Dynamics of an endangered New Zealand skink: accounting for incomplete detectability in estimating patch occupancy

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Abstract: The endangered grand skink (*Oligosoma grande*) is a New Zealand endemic lizard that persists as metapopulations occupying rock patches within matrices of mixed native vegetation and modified agricultural pasture. Parameterisation of metapopulation models applied in conservation biology assumes complete detectability of target species. Incomplete detectability may result in underestimates of occupancy and biased estimates of extinction and colonisation rates. Recent techniques use multiple surveys of sampling sites to model detectability and derive robust estimates of occupancy, and extinction and colonisation rates. Five years (1998–2002) of presence/absence survey data were analysed to determine grand skink site occupancy and estimate colonisation and extinction rates. Mean site occupancy was 0.38 (SE 0.07), compared with a naïve estimate of 0.29. Occupancy, extinction and colonisation probabilities were habitat specific, varying according to tussock or a modified pasture matrix. Colonisation probability was higher in tussock than in pasture, whereas extinction probability was higher in pasture. Derived model-averaged estimates showed that occupancy was higher in tussock (range 0.515(0.02) – 0.532 (0.02)) than in pasture (range 0.226 (0.03) – 0.234 (0.01)), with a slight trend of decline in pasture areas and increase in tussock areas over time, with the result that overall occupancy has been reasonably static over the 5 years. Detectability varied interannually, ranging from 0.63 to 0.83. The difference between the naïve occupancy estimate and the model-averaged estimate highlights the importance of deriving robust estimates of metapopulation parameters that take incomplete detectability into account. Unbiased estimates allow managers to predict and track responses to management interventions.

Keywords: colonisation; extinction; grand skink; metapopulation; *Oligosoma grande*; presence; survey

Introduction

Many species of conservation concern persist in fragmented environments, occupying patches of suitable habitat where the application of metapopulation theory is appropriate (Caughley & Gunn 1996). Although established contemporaneously with the theory of island biogeography (MacArthur & Wilson 1963), Levins' concept of metapopulation (Levins 1969, 1970, cited in Hanski & Gyllenberg 1993) attracted relatively limited theoretical attention until recently. As conservation biologists increasingly grapple with the challenge of managing wildlife populations in the face of habitat loss and fragmentation there has been a resurgence of interest in metapopulation theory and its empirical implications (Hanksi 1994a, b; Etienne & Heesterbeek 2000; Hanski & Ovaskainen 2000; Barbraud et al. 2003; Frank 2005; McCarthy et al. 2005; Oborny et al. 2005, and references therein). Effective management of metapopulations requires an understanding of localised extinction and colonisation rates, and the processes that determine these rates.

Two approaches have been applied to model metapopulation processes, incidence function models (IFMs) (Hanski 1994b) and logistic regression models (LRMs) (Thomas & Jones 1993). Both modelling approaches consider patch-specific rates of extinction and colonisation and make assumptions about how these rates are affected by spatial variation in patch size and patch isolation. Metapopulation models can be parameterised using snapshot presence/absence surveys to determine levels of and changes in individual patch occupancy, and assume that a steady state exists, i.e. no long-term trends in occupancy (Clinchy et al. 2002; Hanski 2002).

Traditionally presence/absence surveys make the implicit and untested assumption of complete detection of the target species (i.e. if the species is present at a given site it will be seen and recorded), but for many species the probability of detection under all reasonably rigorous survey regimes may be less than one (Gu & Swihart 2004). Failure to record a species as present when it is in fact there will result in underestimation of the proportion of the patches occupied and biased estimates of patch colonisation and extinction rates. Thus reliance on simple presence/absence survey data may bias both IFM and LRM approaches since it is impossible to exclude the possibility that recorded colonisations arise through the misclassification of a patch as vacant in earlier surveys (Hanski 2002; Moilanen 2002). Use of naïve parameter estimates is not a sound basis for conservation management since there is a risk of expending scarce resources to address non-existent problems, or of directing effort to the wrong sites or wrong components of metapopulation dynamics (Gu & Swihart 2004).

Models have recently been developed to estimate the proportion of sites occupied by a species when the detection probability is less than one (MacKenzie et al. 2002, 2003; Royle & Nichols 2003). The basis for these modelling approaches is the survey of a sample of sites repeatedly within a relatively

short time interval during which it is assumed there have been no systematic changes in the occupancy state of sites. These models can be applied to data collected from a single year to assess the status of the population (MacKenzie et al. 2002; Royle & Nichols 2003) or to data collected over longer time frames, such as multiple years, to assess trends in occupancy and to estimate localised extinction and colonisation rates (MacKenzie et al. 2003). The model consists of N sites being visited on T sampling occasions. The presence or absence of the species is recorded at each visit, and the detection histories for each site are then constructed and site occupancy rates estimated (MacKenzie et al. 2002, 2003).

The grand skink (*Oligosoma grande)* is one of New Zealand's most endangered endemic reptiles, currently ranked by the New Zealand Department of Conservation as Nationally Critical (Hitchmough et al. 2007). *Oligosoma grande* was believed once to have been found over much of the central south-eastern region of the South Island of New Zealand (see Berry & Gleeson (2005) for details). Concern over the future of the species has been driven by the belief that the present-day fragmented distribution of skinks into eastern and western clusters is the result of historical anthropogenic impacts, and by apparent historical population declines recorded within a core management area since the late 1980s (Whitaker & Housten, unpublished draft report dated 2002, cited in Berry & Gleeson 2005). Recent work has indicated that a high level of genetic structuring among extant populations makes it likely that the distribution was naturally discontinuous; however, it does support the anecdotal suggestion that the grand skink population has declined in historical times (Berry & Gleeson 2005). Data on the rates and magnitude of population declines is equivocal, however. Total population estimates for grand skinks vary from 1400 (Patterson 1992) to 5000 (Whitaker & Loh 1995), with the population currently thought to be around 2000 individuals (Marshall 2000). Total counts in selected sites in the mid-1990s indicated that skink populations were depressed in modified pasture landscapes, with the finding of lower rock-tor occupancy levels in pasture compared with unmodified tussock being used to postulate population declines since 1980 (Whitaker 1996). A review of count data up to 2001 showed no evidence of a decline in the total number of rock tors occupied by grand skinks, but did confirm lower levels of occupancy of rock tors in pasture versus tussock habitat (Houghton & Linkhorn 2002). Although these studies recognised the need to treat grand skinks as a metapopulation and to consider local-scale colonisation and extinction events, counting techniques did not explicitly consider incomplete detectability and thus derived only naïve estimates of occupancy and calculated absolute numbers of extinctions and colonisations rather than rates (Houghton & Linkhorn 2002). To date management of grand skinks has proceeded on the assumption that a marked decline in population numbers and distribution is real, is ongoing, and is due principally to habitat loss as tussock habitat is converted to pasture for farming and predation by a suite of introduced predatory mammals. Recent work (e.g. Tocher 2006) has not conclusively confirmed the impact or relative importance of these two factors.

Unbiased estimates of trends in skink occupancy are required as a basis for future management planning, to assess both the urgency and direction of conservation interventions. The processes mediating any declines and the responses to ameliorate these could be profoundly different depending on which of the postulated causal factors is predominant.

For example loss of habitat would be expected to increase rates of localised extinction and might best be addressed through active habitat restoration, whereas features of the habitat matrix may limit dispersal (Berry et al. 2005), e.g. as higher rates of predation in modified habitat, and thus reduce rates of colonisation of unoccupied patches and may require interventions such as vigorous predator control. Alternatively there may be some other interaction between habitat and predation, e.g. whereby unmodified habitat provides refugia for skinks from predators, or even some as yet unrevealed factors.

The aim of this study was to apply recently developed presence/absence modelling techniques to 5 years of grand skink count data in order to quantify trends in site occupancy and to derive estimates of extinction and colonisation rates that take into account incomplete detectability.

Materials and methods

Study site
Skink surveys have taken place in the c. 250-ha Grande Ridge (Trig E) study area, within the Macraes Ecological District (45°27' S, 170°26' E), Central Otago – a mosaic of close-cropped introduced grassland (pasture) and remnants of native vegetation. The area consists of extensive Haast schist rock outcrops and rock tors at an altitude of c. 440–540 m (Bibby 1997). Mixed shrubland occurs in many areas of the hill-slopes, with mānuka (*Leptospermum scoparium*) being the dominant species. Tussock habitat is dominated by narrow-leaved snow tussock (*Chionochloa rigida*) grassland, with golden spaniard (*Aciphylla aurea*) and mountain flax (*Phormium cookianum*) also present on the steeper slopes, while in lower areas *C. rigida* dominates along with hard tussock (*Festuca novaezelandiae*) and matagouri (*Discaria toumatou*) (Bibby 1997). The region experiences coastal climatic conditions. Westerly-moving depressions result in higher rainfalls and more moderate temperatures than in the rest of Central Otago (Bibby 1997).

Rock-tor surveys
The rock-count method for monitoring grand skinks was developed in 1994 (Whitaker 1996) with the aim of determining the presence or absence of *Oligosoma grande*. Rock tors (henceforth 'rocks') were defined as a rock outcrop at least 10 m away from its nearest neighbouring rock. Clusters of rocks within 10 m of each other were classified as one rock (Whitaker 1996). Rock counts have been carried out in January each year to take advantage of periods of relatively good weather conditions and long day length. Counts are carried out by teams of observers, comprising people with varying experience in identifying and finding skinks. Counts are primarily undertaken during the morning to take advantage of optimum basking conditions and thus the presumed best chance of finding skinks.

The usual search procedure is to scan a rock for basking skinks from nearby using binoculars, then to approach the rock to search crevices that might be skink refuges (Whitaker 1996). The presence and total number of *Oligosoma grande* is recorded for each rock for each visit (Department of Conservation, unpubl. data); only presence/absence data were used in this study.

The presence or absence of grand skinks on a random

sample of up to 120 rocks was recorded during each of up to three separate visits during January in 1998–2002. Equal numbers of survey rocks were located in both modified pasture and indigenous vegetation for each survey period (Whitaker 1996). Management at the site did not vary significantly over this period, with varying intensity of predator control via trapping taking place throughout the area (JR, unpubl. data).

Analyses

Rock-count data were converted into presence/absence data for each rock over all survey periods. Presence (i.e. at least one skink observed) was recorded as a 1, whereas absence (i.e. no skinks observed) was recorded as a 0. This resulted in five primary sampling periods (years) with absolute totals of 15 surveys and 352 different rocks. Rocks for which there was just one survey were deleted from the dataset as they would not contribute to the results. This resulted in a total of 299 individual rocks, comprising 116 in pasture and 183 in tussock, being represented in the final analysis. Data were then entered into the computer program PRESENCE (Mackenzie et al. 2003). The multiple seasons' analysis was used to provide estimations of site occupancy, colonisation, and local extinction probabilities when a species has imperfect detectability (MacKenzie et al. 2003). It uses repeated surveys of sites over several seasons to model presence, allowing for the possibility that the species of interest may be present but undetected during a given survey.

The model consists of N units being surveyed over time where the aim is to determine the presence or absence of a species. The occupancy status of the different states may not be constant over time. The study therefore comprises T primary sampling periods, between which changes in the occupancy state of sites may occur. Within each primary sampling period, investigators use an appropriate technique to detect the species at k_t surveys of each site, where k_t is the number of surveys per primary period. The detection history for each site may be expressed as T vectors of 1's and 0's (detection and non-detection, respectively). The detection history for the k_t surveys of site i at primary sampling period t is $X_{i,t}$, and the complete detection history for site i over all primary periods is X_i. Detection histories for the sites can then be used to estimate site occupancy, colonisation, and local extinction probabilities.

Three different models may then be fitted to the data (Mackenzie et al. 2006). The first is the model in which the proportion of sites occupied in the first season is estimated, along with colonisation and extinction probabilities; the model utilised in this study. The second and third models both allow the proportion of sites occupied in each season to be estimated, along with one of the two parameters (colonisation and extinction, respectively). Potential models can then be compared using Akaike's Information Criterion (AIC) (Burnham & Anderson 2001) to select which best describes the data (MacKenzie et al. 2003):

$$AIC = \left[-2\log_e(L(\hat{\theta}|data)) \right] + 2K$$

where $\log(L(\hat{\theta}))$ is the maximised value of the log-likelihood, and K is the number of estimatable parameters. Following the recommendations of Burnham and Anderson (2001), models were ranked using the relative difference in AIC:

$$\Delta_i = AIC_i - \min AIC,$$

so that the model with the minimum AIC has a value of 0 and the larger the Δ_i, the less plausible it is that model i is the best approximation. Because we have a large dataset of rocks the number of parameters in our candidate models is well below the number of observations, so we used unadjusted AIC. We also calculated Akaike weights for the R models in the candidate set:

$$w_i = \frac{\exp(-\Delta_i/2)}{\sum_{r=1}^{R} \exp(-\Delta_r/2)},$$

where the w_i sum to 1 and can be interpreted as the probability that model i is the best model for the data.

Model-averaging (Anderson 2008) was carried out on each parameter to account for model-selection uncertainty:

$$\hat{\theta} = \sum_{i=1}^{R} w_i \, \hat{\theta}_i.$$

This allocates more weight to parameter probabilities from higher ranked models to provide a more realistic average probability.

Estimates of occupancy over time were derived:

$$\psi_t = \psi_{t-1}(1-\varepsilon_{t-1}) + (1-\psi_{t-1})\gamma_{t-1},$$

where:

ψ_t = occupancy, or the probability that a skink is present at a site a time t

ε = the local probability of extinction

γ = the probability of colonisation.

So that occupancy (ψ_t) is dependent on previous occupancy (ψ_{t-1}) via the probabilities that previously occupied sites do not become empty ($\psi_{t-1}(1-\varepsilon_{t-1})$) and previously unoccupied sites are colonised ($(1-\psi_{t-1})\gamma_{t-1}$).

Results

In this study $N = 299$ different rock tors were sampled for $T = 5$ primary sampling periods, compiled from counts in January each year from 1998 to 2002. Surveys were carried out by the Department of Conservation at Trig E Ridge, Macraes Flat, Otago.

A number of candidate models were fitted to the data. Table 1 presents the candidate models and their respective AIC values. Two of the models had ΔAIC values less than 2, and very similar model weights indicating they both provide good descriptions of the data. The most parsimonious model (lowest AIC) suggests that occupancy, colonisation, and extinction probabilities are best modelled as being habitat-specific but constant over time. The second-ranked model is very similar but also suggests annual variation in colonisation probabilities. The other models that were tested have limited support in terms of AIC, with a sharp contrast between models in which occupancy was related to habitat, which had greater support over models where occupancy was constant. Habitat thus appears to be a critical factor. Detection probability was best modelled as year-specific, varying from 0.63 to 0.83, in contrast to a probability of detection of 0.8 (assumed by managers based on Whitaker (1996)) (Fig. 1).

The average overall naïve estimate of occupancy, i.e. the proportion of sites where a grand skink was seen at least once based on the first survey of each year, was 0.29, whereas the

Table 1. Relative difference in AIC (ΔAIC) of each grand skink (*Oligosoma grande*) model tested, parameter estimates for each year, and model-averaged parameter estimates. ψ = probability that a species is present at a site, ε = local extinction probability, γ = colonisation probability, p = detection probability, (.) = probability is constant (Habitat) = parameter is a function of habitat type and constant across years, (t+habitat) = parameter is a function of habitat type and different in each year, (time, .) = detection probability different in each year, constant over surveys.

Model	AIC	ΔAIC	w_i	K	ψ_{1998}(Tuss)	ψ_{1998}(Past)	γ_{1998}(Tuss)	γ_{1998}(Past)	γ_{1999}(Tuss)	γ_{1999}(Past)
ψ(habitat) ε(habitat) γ(habitat)p(time,.)	1741.9	0.00	0.34	11	0.51	0.23	0.10	0.05	0.10	0.05
ψ(habitat) ε(t+habitat) γ(habitat)p(time,.)	1742.0	0.10	0.31	14	0.50	0.23	0.16	0.07	0.03	0.01
ψ(habitat) ε(habitat) γ(habitat)p(t+habitat,.)	1743.9	2.00	0.13	11	0.51	0.23	0.10	0.05	0.10	0.05
ψ(habitat) ε(t+habitat) γ(t+habitat)p(time,.)	1744.4	2.50	0.1	15	0.49	0.23	0.16	0.07	0.02	0.01
ψ(habitat) ε(habitat) γ(t+habitat)p(time,.)	1744.7	2.80	0.08	14	0.51	0.23	0.10	0.05	0.10	0.05
ψ(habitat) ε(t+habitat) γ(t+habitat)p(t+habitat,.)	1746.4	4.50	0.04	15	0.49	0.23	0.16	0.07	0.02	0.01
ψ(.) ε(habitat) γ(habitat)p(time,.)	1759.9	18.00	<0.0001	10	0.39	0.39	0.11	0.04	0.11	0.04
ψ(.) ε(habitat) γ(habitat)p(t+habitat,.)	1760.8	18.90	<0.0001	10	0.40	0.40	0.11	0.04	0.11	0.04
ψ(.) ε(t+habitat) γ(t+habitat)p(time,.)	1760.9	19.00	<0.0001	14	0.37	0.37	0.19	0.07	0.02	0.01
ψ(.) ε(t+habitat) γ(t+habitat)p(t+habitat,.)	1762.2	20.30	<0.0001	14	0.38	0.38	0.20	0.07	0.01	0.003
Model averaged estimates (1 SE)					0.49 (0.02)	0.23 (0.03)	0.12 (0.01)	0.06 (0.004)	0.07 (0.01)	0.03 (0.006)

Cont'd from above

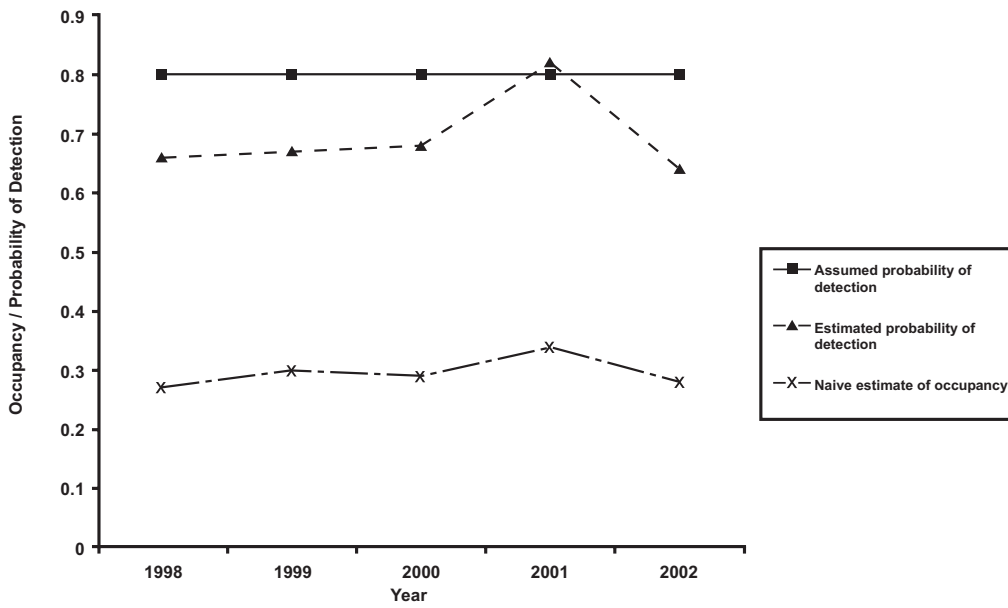| γ_{2000}(Tuss)	γ_{2000}(Past)	γ_{2001}(Tuss)	γ_{2001}(Past)	ε_{1998}(Tuss)	ε_{1998}(Past)	ε_{1999}(Tuss)	ε_{1999}(Past)	ε_{2000}(Tuss)	ε_{2000}(Past)	ε_{2001}(Tuss)	ε_{2001}(Past)
0.10	0.05	0.10	0.05	0.08	0.16	0.08	0.16	0.08	0.16	0.08	0.16
0.10	0.05	0.14	0.06	0.08	0.16	0.08	0.16	0.08	0.16	0.08	0.16
0.10	0.05	0.10	0.05	0.08	0.17	0.08	0.17	0.08	0.17	0.08	0.17
0.10	0.04	0.14	0.04	0.06	0.12	0.06	0.12	0.12	0.22	0.14	0.25
0.10	0.05	0.10	0.05	0.06	0.12	0.06	0.12	0.11	0.21	0.14	0.26
0.10	0.05	0.14	0.06	0.06	0.12	0.06	0.12	0.12	0.22	0.14	0.25
0.11	0.04	0.11	0.04	0.08	0.17	0.08	0.17	0.08	0.17	0.08	0.17
0.11	0.04	0.11	0.04	0.08	0.15	0.08	0.15	0.08	0.15	0.08	0.15
0.11	0.04	0.15	0.05	0.06	0.12	0.06	0.12	0.11	0.22	0.13	0.25
0.11	0.04	0.15	0.05	0.06	0.11	0.06	0.11	0.11	0.20	0.14	0.24
0.10 (0.002)	0.05 (0.002)	0.11 (0.007)	0.05 (0.002)	0.07 (0.003)	0.13 (0.008)	0.07 (0.003)	0.15 (0.008)	0.09 (0.006)	0.17 (0.009)	0.09 (0.01)	0.18 (0.015)

Figure 1. Assumed (solid squares) and estimated (solid triangles) probabilities of detecting grand skinks (*Oligosoma grande*) on rock tors, and naïve estimates (crosses) of rock-tor occupancy based on the proportion of sites where grand skinks were detected at least once, between 1998 and 2002.

average overall occupancy probability for those models that included it was 0.38 (SE 0.07). In pasture habitat the model-averaged occupancy probability was 0.23 (0.03), while in tussock habitat it was 0.49 (0.02) (Table 1); both are higher than the naïve estimates of occupancy for pasture and tussock at 0.20 and 0.44, respectively (Table 2). Model-averaged estimates suggest that the probability of colonisation tends to be higher in tussock habitat than in pasture habitat, with values in tussock being around double those in pasture (Table 1). The opposite is true for extinction, with values in pasture habitat being higher than those in tussock habitat. Extinction rates in pasture habitat appear to be increasing over time (Table 1). The derived estimates, based on the top-ranked model, of site occupancy over time show only a very slow trend in either tussock or pasture habitat, suggesting that occupancy was reasonably static over the period 1998–2002 (Table 3). Detection probability did not differ between tussock and pasture habitat; the average detection probability for tussock habitat over the 5 years was c. 0.70, while in pasture it was c. 0.69 (Table 4).

Discussion

The results suggest that between 1998 and 2002 the overall level of occupancy of rock tors by *Oligosoma grande* at Trig E Ridge in Macraes Flat has been constant, but there may be systematic changes in the occupancy state of individual sites that are consistent with viewing grand skinks as a metapopulation. The naïve estimates of site occupancy would indicate lower and more variable levels of occupancy than is apparent when incomplete detectability is taken into account. This may be in part due to inter-annual changes in detectability, possibly arising from differences in weather condition during surveys, and/or observer experience. The overall model-averaged estimate of detection probability was c. 0.7 for tussock and c. 0.69 for pasture. The model-averaged estimates produced for each year of the study showed that detection probabilities may vary between years. This variation may be a result of observer error and skill level. Unaccounted for variation in detectability may yield spurious patterns of naïve occupancy, whereby a high probability of detection in one year could be interpreted

Table 2. Naïve estimate of occupancy expressed as the proportion of sites where a grand skink (*Oligosoma grande*) was seen at least once in tussock and pasture habitat based on the first survey of each year. Average for tussock = 0.44, average for pasture = 0.20.

Year	Tussock	Pasture
1998	0.41	0.19
1999	0.43	0.19
2000	0.44	0.20
2001	0.48	0.24
2002	0.43	0.19

Table 3. Derived estimates, using the starting estimate of extinction and colonisation probabilities from the top-ranked model (Table 1), and (SE) of grand skink (*Oligosoma grande*) occupancy probabilities for tussock and pasture habitat between 1998 and 2002.

Year	Tussock	Pasture
1998	0.515 (0.02)	0.234 (0.01)
1999	0.520 (0.05)	0.232 (0.05)
2000	0.525 (0.03)	0.229 (0.03)
2001	0.529 (0.03)	0.228 (0.02)
2002	0.532 (0.02)	0.226 (0.03)

Table 4. Model-averaged estimates of grand skink (*Oligosoma grande*) detection probability in tussock and pasture habitat between 1998 and 2002.

Year	Tussock	Pasture
1998	0.68	0.67
1999	0.67	0.66
2000	0.69	0.68
2001	0.83	0.82
2002	0.64	0.63

as an increase in occupancy and cause for optimism, whereas a low level of detectability in a subsequent year would be mistakenly interpreted as a decline in occupancy warranting urgent management intervention. The robust estimates derived in this study suggest that the true occupancy level is higher than the simple proportion of sites where skinks were detected at least once, and indicates the importance of surveying sites more than once to enable season-specific estimates of detectability to be used to derive an accurate estimate of site occupancy. Claims and apparent evidence of the marked decline of *Oligosoma grande* over time (Whitaker 1996; Houghton & Linkhorn 2002) appear to be contradicted by the results of this study, which show only very slow trends in occupancy in pasture or tussock habitats. Declines may be obscured somewhat when looking at occupancy alone due to the lowering of population sizes rather than restriction of distribution in the area studied. The number of rocks occupied by *Oligosoma grande* may not have declined, but the number of skinks on rocks may be lower. Dispersal of both juveniles and breeding adults, and movements of skinks within home ranges, may account for the apparently static levels of site occupancy. It is known that adult *Oligosoma grande* inhabit home ranges of around 200–800 m^2 (Marshall 2000). This may result in enough movement over the period of the rock-tor counts to ensure that there is little change in site occupancy (i.e. the same number of rocks are occupied at all times).

There is strong support in the results for models that state local extinction as habitat-specific. The variability in average extinction probabilities suggest that if *Oligosoma grande* populations are indeed going through fluctuations in site occupancy, there may be some extinction pattern occurring at certain time intervals. The same may be said for colonisation, which also seems to be habitat-specific.

Average extinction probabilities tended to be higher than average colonisation probabilities. Reasons for this are unclear; though habitat degradation and habitat loss seem likely (Whitaker 1996; Houghton & Linkhorn 2002). Even though the overall level of occupancy appears to be constant, there may be individual sites that are experiencing higher levels of extinction than others. This could increase the risk of isolating rock tors thus reducing the likelihood of dispersal-mediated recolonisation of vacant patches or rescue effects whereby small populations on individual rock tors are prevented from going extinct by immigration (Le Galliard et al. 2005).

Management implications and future research directions

This study has highlighted the importance of considering incomplete detectability when using presence/absence data to estimate metapopulation parameters to guide management of endangered species. Future work should aim to achieve multiple annual presence/absence surveys of suitable habitat patches in order to track trends in site occupancy and to derive estimates of colonisation and extinction rates that take incomplete detectability into account. Concurrent recording of patch characteristics will enable estimates derived from robust empirical presence models to be compared with predictions derived from models that assume patch-specific rates.

Acknowledgements

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