Assessment of site-occupancy modeling as a technique to monitor Hochstetter's frog (*Leiopelma hochstetteri*) populations

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ABSTRACT

Hochstetter's frog is a small, cryptic, semi-aquatic species. Isolated populations are found in forested catchments in the northern half of the North Island of New Zealand. The current status of these populations is unknown due to the lack of a rigorous monitoring technique. This study assessed the potential of site-occupancy modeling as a tool for monitoring Hochstetter's frog populations. The primary aim of the study was to obtain estimates of detection probability for Hochstetter's frog, to determine whether the amount of sampling effort required for a fully implemented monitoring programme is likely to be prohibitive. Multiple sites were established in each of three different stream habitats, and the presence / absence of frogs was recorded for each site during repeat surveys in winter / spring 2003 and summer / autumn 2004. The estimates of detection probability obtained indicate that the models have the potential to generate unbiased estimates of occupancy based on low sampling effort (four to six repeat surveys per site), and that in many instances it may be possible to separately monitor juvenile and sub-adult / adult frogs within a population. No major difficulties were encountered when implementing the technique in the field. It is recommended that anyone considering monitoring Hochstetter's frog populations trial this technique, to determine its applicability in specific locations. Results indicate that site-occupancy modeling also may be applicable to monitoring other species in situations where more traditional rigorous methods (e.g. capture-recapture or distance sampling) cannot be applied.

Keywords: Population monitoring, amphibians, threatened species, cryptic species, semi-aquatic, streams, Hunua Ranges, Brynderwyn Hills, Mahurangi Forest, New Zealand

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1. Introduction

In recent years, population declines of many amphibian species have been documented throughout the world (see reviews by Alford & Richards 1999; Gardner 2001), including in New Zealand (Bell, Carver et al. 2004). Despite the acknowledged difficulties in discriminating between anthropogenic impacts and natural population dynamics (Pechmann et al. 1991; Pechmann & Wilbur 1994), it is now generally accepted that these declines are real and pose a serious threat to the global diversity of herpetofauna. A variety of potential causal agents have been postulated, including habitat alteration, climate change, increased levels of ultraviolet radiation, introduced predators, chemical pollutants, emerging infectious diseases, parasitic infections and collection for trade (summaries in Alford & Richards 1999; Young et al. 2001; Green 2003). In many instances, the precise mechanisms of decline remain speculative, and may involve complex synergistic interactions (e.g. Kiesecker et al. 2001). In order to conserve and manage amphibian populations, there is an urgent need to develop and implement robust monitoring techniques. This requirement has been identified as a major priority by the Native Frog Recovery Group in New Zealand (Newman 1996).

Four extant species of frog are currently identified as being endemic to New Zealand (Bell, Carver et al. 2004; Bell, Pledger et al. 2004). Hochstetter's frog (*Leiopelma hochstetteri*) is the most widely distributed of these, occurring in disjunct populations throughout the northern half of the North Island, from the King Country and East Cape regions to south of Whangarei in Northland, including the Coromandel Peninsula and Great Barrier Island (Robb 1986; Pickard & Towns 1988). Hochstetter's frog is typically described as semi-aquatic, often being found alongside small streams and seepages in forested catchments (Gill & Whitaker 1996). It is a small (up to 50 mm length), cryptically coloured frog that shelters during the day in cracks and crevices (e.g. under rocks, logs and leaves, and in rock fissures). Although aspects of the species' physiology, biology, behaviour and genetics have been studied (summaries in Bell 1978, 1985; Cree 1985; Tessier et al. 1991 and references cited therein; Gemmell et al. 2003), much of its ecology remains poorly understood. Hochstetter's frog is currently classified as 'Sparse' under the New Zealand threat classification system (Hitchmough 2002). However, it should be acknowledged that this classification is based on a qualitative assessment of existing populations, as no rigorous quantitative monitoring technique currently exists.

1.1 MONITORING ISSUES

Previous attempts to monitor Hochstetter's frog populations have involved either estimates of relative abundance based on count indices (typically number of frogs observed per unit search area: e.g. Green & Tessier 1990; McNaughton & Greene 1994; Perfect 1996), or estimates of population size based on capture-recapture (e.g. Slaven 1992; Whitaker & Alspach 1999). Both approaches are commonly used in amphibian population studies (Heyer et al. 1994). However, neither approach has proven to be effective for monitoring Hochstetter's frog populations, due to either fundamental or applied constraints. To monitor Hochstetter's frog populations effectively, these constraints need to be acknowledged and redressed.

1.1.1 Previously used techniques

Count indices

It is important to recognise that any count of abundance is the product of two factors: the actual number of individuals present in the study area and the likelihood of detecting those individuals (i.e. detection probability) (e.g. Anderson 2001; Yoccoz et al. 2001; MacKenzie & Kendall 2002; MacKenzie et al. 2002). Consequently, it is impossible to make accurate inference about the abundance of a species in an area without considering its detection probability. Interpretation of trends in abundance based on index counts is problematic, because this approach assumes that detection probability is constant; such an assumption is unlikely to be true, because species detection probability can vary on both spatial and temporal scales for a number of reasons (Anderson 2001, 2003; Hyde & Simons 2001; Bailey et al. 2004). Therefore, since index counts do not incorporate estimates of detection probability, it is impossible to determine whether any change in index counts actually reflects a change in population size or is simply due to a change in detection probability (Buckland et al. 2000; Yoccoz et al. 2001).

Capture-recapture

Capture-recapture methodology incorporates an estimate of detection probability, and is therefore a more statistically robust approach than index counts. However, previous attempts to monitor Hochstetter's frog populations using capture-recapture have often been hampered by low recapture rates (Slaven 1992; Whitaker & Alspach 1999; but see Tessier et al. 1991 for an exception). In addition, this method requires the identification of individual frogs. This has previously been achieved using toe-clipping. However, due to concerns about the potential sub-lethal or lethal effects of toe-clipping (McCarthy & Parris 2004; summary in Bradfield 2004), this method of identifying individual frogs is not desirable. The possibility of using non-invasive identification techniques, such as natural markings (as has been developed for Archey's frog: Bradfield 2004), is currently being assessed for Hochstetter's frog (T. Beauchamp, pers. comm.).

Another limitation of the capture-recapture methodology relates to the issue of the appropriate spatial scale for monitoring Hochstetter's frog populations. Although the species is sometimes described as sedentary (e.g. Tessier et al. 1991), such generalisations are questionable. It is known that Hochstetter's frog can, at times, be found in the forest some distance away from streams (Stephenson & Thomas 1945; Stephenson & Stephenson 1957; Perfect 1996; Robb 1986; pers. obs.), and individual frogs have been documented moving within and between streams in a catchment (Slaven 1992). These latter observations, as well as genetic data (Slaven 1992), indicate that local populations may function as a metapopulation, a common feature of many amphibian populations (Alford & Richards 1999). This has significant implications for population monitoring, as temporal fluctuations in the size of local populations may not accurately reflect the overall status of the metapopulation (Alford & Richards 1999). Therefore, monitoring of Hochstetter's frog populations in any given area should include numerous sites to account for potential metapopulation dynamics. This approach is likely to be prohibitively costly using capture-recapture, even if a non-invasive technique for identifying individual frogs was available.

1.1.2 Habitat variability

The physical structure of stream habitat utilised by Hochstetter's frog varies widely throughout the species' distribution range. For example, streams in southern and central areas are often dominated by long (> 50 m) sections of streamside rocks, while in the northern region such rocky areas are typically restricted to small isolated patches (as small as 5 m in length) interspersed with longer sections of bedrock or silt. In both habitat types, frogs are most easily found by searching under streamside rocks (and associated fallen branches or logs) during the day. In other areas (e.g. near Warkworth) such rocky sections are often sparse or absent. Instead, stream structure is dominated by cascades and waterfalls, containing numerous tunnels and fissures. In this habitat, frogs are most easily found by daytime searches of the tunnels and fissures. In many instances, frogs can be seen within crevices, but due to their position would be very difficult to capture without risking injury to the frog (pers. obs.). Ideally, a standardised monitoring technique would be able to accommodate such variation in stream habitat structure.

In summary, a monitoring technique with the following attributes is required:

- Statistically robust
- Preferably non-invasive
- Able to be applied efficiently at an appropriate spatial scale
- Able to incorporate variation in stream habitat type

Site-occupancy modeling has the potential to meet all of these criteria.

1.2 SITE-OCCUPANCY MODELING

Rather than estimating the number of individuals present in an area, site-occupancy modeling estimates the number of sites occupied by a species in an area. 'Sites' may be naturally occurring (e.g. stream reaches or ponds) or arbitrarily defined (e.g. transects or quadrats) sampling units. In some instances, occupancy may be regarded as a surrogate for population size; in other situations, occupancy itself may be the primary ecological measure of interest (e.g. for assessing a species' range or distribution, and in metapopulation studies). One advantage of site occupancy over actual abundance as a monitoring metric is that less effort may be required, since it is only necessary to detect evidence that the species is present within a sampling unit. Observing individual animals, hearing their calls, or locating tracks, territorial markings or other sign would all constitute such evidence. However, for most species, not detecting any evidence that the species is present at a site does not equate to the species being absent (i.e. the species may be present but simply undetected by a survey).

When a species is present at a site, the probability of detecting that species in a survey of that site is the detection probability (MacKenzie et al. 2002). To make reliable inferences about occupancy, it is important to account for detection probabilities, as these may vary spatially and / or temporally. Using the method developed by MacKenzie et al. (2002), sites are surveyed repeatedly within a relatively short timeframe (for useful extensions see MacKenzie et al. 2003; Royle & Nichols 2003; MacKenzie et al. 2004). Detection or non-detection of the species of interest is recorded for each site search. The likelihood of observing a particular sequence of detections and non-detections from repeated surveys of a site can then be expressed as a function of occupancy and detection probabilities. Importantly, for those sites where the species was never detected, the likelihood consists of two components, which represent the two possible explanations: either the species was present but was never detected, or the species was genuinely absent from the site (see MacKenzie et al. 2002 for additional details). Using this approach, an unbiased estimate of overall site occupancy is obtained. Note that if each site is only surveyed once, occupancy and detection probabilities are entirely confounded; hence it is not possible to obtain an unbiased estimate of occupancy without additional information.

The key assumptions of the models of MacKenzie et al. (2002) are:

- Sites remain closed to changes in occupancy state during the survey period (i.e. occupied sites remain occupied, and unoccupied sites remain unoccupied).
- The species is not falsely detected at a site when it is absent.
- Species detection at any site is independent of detection at all other sites.
- There is no unmodeled heterogeneity in detection probability, so that detection probability calculated from sites where the species was detected can validly be applied to sites where the species was never detected.

Computer simulations indicate that the models can provide unbiased estimates of site occupancy irrespective of a species' detection probability (MacKenzie et al. 2002). However, the amount of sampling effort required to obtain these estimates of occupancy is a function of the detection probability: more sampling effort is required at lower detection probabilities (MacKenzie & Royle in press). When the detection probability is very low, it is still theoretically possible to use site-occupancy modeling as a monitoring tool; however, the amount of sampling effort required may make the technique unfeasible in practical terms.

2. Objectives

The primary aim of this pilot study was to obtain estimates of the spatial and temporal variation in detection probability for Hochstetter's frog, and to use this information to determine the sampling effort likely to be required to implement a monitoring programme based on the site-occupancy models of MacKenzie et al. (2002). Thus, provided detection probability for Hochstetter's frog is greater than zero, the assessment of the technique will be based on the sampling effort required, as well as any practical difficulties identified when applying the technique in the field.

3. Methods

3.1 SITE LOCATIONS

Three areas were chosen from within the distribution range of Hochstetter's frog. These varied in stream habitat structure, each representing one of the three habitat types outlined above: the Hunua Ranges (long sections of streamside rock), the Brynderwyn Hills (small isolated patches of streamside rock), and Mahurangi Forest (cascades / waterfalls with numerous tunnels and fissures but few streamside rocks).

A number of sites were established within each stream habitat type (Table 1; specific information about site locations is lodged at the Waikato Conservancy Office). In the Hunua Ranges, a 'site' was defined *a priori* as a 40-m streamside transect (based on data provided in Slaven 1992; Perfect 1996). All of these sites were located in native hardwood / broadleaf forest dominated by tawa (*Beilschmiedia tawa*) that receives intensive predator control for rats (*Rattus rattus*), stoats (*Mustela erminea*) and possums (*Trichosurus vulpecula*). In the Brynderwyn Hills, a 'site' was defined as a single small patch of streamside rocks (5–23 m long; site length was determined by the size of each individual rock

TABLE 1. SUMMARY OF SURVEY DETAILS.

SITE TYPE	LOCATION	SURROUNDING VEGETATION	TIME OF SURVEYS	NO. SITES	NO. REPEAT SURVEYS PER SITE
40-m transect	Hunua Ranges	Native forest	Aug–Sept 2003	10	6–7
			Jan–Mar 2004	10	5–6
Small rock-patch	Brynderwyn Hills	Native forest	Aug–Sept 2003	6	6
			Jan–Mar 2004	6	8
Cascade / waterfall	Mahurangi Forest	Mature pine forest	Sept–Oct 2003	6	3
		Harvested area	Mar–May 2004	4	5–6
		Native forest	Mar–May 2004	4	6

patch). All of these sites were located in native broadleaf forest. In Mahurangi Forest, a 'site' was defined as a single cascade or waterfall (2.5–18 m long; site length was determined by the size of each individual cascade / waterfall). The cascade / waterfall sites were initially established in mature plantation pine (*Pinus radiata*) forest (planted in 1977: C. Zinsli, Carter Holt Harvey, pers. comm.). However, due to unforeseen circumstances (described below), these sites had to be re-established during the study. New cascade / waterfall sites were established in Mahurangi Forest in two areas: in native hardwood / podocarp forest, and in a small stand (approximately 2.03 ha) of mature plantation pine forest and native vegetation. The small stand of pine and native vegetation extended up to 40 m on both sides of the stream; the remainder of the sub-catchment had been mature plantation pine forest but was harvested in early 2003 and 2004 (C. Zinsli, pers. comm.). In this report, the three study locations within Mahurangi Forest are referred to as 'mature pine forest', 'native forest' and 'harvested area'. With the exception of the harvested area in Mahurangi Forest, all sub-catchments surrounding study streams in the Hunua Ranges, Brynderwyn Hills and Mahurangi Forest were comprised of intact vegetation.

3.2 SITE SURVEY PROTOCOL

The presence of frogs was verified at all sites prior to the study to ensure that sites were occupied. Once this was achieved, each site was searched during the daytime (one to three searchers per site survey) at approximately weekly intervals on three to eight occasions. In some instances, site searches had to be postponed due to inclement weather or logistical constraints. Daytime searches were chosen (as opposed to night-time searches) due to practical and safety considerations, and because previous data indicate that Hochstetter's frogs are more likely to be detected during the daytime (McLennan 1985; Slaven 1992).

The search protocol followed the recommendations of Bell (1996). Each site was searched by slowly moving upstream from the start point, carefully examining all available refugia for frogs (underneath rocks, logs and leaves, and inside crevices and tunnels). All objects that had to be moved were carefully replaced in their original position to minimise habitat disturbance. If replacing an object posed a risk to a frog, the frog was gently nudged aside using a blunt object (e.g. a leaf or twig). After the object was returned to its position, the frog was gently nudged back under it. Both sides of the stream at each site were searched from the water's edge to the stream bank. Due to low light levels and the cryptic colouration of frogs, searches were conducted with the aid of a torch. Only one observer searched a site at any given time, and each observer searched a site until they found one sub-adult / adult frog (> 1 yr old, > 18 mm snout-vent length (SVL); Whitaker & Alspach 1999) and one juvenile frog (≤ 1 yr old, ≤ 18 mm SVL; Whitaker & Alspach 1999), or until they had finished searching the site completely. This allowed separate calculations to be made of the detection probabilities of sub-adults / adults and juveniles, in addition to the overall detection probability (i.e. the detection of a frog regardless of size or age).

Previous experience showed that frogs occasionally jump away (often into the stream) when rocks or logs are lifted, or move deep into fissures (and out of view) when a light is shone into the fissure. There is some evidence that frogs disturbed in this manner may return to their original location or nearby within a short time period (Tessier et al. 1991; pers. obs.). In an attempt to account for this potential temporary 'flight response', multiple searches of a site on a given day were conducted 20 minutes apart. To ensure independence of results, any observer(s) not involved in a search deliberately looked away from any observer(s) currently searching for frogs. In addition, when two or three observers searched a site on a given day, all observers only stopped looking for frogs after they had all met one of the criteria listed above. This allowed the last observer to remain naïve to the search results of any previous observer(s), hence ensuring independence of the surveys.

The SVL of each frog was measured by holding a small ruler parallel to the frog. When this was not possible (e.g. when the frog jumped into the stream or was deep within a crevice), size was estimated. The vast majority (84.4%; n = 128) of frogs that could not be measured directly were obviously large; the remainder were obviously small (< 15 mm SVL). Therefore, there will have been no significant bias when assigning these frogs to an age-class category. For each frog detected, colour, search time, number of cover objects turned, and relative position within the site were noted. The following environmental variables were also recorded during each site search: ambient temperature (air, water and substrate), relative humidity (measured using a sling psychrometer), general weather conditions, and stream condition (e.g. water present / absent). A rain gauge and maximum / minimum thermometer located at each of the three geographic areas recorded rainfall and temperature fluctuations between site searches.

The observers involved in the study had varying degrees of prior experience in searching for Hochstetter's frog. All observers were given specific search instructions (verbal and written) and shown photographs and / or live frogs before commencing their first search. Standard procedures were followed to minimise the possible spread of chytrid fungus (*Batrachochytrium dendrobatidis*), which has been implicated in frog population declines at various locations around the world (summary in Gardner 2001), including New Zealand (Bell, Carver et al. 2004). All equipment (clothing, boots, packs, etc.) was thoroughly cleaned of mud and dried before moving from one region to another. In addition, the footwear and gaiters of all observers were sprayed with Virkon™ prior to entering sites.

It was planned to conduct a series of repeat searches of each site in winter 2003, and again in summer 2004, in an attempt to maximise variation in environmental conditions and, potentially, detection probabilities. This seasonal comparison was achieved for sites in the Hunua Ranges and Brynderwyn Hills, with sites in these areas being monitored in August–September 2003 and January–March 2004. However, due to logistical constraints, sites in Mahurangi Forest could not be established and monitored until September–October 2003 (spring). Unfortunately, we established these sites in the wrong area (due to a misunderstanding regarding the location of protected frog enclaves) and the sites were logged at the commencement of the summer 2004 surveys. Therefore, we established and monitored new cascade / waterfall sites at the correct location and in nearby native forest in March–May 2004 (autumn). This situation precludes a direct seasonal comparison of detection probabilities at the cascade / waterfall sites, but nonetheless provides data on the general variation in detection probabilities in this habitat type.

3.3 CALCULATION OF DETECTION PROBABILITIES

We estimated three categories of detection probability for Hochstetter's frog (overall detection, juvenile detection, and sub-adult / adult detection) for each location during each season. Many factors are likely to affect the probability of detecting Hochstetter's frog, particularly environmental variables and observer experience. We assessed the feasibility of modeling these covariates to estimate detection probabilities; however, this was not possible due to the limitations of the pilot study data (small number of sites surveyed, and insufficient variation in frog detection / non-detection at sites). Since the presence of frogs was confirmed at each monitoring site prior to the study, detection probabilities ($\hat{p}$) were simply estimated as a binomial proportion (assuming that, within each site and season, each survey was independent and had a constant probability of detecting frogs in any given category). That is, $\hat{p} = x/n$ where n is the total number of surveys conducted at any location within a season and x is the number of those surveys where frogs of a particular category (overall, juvenile or sub-adult / adult) were detected. The standard error for $\hat{p}$ ($SE(\hat{p})$) is thus:

$$SE(\hat{p}) = \sqrt{\frac{\hat{p}(1-\hat{p})}{n}}$$

4. Results

4.1 ENVIRONMENTAL CONDITIONS

Summaries of environmental conditions during the study are provided in Appendix 1. In the Hunua Ranges, surface water was always present at eight sites (= 'wet' sites), but was always absent from two sites (= 'dry' sites). All sites in the Brynderwyn Hills and Mahurangi Forest had surface water present during the study.

4.2 DETECTION PROBABILITIES

Estimates of detection probabilities are presented in Tables 2–4. Results for sites in the Hunua Ranges are further divided into wet and dry sites (Table 2).

Detection probabilities for all categories (overall, sub-adult / adult and juvenile) at the wet Hunua sites were ≥ 0.66 (Table 2). There was no evidence of a seasonal difference in the detection probability of sub-adult / adult frogs at these sites. However, the detection probability of juvenile frogs was lower at wet Hunua sites in January–March 2004. In contrast, detection probabilities (particularly for sub-adult / adult frogs) at dry Hunua sites tended to be higher in January–March 2004 than in August–September 2003, although the limitations of these data must be acknowledged (n = 2 sites). Nonetheless, the relatively frequent detection of frogs at dry sites was surprising given that this species is considered to be semi-aquatic and these sites were completely devoid of surface water during the winter and summer monitoring periods.

There was remarkably little seasonal variation between detection probabilities at the Brynderwyn sites (Table 3). In both seasons, detection probabilities for juvenile frogs ($\hat{p}$ = 0.28) were markedly lower than for sub-adult / adult frogs ($\hat{p}$ = 0.63–0.66).

Detection probabilities for all categories at cascade / waterfall sites ranged from 0.51–0.89 in mature pine forest (September–October 2003), and 0.79–0.97 in native forest (March–May 2004) (Table 4). The lowest detection probabilities for cascade / waterfall sites were recorded at the harvested area, with the juvenile detection probability ($\hat{p}$ = 0.11) being much lower than the sub-adult / adult detection probability ($\hat{p}$ = 0.51).

TABLE 2. DETECTION PROBABILITIES (± SE) FOR 40-m TRANSECT SITES IN THE HUNUA RANGES.

SITE TYPE	CATEGORY	AUG–SEPT 2003	JAN–MAR 2004
Wet	Overall	0.94 ± 0.02	0.86 ± 0.04
	Sub-adult / Adult	0.80 ± 0.04	0.82 ± 0.04
	Juvenile	0.90 ± 0.03	0.66 ± 0.05
Dry	Overall	0.61 ± 0.11	0.83 ± 0.09
	Sub-adult / Adult	0.40 ± 0.13	0.71 ± 0.11
	Juvenile	0.50 ± 0.13	0.61 ± 0.11
Wet and dry	Overall	0.89 ± 0.03	0.86 ± 0.03
	Sub-adult / Adult	0.74 ± 0.04	0.80 ± 0.04
	Juvenile	0.84 ± 0.04	0.65 ± 0.05

TABLE 3. DETECTION PROBABILITIES (± SE) FOR SMALL ROCK-PATCH SITES IN THE BRYNDERWYN HILLS.

CATEGORY	AUG–SEPT 2003	JAN–MAR 2004
Overall	0.77 ± 0.05	0.75 ± 0.04
Sub-adult / Adult	0.66 ± 0.06	0.63 ± 0.05
Juvenile	0.28 ± 0.05	0.28 ± 0.05

TABLE 4. DETECTION PROBABILITIES (± SE) FOR CASCADE / WATERFALL SITES IN MAHURANGI FOREST.

CATEGORY	SEPT–OCT 2003 (MATURE PINE FOREST)	MAR–MAY 2004 (HARVESTED AREA)	MAR–MAY 2004 (NATIVE FOREST)
Overall	0.89 ± 0.05	0.57 ± 0.08	0.97 ± 0.03
Sub-adult / Adult	0.80 ± 0.07	0.51 ± 0.08	0.85 ± 0.06
Juvenile	0.51 ± 0.08	0.11 ± 0.05	0.79 ± 0.06

4.3 SAMPLING EFFORT

Recent research by MacKenzie & Royle (in press) has shown that, for given probabilities of detection (and occupancy), there is an optimal number of repeat surveys that should be conducted at each site to obtain unbiased estimates of site occupancy, assuming that detection probability is reasonably constant over the sampling period (Table 5).

In this study, the overall detection probability for Hochstetter's frog at all sites during all seasons was 0.57–0.97. Therefore, two to four repeat surveys per site would be required to obtain unbiased estimates of site occupancy using the methodology outlined (Table 5). Given the detection probabilities of sub-adult / adult frogs in all site types during both seasons ($\hat{p}$ = 0.40–0.85 for all sites; $\hat{p}$ = 0.51–0.85 for sites where surface water was present), and the detection probabilities of juvenile frogs at sites in the Hunua Ranges ($\hat{p}$ = 0.50–0.90) and at sites located in mature pine forest and native forest in Mahurangi Forest ($\hat{p}$ = 0.51 and 0.79 respectively), separate monitoring of sub-adult / adult and juvenile frogs may be achievable with two to five repeat surveys per site (Table 5). However, at sites in the Brynderwyn Hills, where the detection probability of juvenile frogs was lower ($\hat{p}$ = 0.28), a minimum of five repeat surveys per site would be required, and at sites in Mahurangi Forest, where the juvenile detection probability was much lower ($\hat{p}$ = 0.11), 14–34 repeat surveys per site would be required to accurately monitor different age classes (Table 5).

TABLE 5. OPTIMUM NUMBER OF SURVEYS REQUIRED AT EACH SITE FOR SELECTED PROBABILITIES OF OCCUPANCY (ψ) AND DETECTION (p)[a].

	ψ								
p	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
0.1	14	15	16	17	18	20	23	26	34
0.2	7	7	8	8	9	10	11	13	16
0.3	5	5	5	5	6	6	7	8	10
0.4	3	4	4	4	4	5	5	6	7
0.5	3	3	3	3	3	3	4	4	5
0.6	2	2	2	2	3	3	3	3	4
0.7	2	2	2	2	2	2	2	3	3
0.8	2	2	2	2	2	2	2	2	2
0.9	2	2	2	2	2	2	2	2	2

[a] Data refer to sites being surveyed an equal number of times using a standard design. Note that MacKenzie & Royle (in press) suggest that in practice a minimum of three surveys per site should be conducted. Data sourced from MacKenzie & Royle (in press).

4.4 OBSERVER BIAS

Comparison of bias estimates and associated standard errors for sites that were searched by two observers on the same day provides little indication of a bias favouring one observer over the other with regards to detecting either a frog of any size (overall detection probability) or a juvenile frog (Table 6). However, there was potentially a positive bias towards the first observer detecting a sub-adult / adult frog (Table 6).

TABLE 6. MEAN PERCENT (± SE) OF SURVEYS WHERE SITES WERE SEARCHED BY TWO OBSERVERS ON THE SAME DAY, BUT FROGS WERE ONLY DETECTED BY ONE OF THE OBSERVERS.

CATEGORY	% SEARCHES FROG DETECTED ONLY BY	
	OBSERVER 1	OBSERVER 2
Overall	10.0 ± 2.5	8.7 ± 1.0
Sub-adult / Adult	16.4 ± 3.2	9.2 ± 1.8
Juvenile	10.7 ± 2.3	12.0 ± 3.5

5. Discussion

5.1 ASSESSMENT OF DETECTION PROBABILITIES WITH RESPECT TO SAMPLING EFFORT

In the present study, the overall detection probabilities of Hochstetter's frog at all site types in all seasons ranged from 0.57–0.97. This indicates that the models of MacKenzie et al. (2002) could be used to obtain unbiased estimates of site occupancy for Hochstetter's frog *per se* based on a very small amount of sampling effort (two to four repeat surveys per site). This in itself is a significant advance in the development of an effective technique for monitoring Hochstetter's frog populations.

The major drawback of designing a monitoring programme based on the detection / non-detection of one frog of any age at a site is that trends in the status of different age classes within a population are unknown. Clearly, it would be preferable to separately monitor sub-adult / adult and juvenile frogs within a population. The results of this study indicate that, in many instances, this may be possible. The detection probabilities of sub-adult / adult frogs at all site types regardless of season, and the detection probabilities of juvenile frogs in the Hunua Ranges and in mature pine forest and native forest in Mahurangi Forest, suggest that separate monitoring of sub-adult / adult and juvenile frogs may be achievable with small sampling effort (two to five repeat surveys per site) at these sites. Monitoring of sites in the Brynderwyn Hills, where the detection probability of juvenile frogs is lower, may still be reasonable in terms of sampling effort (minimum of five repeat surveys per site). However, if the very low estimate of juvenile detection probability at the harvested site in Mahurangi Forest is representative, then the required sampling effort (14–34 repeat surveys per site) is likely to be prohibitively large for monitoring juvenile frogs in this habitat type.

5.2 OBSERVER BIAS

When a site is searched by more than one observer on the same day, the act of searching by one observer may affect the likelihood of any other observer(s) detecting the target species. In this study, there was some indication that the first observer was more likely to detect sub-adult / adult frogs than the second observer. However, there was little indication of observer bias with regard to the detection of juvenile frogs. This is consistent with field observations: juvenile frogs usually remained motionless or only moved very short distances when detected, while sub-adult / adult frogs were more likely to jump away. Although we tried to account for such 'escape behaviour' by having a 20-minute interval between multiple site searches on the same day, field observations indicated that 'escaped' frogs did not always return to their original refuge (or nearby) within this time. This type of observer bias can be accounted for in a monitoring programme in one of two ways. If it is feasible and appropriate, sites could be searched by only one observer per day. Alternatively, sites could be searched by two observers per day, in which case 'observer number' should be included as a covariate in the data analysis. Either option will minimise the significance of such observer bias on estimates of site occupancy.

5.3 CONCLUSIONS OF THIS PILOT STUDY

The results indicate that it may be possible to monitor Hochstetter's frog populations (either overall presence or specific age classes) with low sampling effort. Thus, the site-occupancy models of MacKenzie et al. (2002) have significant potential as a tool for monitoring Hochstetter's frog populations.

5.4 ALTERNATIVE SITE-OCCUPANCY MODELS

The development of site-occupancy models is an ongoing field of research. For all these models, the accuracy of the estimate of site occupancy is dependent upon the accuracy of the estimate of detection probability. Therefore, heterogeneity in detection probability, which can result from a variety of sources, needs to be accounted for in the models. The models of MacKenzie et al. (2002) can include many potential sources of heterogeneity as covariates when estimating detection probability (e.g. observer experience, weather conditions, time of search, site habitat structure and number of refugia present at the site). However, because these models are based on the detection / non-detection of one individual at each site, they do not explicitly incorporate variation in species abundance, which can also affect detection probability:

if there are fewer individuals at a site, then detecting the species (at least one individual) is less likely during any given survey. This is not a problem if any covariates being modeled are correlated with abundance (see below).

Recently, Royle & Nichols (2003) proposed a method for estimating site occupancy where modeling of detection probability could incorporate heterogeneity in abundance at sites. While this approach offers the potential to optimise the modeling of heterogeneity in detection probability, it is based on the assumption that abundance at occupied sites remains constant during the period of repeat surveys. In contrast, the models of MacKenzie et al. (2002) only assume that sites remain either occupied (i.e. at least one individual is present) or unoccupied during the sampling period. Given that we know very little about the movement patterns of Hochstetter's frog (even over short time-periods), it does not seem defensible to assume constant abundance at sites during the period of repeat surveys. It is worth noting that heterogeneity in detection probabilities arising from variation in abundance at sites can, to some degree, be accommodated for in the models of MacKenzie et al. (2002) by including appropriate covariates that act as a surrogate for abundance. A second consideration is that the approach of Royle & Nichols (2003) requires each site to be completely searched, whereas the approach of MacKenzie et al. (2002) only requires each site to be searched until one individual is found. The latter approach may thus be more time-efficient and, in terms of monitoring Hochstetter's frog populations, may minimise habitat disturbance and the chances of accidentally crushing frogs during surveys.

When modeling heterogeneity in detection probability, there is a potential risk that if abundance (or a correlated covariate) is not included, occupancy will be underestimated. However for the purposes of monitoring occupancy over time, the relative change in the estimated levels of occupancy may still be indicative of the true situation, provided that the degree of heterogeneity in detection probabilities is relatively constant. That is, if the detection probabilities estimated for each time period are consistently proportional to the average detection probability (across sites) within each time period, then any estimate of the change in occupancy may still be reasonable. Note that this is a much less restrictive assumption than those required for interpreting an index, namely that detection probabilities are constant across time (e.g. Yoccoz et al. 2001; MacKenzie & Kendall 2002), and there is no heterogeneity between sites (MacKenzie et al. 2003 and references cited therein).

6. Recommendations

Based on the results of this study, we recommend that Hochstetter's frog populations be monitored using the site-occupancy models of MacKenzie et al. (2002). Specific advice regarding the establishment of a monitoring programme is available on request from the Waikato Conservancy. In general, monitoring should involve at least 40–50 sites, with each site being searched on four to six occasions. Sites should be chosen randomly, provided that suitable and searchable frog habitat is present; sites should not be chosen based on the initial presence of frogs. To obtain unbiased estimates of occupancy, the required sampling effort can be achieved by either using one observer (four to six site visits) or two observers (two to three site visits) per site on each survey trip. The most suitable approach will depend on practical and financial considerations for the area in question. Sites should be searched using the procedures described in this study. For any given frog population, the monitoring results should be reviewed once the first season's data have been analysed to determine whether any refinements need to be made (e.g. definition of a 'site' or assessment of adequate sampling effort with respect to detection probability).

Finally, we re-iterate the need to explicitly estimate detection probability in population-monitoring programmes. Abundance indices (e.g. transect counts) fail to do so, meaning that they contribute no rigorous data for assessing spatial or temporal trends in population size. Although this approach is sometimes defended because it is the 'easiest' option, it constitutes a waste of valuable resources (Anderson 2001).

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Appendix 1

SUMMARY OF ENVIRONMENTAL CONDITIONS AT STUDY SITES

TABLE A1.1. HUNUA RANGES.

PARAMETER	AUG–SEPT 2003	JAN–MAR 2004
Monitoring dates	11 Aug – 23 Sept 03	12 Jan – 10 Mar 04
Total rainfall (mm)	306	468
Min. air temperature (°C)	4.0–11.0	6.0–15.0
Max. air temperature (°C)	7.0–12.0	16.0–22.0
Ambient air temperature (°C)	7.0–16.0	9.0–21.0
Ambient water temperature (°C)	7.0–11.0	10.0–15.0
Ambient substrate temperature (°C)	7.0–12.0	11.0–17.0
Ambient relative humidity (%)	77–100	81–100

TABLE A1.2. BRYNDERWYN HILLS.

PARAMETER	AUG–SEPT 2003	JAN–MAR 2004
Monitoring dates	14 Aug – 25 Sept 03	15 Jan – 11 Mar 04
Total rainfall (mm)	480	238
Min. air temperature (°C)	5.5–8.5	9.0–13.0
Max. air temperature (°C)	8.0–14.5	20.0–22.5
Ambient air temperature (°C)	9.0–15.0	11.5–21.0
Ambient water temperature (°C)	9.0–13.0	12.0–18.0
Ambient substrate temperature (°C)	9.0–13.5	12.0–15.5
Ambient relative humidity (%)	83–100	80–97

TABLE A1.3. MAHURANGI FOREST.

PARAMETER	SEPT–OCT 2003 (MATURE PINE FOREST)	MAR–MAY 2004 (HARVESTED AREA)	MAR–MAY 2004 (NATIVE FOREST)
Monitoring dates	11 Sept – 2 Oct 03	17 Mar – 21 May 04	25 Mar – 20 May 04
Total rainfall (mm)	127	179	250
Min. air temperature (°C)	3.0–6.5	0.5–6.0	4.0–11.0
Max. air temperature (°C)	16.5–19.0	19.0–22.0	14.0–19.0
Ambient air temperature (°C)	9.8–16.0	11.0–18.0	11.0–17.0
Ambient water temperature (°C)	10.0–13.0	11.0–16.0	10.0–14.5
Ambient substrate temperature (°C)	9.0–14.0	8.0–17.0	10.0–15.5
Ambient relative humidity (%)	70–97	65–95	84–100