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Predator control to protect a native bird (North Island kōkako) also benefits Hochstetter's frog

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Abstract: Control of introduced predators is part of the management strategy for many conservation programs. However, when such programs are designed to protect a single species, the benefits to sympatric native species are usually not assessed. We used site occupancy modelling to investigate whether predator control implemented to protect a native bird species (North Island kōkako) in the Hūnua Ranges, New Zealand also benefits the sympatric native Hochstetter's frog population. We hypothesised this benefit is possible because both native species are vulnerable to introduced mammalian predators that are targeted by control measures. Model results indicate that the predator control history of sites was the only factor to exhibit a strong and consistent relationship with occupancy by frogs. Under a range of realistic model scenarios, the probability of occupancy by juvenile, sub-adult, and adult frogs was consistently higher at sites that receive intensive predator management. Relationships between occupancy probability and other site factors (number of refugia, air temperature) existed but were inconsistent among frog age classes and either occurred independent of predator control history or appear less biologically relevant than predator control. The results support the notion that predator control designed to protect North Island kōkako in the Hūnua Ranges also benefits the Hochstetter's frog population.

Keywords: conservation, cost-effectiveness, impact, invasive species, *Leiopelma hochstetteri*, ship rat

Introduction

Conserving the world's biodiversity requires a huge investment in human and financial resources (Balmford et al. 2003; McCarthy et al. 2012; Diagne et al. 2021). Given that such resources are limited it is important to understand both the effectiveness and cost-effectiveness of conservation programs. Measuring the effectiveness of a conservation program is standard procedure, e.g. measuring target species responses following the initiation of management actions (Townes et al. 2006). However, assessments of cost-effectiveness are frequently lacking (Cullen et al. 2005; Busch & Cullen 2009; Byrom et al. 2016). The cost-effectiveness of a conservation program is defined as "the improvement in biological outcomes attributable to the program, per dollar spent" (Busch & Cullen 2009). Thus, assessing cost-effectiveness not only involves understanding the outcomes for target species (Fairburn et al. 2004), but also understanding any benefits for non-target species (Byrom et al. 2016; Runge et al. 2019). That is, the more native species that benefit from a conservation program,

the greater the cost-effectiveness of the program.

One of the greatest challenges to conserving native biodiversity, and one of the greatest conservation costs, is combatting the continuing spread of invasive species (Mack et al. 2000). Introduced predators in particular can have dramatic impacts on native biota, especially on islands where the native fauna has evolved in the absence of such predators (Savidge 1987; Lodge 1993; Medina et al. 2011). In New Zealand where native terrestrial fauna has evolved in the absence of mammals (except bats), introduced mammalian predators have caused impacts ranging from behavioural shifts (Hoare et al. 2007) to population declines and extinctions of native fauna (Atkinson & Cameron 1993; Towns & Daugherty 1994; Towns et al. 2001; Towns et al. 2006; Towns 2009). In response to this threat, predator control or eradication has been widely implemented as a management strategy (Towns et al. 2001; Towns et al. 2006; Towns 2009; Brown et al. 2015). Such predator control programs can have dramatic benefits for native fauna, although effects may be variable among native taxa (Towns et al. 2006), precise mechanisms of impact may

be difficult to identify (Townes et al. 2006), and indirect effects may make it difficult to predict all ecological consequences (Tompkins & Veltman 2006).

In this study, we assessed the evidence for whether predator control specifically implemented to protect a native bird species (North Island kōkako, *Callaeas wilsoni*) in the Hūnua Ranges also benefits the sympatric native Hochstetter's frog (*Leiopelma hochstetteri*) population. Predator management at this site focuses on three introduced mammalian species: Australian brushtail possums (*Trichosurus vulpecula*), stoats (*Mustela erminea*), and ship rats (*Rattus rattus*). Australian brushtail possums are not known to prey upon any native or introduced frog species in New Zealand (Egeter et al. 2015). However, both stoats and ship rats are known predators of native frogs, including Hochstetter's frog (Thurley & Bell 1994; Egeter et al. 2015; Egeter et al. 2019). Several lines of evidence suggest that rats in particular pose a threat to native frogs. The Pacific rat (kiore, *Rattus exulans*) was introduced to New Zealand c. 1280 CE and historic population declines and extinctions of endemic New Zealand frogs c. 1000 years BP to c. 300 years BP are attributed to this rat species (Worthy 1987; Bell 1994; Towns & Daugherty 1994; Wilmshurst & Ruscoe 2021). Pacific rats disappeared from most of the North Island in 1850–1860, and from most of the South Island in the 1890s, mainly due to the arrival and rapid spread of the ship rat and to a lesser extent the Norway rat (*Rattus norvegicus*; Innes & Russell 2021; Wilmshurst & Ruscoe 2021). The ship rat is now the most abundant and widespread invasive rat species in New Zealand and ship rats have been associated with declines or extinctions of 60 native vertebrate species globally (Townes et al. 2006; Innes & Russell 2021). In New Zealand, a statistically robust field experiment based on capture-recapture data demonstrated that control of ship rats at Whareorino Forest resulted in increased abundance of native Archey's frog, *Leiopelma archeyi* (Haigh et al. 2007; Pledger 2011; Germano et al. 2023). Specifically, the survival benefit occurred for adult frogs but not for sub-adult or juvenile frogs, possibly because younger (smaller) frogs are more vulnerable to other predators such as house mice (*Mus musculus*; Germano et al. 2023). This benefit of rat control for adult Archey's frogs is contrary to a dietary analysis study which found that predation by ship rats on Archey's frog at Whareorino Forest is uncommon (Egeter et al. 2019). Similarly, Nájera-Hillman et al. (2009a) found inconclusive evidence for Hochstetter's frog in the diet of ship rats at a stream in the Waitākere Ranges, although their sample size was very small ($n = 3$ rats). However, caution needs to be applied when interpreting such results because dietary studies can be a poor predictor of population-level impacts (Townes et al. 2006; Egeter et al. 2019). This may be especially so for native prey species that are not a primary food source for introduced predators. For example, ship rats are generalist omnivores with the animal component of their diet consisting primarily of arthropods (Innes & Russell 2021). If native frogs are consumed by ship rats as secondary prey at certain locations or times, then frogs would only be occasionally detected in dietary studies conducted at those locations or times. Consequently, dietary data should not be used in isolation to predict the population-level threat posed by introduced predators (Townes et al. 2006; Egeter et al. 2019).

Few data exist regarding the ability of extant native New Zealand frog species to defend themselves against introduced mammalian predators. Melzer et al. (2012) demonstrated that the Maud Island frog (*Leiopelma pakeka*) produces secretions from dorsal skin glands that are avoided

by Norway rats. Whether other native frog species produce such skin secretions, or whether ship rats are deterred by these secretions, has not been assessed. However, examination of dead Archey's frogs killed by rats (most likely ship rats) indicates the frogs were bitten on the head, and the body cavity was opened from the ventral side, thereby avoiding any dorsal gland secretions (Thurley & Bell 1994; SH pers. obs.). This observation suggests that ship rats may be adept at avoiding any chemical defences of native frogs. Such avoidance is known for other rat species: native water rats (*Hydromys chrysogaster*) in Australia avoid the toxic dorsal parotoid glands of invasive cane toads and attack toads by the ventral surface to consume non-toxic internal organs (Parrott et al. 2019).

Several previous studies have attempted to quantify the population-level effects of introduced mammalian predator control for Hochstetter's frog. Mussett (2005) found that Hochstetter's frog in the Hūnua Ranges was more abundant at sites that receive predator control, while Longson et al. (2017) found that the abundance of Hochstetter's frog at Maungatautari Scenic Reserve increased in the years following commencement of predator control. In contrast, Nájera-Hillman et al. (2009b) found no effect of predator control on the abundance of Hochstetter's frog in the Waitākere Ranges. All these studies assessed spatial or temporal change in frog population size by using an index of relative abundance (in this case, raw count of number of frogs seen per transect). There are two issues to consider with this approach. Firstly, any count of abundance is the product of two factors: the number of individuals present, and the likelihood of observing those individuals (i.e. detection probability: Anderson 2001; Yoccoz et al. 2001; MacKenzie & Kendall 2002; MacKenzie et al. 2002; Schmidt 2003; MacKenzie et al. 2005). Indices of abundance assume that detection probability does not vary in space or time, an assumption that is rarely likely to be valid (Anderson 2001, 2003; birds: Hardy & Morrison 2000; amphibians: Smith et al. 2006; mammals: Molinari-Jobin et al. 2018). Consequently, interpretation of indices of abundance is problematic because it is impossible to determine whether any change in the index represents a change in detection probability or a change in population size (Buckland et al. 2000; Yoccoz et al. 2001). For Hochstetter's frog, detection probability is known to vary among sites, seasons, and frog age classes (Crossland et al. 2005) and hence needs to be taken into consideration. The second issue with indices of abundance is that the functional relationship (linear, non-linear) between the abundance index and the population metric in question (e.g. density, distribution range) is unknown (Williams et al. 2002; MacFarland & Van Deelen 2011). Few studies using an index of abundance attempt to calibrate this relationship (Brown et al. 1996; Huijser & Bergers 2000; Mills et al. 2005) and incorrect assumptions can lead to misinterpretation of data (MacFarland & Van Deelen 2011). As indices of abundance can produce misleading results regarding changes in population status (MacFarland & Van Deelen 2011; Molinari-Jobin et al. 2018), it is difficult to confidently interpret the existing data regarding the effect of introduced mammalian predators on Hochstetter's frog populations.

In this study, we used the site occupancy model of MacKenzie et al. (2002) to assess the evidence for population-level effects of mammalian predator control for Hochstetter's frog. Site occupancy models estimate the proportion of sites occupied by a species in an area and use this as a population monitoring metric (see Votja 2005 for summary). The model of MacKenzie et al. (2002) explicitly incorporates detection

probability, and hence produces statistically robust estimates of occupancy patterns provided the detection component of the model has sufficient flexibility to allow for the main sources of variation in detection probability. This model is particularly useful for monitoring cryptic or rare species, or species that exist as meta-populations and hence must be monitored over a large spatial scale (e.g. many amphibian populations; Alford & Richards 1999).

Methods

Study species

Hochstetter's frog is a cryptic species that exists as a series of isolated populations across the northern half of the North Island of New Zealand (Fouquet et al. 2010a,b; Newman et al. 2010). There is strong genetic structuring within the species (Gemmell et al. 2003), such that extant populations exist as 13 separate evolutionary significant units (ESU's: Fouquet et al. 2010a). Hochstetter's frog is typically associated with seepages and small rocky streams in heavily forested areas (Bell 1978; Fouquet et al. 2010b), and modelling indicates that populations across the North Island are strongly associated with areas where summer temperatures exceed 20°C and winter precipitation exceeds 200 mm (Fouquet et al. 2010b). Individuals are sedentary at stream sites over short time frames (8 days to 2 months: Tessier et al. 1991). However, Hochstetter's frogs have been observed in the forest some distance from streams, including on ridge tops (Stephenson & Thomas 1945; Bell 1978; Perfect & Bell 2005; MRC pers. obs.). Slaven (1992) recorded marked individuals moving between streams within a catchment, indicating that Hochstetter's frog populations likely function as a meta-population (Crossland et al. 2005).

In addition to the threat posed by invasive predators, Hochstetter's frog populations are also thought to be at risk from alteration of stream habitat arising from land management activities (e.g. silt sedimentation, high gravel cover; Nájera-Hillman et al. 2009b; Easton et al. 2016). The pathogenic fungus chytridiomycosis responsible for global amphibian declines (Lips et al. 2006) is not believed to pose a threat to Hochstetter's frog populations. Field surveys have failed to detect infection in this species (Moreno et al. 2011), likely because Hochstetter's frog has low susceptibility to the fungus and clears infection quickly (Ohmer et al. 2013). The conservation status of extant Hochstetter's frog populations is classified as Declining, although the Otawa population is considered Nationally Critical (Burns et al. 2018).

Study site

The study was conducted in the Hūnua Ranges Regional Parkland (HRRP) located approximately 40 km south-east of Auckland. The HRRP consists of approximately 17 000 ha of native broadleaf/podocarp forest and contains a Hochstetter's frog population that is classified as a "relict" population (Newman et al. 2010) and an evolutionary significant unit in its own right (Fouquet et al. 2010a).

The HRRP has a history of predator control operations. Prior to 1994, small areas adjacent to roads and tracks were treated with cyanide to remove 2000–6000 possums per year

(Sweetapple & Fitzgerald 1994). In mid-1994, the entire HRRP was treated with an aerial application of sodium monofluoroacetate (1080) at 5 kg ha⁻¹ which killed an estimated 86% of the possum population and 83% of the rat population (Sweetapple & Fitzgerald 1994). In late 1994, intensive localised predator control was initiated at each territory of five pairs of North Island kōkako. Specifically, poison bait stations (Talon® bait; active ingredient: 0.02% brodifacoum) were established on either a 100 × 50 m grid (breeding pairs) or 100 × 100 m grid (non-breeding pairs) for a total minimum coverage of 300 × 300 m per territory. In addition, each nest was surrounded by a ring of up to 30 traps (Victor® Ez Set snap traps for rats, Victor® leg-hold traps for possums and rats, Fenn traps for stoats and other mustelids). Fenn traps were baited with chocolate, peanut butter, and a plastic egg. Snap traps were baited with chocolate and peanut butter, while leg-hold traps were baited with flour. Fenn traps were also set along spurs and ridges adjacent to nests. These control measures were implemented from October 1994 to March 1995 (the kōkako breeding season) and were repeated each subsequent breeding season until 1997 based on the number of breeding pairs detected (Nicolaou 1994; Rudolph 1997; R. Gatland, Auckland Council, pers. comm.).

In the 1997–1998 breeding season, predator management shifted to establishing a single 350 ha block that encompassed all known kōkako territories (referred to as the Kōkako Management Area, KMA). Baits (Talon®, 0.02% brodifacoum) were deployed in bait stations on a grid system of approximately 100 × 100 m throughout the KMA, while retaining the ring of traps at each nest (as described above). In subsequent years, the size of the KMA expanded (1998: 500 ha; 1999: 600 ha; 2003: 800 ha) and in 2006 (the time of our study) covered a single block of 850 ha (100 × 100 m bait station grid system throughout, trapping protection at each nest site). During this period of expansion, several adjustments were made to predator management. From 1998–1999 onwards, nest protection was increased by placing cyanide baits (Feratox®) 20–30 cm above ground on trees (nest trees, trees located on spurs and ridges adjacent to nests) and in some bait stations throughout each territory. Freshly dead rats or freeze-dried rats were occasionally used as trap lures from 1998–1999 onwards, while Fenn trap bait changed to a single live hen's egg and a plastic egg from 2001–2002 onwards. In 1999–2000, Talon® (0.02% brodifacoum) was replaced with Pestoff® (0.02% brodifacoum) as the primary bait deployed in bait stations. From 2003–2004 onwards, additional baited traps ($n = 194$ –244 Fenn traps, $n = 50$ –80 Thumper traps) were deployed on main ridges and spurs. In 2005–2006, the ring of rat traps surrounding each nest was replaced with lines of baited Victor® Professional traps throughout each nesting territory (whilst retaining the use of cyanide pellets and other traps at nest sites as described above). Details of these changes are provided in Gatland (1999, 2000, 2004, 2006). Despite these adjustments, predator control inside the KMA remained broadly consistent from 1998–2006 in that for each year (1) predator management consisted of both broadscale control (100 × 100 m bait station grid) and intensive control at nest sites (traps, cyanide pellets), (2) the active ingredient in baits deployed in bait stations was 0.02% brodifacoum, and (3) control operations were conducted on an annual basis within the period of August–March (i.e. during the kōkako breeding season).

Although predator control inside the KMA targets possums, stoats and rats, other invasive species are present that may

be potential frog predators including mice (*M. musculus*), hedgehogs (*Erinaceus europaeus*), ferrets (*Mustela furo*), weasels (*Mustela nivalis*), feral cats (*Felis catus*), and feral pigs (*Sus scrofa*). These species are susceptible to one or more of the predator control methods used: all these species are vulnerable to primary and/or secondary poisoning from baits, while mice, hedgehogs, ferrets and weasels are also caught in traps (Alterio 1996; Berry 1999; Gatland 2006; Byrom et al. 2016; HJS pers. obs.). Pigs are also controlled by shooting in the Hūnua Ranges (Baber et al. 2009), although not inside the KMA. However, all these species appear to be in relatively low abundance at our study site (Gatland 2006; Baber et al. 2009; HJS pers. obs.) and hence likely pose a relatively low risk to the Hochstetter's frog population.

In contrast to the intensive annual predator management inside the KMA, the native forest surrounding the KMA is only subject to baseline possum control at c. 3–4 year intervals using brodifacoum baits, Victor® leg-hold traps and Feratox® cyanide pellets (Baber et al. 2009). In 2005, rat control (Feratox®) was attempted in one catchment outside the KMA. However, this was ineffective and so was discontinued after three months (Baber et al. 2009).

Assessment of frog populations

We randomly located a series of monitoring sites along small (<3 m wide) first- and second-order streams inside and outside the KMA using a topographic map. All streams were located within the same contiguous native forest (i.e. the HRRP) and had water flowing at the time of surveys. Fifty sites were established inside the KMA at distances of 50–110 m between sites. Forty-six sites were established outside the KMA at distances of 43–96 m between sites. Streams in both areas were located on underlying sandstone/limestone, had an abundance of rocky habitat suitable as refuge sites for frogs, and were similar in terms of gradient and vegetation. No streams showed evidence of sedimentation or high gravel content.

We defined a monitoring site as a 10 m transect of streamside habitat based on prior studies (Crossland et al. 2005; MRC unpubl. data). Site boundaries were defined as the area between the water's edge and the stream bank, and included both sides of the stream. In practice, this meant that the area searched was up to 1 m from the water's edge and up to 60 cm above the water level on each side of the stream. Sites were surveyed by five trained observers during daylight hours (0800–1630 hrs) between July–August 2006, with similar numbers of sites inside and outside the KMA being surveyed each day. Each site was surveyed completely (i.e. from 0–10 m) on 3–4 separate occasions (1 observer per site survey) within a 10-day period. This timeframe satisfied the model assumption of constant occupancy during the period of repeat surveys (Tessier et al. 1991; Crossland et al. 2005). Each observer surveyed sites inside and outside the KMA, and each site was surveyed by at least two observers during the study.

During each survey, all available retreat sites underneath rocks and fallen vegetation were searched with the aid of a headlamp and all frogs detected were measured by placing a small ruler adjacent to the frog. Care was taken to replace retreat sites in their original position. All frogs observed were classified as juvenile (<18 mm snout-vent length SVL), sub-adult (18–29 mm SVL) or adult (>29 mm SVL) as defined by Bell (1978) and Whitaker and Alspach (1999). Frog abundance data for each site survey were reduced to detection / non-detection data for each age class to obtain estimates of occupancy.

Ambient air temperature and the number of refuge sites

present were recorded during each site survey. Daily rainfall data were obtained from a weather station located in a central region of the study area. All equipment and footwear were disinfected with Trigen™ prior to entering the study area to minimise the risk of disease transmission among sites.

Statistical analyses of frog occupancy data

Frog data were analysed using the single-season occupancy model of MacKenzie et al. (2002) in Program PRESENCE (<http://www.mbr-pwrc.usgs.gov/software.html>). Three predictor variables for occupancy probability at a site were considered: predator control history (PCH = inside KMA vs outside KMA), average number of refugia present (AvR) and average ambient air temperature (AvT). Average number of refugia present was used as a surrogate for habitat quality, while average ambient air temperature was used as a surrogate for environmental conditions. We performed model selection using Akaike's information criterion corrected for small sample bias (AICc; where the number of transects was used as the effective sample size) and summed AICc model weights (Burnham & Anderson 2002) to identify which predictor variables appeared to be most important for explaining occupancy of sites by frogs. For each model, we estimated the probability of occupancy within a range of realistic values for each of the three predictor variables: PCH = inside or outside the KMA; AvT = 5°C, 7°C, 9°C or 11°C; and AvR = 100, 200, 300 or 400 refuge sites. Occupancy estimates were then model averaged to account for model selection uncertainty.

For all models, the same general structure for the detection probability component was used. Detection probability was allowed to vary by time of day, air temperature, number of refugia present, rainfall in the previous 24 hours and observer. Inclusion of all covariates in this manner provided the detection probability component of the model with maximum flexibility. Air temperature, number of refugia present and rainfall were continuous-valued covariates that were presumed to have a linear relationship with detection probability (on the logit scale), while time of day and observer were discrete-valued covariates with no constraints on the potential relationship with detection probability. Data for continuous covariates were standardised ($(x - \text{mean}) / \text{standard deviation}$) prior to analysis.

We assessed the fit of the most global model using the technique developed by MacKenzie and Bailey (2004) based upon a parametric bootstrap procedure as implemented in Program PRESENCE. Ten thousand bootstrap samples were used to assess the significance of the observed test-statistic (TS) and to estimate the overdispersion factor \hat{c} .

Assessment of rat abundance

Data for ship rat abundance in the HRRP were obtained from Auckland Council. The abundance index of ship rats was monitored during March–December 2006 by establishing transects ($n = 5$ outside the KMA; $n = 10$ inside the KMA) at a minimum distance of 100 m apart. Each transect contained 10 tracking tunnels placed at 50 m intervals. All tracking tunnels were baited with peanut butter and set for a single night during fine weather conditions. Brown et al. (1996) previously demonstrated that tracking tunnel usage by ship rats is linearly correlated with ship rat population density. Hence, the tracking tunnel monitoring in the HRRP likely reflects the population density of ship rats inside and outside the KMA.

Results

Assessment of native frog populations

There was no evidence of poor fit of the global model for any frog age-class (juveniles: $TS = 15.11$, $\hat{c} = 0.65$, $p = 0.90$; sub-adults: $TS = 16.18$, $\hat{c} = 0.66$, $p = 0.89$; adults: $TS = 21.21$, $\hat{c} = 0.86$, $p = 0.58$). Therefore, we did not adjust model selection procedures or inflate the estimated standard errors.

Model selection results for juvenile frogs show the two top-ranked models [$\psi(\text{PCH}+\text{AvT}+\text{AvR})$; $\psi(\text{PCH}+\text{AvR})$] have substantial support and together account for 92% of the AICc model weight (Table 1). Summed model weights for PCH (0.98), AvR (0.93) and AvT (0.69) indicate that predator control history and number of refugia are particularly important for explaining variation in occupancy by juvenile frogs, with air temperature also being important but to a lesser degree. The estimated regression coefficients (on the logit scale) are consistently similar across the different models in terms of direction and magnitude (Table 1). The models indicate that juvenile occupancy probability is higher inside the KMA, increases with the number of refugia present, and decreases with an increase in air temperature (Table 2).

Similar model selection results were obtained for sub-adult frogs: the $\psi(\text{PCH}+\text{AvR})$ and $\psi(\text{PCH}+\text{AvT}+\text{AvR})$ models rank the highest and account for 92% of the total AICc model weight (Table 3). The summed AICc model weights for PCH (0.93),

AvR (0.98) and AvT (0.22) again indicate that predator control history and number of refugia are important for explaining variation in occupancy by sub-adult frogs, while air temperature is relatively unimportant. As with juvenile frogs, the estimated regression coefficients and model-averaged estimates indicate that sub-adult occupancy is higher inside the KMA (Tables 3, 4). However, in contrast to juvenile frogs, occupancy probability decreases as the number of refugia increases (Tables 3, 4). The estimated regression coefficients for air temperature are less stable which is expected given that it appears to be a relatively unimportant variable for sub-adult frogs (Table 3).

For adult frogs, 75% of the AICc model weight is evenly spread across the top 3 models [$\psi(\text{PCH})$, $\psi(\text{AvT})$ and $\psi(\text{PCH}+\text{AvT})$] indicating that adult occupancy probability is either a function of predator control history, air temperature or a combination of both (Table 5). The summed model weights for PCH (0.64), AvT (0.63) and AvR (0.22) suggest that predator control history is again one of the most important predictor variables for occupancy. However, predator control history appears less important for adult frogs than for juvenile and sub-adult frogs (i.e. the summed PCH model weight is lower for adult frogs than juvenile or sub-adult frogs), and there is a similar level of importance for air temperature as a predictor variable for adult frog occupancy. In contrast to juvenile and sub-adult frogs, the number of refugia present is relatively unimportant as a predictor variable for adult frog

Table 1. Summary of juvenile frog model selection and associated estimated regression coefficients (standard error) for each factor in the occupancy portion of the model. The factors considered were predator control history (PCH), average air temperature (AvT), and average number of refugia present (AvR). For all models, a global detection probability model was used (see text). ΔAICc is the relative difference in AICc values for each model compared to the top-ranked model, w is the AICc model weight, K is the total number of parameters in the model (with 9 of those parameters required for detection probability) and $-2l$ is twice the negative log-likelihood for the model. Zero values with no standard errors indicate models in which the parameter was set to 0.

Model	ΔAICc	w	K	$-2l$	Intercept	PCH	AvT	AvR
$\psi(\text{PCH}+\text{AvT}+\text{AvR})$	0.00	0.64	13	205.85	0.38 (0.40)	-2.20 (0.73)	-0.44 (0.23)	0.78 (0.31)
$\psi(\text{PCH}+\text{AvR})$	1.61	0.28	12	210.14	0.42 (0.35)	-2.74 (0.68)	0 (-)	0.70 (0.28)
$\psi(\text{PCH}+\text{AvT})$	5.45	0.04	12	213.98	0.29 (0.34)	-1.85 (0.63)	-0.37 (0.20)	0 (-)
$\psi(\text{PCH})$	6.64	0.02	11	217.79	0.40 (0.33)	-2.37 (0.58)	0 (-)	0 (-)
$\psi(\text{AvT}+\text{AvR})$	8.03	0.01	12	216.56	-0.42 (0.29)	0 (-)	-0.73 (0.21)	0.63 (0.27)
$\psi(\text{AvT})$	12.21	0.00	11	223.36	-0.35 (0.28)	0 (-)	-0.63 (0.19)	0 (-)
$\psi(\text{AvR})$	22.22	0.00	11	233.37	-0.46 (0.29)	0 (-)	0 (-)	0.55 (0.28)
$\psi(\cdot)$	25.12	0.00	10	238.82	-0.42 (0.27)	0 (-)	0 (-)	0 (-)

Table 2. Model averaged estimates of juvenile frog occupancy probabilities for 100–400 refugia per site at ambient air temperatures of 5–11°C. Numbers in parentheses indicate lower and upper bounds of 95% confidence intervals.

No. Refugia	Location	5°C	7°C	9°C	11°C
100	Inside KMA	0.475 (0.128, 0.848)	0.329 (0.113, 0.654)	0.218 (0.057, 0.561)	0.153 (0.022, 0.589)
100	Outside KMA	0.107 (0.009, 0.619)	0.055 (0.007, 0.325)	0.030 (0.004, 0.177)	0.018 (0.002, 0.151)
200	Inside KMA	0.770 (0.391, 0.946)	0.664 (0.438, 0.833)	0.518 (0.299, 0.730)	0.378 (0.103, 0.765)
200	Outside KMA	0.297 (0.038, 0.818)	0.174 (0.041, 0.506)	0.097 (0.034, 0.248)	0.058 (0.014, 0.215)
300	Inside KMA	0.919 (0.561, 0.990)	0.881 (0.569, 0.976)	0.807 (0.460, 0.954)	0.689 (0.233, 0.941)
300	Outside KMA	0.587 (0.109, 0.943)	0.452 (0.114, 0.841)	0.307 (0.103, 0.632)	0.198 (0.053, 0.523)
400	Inside KMA	0.966 (0.605, 0.998)	0.952 (0.595, 0.996)	0.926 (0.507, 0.994)	0.879 (0.333, 0.991)
400	Outside KMA	0.803 (0.188, 0.986)	0.743 (0.188, 0.973)	0.642 (0.159, 0.945)	0.503 (0.097, 0.905)

Table 3. Summary of sub-adult frog model selection and associated estimated regression coefficients (standard error) for each factor in the occupancy portion of the model. The factors considered were predator control history (PCH), average air temperature (AvT), and average number of refugia present (AvR). For all models, a global detection probability model was used (see text). ΔAICc is the relative difference in AICc values for each model compared to the top-ranked model, w is the AICc model weight, K is the total number of parameters in the model (with 9 of those parameters required for detection probability) and $-2l$ is twice the negative log-likelihood for the model. Zero values with no standard errors indicate models in which the parameter was set to 0.

Model	ΔAICc	w	K	$-2l$	Intercept	PCH	AvT	AvR
$\psi(\text{PCH+AvR})$	0.00	0.73	12	285.00	1.51 (0.64)	-2.01 (0.75)	0 (-)	-1.29 (0.52)
$\psi(\text{PCH+AvT+AvR})$	2.68	0.19	13	285.00	1.52 (0.73)	-2.03 (1.03)	0.01 (0.35)	-1.30 (0.52)
$\psi(\text{AvT+AvR})$	6.36	0.03	12	291.36	0.75 (0.45)	0 (-)	-0.38 (0.26)	-1.30 (0.51)
$\psi(\text{AvR})$	6.43	0.03	11	294.05	0.72 (0.49)	0 (-)	0 (-)	-1.25 (0.53)
$\psi(\text{PCH})$	8.31	0.01	11	295.92	1.64 (0.85)	-1.98 (0.88)	0 (-)	0 (-)
$\psi(\text{PCH+AvT})$	10.80	0.00	12	295.81	1.72 (1.00)	-1.92 (0.92)	-0.12 (0.38)	0 (-)
$\psi(\cdot)$	14.45	0.00	10	304.62	0.63 (0.41)	0 (-)	0 (-)	0 (-)
$\psi(\text{AvT})$	15.34	0.00	11	302.96	0.72 (0.47)	0 (-)	-0.30 (0.26)	0 (-)

Table 4. Model averaged estimates of sub-adult frog occupancy probabilities for 100–400 refugia per site at ambient air temperatures of 5–11°C. Numbers in parentheses indicate lower and upper bounds of 95% confidence intervals.

No. Refugia	Location	5°C	7°C	9°C	11°C
100	Inside KMA	0.981 (0.750, 0.999)	0.981 (0.758, 0.999)	0.980 (0.740, 0.999)	0.978 (0.694, 0.999)
100	Outside KMA	0.888 (0.391, 0.990)	0.888 (0.437, 0.988)	0.887 (0.453, 0.987)	0.886 (0.429, 0.988)
200	Inside KMA	0.817 (0.521, 0.948)	0.814 (0.550, 0.940)	0.809 (0.510, 0.945)	0.804 (0.438, 0.956)
200	Outside KMA	0.402 (0.140, 0.736)	0.399 (0.173, 0.679)	0.395 (0.197, 0.634)	0.390 (0.173, 0.660)
300	Inside KMA	0.262 (0.046, 0.723)	0.258 (0.051, 0.694)	0.256 (0.046, 0.708)	0.255 (0.038, 0.748)
300	Outside KMA	0.062 (0.005, 0.448)	0.057 (0.006, 0.379)	0.054 (0.006, 0.343)	0.053 (0.006, 0.348)
400	Inside KMA	0.038 (0.002, 0.502)	0.037 (0.002, 0.485)	0.037 (0.002, 0.489)	0.037 (0.001, 0.511)
400	Outside KMA	0.012 (0.000, 0.285)	0.011 (0.000, 0.240)	0.011 (0.000, 0.218)	0.010 (0.000, 0.215)

Table 5. Summary of adult frog model selection and associated estimated regression coefficients (standard error) for each factor in the occupancy portion of the model. The factors considered were predator control history (PCH), average air temperature (AvT), and average number of refugia present (AvR). For all models, a global detection probability model was used (see text). ΔAICc is the relative difference in AICc values for each model compared to the top-ranked model, w is the AICc model weight, K is the total number of parameters in the model (with 9 of those parameters required for detection probability) and $-2l$ is twice the negative log-likelihood for the model. Zero values with no standard errors indicate models in which the parameter was set to 0.

Model	ΔAICc	w	K	$-2l$	Intercept	PCH	AvT	AvR
$\psi(\text{PCH})$	0.00	0.26	11	263.49	0.25 (0.34)	-1.27 (0.49)	0 (-)	0 (-)
$\psi(\text{AvT})$	0.07	0.25	11	263.56	-0.18 (0.27)	0 (-)	-0.42 (0.18)	0 (-)
$\psi(\text{PCH+AvT})$	0.17	0.24	12	261.04	0.18 (0.37)	-0.87 (0.55)	-0.29 (0.20)	0 (-)
$\psi(\text{PCH+AvR})$	2.54	0.07	12	263.42	0.25 (0.33)	-1.27 (0.49)	0 (-)	-0.07 (0.25)
$\psi(\text{AvT+AvR})$	2.60	0.07	12	263.47	-0.18 (0.27)	0 (-)	-0.42 (0.18)	-0.08 (0.25)
$\psi(\text{PCH+AvT+AvR})$	2.77	0.07	13	260.96	0.18 (0.36)	-0.87 (0.55)	-0.29 (0.20)	-0.08 (0.26)
$\psi(\cdot)$	4.59	0.03	10	270.63	-0.31 (0.24)	0 (-)	0 (-)	0 (-)
$\psi(\text{AvR})$	7.07	0.01	11	270.56	-0.31 (0.24)	0 (-)	0 (-)	-0.06 (0.24)

occupancy. The models indicate that adult frog occupancy is higher inside the KMA and decreases with an increase in average air temperature (Tables 5, 6).

There was a partial correlation between PCH and AvT (0.54), with average air temperature outside the KMA being slightly higher than inside the KMA (mean ambient air

temperatures 9.2°C and 7.4°C, respectively). There was no correlation between PCH and AvR (0.00), indicating that sites inside and outside the KMA were similar in terms of number of refugia present.

Table 6. Model averaged estimates of adult frog occupancy probabilities for 100–400 refugia per site at ambient air temperatures of 5–11°C. Numbers in parentheses indicate lower and upper bounds of 95% confidence intervals.

No. Refugia	Location	5°C	7°C	9°C	11°C
100	Inside KMA	0.607 (0.368, 0.804)	0.565 (0.390, 0.725)	0.519 (0.306, 0.724)	0.481 (0.210, 0.763)
100	Outside KMA	0.374 (0.109, 0.745)	0.331 (0.135, 0.612)	0.286 (0.156, 0.464)	0.249 (0.123, 0.439)
200	Inside KMA	0.606 (0.371, 0.800)	0.564 (0.394, 0.719)	0.517 (0.309, 0.720)	0.480 (0.211, 0.760)
200	Outside KMA	0.373 (0.110, 0.741)	0.330 (0.136, 0.606)	0.284 (0.158, 0.456)	0.248 (0.125, 0.432)
300	Inside KMA	0.604 (0.366, 0.801)	0.562 (0.387, 0.723)	0.516 (0.303, 0.723)	0.478 (0.208, 0.762)
300	Outside KMA	0.372 (0.109, 0.742)	0.329 (0.134, 0.607)	0.283 (0.154, 0.460)	0.247 (0.122, 0.435)
400	Inside KMA	0.603 (0.357, 0.806)	0.560 (0.376, 0.730)	0.514 (0.293, 0.729)	0.477 (0.201, 0.767)
400	Outside KMA	0.370 (0.106, 0.744)	0.327 (0.131, 0.612)	0.282 (0.149, 0.467)	0.246 (0.118, 0.442)

Assessment of rat abundance

In the months preceding and following the frog surveys, the ship rat abundance index outside the KMA was more than one order of magnitude greater than inside the KMA (Table 7). This trend is consistent with monitoring results from previous years (Rudolph 1997).

Discussion

Our study assessed spatial variation in occupancy probability for Hochstetter's frog in the Hūnua Ranges Regional Parkland with respect to three predictor variables: predator control history, availability of refugia and temperature. Importantly, we assessed occupancy patterns using a statistical model that explicitly incorporates detection probability (MacKenzie et al. 2002).

Predator control history was the only variable to exhibit a strong and consistent relationship with occupancy probability for all frog age classes: sites inside the Kōkako Management Area (KMA) had a higher probability of being occupied by all frog age-classes than sites outside the KMA. These occupancy patterns were inversely related to the index of ship rat abundance, with rat indices inside the KMA being consistently and dramatically lower than outside the KMA. Previous studies have found that (1) the historic decline and extinction of native frogs in New Zealand coincides with the introduction of rats (the Pacific rat; Worthy 1987; Bell 1994; Towns & Daugherty 1994), (2) ship rats prey upon native frogs including Hochstetter's frog (Thurley & Bell 1994; Egeter et al. 2015; Egeter et al. 2019), and (3) control of ship rats at Whareorino Forest resulted in increased survival and abundance of adult Archey's frog (Haigh et al. 2007; Pledger 2011; Germano et al. 2023). Additionally, control of another invasive rodent (house mouse) has been shown to increase survival and recruitment of Hamilton's frog, *Leiopelma hamiltoni* (Karst et al. 2023). Our results are consistent with these studies and support the notion that the predator control program inside the KMA benefits the resident Hochstetter's frog population. However, caution must be applied when interpreting such correlative results (Clinchy et al. 2002; Towns et al. 2006). In our case, we note that the area receiving intensive predator control (the KMA) exists as a single conservation management area, a situation that is common for mainland island reserves in New Zealand (e.g. Maungatautari Scenic Reserve: Baber et al. 2006, Longson et al. 2017). The KMA is part of a larger patch of contiguous forest, resulting in sites inside and outside

Table 7. Rat tracking indices (% tracking rate) in the Hūnua Ranges Regional Parkland before and after frog surveys (frog surveys conducted July–August 2006). Data are mean tracking index values \pm standard error. Data source and analysis: Auckland Council.

Date	Inside KMA	Outside KMA
March 2006	7.0 \pm 3.0	94.0 \pm 6.0
July–August 2006	Frog surveys	Frog surveys
September 2006	1.0 \pm 1.0	92.0 \pm 5.8
December 2006	4.0 \pm 2.7	92.0 \pm 3.7

the KMA being spatially separated. The question thus arises: could spatial variation in factors other than predator control history contribute to the differences in frog occupancy patterns inside versus outside the KMA?

The models identified refuge availability as an important predictor variable for occupancy by juvenile and sub-adult frogs, but not adult frogs. However, variation in refuge availability was not correlated with predator control history. That is, although occupancy of sites by juvenile and sub-adult frogs was related to refuge availability, these patterns occurred independent of whether sites were located inside or outside the KMA. Thus, we can exclude spatial variation in refuge availability as a confounding factor in our results.

Interestingly, the relationship between refuge availability and occupancy probability was positive for juvenile frogs but negative for sub-adult frogs. The reason for the difference between age classes is unknown but may relate to ontogenetic changes in dispersal behaviour. Hochstetter's frog eggs are laid in close association with streams (e.g. under rocks, in seepages or pools; McLennan 1985; Beauchamp et al. 2010). If sites with greater refuge availability are more favourable as breeding sites, and if juvenile frogs tend to remain close to their natal site, then a positive association between refuge availability and juvenile frog occupancy may occur. Sub-adult frogs may have greater tendency and/or ability to disperse than juvenile frogs, resulting in spatial sorting among age classes, as has been observed in other anurans (Vimercati et al. 2021). In a streamside environment where spatial variation in refuge availability exists, if juvenile frogs tend to be restricted to natal sites with high refuge availability, then dispersing sub-adult frogs may by default be more likely to occupy sites with lower refuge availability. The lack of association between occupancy

probability and refuge availability for adult frogs may reflect a less strict association with streamside habitat, as adult frogs are known to also utilise forest habitat away from streams (Stephenson & Thomas 1945; Slaven 1992; MRC pers. obs.).

The models also indicated that air temperature was an important predictor of site occupancy for juvenile and adult frogs, but not for sub-adult frogs. Temperature was negatively associated with occupancy probability for both juvenile and adult frogs, with the relationship being particularly strong for adult frogs. In contrast to refuge availability, there was a partial correlation between air temperature and predator control history, with sites outside the KMA tending to be warmer than sites inside the KMA. Could these temperature differences contribute to variation in frog occupancy inside versus outside the KMA? There are several reasons why we consider this to be unlikely. Firstly, the ambient air temperature difference was quite small, with sites outside the KMA being on average only 1.8° C warmer than sites inside the KMA (°C: inside KMA mean = 7.4, SD = 1.9, range = 3.0 to 12.0; outside KMA mean = 9.2, SD = 1.4, range = 6.0 to 11.5). This small difference seems unlikely to explain consistent site selection by frogs on a large spatial scale. In addition, Crossland et al. (2005) found that juvenile and adult Hochstetter's frogs frequently occupy sites with much higher ambient air temperatures (up to 22.5°C). This suggests that sites outside the KMA (up to 12°C) are unlikely to be avoided on the basis of temperature. Ohmer et al. (2013) considered 15–17°C to be the optimal temperature for Hochstetter's frog, while modelling by Fouquet et al. (2010b) indicates that Hochstetter's frog populations across the North Island are associated with warmer rather than cooler sites. Based on these latter studies, if temperature was driving occupancy patterns in our study, we would predict the warmer sites outside the KMA to have a higher probability of occupancy than the cooler sites inside the KMA. Instead, we observed the opposite pattern.

Are there other factors that might account for differences in frog occupancy patterns inside versus outside the KMA? All sites were similar in terms of underlying geology, stream width and gradient, and surrounding vegetation structure. Importantly, none of our sites inside or outside the KMA showed evidence of sedimentation or high gravel content, a factor likely to reduce occupancy by Hochstetter's frog via a reduction in availability of refugia (Nájera-Hillman et al. 2009b). Increased levels of ultraviolet-b (UV-B) radiation can adversely affect amphibians that are directly exposed to UV-B (Adams et al. 2001). Although we did not measure levels of ambient UV-B at our sites, this is unlikely to be an issue because Hochstetter's frog eggs are typically laid in covered, cryptic locations (McLennan 1985; Beauchamp et al. 2010), and juvenile, sub-adult, and adult frogs spend daylight hours sheltered in retreat sites away from direct exposure to UV-B (authors' pers. obs.; Bell et al. 2004). We found no sick or diseased frogs inside or outside the KMA. At the time of our study, the disease of most concern was the pathogenic chytridiomycosis fungus which has been associated with global amphibian declines (Lips et al. 2006). However, field surveys have failed to detect this fungus in Hochstetter's frog (Bell et al. 2004; Moreno et al. 2011), and experimental studies show that Hochstetter's frog has low susceptibility to this fungus and clears infection quickly (Ohmer et al. 2013). All sites inside and outside the KMA were exposed to a 1080 operation in 1994. Thus, if there was any long-term effect of this operation on frog populations it would have occurred equally inside and outside the KMA. Shorter-term effects of predator control

operations using brodifacoum-based poison baits and cyanide pellets in the years immediately prior to our study can also be excluded because we found higher occupancy rates of frogs in areas with increased poison-based operations (i.e. inside the KMA). Consistent with this, Perfect & Bell (2005) found no short-term population effect of an aerial 1080 operation on another native Leiopelmid frog species (Archey's frog).

Based on the above arguments, we believe our results provide strong circumstantial evidence that spatial variation in the abundance of introduced mammalian predators (likely most importantly, ship rats) drives patterns of Hochstetter's frog occupancy in the Hūnua Ranges Regional Parkland, and that control of these predators to protect North Island kōkako therefore also benefits the co-occurring frog population. Depending on site conditions (i.e. availability of refugia, temperature), our estimates of occupancy inside the KMA versus outside the KMA were up to 8.5 times higher for juvenile frogs, 4.8 times higher for sub-adult frogs, and 1.9 times higher for adult frogs (Tables 2, 4, 6). This variation may reflect increased susceptibility to predation for earlier age-classes, or greater dispersal ability of adult frogs (e.g. a greater proportion of the adult frog population may be away from streamside habitat during stream surveys; adult frogs may have higher potential to disperse from sites inside the KMA to sites outside the KMA). However, we note that our occupancy estimates are associated with relatively large confidence intervals. In our study, we surveyed streams using 46–50 sites per location; increased sample size in future studies is likely to improve the precision of occupancy estimates. We also note that our sites outside the KMA still receive predator control, just at a lower frequency than sites inside the KMA (c. 3–4 years vs annually). Although predator control outside the KMA targets possums, some rats in this area will likely also be killed by the traps and poison baits. Future studies that compare sites where predator control is present versus completely absent may find greater effects of predator control for Hochstetter's frog populations.

Our study demonstrated the benefits of predator control for Hochstetter's frog inside the KMA in 2006. Is there any evidence these benefits have persisted? The KMA has been further expanded since our study and currently occupies approximately 2000 ha. Predator management inside the KMA has continued to the present day but intensified from seasonal control to year-round control in 2011. Brodifacoum baits were replaced with Pindone (also very effective at controlling rats; Innes et al. 1995) in bait stations from 2016 onwards. In addition, the entire Hūnua Ranges Regional Parkland was treated with aerial drops of 1080 in 2015 and 2018. Rat tracking indices conducted inside the KMA each November from 2007–2020 indicate that suppression of the rat population has continued. With the exception of one year, the November rat index inside the KMA during this period was 0–6% (Auckland Council data). The exceptional year was 2014 (a mast year) when the November rat index was 45% due to low take-up of baits in bait stations, but this declined to 8% later in the season. Based on the general rat index results for 2007–2020, we would predict that predator control inside the KMA is likely to be providing ongoing benefit for the Hochstetter's frog population. However, there have been no further site occupancy studies of Hochstetter's frog at our sites to test this prediction. Stream surveys conducted between 2008–2019 found the relative abundance of Hochstetter's frog to be consistently higher inside the KMA than outside the KMA (Longson 2015, 2020). These results suggest there may be ongoing protection for

the Hochstetter's frog population inside the KMA. Future population assessments that incorporate detection probability would verify these trends.

Understanding the cost-effectiveness of invasive species control programs is a global issue yet is often overlooked (Cullen et al. 2005; Busch & Cullen 2009; Byrom et al. 2016). Fairburn et al. (2004) assessed the cost-effectiveness of predator control to protect North Island kōkako by measuring the change in number of male-female kōkako pairs at a site over time relative to the dollar cost of predator control at that site. Another factor to consider when evaluating the cost-effectiveness of predator control is the additional (often unplanned) benefits for non-target native species (Byrom et al. 2016). Our data show that the predator control program designed solely to protect North Island kōkako in the Hūnua Ranges is more cost-effective than previously understood because the program also benefits the resident Hochstetter's frog population. Baber et al. (2009) reported the relative abundance of several non-target bird species—tūī (*Prosthemadera novaeseelandiae*), kererū (*Hemiphaga novaeseelandiae*), tomtits (*Petroica macrocephala*)—was higher inside the KMA than outside the KMA, suggesting these species may also benefit from the KMA predator control program. As with frog survey data, verification of these trends using a monitoring method that incorporates detection probability would strengthen this argument. More generally, we suspect that for many predator control programs, additional benefits to non-target native species may be more widespread than currently appreciated. We encourage assessing such benefits to improve our understanding of the cost-effectiveness and broader conservation benefits of these programs.

Assessing the effectiveness of predator control programs requires statistically robust population data (i.e. population assessments that incorporate spatial or temporal variation in detection probability). Unfortunately, such data are rare for assessing the effect of introduced mammalian predators on native New Zealand frog populations. Pledger (2011) and Germano et al. (2023) provide the first such data for Archey's frog, while Karst et al. (2023) provide data for Hamilton's frog. Here, we provide the first such data for Hochstetter's frog, and encourage future studies to adopt a similar approach.

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Additional Information and Declarations

Conflicts of interest: The authors declare no conflicts of interest.

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Ethics: This study was conducted as part of Department of Conservation research investigating methods to monitor native frog populations and did not involve handling of live animals.

Data availability: The data from this article are openly available at <https://doi.org/10.6084/m9.figshare.22357996.v1>. There is no code available because the program used to analyse the data (Program PRESENCE, <http://www.mbr-pwrc.usgs.gov/software.html>) does not require written code input.

Author contributions: All authors contributed to the design of the project; HK conducted the field research with logistical support from MRC and HS; DM analysed the data; all authors contributed to the writing of the manuscript.

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