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RESEARCH

A comparison of methods for estimating abundance of unmarked Hochstetter's frogs

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Abstract: The Hochstetter's frog (*Leiopelma hochstetteri*) is a nationally At Risk – Declining species, but management decisions for this species are limited by the lack of established monitoring protocols and analytical methods. We compared methods for inferring spatial and temporal patterns in abundance on Aotea (Great Barrier Island) using count data collected from fifteen 100 m stream transects in 2012, 2015 and 2021. Each transect was surveyed 2–3 times on the same day each year. Frogs were not marked, but individuals were identified in 2021 based on their body sizes and locations to facilitate the use of closed-population capture-mark-recapture (CMR) methods. We compared patterns in abundance estimates derived from Bayesian formulations of CMR (2021 only), N-mixture, Poisson regression of single counts, and occupancy models. Abundance estimates from CMR and N-mixture models were realistic and reasonably precise if detection probability (p) was assumed constant among transects. N-mixture estimates were 17% lower than CMR estimates but closely correlated with them. Relaxing the assumption of constant p among transects made little difference to CMR estimates but greatly reduced the precision of N-mixture estimates. Assuming constant p among transects, the N-mixture abundance estimates for the 15 transects were consistent among years. The 95% credible interval for the change in abundance from 2012–2021 ranged from a 24% decrease to a 10% increase. Mean first counts were 32% as high as N-mixture estimates, reflecting the estimated detection probability for first surveys. However, the spatial and temporal patterns inferred from single counts were consistent with those from N-mixture, and the change over time was estimated with only slightly lower precision. Estimated occupancy probabilities were correlated with N-mixture estimates but could not distinguish among transects with greater than 50 frogs and could not be used to infer changes over time.

Keywords: abundance, capture-mark-recapture, conservation, *Leiopelma hochstetteri*, monitoring, N-mixture, occupancy modelling

Introduction

Robust analytical methods for the estimation of population parameters are essential to inform threatened species management (Nichols & Williams 2006). Identifying the most appropriate methods for determining the status of populations is of utmost importance for amphibians, due to ongoing declines coupled with a high risk of extinction for approximately one-third of amphibian species worldwide (Green et al. 2020). There are a broad range of life history strategies within the Amphibia, necessitating the development of a plethora of population survey and monitoring methodologies. These methods may require the capture and identification of individuals or can use data collected from passive detection of species presence (Bower et al. 2014). They can be further categorised by the type of inference made about the population parameters (e.g.

abundance, survival, species distribution) being examined: index methods, site-based estimation, and individual-based estimation. Population indices and estimates differ in that index methods make no attempt to estimate detection probability; therefore, parameters like abundance are underestimated whenever the probability of detecting individuals is less than 1.0 (Williams et al. 2002). Parameter estimation techniques account for imperfect detection probability; therefore, they can estimate absolute parameter values that are robust to nuisance variables that affect detection (Royle & Dorazio 2008). Site-based estimation requires the detection of a species at replicated independent sites, whereas individual-based estimation generally requires the capture and recapture of multiple identifiable individuals (Royle & Dorazio 2008). Amphibian eggs, larvae, or adults are typically detected at sites by acoustic surveying, non-capture encounter, trapping, netting, search of

artificial retreats, or, more recently, by eDNA assay (Pearman et al. 1995; Rödel & Ernst 2004; Bower et al. 2014; Hobbs et al. 2019). Individual identification of amphibians usually requires capture for microchipping, visible implant elastomer (VIE) tagging, toe clipping, or photography of unique markings (Rödel & Ernst 2004; Schmidt & Schwarzkopf 2010; Bendik et al. 2013; Bower et al. 2014). However, the effectiveness of each technique is constrained by the life history of the study species.

The endemic amphibian fauna of Aotearoa New Zealand once comprised at least nine frog species in the genus *Leiopelma* (Easton et al. 2022). Remnant populations of the three remaining extant species are threatened by habitat destruction, invasive mammalian predators, and climate change (Burns et al. 2018). Hochstetter's frogs (*Leiopelma hochstetteri*; Fig. 1) are the most widespread extant species, with 11 evolutionarily significant units spread over the northern half of Te-Ika-a-Māui (The North Island). It is considered At Risk – Declining at a national level and Regionally Declining in the Tāmaki Makaurau / Auckland region (Burns et al. 2018; Melzer et al. 2022). Compared with Archey's frogs (*L. archeyi*) and Hamilton's frogs (*L. hamiltoni*), monitoring efforts for

Hochstetter's frogs have been relatively unstandardised and short-term (≤ 9 years, Table 1; Bell & Pledger 2023; Germano et al. 2023). Consequently, our relative lack of understanding of the population dynamics of Hochstetter's frogs precludes informed conservation management of this species at local or national scales.

Many standard detection and individual identification techniques for other amphibians are ineffective for Hochstetter's frogs because they are small-bodied, cryptically camouflaged, lack distinctive patterning or areas of transparent skin, and rarely vocalise (Bell 1978; Mellor et al. 2004). Most survey and monitoring programmes have followed the daytime stream transect search protocol of Bell (1996), although transect length and survey replication has varied substantially among studies (Table 1). Protocols for eDNA assay and scent-detection by trained dogs are currently in development (Smith & Feickert 2021; D. Bishop, pers. comm.). The most commonly reported population parameter from monitoring programmes for Hochstetter's frogs is a single-survey count index of relative abundance (Table 1). Open-population capture-mark-recapture (CMR) of toe-clipped frogs has been trialled, but ultimately failed due to insufficient recaptures (Slaven 1992; Whitaker
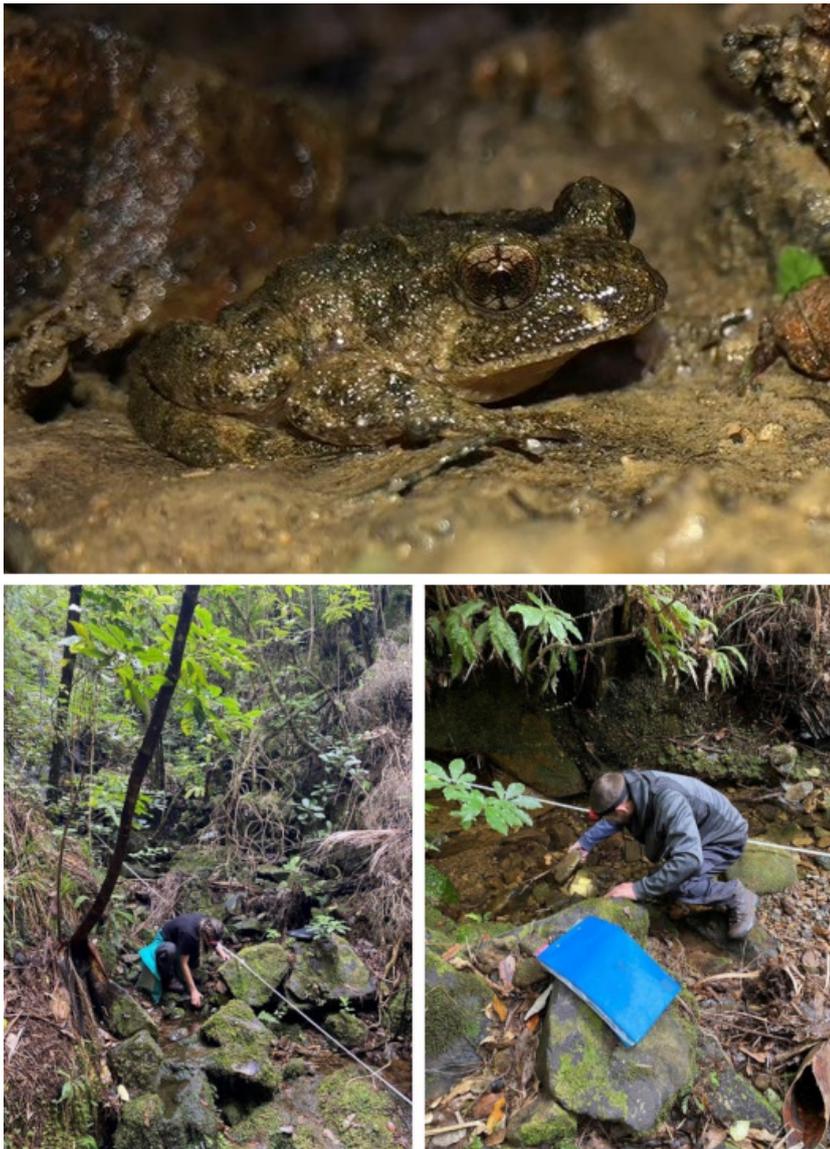

Figure 1. (Top) Adult Hochstetter's frog in Te Paparahi, Aotea, New Zealand. Photo: C. Johnson. (Bottom) Surveyors searching transects for Hochstetter's frogs in April 2021. The 100 m central transect line (white) can be seen. Photos: S. Dwyer.

Table 1. Summary of methods used to monitor or survey abundance or relative abundance of Hochstetter's frogs from surveys of stream transects.

Method	Applications	Advantages/Disadvantages
Closed-population capture-mark-recapture (CMR)	• Slaven (1992): 5 transects (150–200 m) near Golden Cross, Coromandel, surveyed 2–3 times. Duration: 2 years* • Moreno Puig (2009): 50 40 m transects in Waitakere Ranges, surveyed 4 times • This study: 15 100 m transects on Aotea surveyed 2–3 times in 2012, 2015, and 2021	• Can estimate absolute abundance and associated uncertainty • Can accommodate multiple forms of variation in detection probability (p) • Requires individual ID, e.g. from toe-clipping or size and location • Surveys should be done in rapid succession (e.g. hours or days) to meet closed population assumption
N-mixture	• Moreno Puig (2009): as for CMR but without individual ID; p estimated from spatial replicates • This study: as for CMR but without individual ID; p estimated from repeat surveys	• Can estimate absolute abundance and associated uncertainty without the need for individual ID • Do not need temporal replicates if spatial replicates obtained from sites assumed to have equal expected density • Highly sensitive to assumptions, with limited capacity to account for variation in p
Single counts	• Green & Tessier (1990): surveys throughout species' range • Whitaker & Alspach (1999): trends in counts near Golden Cross 1989–1998 • Baber et al. (2006): spatial distribution at Maungatauri • Nájera-Hillman et al. (2009): model habitat factors correlated with counts in Waitakere Ranges • Longson et al. (2017): trend in Maungatautari counts from 2009–2012 • Moreno Puig (2009): as above using first counts only • This study: as above using first counts only	• Lack of temporal replication minimises disturbance and potentially allows wider coverage • Cannot estimate absolute abundance • Can infer changes in relative abundance over time or space if reasonable to assume constant detection probability
Site occupancy	• Crossland et al. (2005): occupancy of 40 m transects in Hunua Ranges, 5–23 m transects in Brynderwyn Hills, and 2.5–18 m in Mahurangi Forest, 2003–2004. 3–8 repeat surveys. • Crossland et al. (2023): occupancy of 96 10 m transects in Hunua Ranges in relation to predator control • Moreno Puig (2009): occupancy of 40 m transects, overall abundance derived from detection probability • This study: occupancy of 10 m segments over 100 m transects, used to derive abundance	• Can reduce effort if stop searching at first detection • Loss of power compared to counts • Can infer distribution & relative abundance • Can potentially derive absolute abundance, depending on replication, scale of sampling and abundance-induced heterogeneity in detection probability

*This design was inappropriate for closed-population CMR due to the intervals between surveys allowing for recruitment, deaths, immigration and emigration.

& Alspach 1999). Whitaker and Alspach (1999) suggested that this was due to high migration rates of previously marked frogs at monitoring sites, or because small proportions of the population inhabiting each site were accessible for capture and marking during each survey. More recent efforts at population parameter estimation for this species have included occupancy estimation, N-mixture modelling, and closed-population CMR on unmarked frogs (Moreno Puig 2009; Crossland et al. 2005 2023). Advantages of not marking unless necessary for estimating individual-based parameters like survival include reduced stress to frogs, increased search efficiency due to less time spent handling animals, and less reliance on highly trained surveyors (Mellor et al. 2004; Schmidt & Schwarzkopf 2010).

Capture-Mark-Recapture are a suite of statistical methods in which recapture or re-sighting data from individually identifiable animals are used to estimate individual-based parameters such as abundance, survival, or recruitment. Estimates derived from CMR therefore can be robust to variation in individual detection probability among surveys, sites, and individual animals (Kellner & Swihart 2014). Capture-Mark-Recapture methods have been applied to long-term monitoring (> 18 years) data from toe-clipped and/or photographically identified Archey's and Hamilton's frogs (Bell & Pledger 2023; Germano et al. 2023). N-mixture methods estimate individual detection probability and population size without identifying individuals (Royle 2004; Kéry & Royle 2015; Ficetola et al. 2018). They achieve this by simultaneously estimating abundance and detection probability based on the likelihood of obtaining an observed sequence of repeated counts over space and/or time. However, N-mixture can be highly sensitive to untestable assumptions inherent in repeated count data (i.e. consistent detection probability among individuals and that no individual has been double-counted), making it less reliable than CMR (Link et al. 2018). Site occupancy modelling provides an alternative means of accounting for imperfect detection in repeated survey data. By treating sites rather than individuals as the unit upon which detection is replicated, presence-absence data can be used to estimate the probability of a species being detected at sites where it is present (MacKenzie et al. 2006). This enables estimation of the number of sites occupied by a species, which can be a useful indicator of species abundance (MacKenzie et al. 2006). In contrast with CMR, N-mixture, and occupancy methods, single-survey counts provide an index of abundance without accounting for detection probability (Williams et al. 2002). The advantages of single-survey count indices are that repeated surveys are not required, thus reducing sampling effort and habitat disturbance. However, count indices often underestimate abundance and robust inference from them relies on the assumption of constant detection probability (Williams et al. 2002).

In this study, we performed CMR, N-mixture, Poisson regression of single-survey counts, and occupancy modelling on data collected from a monitoring programme for Hochstetter's frogs on Aotea / Great Barrier Island between 2012 and 2021. Our primary objective was to investigate whether detection abundance could be estimated from limited multi-observer data collected from stream-transect surveys of unmarked frogs. Our secondary objective was to develop an analysis protocol for understanding temporal change in an island metapopulation of this species that co-exists with invasive mammalian predators.

Methods

Study site

Surveys of Hochstetter's frogs were conducted in five river catchments in the Te Paparahi region of Aotea (catchments 'A–E', Fig. 2). Te Paparahi is densely forested, with large areas of coastal broadleaf forests near the eastern slopes and kānuka (*Kunzea robusta*) forest in patches of secondary regrowth following fires in the 1930s (Esler & Astridge 1974; Perry et al. 2010). Aotea is free of mustelids (*Mustela erminea, M. nivalis, M. furo*), possums (*Trichosurus vulpecula*), Norway rats (*Rattus norvegicus*), goats (*Capra hircus*), and deer (*Dama* spp., *Cervus* spp., *Odocoileus* spp.), but has ship rats (*Rattus rattus*), kiore (*Rattus exulans*), mice (*Mus musculus*), feral pigs (*Sus scrofa*), and feral cats (*Felis catus*) (Great Barrier Local Board 2017). At the time of survey, there were no pest control operations within Te Paparahi.

Fifteen 100 m stream transects were selected within the headwaters of the five catchments and at various altitudes (143–467 m a.s.l.) (Herbert et al. 2014; Fig. 2). Transect locations were based on accessibility to maximise the number of sites that could be surveyed in this rugged and densely forested terrain. Transects were marked with flagging tape and global positioning system coordinates were recorded to enable the same locations to be surveyed over multiple years.

Field methods

Surveys were conducted by 2–5 people over 10–12 days in April–May 2012, 2015, and 2021. There was a deliberate interval of at least three years between sampling occasions to avoid excessive disturbance. Each transect was surveyed twice (2012, 2015) or thrice (2021) on the same day. However, we excluded data from the first transect surveyed in 2012 (A1) as this survey was used to train field staff.

Surveying followed the daytime search protocol specified by Bell (1996), which involved walking in an upstream direction searching under rocks and refugia (Fig. 1). The replicate surveys for each transect were conducted simultaneously by two or three observers. That is, the surveyors divided the transect into two (50 m) or three (33–34 m) sections, searched one section each, and then switched sections until each person had searched the whole transect. The time to complete a transect was c. 4 hours but depended on the number of refugia, i.e. transects with more rocks took longer to search. The independence of repeated surveys was maintained by observers not discussing results until all surveys of a transect were completed. Surveys were not conducted during heavy rain or in drought or flood conditions.

Upon encountering a frog, the observer recorded the distance along the transect (0–100 m) and measured the approximate snout-to-vent length (SVL, mm) by holding a ruler over the frog. In 2021, the perpendicular distance of the frog to the right (+) or left (−) of the central transect line (Fig. 1) was also recorded to give the position of each sighting. This allowed frogs found in surveys 2–3 to be tentatively divided into new captures and recaptures (the terms 'captures' and 'recaptures' were used to conform to standard CMR terminology despite frogs not being handled). We considered a frog to be a recapture if located within 20 cm of a previous record and if the SVL matched within ± 5 mm. This assumption is reasonable given Hochstetter's frogs are sedentary during daylight (Tessier et al. 1991), and all replicate surveys were completed within a few hours.
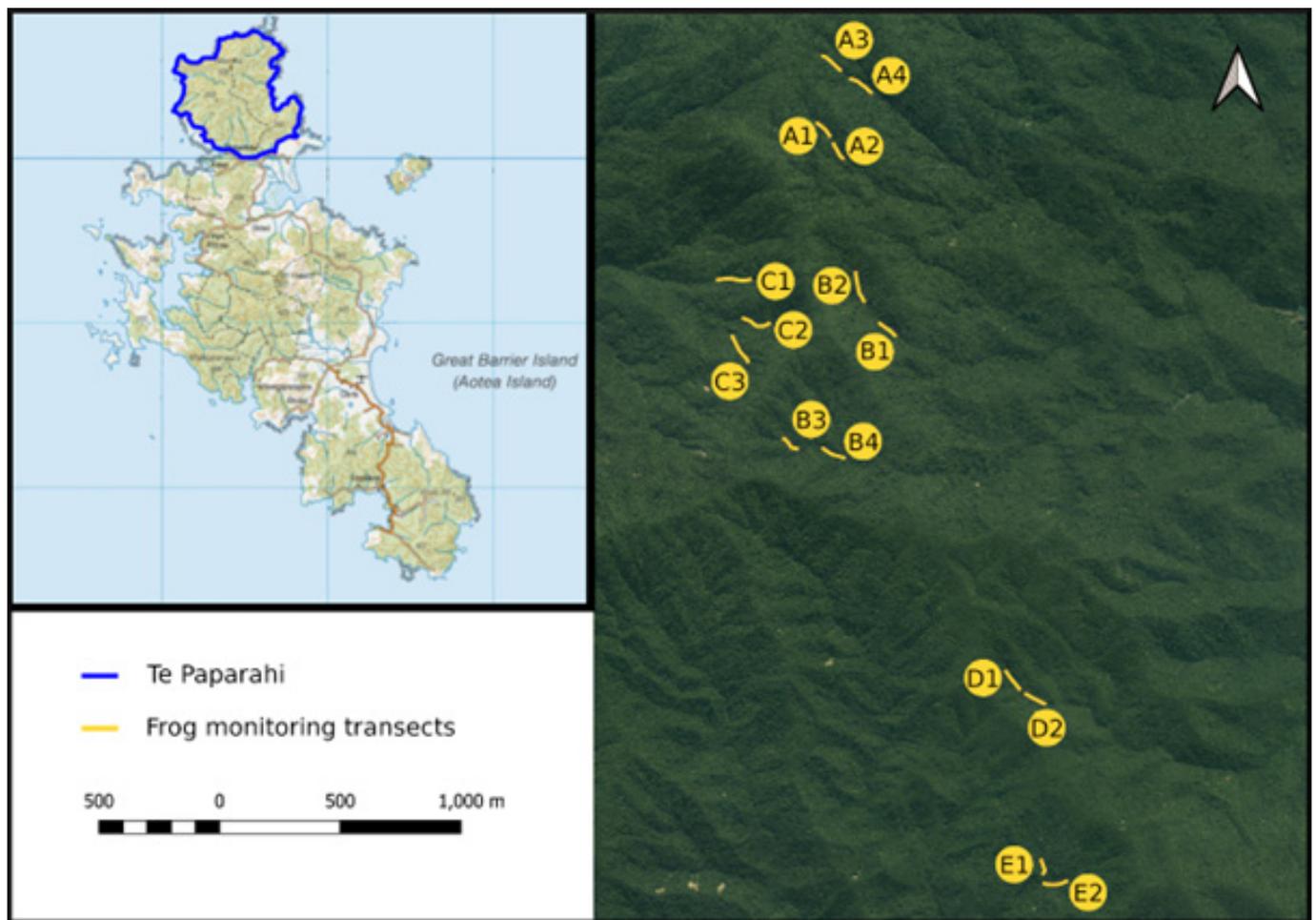
Figure 2. The fifteen 100 m stream transects (shown in yellow) where Hochstetter's frogs were surveyed in the Te Paparahi region (shown in blue on the Topo 250 Map insert) at the north of Aotea (Great Barrier Island), New Zealand. The aerial photography used in the map of transects are from the Auckland 0.5 m Rural Aerial Photos series taken in 2010–2012 (https://data.linz.govt.nz/layer/51769-auckland-05m-rural-aerial-photos-2010-2012/).

Analytical methods

The raw data consisted of one row for each frog found, with columns showing the year, transect, survey (1, 2, or 3), observer, SVL, distance along the transect and perpendicular distance. We used R scripts (R Core Team 2021) to convert these observations into four matrices for analysis (see Appendix S1 in Supplementary Material). To facilitate CMR modelling, we generated two matrices showing the numbers of captures and recaptures for each survey of each transect with 2021 data. To perform N-mixture modelling, we generated a matrix showing the total number of frogs found in each survey of each transect each year. The first column of this matrix (first surveys) was also used for the modelling of single counts. For site occupancy modelling, we divided each transect into ten 10 m segments and generated a matrix showing whether one or more frogs were detected in each segment for each survey. The 10 m scale matched that used in Crossland et al.'s (2023) occupancy data and allowed segment occupancy probability to be estimated separately for each transect as a possible surrogate for abundance.

We fitted the data to purpose-built models coded using the Bayesian updating software OpenBUGS 3.2.3 (Spiegelhalter et al. 2014). The flexibility of this modelling approach allowed us to construct models suitable for the sampling design and for the different types of models to be constructed in a uniform framework, facilitating direct comparison of results. We used uninformative priors for all parameters except where specified. All code and data are available in OpenBUGS format in Appendix S2. To allow direct comparison to this code, we summarise the structures here using OpenBUGS pseudocode rather than traditional mathematical notation. Consequently, the parameters shown in the normal distributions below are means and precisions ($1/SD^2$) rather than means and standard deviations.

We fitted each model using three Markov Chain Monte Carlo (MCMC) chains to check convergence, discarding a burn-in of at least 1000 samples. In all cases the R-hat convergence diagnostic (Brooks & Gelman 1998) was < 1.01 for the samples used. We performed posterior predictive checks (Gelman et al. 2004) to ensure that all models had reasonable fit to the data (Appendix S3).

Closed-population CMR

The CMR model for the 2021 data was adapted from code used by Hotham et al. (2023) to estimate the abundance of Archey's frogs. The capture probability (*c*) and recapture probability

(p) for survey j of any transect were given by:

$$logit(c[j]) <- a.p + re.j.p[j] \qquad (1)$$
$$logit(p[j]) <- logit(c[j]) + b.B \qquad (2)$$

where $a.p$ is the intercept, $b.B$ is the behaviour effect (change in detection probability after initial detection), and $re.j.p[j]$ is a random effect allowing for variation among the three surveys due to disturbance. The prior for the standard deviation of these random effects ($s.j.p$) was constrained from 0–1, which was mildly informative (Banner et al. 2020) as necessitated by having just 2–3 surveys. We assumed that detection probability was similar among transects but tested the sensitivity of the results to this assumption. The model is therefore similar to Otis et al.'s (1978) M_{tb}, except that time and behavioural effects apply across multiple sites and the time effect is random rather than fixed.

The numbers of captures (u) and recaptures (m) in survey j of transect i were taken to be binomial samples from the "marked" frogs (M) and "unmarked" frogs (U) present, as shown by the code:

$$u[i,j] \sim dbin(c[j], U[i,j]) \qquad (3)$$
$$m[i,j] \sim dbin(p[j], M[i,j]) \qquad (4)$$
$$U[i,j+1] <- U([i,j]) - u[i,j] \qquad (5)$$
$$M[i,j+1] <- M[i,j] + u[i,j] \qquad (6)$$

The initial number of unmarked frogs ($U[i,1]$) is the abundance ($N[i]$), hence the abundances are estimated through this sampling process as well as the detection parameters described above.

The abundance on each transect was taken to be a Poisson sample from an expected number ($mu[i]$) with a log-normally distributed prior, as shown by the code:

$$a.N[i] \sim dnorm(0, 0.1) \qquad (7)$$
$$log(mu[i]) <- a.N[i] \qquad (8)$$
$$N[i] \sim dpois(mu[i]) \qquad (9)$$

This prior was also mildly informative, specifying that we believed there was a 95% prior probability that there were fewer than 500 frogs on a transect (97.5% credible limit for $N[i]$ = 490). This number needed to be large enough to ensure abundance was not underestimated due to model-imposed constraints, but kept within a plausible range to allow all the models to converge.

N-mixture
In N-mixture models there is no distinction between captures and recaptures. We therefore simplified the CMR model by replacing Equations 1–2 with:

$$logit(p[j]) <- a.p + re.j.p[j] \qquad (10)$$

where $p[j]$ refers to survey-specific individual detection probability regardless of previous detection, and Equations 3–4 with:

$$n[i,j] \sim dbin(p[j], N[i]) \qquad (11)$$

where $n[i,j]$ is the number of frogs detected during survey j of transect i. The N-mixture model fitted to the 2021 data was otherwise identical to the CMR model.

We fitted two types of N-mixture models to multi-year

data. We first obtained unconstrained estimates of abundance for each transect each year using a model identical to that used for the 2021 data but with the additional assumption that detection probability was constant among years. We then fitted a log-linear time-trend model to estimate the change in abundance from 2012–2021. Under this model the priors for the expected number of frogs on each transect each year (Equations 7–8) were replaced with:

$$a.N \sim dnorm(0,1) \qquad (12)$$
$$s.trans.N \sim dunif(0,5) \qquad (13)$$
$$log(mu[i]) <- a.N + b.year*(year[i] - 2012) \qquad (14)$$
$$+ re.trans.N[transect[i]]$$

where $a.N$ is the intercept (average abundance in 2012), $b.year$ is the intrinsic rate of increase, and $re.trans.n[transect[i]]$ is a random transect effect drawn from a normal distribution with mean 0 and standard deviation $s.trans.N$. In combination, the priors for $a.N$ and $s.trans.N$ also limit the number of frogs on a transect to less than c. 500, similar to the unconstrained model. The form of the two models allowed us to directly compare the time-trend model to the model fitted to single counts while checking that it adequately captured temporal and spatial patterns in abundance.

Single-survey counts
Single-survey count data from one year could not be modelled due to lack of replication, but the multi-year data could be fitted to a time-trend model using Poisson regression. To do this, we simplified the time-trend N-mixture model by removing the detection component (Equation 10) and replacing Equation 11 with:

$$n[i,1] \sim dpois(mu[i]) \qquad (15)$$

where $n[i,1]$ is the number of frogs detected in the first survey and $mu[i]$ is the expected count rather than the expected abundance.

Site occupancy
In our site occupancy models, the detection component was the same as for N-mixture models (Equation 10), but $p[j]$ is the probability of the species being detected in a 10 m segment if present rather than the probability of an individual frog being detected. Whether or not a segment was occupied was considered to be a Bernoulli sample based on occupancy probability for the transect it belongs to. Whether or not frogs were detected in a survey depended on the segment's occupancy status and the detection probability. This is represented by the following code, where the subscript i refers to a segment rather than a transect:

$$present[i] \sim dbern(p.present[transect[i]]) \qquad (16)$$
$$p.detect[i,j] <- present[i]*p[j] \qquad (17)$$
$$detected[i,j] \sim dbern(p.detect[i,j]) \qquad (18)$$

where $present[i]$ is the occupancy status of the segment, $p.present[transect[i]])$ is the occupancy probability for the transect containing that segment, and $detected[i,j]$ indicates whether frogs were detected in the segment during survey j.

The prior distribution for each transect's occupancy probability was derived from its prior distribution for abundance. Assuming individuals are Poisson distributed within their habitats, the probability of a species occurring in

a sample area is 1-exp(-*D*), where *D* is the expected number (Caughley 1977). The probability of a 10 m segment being occupied is therefore:

$$p.present[i] <- 1-exp(-N[i_i]/10) \qquad (19)$$

where *N[i]* is the number of frogs on a 100 m transect divided by 10 to get the expected number of frogs in a 10 m segment. This form of prior not only maximised consistency with the CMR and N-mixture models but also allowed the abundance of frogs on each transect to be automatically derived from its occupancy probability.

We fitted site occupancy models where the priors for abundance matched either those from the unconstrained N-mixture model (Equations 7–8) or the time-trend N-mixture model (Equations 12–14). The first of these models allowed us to assess the correlation between estimated occupancy probabilities and abundance, and the second allowed us to assess whether it was possible to estimate the change in abundance over time from occupancy data alone.

Results

A total of 1068 Hochstetter's frog observations were recorded on the Te Paparahi transects during the surveys in 2012, 2015, and 2021 (Table 2). Approximately 17% of observations were of juvenile frogs (SVL < 18 mm; Whitaker & Alspach 1999). In 2012, 155 individual frogs were recorded during the first survey (mean 11.1, range 0–38, data from transect A1 excluded). In 2015 and 2021, 190 (mean 12.7, range 0–54) and 172 individual frogs (mean 11.5, range 0–30), respectively, were recorded during the first survey. The highest number of observations each year were consistently made in catchment A and the lowest in catchments D and E (Table 2, Fig. 2).

CMR abundance estimates generated from the 2021 data ranged from 0 to 118 frogs per transect, whereas the corresponding N-mixture abundance estimates were 17% lower, ranging from 0 to 98 frogs per transect (Fig. 3; Appendix S4). However, the abundance estimates generated by CMR

and N-mixture models were strongly correlated (Spearman's $\rho = 0.989$; Fig. 3). The CMR models indicated a behavioural effect of observation on individual frogs. That is, the probability of re-sighting an individual (the recapture probability, *p*) during a given survey was lower than the probability of observing a new individual (the capture probability *c*; Table 3). Under the N-mixture model, which makes no distinction between captures and recaptures, the detection probability *p* was interpreted as declining after the first survey (Table 3). Per-transect abundances estimated by CMR models were more precise than those generated by N-mixture models, with N-mixture estimates having Coefficients of Variation (CVs) c. 30% higher (Fig. 3, Table 4). This difference became much more pronounced when we relaxed the assumption of equal detection probability among transects, i.e. relaxing this assumption made little difference to the precision around CMR abundance estimates but greatly reduced the precision of N-mixture abundance estimates (Appendix S5).

Assuming constant detection probability among transects, abundance estimates from the unconstrained N-mixture model were very consistent among years (Fig. 4a). Estimates from the time-trend N-mixture model were closely correlated with the unconstrained model estimates ($\rho = 0.992$; Fig. 5), meaning the random transect effect in the time-trend model (Equation 14) fitted the observed variation among transects well. Under the time-trend model, the 95% credible interval (CRI) for the intrinsic rate of increase (*b.year*) ranged from −0.03 to 0.01, meaning there was no evidence of change. This corresponds to a proportional annual changes in abundance ($\hat{\lambda} = e^{b.year}$) ranging from 0.97 to 1.01, and a proportional change in abundance from 2012–2021 ($\hat{\lambda}^9$) ranging from 0.76 to 1.10.

Patterns in relative abundance inferred from single counts were strongly correlated with those estimated by N-mixture (cf. unconstrained model: Spearman's $\rho = 0.909$; cf. time-trend model: $\rho = 0.933$; Fig. 4). The estimated median counts from Poisson regression were 32% of the size of corresponding estimates from the time-trend N-mixture model, reflecting the estimated detection probability for first surveys (Table 3), and were more precise than the N-mixture estimates based on their CVs (Table 4). The estimated change in relative abundance

Table 2. Number of individual Hochstetter's frogs observed in each 100 m stream transect during each survey in Te Paparahi, Aotea, New Zealand.

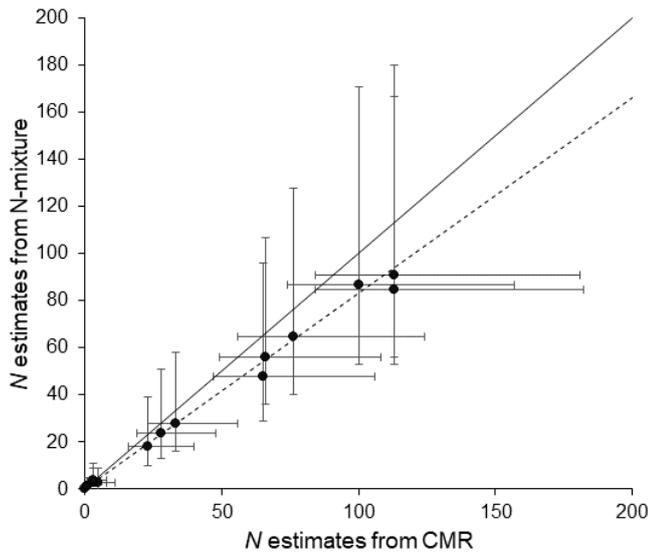| Transect | 2012 | | 2015 | | 2021 | | |
	Survey 1	Survey 2	Survey 1	Survey 2	Survey 1	Survey 2	Survey 3
A1	NA	NA	20	30	29	20	25
A2	29	28	35	33	28	23	27
A3	38	25	54	45	30	26	16
A4	17	8	11	12	10	12	19
B1	20	16	10	16	8	6	7
B2	10	6	12	13	28	4	12
B3	7	5	2	4	0	1	0
B4	0	0	2	2	1	1	1
C1	12	9	26	9	3	6	7
C2	14	5	11	10	24	14	17
C3	3	1	0	0	9	6	9
D1	3	2	3	3	0	2	1
D2	0	0	0	0	0	0	0
E1	1	1	1	1	1	0	0
E2	1	0	3	2	1	1	2

Figure 3. Relationship between abundance (N) estimates from closed-population capture-mark-recapture (CMR) and N-mixture models fitted to count data for Hochstetter's frogs in fifteen 100 m transects on Aotea in 2021. The dotted line shows the fitted relationship indicating that N-mixture estimates were 17% lower than CMR estimates. The solid diagonal line shows a 1:1 relationship. Error bars show 95% credible intervals. See Appendix S4 for data.

Table 3. Mean, median, standard deviation (SD), and 95% credible intervals (2.5% and 97.5%) for detection parameters under closed-population capture-mark-recapture (CMR) and N-mixture models fitted to counts of Hochstetter's frogs conducted on fifteen 100 m transects on Aotea in 2021. In CMR there is a distinction between capture probability (probability of a previously undetected frog being seen) and recapture probability (probability of a previously detected frog being seen), whereas there is no such distinction in N-mixture. See Equations 1, 2, and 10 for explanation of how the capture and recapture probabilities were derived from parameters *a.p, b.B*, and *s.j.p*.

Model	Parameter	Meaning	Mean	SD	2.5%	Median	97.5%
	a.p	intercept	−1.00	0.40	−1.83	−0.99	−0.23
	b.B	behaviour effect	−0.89	0.41	−1.66	−0.94	−0.05
	s.j.p	SD in logit(p) among 3 surveys	0.33	0.23	0.04	0.27	0.90
CMR	*c[1]*	capture probability 1st survey	0.26	0.05	0.16	0.27	0.36
	c[2]	capture probability 2nd survey	0.23	0.05	0.12	0.23	0.35
	c[3]	capture probability 3rd survey	0.29	0.08	0.14	0.28	0.46
	p[2]	recapture probability 2nd survey	0.10	0.01	0.07	0.10	0.14
	p[3]	recapture probability 3rd survey	0.13	0.01	0.10	0.13	0.17
	a.p	intercept	−0.91	0.44	−1.78	−0.91	−0.04
	s.j.p	SD in logit(p) among 3 surveys	0.40	0.22	0.08	0.34	0.92
N-mixture	*p[1]*	capture probability 1st survey	0.32	0.08	0.17	0.32	0.51
	p[2]	capture probability 2nd survey	0.24	0.06	0.12	0.24	0.38
	p[3]	capture probability 3rd survey	0.27	0.07	0.14	0.27	0.43

from 2012–2021 was similar to that derived from N-mixture but slightly less precise (95% CRI: 0.77–1.17).

The estimated probability of a 10 m segment being occupied ranged from 0 to 1 among transects (Fig. 6a), with consistent variation among transects in 2012, 2015, and 2021 (Appendix S4). These occupancy estimates were strongly correlated with N-mixture estimates (ρ = 0.966 for unconstrained N-mixture, ρ = 0.923 for time-trend N-mixture) but had poor precision (Appendix S4). Furthermore, occupancy estimates were near one for transects estimated to contain > 60 frogs (e.g. Fig. 6a). Abundance estimates derived from the unconstrained occupancy model were strongly correlated with unconstrained N-mixture estimates (ρ = 0.966). However, occupancy-derived estimated abundances were around half the size of N-mixture estimates at the low end of the scale (e.g. Fig. 6b). At the high end of the scale, abundances were inestimable due to occupancy rates near 100% placing no

upper constraint on abundance. Changes in abundance over time could not be estimated using the time-trend occupancy model, i.e. the posterior distribution for *b.year* matched the uninformative prior specified rather than being updated based on the data.

Discussion

We trialled closed-population CMR and N-mixture modelling on single-year count data of Hochstetter's frogs collected in 2021 from a survey of 15 stream transects in Te Paparahi, Aotea. These models produced strongly positively correlated abundance estimates with reasonable precision. However, per-transect abundance estimates derived by N-mixture were lower than those from CMR. Because data from previous surveys of the same transects in 2012 and 2015 were insufficient for
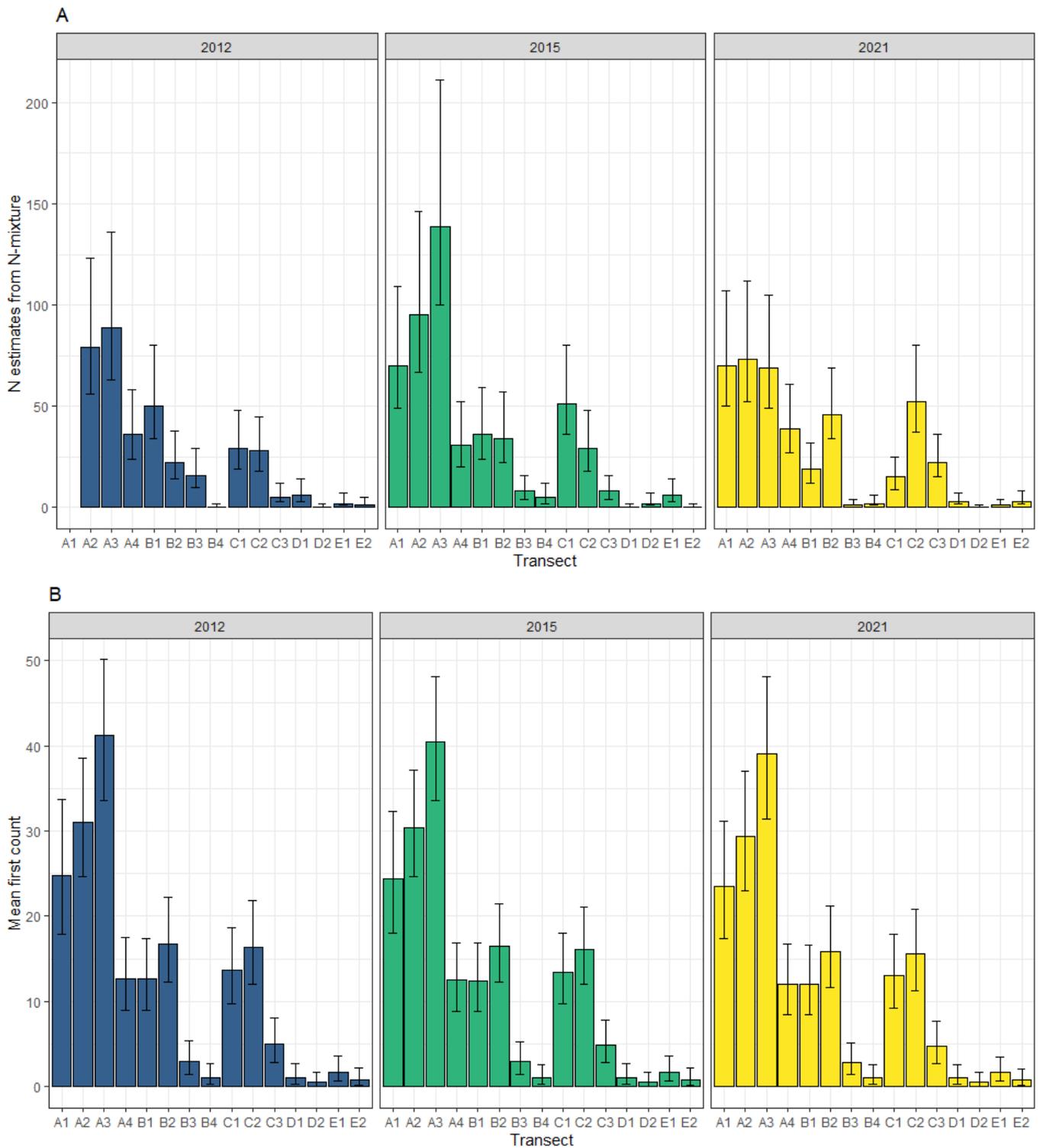
Figure 4. (a) Estimates of Hochstetter's frog abundance for each 100 m transect on Aotea in 2012, 2015, and 2021 generated using an unconstrained N-mixture model. (b) Mean first counts of Hochstetter's frogs for each transect in 2012, 2015, and 2021 generated using a log-linear model with year as a fixed effect and transect as a random effect. In both graphs, the error bars represent 95% credible intervals. See Appendix S4 for data.

Table 4. Comparison of Coefficient of Variation (CV) for estimates of abundance from CMR and N-mixture models fitted to 2021 data, and for estimates from time-trend single-count and N-mixture fitted to data for all years. CVs are calculated as SD / mean from data available in Appendix S2 Values are excluded for transects with means < 10 because C.V.s are not comparable when means are small (Reed et al. 2002).

Transect	2021 data		Time-trend models*	
	CMR	**N-mixture**	**Single counts**	**N-mixture**
A1	0.22	0.33	0.15	0.21
A2	0.21	0.33	0.12	0.21
A3	0.21	0.33	0.11	0.23
A4	0.22	0.34	0.17	0.21
B1	0.25	0.38	0.17	0.28
B2	0.22	0.31	0.15	0.17
B3	-	-	-	-
B4	-	-	-	-
C1	0.27	0.38	0.17	0.29
C2	0.22	0.34	0.16	0.19
C3	0.25	0.37	-	0.21
D1	-	-	-	-
D2	-	-	-	-
E1	-	-	-	-
E2	-	-	-	-

*These models generate separate values for each year, but only the 2021 values are shown here for simplicity.
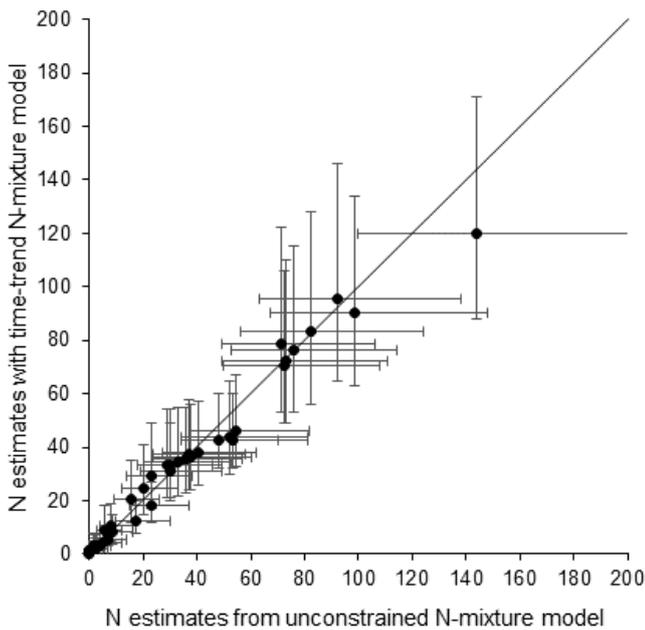
Figure 5. Comparison between abundance (*N*) estimates from the time-trend N-mixture model (incorporating log-linear function with year as a fixed effect and transect as a random effect) with estimates using the unconstrained N-mixture model. The diagonal line shows a 1:1 relationship. Error bars show 95% credible intervals.

constructing CMR models, we compared the performance of N-mixture models with occupancy modelling and Poisson regression of single-survey counts on the 2012–2021 data. Single-survey counts and N-mixture abundance estimates among transects and years were strongly positively correlated. Occupancy and abundance estimates derived from occupancy modelling of 10 m segments of transects were also closely corelated with N-mixture abundance estimates. However, occupancy estimates were relatively imprecise and could not distinguish among transects with greater than 60 frogs. Occupancy-derived abundance estimates were much lower than N-mixture estimates at the low end of the scale and extremely imprecise at the high end of the scale. It therefore appears that closed-population CMR and N-mixture methods were capable of estimating abundance from our multi-observer data and may be promising techniques for understanding temporal change in the Te Paparahi Hochstetter's frog metapopulation. We further discuss the appropriateness and limitations of each method below.

The actual numbers of frogs occupying transects are unknown, so it is uncertain whether the N-mixture or CMR model estimated abundances more accurately. N-mixture estimates were 17% lower than the corresponding CMR estimates, reflecting different interpretations of the data under the two models. A critical advantage of CMR over N-mixture is the capacity to distinguish detection probabilities based on whether individuals have been previously detected, i.e. capture *vs* recapture probabilities (Joseph et al. 2009). The detection process often has behavioural effects that lower subsequent detection probability (Fegatelli & Tardella 2013). This was the case in a CMR study of Archey's frogs where individuals were caught, photographed, and measured on first detection (Hotham et al. 2023). It is thus plausible that the disturbance to Hochsetter's frogs from lifting rocks and holding rulers over caused the estimated negative effect of prior capture on recapture in our study (Table 3). In N-mixture models, the decline in the number of frogs detected in successive
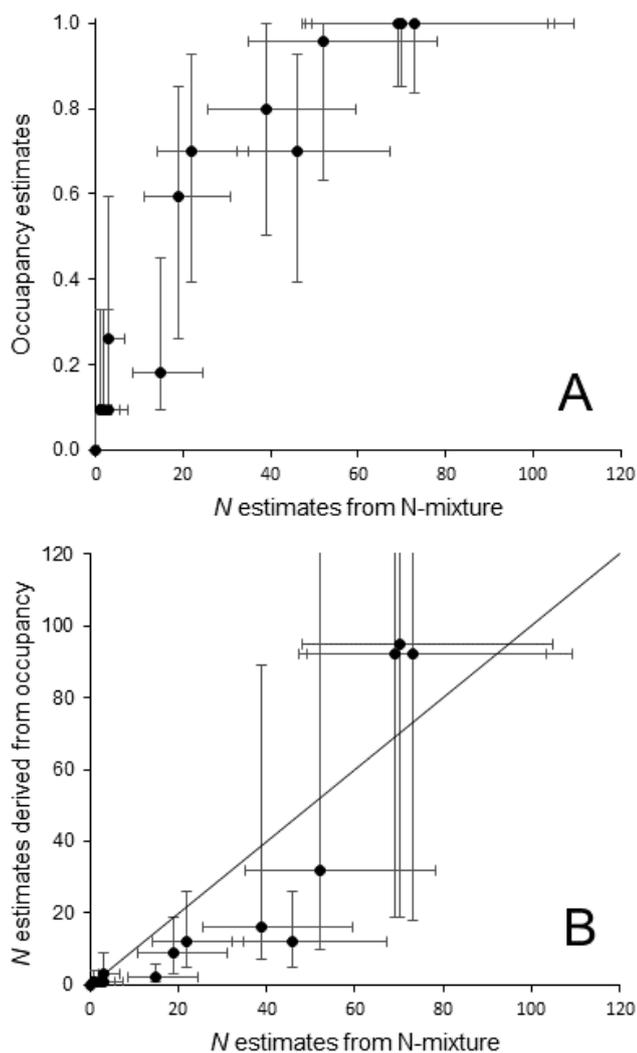
Figure 6. Comparison between (a) occupancy estimates from an unconstrained model for each 100-m transect (probability that a 10-m segment occupied) and (b) abundance estimates derived from those occupancy estimates, against median abundance estimates derived from an unconstrained N-mixture model. The estimates shown are for 2021 but similar patterns occurred in other years. The diagonal line shows a 1:1 relationship. Error bars show 95% credible intervals (note that these intervals extend to > 1800 where no upper limits are shown). See Appendix S4 for data.

surveys is interpreted as a reduced detection probability for all frogs, regardless of their capture history. It seems more plausible that behavioural effects apply to frogs whose cover was lifted, suggesting that abundance was underestimated using N-mixture. However, our CMR method required the identification of recaptures based on size and location, and incorrect classification could also have biased estimates. For example, while most frogs showed no obvious sign of disturbance, 6% of detections resulted in frogs jumping under adjacent rocks or into water pools. This could have made them harder to detect in subsequent surveys, consistent with the behavioural effect identified by the CMR model, but could also have resulted in them moving greater than 20 cm and being misidentified as new individuals, resulting in abundance being overestimated.

The other key consideration when comparing CMR and N-mixture is the precision around the abundance estimates. As expected, N-mixture estimates were slightly less precise than CMR estimates when we assumed detection probability was equal among transects, but this difference became much more pronounced when we relaxed this assumption. This finding is consistent with Link et al.'s (2018) simulations showing that N-mixture is less robust to the violation of assumptions than CMR.

We could not estimate temporal change in abundance with CMR because the positional data used to identify recaptures were only collected in 2021, but we could do so using the time-trend versions of the single-count and N-mixture models. Such inference was impossible from the time-trend occupancy model. The λ parameter estimated in the single-count and N-mixture models did not show a clear trend from 2012–2021. However, based on the 95% credible intervals it is possible that the Te Paparahi population may be gradually declining, akin to Hochstetter's frog populations on the mainland which are suspected to be to be declining due to predation (by rodents, pigs, and cats) and/or habitat degradation (Bishop et al. 2013; Burns et al. 2018). Apparent increases in Hochstetter's frog densities following the exclusion and control of most mammalian predators (Longson et al. 2017; Crossland et al. 2023) suggest they negatively affects Hochstetter's frogs in Te Paparahi where there has been no predator management. The uncertainty in λ illustrates the difficulty in detecting population trends, especially given that populations fluctuate rather than changing exponentially, meaning data may need to span several decades to capture the dynamics (Lester et al. 2017).

The ideal monitoring method for other populations of Hochstetter's frogs will ultimately depend on the objectives and scale of the programme as well as the assumptions people are prepared to make (Table 1). CMR provides the strongest inferences about abundance, but the accuracy of CMR estimates depends on the accuracy of individual identification, which is problematic for Hochstetter's frogs unless toe-clipping is used. N-mixture is a reasonable alternative but requires stronger assumptions about detection probability, including the assumption that the initial detection of frogs does not affect their subsequent detection probability. Royle's (2004) N-mixture model invokes the additional assumption that spatial replicates are random samples from an area with uniform density, meaning detection probability can be estimated from spatial replicates alone. Moreno Puig (2009) found that Royle's (2004) model greatly overestimated abundance, as was expected given there was high variation in counts among transects that were inconsistent with the assumption of uniform density. We avoided this problem by using N-mixture models that estimated detection probability based on repeat counts of the same transects.

Single counts are useful if it is most important to reduce disturbance or survey effort. Reducing survey effort per transect may increase the number of transects surveyed, increasing the scale of surveying possible (Green & Tessier 1990) and potentially increase the power to determine factors affecting relative abundance (Nájera-Hillman et al. 2009). We found that single counts repeated over multiple years were strongly correlated with N-mixture abundance estimates and were only slightly less precise. However, this finding is contingent on the assumption that detection probability is constant among transects and years, and the inability to relax such assumptions is the key limitation of single counts (Williams et al. 2002).

If occupancy modelling is used, this method will need

to be tailored to the system being monitored and the number of surveys. For monitoring fifteen 100 m transects, it was not sensible to record occupancy at the transect level, so we instead recorded occupancy in 10 m segments and estimated the probability of a segment being occupied over each transect. In contrast, Moreno Puig (2009) monitored fifty 4 m transects, so recorded occupancy of transects and estimated occupancy probability over the whole landscape. As each transect was surveyed four times (Moreno Puig 2009) the model developed by Royle and Nichols (2003) could be used to estimate abundances based on detection probabilities inferred from replicate surveys. Like our occupancy analysis, Moreno Puig (2009) found that site occupancy gave a rough indication of relative abundance, but substantially underestimated absolute abundance.

It would not make sense to undertake counts and then reduce them to binary occupancy data, as this entails throwing away data and therefore statistical power. If using standard search methods for Hochstetter's frogs, it would only make sense to use an occupancy approach if transects are short or if substantial survey effort can be saved by stopping each survey when the first frog is detected. Using the latter method, the time taken to find the first frog can potentially be used to model abundances (Halstead et al. 2021). Although occupancy modelling was not the best methodology for our search methods, it would be highly applicable to broader-scale eDNA surveying (Willoughby et al. 2016; Buxton et al. 2021; Smith & Feickert 2021).

Coordinating a national monitoring strategy for Hochstetter's frogs will require balancing the need for consistency against the need for methods that meet objectives and constraints at a local level. It is important to ensure that surveys for Hochstetter's frogs are conducted when frogs are likely to be detectable and sedentary, meaning surveys should be conducted during daylight and not in rainy weather, nor during drought or flood conditions (Slaven 1992; Bell 1996; Whitaker & Alspach 1999). However, it is likely that the number of surveys and lengths of transects will continue to vary, and some surveyors may choose to stop when the first frog is detected (providing occupancy data) rather than completing counts. As illustrated in our study, the flexibility of MCMC fitting using Bayesian updating software such as OpenBUGS (Spiegelhalter et al. 2014), JAGS (Plummer 2017) or NIMBLE (de Valpine et al. 2017) allows multiple data types to be modelled in a uniform structure. It is also possible to integrate multiple data types within a single model, and such integration would be invaluable for a wider comparative analysis of data from Hochstetter's frog monitoring programmes.

Acknowledgements

Additional Information and Declarations

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Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

Appendix S1. Count and occupancy data for Hochstetter's frogs for fifteen 100 m transects at Te Paparahi, Aotea, New Zealand.

Appendix S2. OpenBUGS code for closed-population mark-recapture (CMR), N-mixture, and occupancy models fitted to data for Hochstetter's frogs at Te Paparahi, Aotea, New Zealand.

Appendix S3. Posterior predictive checks of models fitted to count and occupancy data for Hochstetter's frogs at Te Paparahi, Aotea, New Zealand.

Appendix S4. Output from models fitted to data for Hochstetter's frogs at Te Paparahi, Aotea, New Zealand.

Appendix S5. Robustness of closed-population mark-recapture (CMR) and N-mixture models to variation in detection probabilities among transects.

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