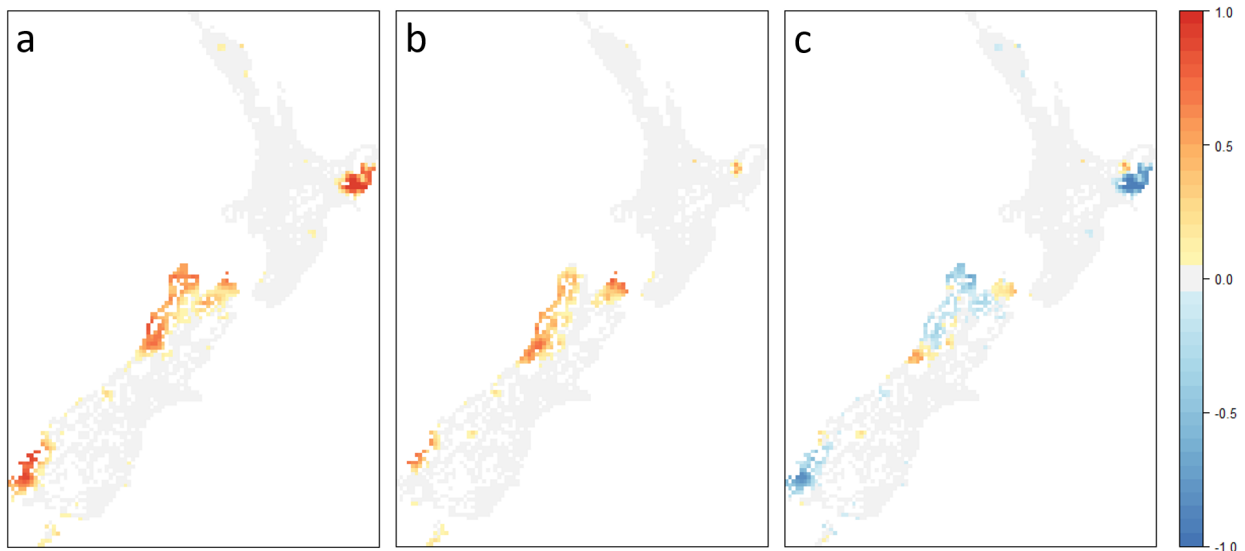
a range of unique issues, including faunas characterised by dispersal limitation, species radiations with high degrees of specialisation, high rates of endemism, and high rates of human-induced species declines and extinctions (Wood et al. 2017). Insular native New Zealand prey populations may therefore be particularly vulnerable to predation pressure from native predators in contemporary ecosystems (Innes et al. 2010). Conversely, the reintroduction of native predators may provide opportunities for native predators to control introduced species (Carlsson et al. 2009; Letnic & Dworjanyn 2011), such as New Zealand falcons (*Falco novaeseelandiae*) being introduced to vineyards to control the impact of introduced pest birds (Kross et al. 2013). Ritchie et al. (2012) stress that holistic views of predators are key if restoration attempts are likely to succeed, and that future research examining predator restoration must incorporate biodiversity, economic, and social aspects.

New Zealand's prehistoric terrestrial predator guild was devoid of mammals and almost completely dominated by birds, including the world's largest known eagle (Haast's eagle *Aquila moorei*) and largest known harrier (Eyles' harrier *Circus eylesi*). These avian predators would have played an important role in regulating New Zealand's ecosystems (Lee et al. 2010). However, the original predator guild has been reduced since human arrival in New Zealand (c.1280 AD; Wilmshurst et al. 2008), and has now been augmented by introduced mammals, in particular ship and Norway rats (*Rattus rattus*, *R. norvegicus* respectively), stoats, ferrets and weasels (*Mustela erminea*, *M. furo*, *M. nivalis* respectively) and brushtail possums (*Trichosurus vulpecula*). The replacement of the original avian predator guild with a guild dominated by mammalian predators is the key cause of most current New Zealand vertebrate declines (Innes et al. 2010; O'Donnell et al. 2010; Buxton et al. 2014). Perhaps as a consequence of avian predator loss, the importance of native predation is rarely considered in New Zealand restoration scenarios. For example, the initiative to eradicate several species of introduced mammals from New Zealand by 2050 is known as the Predator Free New Zealand programme (Russell et al.

2015), and offshore islands and sanctuaries that have undergone eradications of introduced mammals are commonly referred to as "predator free" (Ryan & Jamieson 1998; Bellingham et al. 2010; Carpenter et al. 2018). Yet many native avian predators are still extant, although much reduced from their previous densities and distributions.

Restoring New Zealand's native extant predators to the regions they historically inhabited will in part increase ecological integrity, a key goal guiding restoration in New Zealand (McGlone et al. 2020). High ecological integrity can be defined as the composition and abundance of native species typical of a region are present, together with the key ecosystem processes that sustain functional relationships between these components (Lee et al. 2005; McGlone et al. 2020). Some definitions of ecological integrity portray humans as having predominantly negative impacts on ecological integrity, whereas others recognise that people (and their relationships with species such as native predators) are an integral part of ecosystems (Roche & Campagne 2017). With the latter approaches, conservation puts greater emphasis on deepening, rather than decoupling, the relationships between people and nature (Gavin et al. 2015; Lyver et al. 2016). Social-ecological approaches like these should be an important component of predator restoration in New Zealand, as restoring native predators is socially, culturally, and ecologically complex.

Weka epitomise many issues around native predator restoration in New Zealand. The gregarious, inquisitive nature of weka make them a special species for many New Zealanders, and Māori historically harvested them for food, feathers, and oil (Miskelly & Beauchamp 2004; Williams 2010). These flightless rails once occurred in diverse habitats across most of the New Zealand mainland (North, South, and Stewart Islands), but over the last century have been extirpated from most of their natural range, mainly due to predation by introduced predators and starvation during droughts (Beauchamp et al. 1999; Tinnemans et al. 2019). Their range shrank further between the 1970s and early 2000s (Fig. 1), and mainland populations have often been subject to large



**Figure 1.** Mean probability of occupancy for weka in  $10 \times 10$  km grid squares, derived from the two bird atlases of New Zealand: a) Atlas 1 (1969–1979); b) Atlas 2 (1999–2004), and; c) the change in the probability of occupancy between the Atlases (calculated as occupancy in Atlas 2 minus occupancy in Atlas 1), with warm colours indicating increases and cold colours indicating decreases. Probability of occupancy is the probability that each 10 km by 10 km grid cell contains weka. Occupancy probabilities from Walker and Monks (2018) and <https://datastore.landcareresearch.co.nz/organization/osnz-atlas-data>.

fluctuations (Beauchamp et al. 1999). The International Union for the Conservation of Nature currently classify weka as 'vulnerable', with a decreasing population trend. Population declines are predicted to intensify due to climate change, so human assistance is likely needed to conserve and protect weka (Beauchamp et al. 1999). However, their conservation has been controversial in New Zealand, because weka are a threatened species that can prey on other threatened species. Because of this conflict, they have been eradicated from at least eleven offshore islands (Miskelly & Beauchamp 2004), including some where they occurred naturally (e.g. Entry Island, Fiordland). They are frequently excluded from mainland restoration projects (Smuts-Kennedy & Parker 2013) despite their historical presence at ecosanctuary sites, mainly due to fears that weka will preclude opportunities to introduce other threatened fauna.

Conservation practitioners require a nuanced understanding of the ecological functions carried out by weka, so that the benefits of their restoration or reintroduction can be balanced against their possible negative impacts on other threatened native fauna. In this review paper, we highlight the role of weka in New Zealand's prehistoric and contemporary ecosystems. We (1) review studies of weka diet and summarise the impacts of weka feeding on native fauna and introduced vertebrates; (2) contrast prehistoric and contemporary predation webs focused on weka, to highlight New Zealand's original predator guild and to demonstrate the dramatic shifts that have occurred in predator guilds since human arrival; and (3) consider the role of social-ecological approaches in the management and restoration of weka.

## Weka feeding and diet

Weka are flightless, so their foraging is predominantly confined to the ground, although they have some climbing ability and can jump vertically up to 90 cm (Thomson et al. 2001). Their most common foraging method is moving across the ground and flicking litter with their beak (Beauchamp 1987). They can move logs up to three times their body weight. Weka also sometimes probe with an open bill at surface objects, such as fruits, fallen flowers, and worms (Beauchamp 1987). Occasionally, they pound large objects before feeding on them. This method is used to break up flesh, puncture eggs and the skulls of chicks, and obtain roots and tubers of orchids (Beauchamp 1987). Some food selection may be based on bright colour (e.g. fruits and fallen petals), as weka show strong colour-based feeding preferences; red and yellow are preferred over blue, green, and brown (Hartley et al. 2000). A combination of iridescence and movement may help weka detect invertebrates (Beauchamp 1987) and lizards. Weka can forage at all times of day and night but have crepuscular peaks of activity (Beauchamp 1987; Bramley 1994; Lamb et al. 2021).

Our literature search revealed ten studies that assessed weka diet using either faecal examinations ( $n = 3$ ), analyses of gizzard contents ( $n = 5$ ), or both methods ( $n = 2$ ). Half of these studies were conducted at mainland sites, while half were conducted on offshore islands with mammals present. The results demonstrate that weka are opportunistic omnivores generally consuming food items in proportion to availability (Beauchamp 1987; Bramley 1994; Beauchamp et al. 2009). Their diet is typically dominated by fruit, seeds, and invertebrates (Table 1). Vegetative matter such as flowers, leaves, and moss are also frequently eaten, although this may

be incidentally ingested while taking other food items off the ground. Beauchamp (1987) notes that preferred foods are vertebrate flesh and eggs. This is apparently more important on islands, perhaps reflecting the greater availability of vertebrate food on some islands compared to the mainland. Petrel eggs and chicks were common food items on offshore islands such as Whenua Hou (Beauchamp 1987) and Taukihepa (Harper 2007), and rodents were important foods for weka on Macquarie Island (Brothers & Skira 1984). Most mainland studies did not record vertebrates as a large component of weka diet. It should also be noted that most of the studies carried out on weka diet thus far do not determine how often prey items were scavenged, as opposed to depredated.

## Impacts of weka on native species

As a consequence of weka predation, prey individuals can be injured or die, or alter their behaviour in ways to avoid predation. These effects aggregate with other factors into population characteristics such as density, sex ratio, age structure, and mortality rates. Population impacts are especially sensitive to the proportion of individuals in the effective breeding population that are killed, relative to the rate of population recruitment, including for example whether species are K- or r-selected (Spurr 1979). Evidence for individual level impacts of weka on native vertebrates is abundant, yet compelling evidence for population level impacts is scarce. Weka have been recorded destroying the eggs and chicks of ground nesting birds including kiwi (*Apteryx* spp.; Jolly 1989), Fiordland crested penguin (*Eudyptes pachyrhynchus*; St. Clair & St. Clair 1992), tūī (*Puffinus griseus*; Harper 2006), southern Buller's albatross (*Thalassarche bulleri bulleri*; Taylor 2000), mottled and Cook's petrels (*Pterodroma inexpectata*; *P. cookii*; Taylor 2000), fairy prion (*Pachyptila turtur*; St. Clair & St. Clair 1992), kākāpō (*Strigops habroptilus*; Elliott & Eason 2002), Chatham Island oystercatcher (*Haematopus chathamensis*; Moore & Reid 2010), takahē (*Porphyrio hochstetteri*; Crouchley 1994), and whio (*Hymenolaimus malacorhynchus*; Whitehead et al. 2008). They can also kill the fledglings and chicks of volant birds such as tūke (*Philesturnus* spp.), robins (*Petroica* spp.), tūī (*Prosthemadera novaeseelandiae*), and kākā (*Nestor meridionalis*) (Hooson & Jamieson 2003; Miskelly & Beauchamp 2004; Van Horik 2011). Weka also consume lizards and introduced frogs (Carroll 1963; Coleman et al. 1983). However, captive weka rejected live Archey's (*Leiopelma archeyi*) and Hochstetter's frogs (*L. hochstetteri*) unharmed after holding them in their bill, possibly due to the frogs' gland secretions (Beauchamp 1996).

Manipulative experiments would provide the best assessment of whether weka predation impacts any of these species at the population level, but we could find only two published studies that had attempted this. Harper (2007) experimentally removed weka from sites on Taukihepa (Big South Cape) and assessed tūī nesting success. Chick losses were reduced by 75% in the year that weka were removed, but the study was confounded by the effect of year. On Kāpiti Island, Colin Miskelly carried out a five year study beginning in 1996 (the year that Norway rats and kiore (*R. exulans*) were eradicated) to determine the impacts of weka on lizards and invertebrates, using fenced enclosures to exclude weka (mentioned in Miskelly & Beauchamp 2004). Ground-dwelling lizards were nearly absent from forested sites, presumably due to both weka and rat predation. However, three lizard species were abundant at the coastal site, and their recovery following rat eradication appeared unaffected by the presence or absence of weka.

**Table 1.** Summary of studies on weka (*Gallirallus australis*) diet.

Study	Method	Vegetation	Fruits and seeds	Invertebrates	Birds	Herpetofauna	Mammals	Miscellaneous
Beauchamp, 1987 Kapiti Island	Examined 360 faecal samples and 20 gizzards and calculated percentage frequency	Deliberate root/shoot consumption for 13% faeces. Consumed hinau flowers, roots and tubers of orchids, <i>Ripogonum scandens</i> shoots. Most other veg consumption deemed accidental	23% of faeces, 90% of gizzards. Mainly <i>Elaeocarpus dentatus</i> , <i>Pseudopanax</i> spp., <i>Coprosma</i> spp., <i>Coprosma grandifolia</i> , and <i>Geniostoma ligustrifolium</i> . Mentions when it was dry weka relied heavily on fallen <i>Pennantia corymbosa</i> , <i>Pseudopanax arboreus</i> , <i>Corynocarpus laevigatus</i> , <i>Tetrapathaea terandra</i> , and <i>Piper excelsum</i>	Most important were amphipods (100% faeces), small worms, Coleoptera, small snails of the genus <i>Charopa</i> and short legged harvestman. Other inverts that were regularly taken were Chilopoda, Diploida, Dermaptera, Carabidae and Elateridae larvae, and dipteran adults and larvae from Tipulidae			Rats in 20% of gizzards. Scavenged on possums when available (45% of gizzards)	
Beauchamp, 1987 (unpublished data listed in thesis) Whenua Hou/Codfish Island	45 gizzards sampled, calculated percentage frequency	"Dicots" 44.4%	Fruit in 79.5%	Coleoptera in 73%, followed by Arachnids, Amphipods, Diptera, Annelids, Orthoptera, Mollusca, and other inverts in smaller quantities	Petrels in 76% of gizzards. Kakariki in 2.2%		Rodents in 6.7%, possum in 2.2% (probably scavenged)	
Beauchamp et al., 1998 Bay of Islands	Sieved through 37 faeces collected in March, June, Sept, Dec, and calculated percentage occurrence by volume for each month	3% in March, 9% in June, 51% Sept, 16% Dec	3% March, 9% June, 10% Sept, 5% Dec	Exotic crickets made up 60% diet in March, 13% in Sept and Dec. Other inverts 23% March, 23% June, 26% Sept, 75% Dec	"Vertebrates" made up 5% diet in March			
Beauchamp et al., 2009 Pakatoa Island, Hauraki	Examined faeces of weka, made feeding observations	Shoots, grass, flower parts	Figs, <i>Gahnia</i> spp., palm, nightshade fruits, other fruit cases	Main food of weka were earthworms. 93% of faeces contained 100s to 1000s of earthworm chaetae. Coleoptera, Orthoptera, Hymenoptera, Lepidoptera, Hemiptera, Diptera, Arachnida, Isopoda, Amphipoda, Diplopoda, Mollusca also occasionally eaten				
Bramley, 1994 Rakaurua, Gisborne	Sorted 86 faecal samples and 13 gizzard examinations	"Plant material" dominated the samples	Seeds were important in autumn and winter	Dominated by annelids, carabids, slugs. Some items, for example slugs, were not seen in the faeces but were clearly eaten by weka (seen in gizzards). Some very hard fragments such as weta mandibles were also found in gizzards	Bird carrion occasionally noted. Eggshells present but only in very small abundances		Mammal carrion occasionally noted	

**Table 1.** Summary of studies on weka (*Gallirallus australis*) diet continued.

Study	Method	Vegetation	Fruits and seeds	Invertebrates	Birds	Herpetofauna	Mammals	Miscellaneous
Bramley 1994 Karangahake, Coromandel Peninsula	Sorted 17 faecal samples and calculated percentage frequency	Plant in 94%	Seeds in 29%	Scarabaeids, amphipoda, annelida, chilopoda, beetles most common inverts in faeces	No remains noted			Were also eating pellets
Brothers and Skira 1984 Macquarie Island	Examined gizzard contents of 98 birds and calculated percentage frequency of occurrence sometimes	In 80% gizzards. Fibrous material with some seed. Kelp	Fruit present, quantity unspecified	Marine shells in 72% birds and land snails in 8%. <i>Tigriopus</i> <i>angulatus</i> in 2% birds, crab claw in 1%. Kelp fly larvae ( <i>Coelopa curvipes</i> and <i>C. nigriffons</i> ) and adult <i>Apetaemis watsoni</i> in 33% gizzards. <i>Erioptera</i> <i>macquariensis</i> pupa, <i>Drosophila</i> <i>melanogaster</i> , Dolichopodidae larvae. <i>Eudoria mawsonii</i> larvae in 37%. Collembola in 5%, Coleoptera in 10%. Arachnids often in diet	Eggshell fragments in 2% gizzards. Penguin and weka feathers in 28% gizzards, inferred to be accidental consumption	In 41% gizzards. Mice in 23%, rats in 19%, and rabbits in 2%.		
Carroll 1963 Gisborne	Examined gizzard contents of 86 birds and calculated mean percentage volume of each food type	56% over whole year. Grass leaves and stalks, fibres, clover leaves, small leaves, manuka, moss	13% over whole year. <i>Bromus mollis</i> , <i>Cynosurus echinatus</i> , <i>Sporobolus capensis</i> , <i>Anthozanthum</i> <i>odoratum</i> , <i>Trifolium</i> <i>repens</i> , <i>T. glomeratum</i> , <i>Mariscus ustulatus</i> , <i>Solanum nigrum</i> , <i>Rumex acetosella</i> , <i>Cirsium vulgare</i> , <i>C.</i> <i>lanceolatum</i> , <i>Coprosma</i> , <i>Phytolacca octandra</i> , <i>Rubus sp.</i>	29% was animal matter. Click beetles, ground beetles, luhu beetles, Carabids, brown and green chafers. <i>Hemideina crassidens</i> , grasshoppers, locusts, cockroaches, ants, ichneumon flies, lepidopterous pupae ( <i>Porina</i> spp.), shield bugs, insect eggs. Slugs ( <i>Limax</i> ), snails (particularly <i>Potamopyrgus</i> ), one <i>Helix</i> land snail, slaters, small fresh water shrimps, spiders. One <i>Peripatus</i> <i>novae-zealandiae</i> . Earthworms, millipedes were common	Eggshell fragments in 7 stomachs	<i>Hyla aurea</i> bones found in 4 birds		3%. Fragments of sheep hoof, piece of wire

**Table 1.** Summary of studies on weka (*Gallirallus australis*) diet continued.

Study	Method	Vegetation	Fruits and seeds	Invertebrates	Birds	Herpetofauna	Mammals	Miscellaneous
Coleman et al. 1983 Bryan O'Lynn, Greymouth	Examined gizzard contents of 35 birds	Foliage occurred in many stomachs, mostly unidentified dicot tissue, but grasses, fern and moss leaves also common	Most common food. Large numbers of <i>Coprosma</i> seeds (particularly <i>C. pseudocuneata</i> , <i>C. parvifolia</i> , <i>C. rigida</i> , <i>C. rhamnoides</i> ), also <i>Carpodetus serratus</i> , <i>Myrsine divaricata</i> , <i>Pennantia corymbosa</i> . Also <i>Nertera</i> , <i>Prumnopitys ferruginea</i> , <i>Podocarpus totara</i> , <i>Dacrydium</i> , <i>Carex</i> seeds. Some Gramineae seeds	Wide range eaten, mostly insects, spiders and worms		1 bird had eaten a lizard, 1 bird a frog	Remains from two rodents and several possums noted	
Harper 2007 Taukihepa, Stewart Island	Crop and pectoral muscle sample taken from 15 birds for dietary and stable isotopic analysis. Food items in crops estimated by % volume	Approx 8%	Approx 15%	38.80%	39.60%			

In the absence of controlled, replicated studies, the next best evidence of population level impacts of weka are accounts of changes in native fauna after weka introduction or following weka eradication. When weka were removed from Te Kakaho (Chetwode Islands), detections of two skink species increased, although this may have reflected a change in lizard behaviour rather than increased density (Rufaut & Clearwater 1997). South Island snipe (*Coenocorypha iredalei*) disappeared from Solomon, Poutama, Jacky Lee, and Green Islands following the introduction of weka (Miskelly 1987). The annual population growth rate of tīeke on Kundy Island increased from a mean of 9.8% in the presence of weka, to 14.5% with weka removed (Hooson & Jamieson 2003).

Most evidence for population-level impacts of weka on native vertebrates is circumstantial. They have been implicated in the extinction of the Macquarie Island parakeet (*Cyanoramphus novaezelandiae erythrotis*), which occurred after populations of cats (*Felis catus*) and weka increased in response to the introduction of rabbits (*Oryctolagus cuniculus*) (Taylor 1979); although weka impacts cannot be disentangled from those of cats and rabbits in this case. The extreme rarity of the Open Bay Islands skink (*Oligosoma taumakae*) and gecko (an undescribed species from the *Mokopirirakau* genus) has been attributed to weka predation (Lettink et al. 2010). Weka were introduced to the Open Bay Islands in the early 1900s (Stirling & Johns 1969), and although weka have not been observed preying on either species, they have been observed hunting for skinks (Lettink et al. 2010) and the skinks are now found mostly in habitat inaccessible to weka (Chapple & Patterson 2007). Dramatic declines in mottled and Cook's petrel populations on Whenua Hou in the 1940s were attributed to weka predation, although kiore and possums were also present at the time (Blackburn 1968). On Jacky Lee Island, Wilson (1959, cited in Miskelly 1987) reported an irrupting weka population decimated diving petrel and prion populations. Similarly, weka predation is believed to have driven declines of tītī on Kāpiti Island over the last 30 years, and a weka-proof fence has been constructed to protect the last breeding colony (Brown et al. 2016). However, a population of Westland petrels (*Procellaria westlandica*) on the South Island has high adult survivorship and fledging success in the presence of weka (Hawke & Holdaway 2005; Waugh et al. 2006). Tīeke populations on Kāpiti Island did exceedingly well in the presence of weka, with an annual population growth rate of 33.2% (Hooson & Jamieson 2003). Despite initial fears (Jolly 1989), weka predation on eggs seems to have little impact on the little spotted kiwi (*Apteryx owenii*) population on Kāpiti Island, with more kiwi chicks surviving than territories available (Miskelly & Beauchamp 2004).

Although invertebrates make up a large part of weka diet (see Table 1), the impacts of weka feeding on invertebrate populations are often not well studied, except for some of the larger, more charismatic species. Meads et al. (1984) recorded highly variable levels of weka predation on *Powelliphanta* species and concluded that although native predators like weka should not seriously threaten *Powelliphanta* species by themselves, weka predation combined with introduced predators, habitat modification, and habitat loss could have serious consequences. The rarity of the Open Bay Islands' leech (*Hirudobdella antipodum*) has been attributed to predation by introduced weka (Miller 1999). Conversely, the eradication of both weka and kiore from the Chetwode Islands did not result in an increase in tree weta (*Hemideina crassidens*) abundance, although weta did change their behaviour once both predators were removed (Rufaut & Gibbs 2003).

In summary, observations suggest that weka are more likely to have deleterious impacts on native species on certain offshore islands, such as the Rakiura Tītī (Muttonbird) Islands adjacent to Stewart Island (Harper 2006, 2007; McKechnie et al. unpubl. data). There are three reasons why weka may have greater impacts on these islands than on the larger mainland. First, weka may reach higher densities on seabird islands than on the mainland, perhaps due to the high productivity of these systems (Bellingham et al. 2010), the lack of consistent top-down predation pressure on weka, and the natural restriction of weka dispersal off some islands. Several islands that weka have been introduced to (e.g. Rakitu, Kawau, Mokoia, Rotoroa) have also been dramatically altered by habitat destruction, and weka seem to thrive in these disturbed environments (Rhys Burns, pers. comm.). Second, weka have been introduced to most islands by people, and therefore may present a novel threat to fauna (e.g. the Open Bay Islands endemic species) that did not previously co-exist with weka. Finally, the small size of offshore islands might intensify the impact of weka predation by limiting spatial heterogeneity in predation. For example, weka may occur patchily across a large, contiguous landscape. Increased predation by weka in some areas would be mitigated by decreased predation in other areas, allowing meta-population dynamics to develop that buffer the prey from decline. These dynamics may not occur on small, offshore islands, where weka may occur almost everywhere. Furthermore, prey species that may have found refuge in mature vegetation may be vulnerable to weka on islands with severe habitat modification. Islands also limit recolonization if prey are locally eliminated.

Weka are also more likely to reduce prey populations when the prey species is already limited or has been limited by other factors, such as predation by introduced mammals (Innes et al. 2010). Habitat loss and degradation may also play a part, as the loss of habitat that acts as refuges from predation could amplify the impact of weka on prey populations. For example, browsing by ungulates removes understorey and ground cover, exposing *Powelliphanta* snails to weka and other predators (Meads et al. 1984). Although this situation is less of a concern in the many fenced ecosanctuaries and offshore islands that have eradicated most mammals with the exception of mice (*Mus musculus*), lizards and large invertebrates may still be at risk, as they are also vulnerable to predation by mice (Watts et al. 2014; Nelson et al. 2016). Little is known about whether native avian predators such as weka inhibit the recovery of remnant lizard populations, although it has been considered as a possible mechanism behind slow population growth of some lizard species in fenced ecosanctuaries (Van Winkel & Ji 2012; Nelson et al. 2016) and on offshore islands following the removal of mammalian predators (Gollin et al. 2020). On Rotoroa Island, weka exclosures were erected to enable establishment and growth of translocated moko skinks (*Oligosoma moco*) and shore skinks (*O. smithii*) in the presence of weka, by providing weka-free habitats which 'leaked' lizards as the population grew. However, owing to changes in island management follow-up monitoring has not yet occurred (Richard Gibson, pers. comm.). Because weka may limit lizard recovery, it is likely to be difficult to establish new populations of threatened lizard species on islands where weka are already present, impacting on the ability to achieve species conservation goals for some lizard species (Jo Monks, pers. comm.). For example, the Sinbad skink (*Oligosoma pikitanga*) is a Nationally Critical species that currently occurs in one location only, and the most ecologically suitable translocation site has a high density weka population (Jo Monks, pers. comm.).

**Impacts of weka on introduced vertebrates**

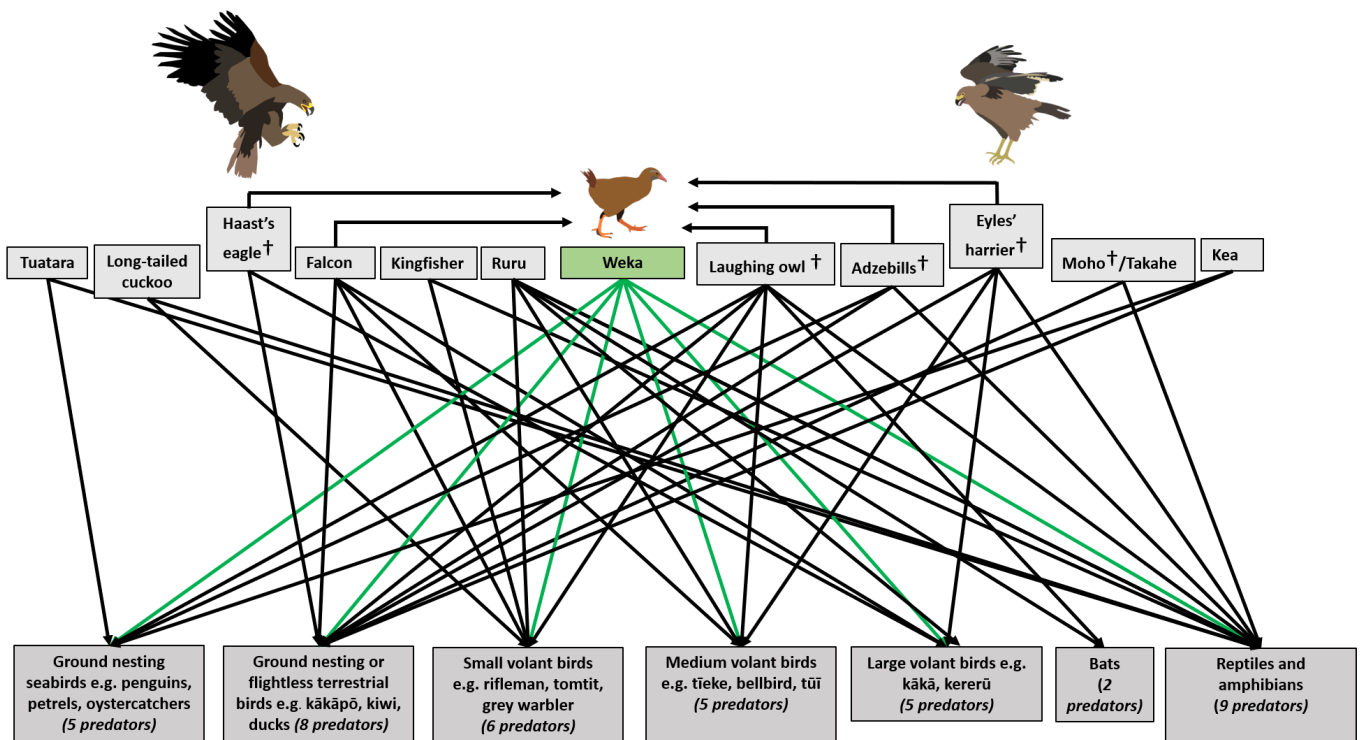
Native predators that consume exotic prey have the potential to suppress invasions and confer biotic resistance to ecosystems (Carlsson et al. 2009; Glen et al. 2017). Weka have been observed killing introduced vertebrates, including rats, mice, mustelids, and lagomorphs. King (2017, and references within) notes that "...during an irruption of forest rodents in Fiordland, western weka (*G. a. australis*) could be seen eagerly snapping up mice and swallowing them head first." Similarly, McConachie (1966, p. 55) observed weka eating so many mice during a plague that the birds' intestines became bound up in fur, killing them. Ogilvie (2010) recorded a weka competently killing a mouse, and suggested that mice might be a common prey item for weka in the wild, while Blackburn (1968) attributed the low density of kiore on Whenua Hou to predation by weka. European settlers were well aware of the potential value of the weka as a predator of rabbits, with many agreeing that weka were a better weapon against rabbits than introduced mustelids or poisoned bait. A marked decrease of rabbits in South Canterbury in the late 1800s was attributed to predation by weka (King 2017).

No studies have experimentally tested whether weka are capable of suppressing populations of introduced mammals. It would be particularly useful to know whether weka could suppress mouse populations in the absence of other mammalian predators. Mice are present in most fenced ecosanctuaries in New Zealand and can reach high densities once other mammalian competitors and predators have been removed

(Goldwater et al. 2012; Wilson et al. 2018). Burgeoning mouse populations are also likely to become an increasing problem across New Zealand if Predator Free 2050 is successful, as this initiative involves removing several introduced species that currently suppress mouse populations (Russell et al. 2015). If weka are capable of suppressing mice, they could become a useful tool for both ecosanctuaries and the Predator Free 2050 initiative. Weka were unable to prevent house mice establishing and becoming widespread over Maud Island (Ralph Powlesland, pers. comm.) or Mokoia Island (Rhys Burns, pers. comm.), but there may be a time lag before weka switch to a novel prey item (Beauchamp 1987).

**The roles of weka in past and present ecosystems**

We compiled prehistoric and contemporary predation webs to demonstrate the changed roles of weka as a mesopredator, and to highlight shifts in New Zealand predator guilds between two snapshots of time. In the prehistoric predation web (Fig. 2), avian predators dominated, with the Haast's eagle and Eyles' harrier the largest of their kinds anywhere in the world. Lee et al. (2010) suggested that these avian apex predators would have had a strong influence on the feeding activity of herbivorous birds like moa (*Dinornithiformes*), with potential consequences for the composition and abundance of plant communities. Trophic cascades mediated by carnivorous



**Figure 2.** Prehistoric predation web focused on the endemic mesopredatory rail, the weka (green feeding links), including other widespread native species (top row) that preyed on native vertebrates (bottom row) in New Zealand's forest or shrubland systems (black links). Dagger symbols mark species that are now extinct. The italic numbers in the captions of the bottom row refer to the number of predatory species that prey on that prey group. Predatory interactions between predators were common, but we have only shown predation on weka, to simplify the diagram. Many of the predators also ate invertebrates as a (sometimes major) diet component. Eyles' harrier and Haast's eagle were apex predators that were not eaten as adults. Trophic connections have been inferred from palaeoecological evidence where possible (e.g. Worthy & Holdaway 1994; Worthy & Holdaway 1995; Worthy & Holdaway 1996; Holdaway & Worthy 1996), but in some cases (e.g. the adzebills) expert opinion has been used to infer trophic links.



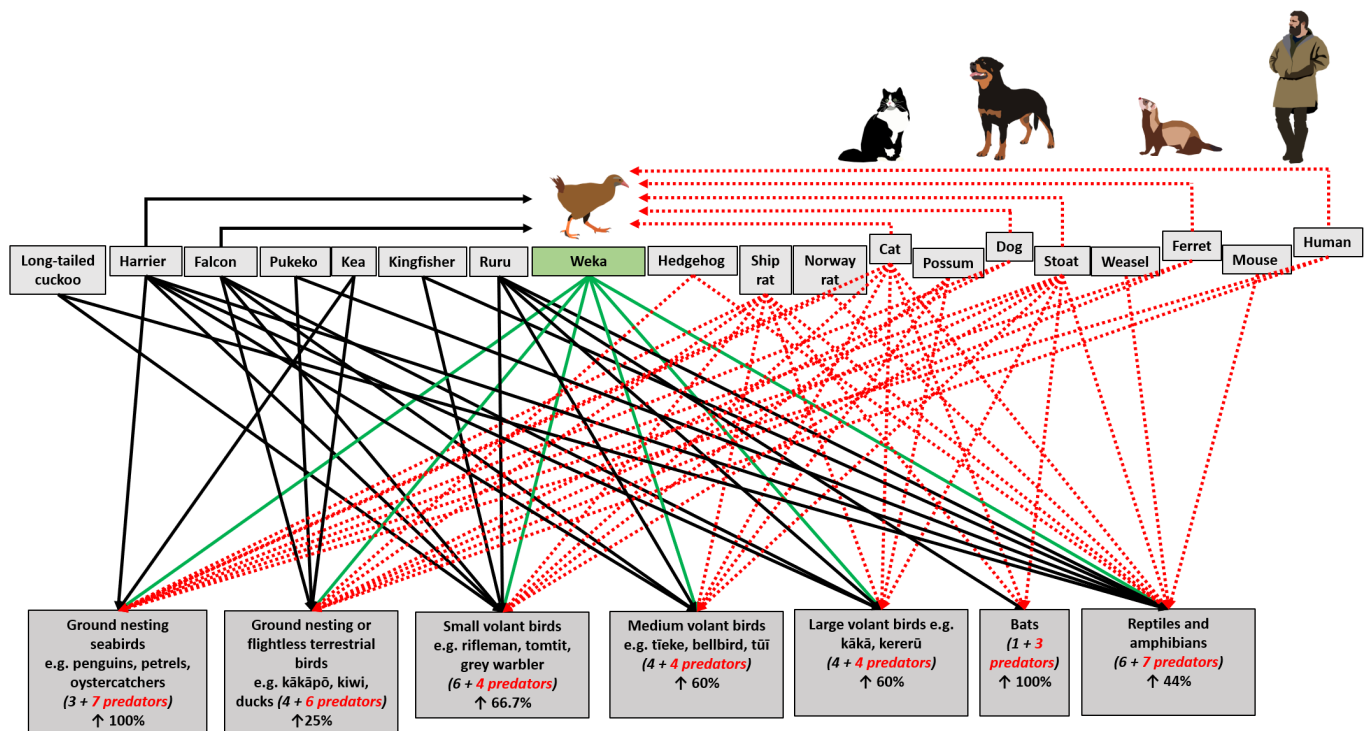
birds are prevalent across different environments and climatic areas globally (Mäntylä et al. 2011), and it seems likely that New Zealand’s avian predators could also have regulated the impact of herbivores and suppressed populations of mesopredators, thereby moderating the impact of predation on smaller prey (Ritchie & Johnson 2009). In prehistoric New Zealand, the laughing owl (*Sceloglaux albifacies*), Haast’s eagle, Eyles’ harrier, falcon, and probably adzebills (*Aptornis* spp.) all likely preyed upon and competed with weka. These species could have suppressed weka populations by directly killing chicks and adults, and by inducing behavioural changes in weka that consequently limited their populations. Weka may have changed their habitat use in favour of habitats that offered refuge from these predators and altered their foraging behaviour and activity. These behaviours would reduce the availability of space and prey resources for weka, with potential demographic impacts. For example, tawny owls (*Strix aluco*) change their behaviour and habitat use in response to their intraguild predator, the eagle owl (*Bubo bubo*), which lowers their breeding output despite actual kill rates being low (Sergio et al. 2007).

The prehistoric predation web demonstrates that birds, bats, and herpetofauna co-existed and evolved with weka and other avian predators. These prey species evolved attributes that facilitated their survival in the face of avian predation, for example cryptic colouration and nocturnal or crepuscular feeding habits (Holdaway 1989; Atkinson & Millener 1991; Lee et al. 2010). Robins (*Petroica* spp.) have been observed building higher nests when weka are present on Allports Island

(Archie Macfarlane, unpub. data), and *Leiopelma* frogs may excrete defensive chemicals to deter weka and other predators, suggesting that some species retain adaptive weka-avoidance behaviours and defences. However, we have little data on the abundances of species before human arrival in New Zealand. Offshore and fenced mainland sanctuaries that have removed all introduced mammals will now most closely approximate this prehistoric predation web, although of course they will always lack the species that have gone extinct.

Some species, such as takahē and kea (*Nestor notabilis*), that are or could have been included in our prehistoric predation web may have been more predatory than they currently appear. Takahē have been observed killing lizards and ducklings on offshore islands and in mainland ecosanctuaries where these prey are available, and kea kill Hutton’s shearwaters (*Puffinus huttoni*) and prey on whoo nests (Cuthbert 2003; Whitehead et al. 2008). These species could have consumed more vertebrate prey in pre-human ecosystems, when some native vertebrate prey items were more abundant.

In the contemporary predation web (Fig. 3), the primacy of introduced mammalian predators is clear, with the four apex predators all being introduced mammals. Weka are now predominantly preyed on by mustelids, cats and dogs (*Canis lupus*), and to a lesser extent native Australasian harriers (*Circus approximans*), falcons, and people (see next section). The mammalian species exert considerable top-down pressure on weka, and are key drivers behind contemporary weka declines (Beauchamp et al. 1999; King 2017). Numerous pest mammals also compete with native predators for the same vertebrate



**Figure 3.** Contemporary predation web focused on the endemic mesopredatory rail, the weka, including other widespread native and introduced species (top row) that prey on native vertebrates (bottom row) in New Zealand’s forest or shrubland systems. Feeding by native avian predators is shown with solid lines, by weka with green lines, and by widespread introduced mammals with dotted red lines. The italic numbers in the bottom row captions refer to the number of native (black) and introduced (red) predator species that now prey on that group, and the change in number of predatory species compared to the prehuman predation web (shown as a percentage). Predatory interactions between these predators are common, but we have only shown predation on weka, to simplify the diagram. All of the predators listed also eat invertebrates as a (sometimes major) diet component. Cats, dogs, ferrets, and humans are apex predators that are not eaten as adults. Diets of all species are described in <http://nzbirdsonline.org.nz/> (birds) and in King (2005; mammals).

prey, and all vertebrate prey groups have undergone increases in the number of species that now prey on them compared to the prehistoric predation web. Although the introduced apex predators affect both introduced and native mesopredators (Innes et al. 2010; Ruscoe et al. 2011), their effects have been particularly severe on native New Zealand species, as also seen on many other oceanic islands where species evolved without mammalian predators (Courchamp et al. 2003; Innes et al. 2010; Duncan et al. 2013; Jones et al. 2016).

Weka are involved in several ecological processes in New Zealand's ecosystems besides predation. Their large gape and fruit consumption make them an important seed disperser, especially for species such as hīnau (*Elaeocarpus dentatus*) which may rely on dispersal by flightless birds (Carpenter et al. 2018, 2019). They can retain seeds in their guts for almost six weeks (the longest avian seed retention times ever recorded), which gives them the potential to carry out important long distance (> 1 km) seed dispersal (Carpenter et al. 2019). Similarly, mammalian predators overseas have been shown to be important long distance seed dispersers (Jordano et al. 2007). The weka habit of opportunistically picking up interesting looking items from the forest floor suggests that they also may consume and disperse ectomycorrhizal fungi, much like moa and kākāpō (Boast et al. 2018), although this has not been studied. Finally, they opportunistically scavenge on carcasses, removing carrion and potentially reducing disease transmission.

### Customary harvest of weka for socio-ecological benefits

Opportunities to achieve cultural and ecological outcomes through biocultural approaches to restoration exist on some offshore islands where weka are not naturally present but have been introduced by humans. Weka are valued by Māori as food, a source of feathers for korowai (cloaks), and topical oil to treat inflammation, but also as a method of rat suppression (Miskelly & Beauchamp 2004). These are thought to be some of the reasons that weka were introduced to some Rakiura Tītī Islands. In the South Island of New Zealand, the people of Ngāi Tahu, Kati Mamoe and Waitaha hunted buff weka seasonally in inland Otago and Southland (Edwards & Logan 1999).

However, where present on the Rakiura Tītī Islands, weka can impact the abundant tītī populations (Harper 2006, 2007; McKechnie et al. unpubl. data). Weka often have no predators on these islands, other than sporadic human hunting, and can reach high densities as a result. Tītī is an important cultural keystone species for the Rakiura Māori community, who maintain a traditional annual harvest of tītī chicks from 35 islands adjacent to Rakiura (Moller et al. 2009). Eradication or control of weka populations on the islands that contain weka could have immediate and substantial benefits for sustainability of the tītī harvest (McKechnie et al. unpubl. data). Alleviating the predation pressure of weka on the Rakiura Tītī Islands may also provide an opportunity to test whether weka are having population level impacts on other species. Eradication or different forms of control of Stewart Island weka on the Rakiura Tītī Islands are options for the Rakiura Tītī Islands birding community and management authorities.

The sustained customary harvest of weka on these specific islands offers itself as a restoration management tool that contributes both biological and cultural benefits. Under this system, weka could be harvested at a prescribed rate by kaitiaki and tangata tiaki (environmental guardians) to relieve predation

pressure on native fauna in those habitats. The practice would contribute to annual mahinga kai (customary food procurement and security) options, help facilitate connection to place, and offer opportunities for regeneration and transmission of mātauranga (Māori traditional knowledge) around the species, its environment, and the practices associated with using the bird (e.g. feathers for raranga [weaving]; oils for rongoa [medicinal purpose]). Under Schedule 3 of the Wildlife Act (1953) "South Island weka (*Gallirallus*): on Chatham Islands only; Stewart Island weka (*Gallirallus*): on islets off Stewart Island and in Foveaux Strait only" can be legally hunted or killed subject to the Minister's notification. Therefore, legislation already exists at these sites for a customary harvest of weka. Where weka populations can sustain it, broadening the legislation to support a customary harvest on other islands where they have been introduced could deliver dual benefits to both communities and biodiversity. Opportunities to actively manage weka on islands where they have been introduced as part of a biocultural restoration design for other ecosystems could be therefore considered in partnership with Māori tribal entities. However, it must be noted that harvesting weka on the New Zealand mainland where weka populations are often insecure may impact the viability of the species, and is illegal.

### Conclusions and recommendations

On the whole, our review found surprisingly little evidence of weka predation having population level impacts on prey populations. However, this is mainly because definitive experimental tests are lacking, and more replicated manipulative experiments are needed before it can be concluded that weka do not reduce populations of native prey species. Studies which experimentally add or remove weka from sites of biological and cultural significance are a logical next step, given the knowledge gaps around impacts of weka on both native and introduced fauna. Using fenced ecosanctuaries or island sites that harbour mice and species thought to be sensitive to weka predation would be particularly useful. Mice, ground nesting birds, lizards, and invertebrates could be monitored before and after weka removal or addition, at treatment and control sites. Seedling density, fungal fruiting bodies, and carrion could also be monitored to quantify the contribution of weka as seed dispersers and scavengers, and to see whether they disperse fungal spores.

The way that weka are managed is highly dependent on the situation and desired conservation outcomes of a restoration project. Therefore, conservation practitioners must clearly identify the relative importance of the goals they are trying to achieve through restoration, whether that be ecosystem restoration, species-focused conservation (and for which species), or biocultural outcomes, in order to make informed decisions on the role of weka.

Restoring and conserving entire ecosystems is an increasingly common aim (or at least claim) for conservationists (Higgs 2003; SER 2004). Under this umbrella, the role of all species, including humans, that are considered part of that ecosystem are restored where possible, and ecosystem processes and functions are rebuilt. Native predators such as weka are a key part of ecosystems, so attempts to achieve ecosystem restoration with ecological integrity should weight the presence of native predators highly. However, the raft of faunal extinctions and declines caused by exotic predators on islands often means that the role of indigenous predators

is overlooked. Therefore, while the importance of restoring species interactions is now widely acknowledged, most research has focused on restoring mutualistic interactions, such as seed dispersal and pollination (e.g. Kaiser-Bunbury et al. 2010; Iles & Kelly 2014). These processes are inarguably important, however, antagonistic processes such as predation, herbivory, seed predation, and parasitism were also a part of historic ecosystems, and should be considered integral components of restored ecosystems (Carpenter et al. 2020). Weka were historically a part of many ecosystems across the New Zealand mainland, so projects truly dedicated to ecosystem restoration should welcome their presence as an archetypal generalist that carries out many ecological processes. However, reintroductions of weka to mainland sites will probably fail unless intensive control of mammalian predators also takes place (Watts et al. 2017). Indeed, North Island weka (*G. a. greyi*) are the most translocated bird in New Zealand conservation history, with 79 recorded translocations, yet only 8 (6 of which were to islands) have been successful (Miskelly & Powlesland 2013), probably due to a combination of predation by exotic mammals and widespread dispersal by released birds (Bramley 1994; Watts et al. 2017).

Conservationists focused on intensive management of highly threatened species may reach different conclusions on the importance of weka, if there is a chance that weka may impact the managed species. Weka are frequently controversial in New Zealand conservation projects due to concerns that they will impact other threatened species, yet our review found that surprisingly few experimental studies have tested the population level impact of weka on native species. However, the evidence accumulated so far suggests that weka may impact on a prey population when weka reach high densities (e.g. at sites free of most introduced mammals such as offshore islands or fenced ecosanctuaries), or when the prey abundance is already small due to other factors. In some cases there may be ways to manage or mitigate the impacts of weka on threatened prey, so that restoration of weka and highly threatened species does not always have to be mutually exclusive. Impacts of weka on particularly sensitive taxa like lizards could be mitigated by creating weka-free 'cells' or exclosures, such as on Ulva Island and Rotoroa Island (to protect skinks). Weka exclosures must be carefully designed to avoid breaches, which may be difficult or even impossible when exclosures must be accessible to other species such as breeding seabirds (Lettink et al. 2010). Alternatively, weka numbers could be controlled by harvesting for translocation or cultural purposes.

Lastly, restoration that focuses on partnership with indigenous peoples offers alternate cultural worldviews, values, perspectives and outcomes which are likely to have complex, situation-dependent views on the role of native predators. In some cases, the predator may hold relational value (e.g. cultural identity; oral history narrative), but also instrumental values (e.g. nutrition; medicinal benefits). In other cases, the presence of the predator may need to be weighed against its impact on other culturally important species. In each of these situations the management would need to be thought through carefully to enhance both ecological values and human values. Weka are engaging and charismatic (Miskelly & Beauchamp 2004), although they can have several nuisance behaviours, and can live in human-dominated, peri-urban and rural landscapes. Therefore, restoring weka also provides an opportunity to restore lively relationships between people and native birds in the places where most people live.

## Author contributions

JKC and JGI conceived the idea for the paper. JKC performed the literature review and collected the data. JRW collected data for the prehistoric predation webs. PO'BL wrote the section 'Customary harvest of weka for socio-ecological benefits.' JKC wrote the rest of the paper and all other co-authors provided editorial input.

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