

Spatial occupancy models for predicting metapopulation dynamics and viability following reintroduction

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Summary

1. The reintroduction of a species into its historic range is a critical component of conservation programmes designed to restore extirpated metapopulations. However, many reintroduction efforts fail, and the lack of rigorous monitoring programmes and statistical models have prevented a general understanding of the factors affecting metapopulation viability following reintroduction.

2. Spatially explicit metapopulation theory provides the basis for understanding the dynamics of fragmented populations linked by dispersal, but the theory has rarely been used to guide reintroduction programmes because most spatial metapopulation models require presence–absence data from every site in the network, and they do not allow for observation error such as imperfect detection.

3. We develop a spatial occupancy model that relaxes these restrictive assumptions and allows for inference about metapopulation extinction risk and connectivity. We demonstrate the utility of the model using six years of data on the Chiricahua leopard frog *Lithobates chiricahuensis*, a threatened desert-breeding amphibian that was reintroduced to a network of sites in Arizona USA in 2003.

4. Our results indicate that the model can generate precise predictions of extinction risk and produce connectivity maps that can guide conservation efforts following reintroduction. In the case of *L. chiricahuensis*, many sites were functionally isolated, and 82% of sites were characterized by intermittent water availability and high local extinction probabilities (0.84, 95% CI: 0.64–0.99). However, under the current hydrological conditions and spatial arrangement of sites, the risk of metapopulation extinction is estimated to be < 3% over a 50-year time horizon.

5. Low metapopulation extinction risk appears to result from the high dispersal capability of the species, the high density of sites in the region and the existence of predator-free permanent wetlands with low local extinction probabilities. Should management be required, extinction risk can be reduced by either increasing the hydroperiod of existing sites or by creating new sites to increase connectivity.

6. *Synthesis and applications.* This work demonstrates how spatio-temporal statistical models based on ecological theory can be applied to forecast the outcomes of conservation actions such as reintroduction. Our spatial occupancy model should be particularly useful when management agencies lack the funds to collect intensive individual-level data.

Key-words: Allee effects, amphibian, connectivity, ecological forecasts, extinction, hierarchical models, *Lithobates chiricahuensis*, spatial correlation, spatio-temporal models, translocation

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Introduction

Reintroducing species into historic portions of their ranges has become an important conservation tool to counteract biodiversity loss, and it has spurred the development of reintroduction biology, a new scientific discipline aimed at understanding the dynamics and viability of reintroduced populations (Ewen, Armstrong & Parker 2012). Advancing the field of reintroduction biology requires that managers and scientists develop rigorous monitoring programmes and statistical models to answer research questions and predict persistence under different management scenarios (Dodd 2005; Seddon, Armstrong & Maloney 2007; Armstrong & Seddon 2008; Nichols & Armstrong 2012; Ewen, Soorae & Canessa 2014).

Most reintroductions involve releasing a small number of individuals to a single site, yet even in these simple situations, limited resources often preclude research past the initial stages of site selection and reintroduction (Seddon, Strauss & Innes 2012). The challenge of monitoring becomes even more daunting when species occur as metapopulations, i.e. fragmented populations experiencing occasional local extinction and colonization events (Hanski 1999). In the context of metapopulation reintroductions, it would be ideal to model subpopulation abundance and vital rates as well as movement among subpopulations, but this is rarely accomplished due to the high costs of marking and monitoring individuals over time and space (Armstrong & Ewen 2002; Larkin *et al.* 2003; Muths, Bailey & Watry 2014; Servanty, Converse & Bailey 2014).

A cost-efficient alternative to modelling metapopulation abundance is to model site occupancy dynamics (Nichols & Armstrong 2012). In addition to being easier to monitor, occupancy is the standard state variable of interest in metapopulation theory, which is one of the most well-developed branches of ecological theory and one with tremendous potential for predicting the success of reintroductions (Hanski & Ovaskainen 2000). Although early metapopulation models were deterministic, non-spatial, and did not admit variation in site quality (Levins 1969), modern stochastic patch occupancy models (hereafter spatial metapopulation models) overcome these deficiencies (Day & Possingham 1995; Frank & Wissel 1998; Hanski & Ovaskainen 2003; Harrison, Hanski & Ovaskainen 2011). Spatial metapopulation models regard occupancy dynamics as a function of site-level colonization and extinction probabilities, which themselves may be functions of the spatial arrangement of sites or environmental variables associated with the sites.

The transition from non-spatial to spatial models has made it possible to assess the relative effects of connectivity and habitat quality on extinction risk, which is important for predicting the outcomes of reintroductions (Moilanen & Hanski 2001; Tischendorf & Fahrig 2001; van Teeffelen, Cabeza & Moilanen 2006). In fact, Hanski *et al.* (1996) argued that non-spatial models have little

value in applied settings because colonization is determined by dispersal capacity and the spatial arrangement of sites, and ignoring these factors results in implausible predictions such as colonization when all sites are unoccupied. As a result, non-spatial models preclude the possibility of metapopulation extinction and therefore cannot be used for inference about metapopulation viability following reintroduction.

Despite the enormous potential of spatially explicit metapopulation models for predicting dynamics and viability, there are several challenges to fitting these models that have prevented widespread application (Baguette 2004). One important challenge is that most spatial models require presence-absence data for *all* sites in the metapopulation network. Without this information, the influence of surrounding sites on colonization probability is unknown, and unmodelled heterogeneity in colonization can produce bias (Moilanen 2002; Etienne, Braak & Vos 2004; Risk, De Valpine & Beissinger 2011). In practice, insufficient funds, restricted access or limited knowledge of the study system usually make it impossible to survey all sites.

A second problem hindering the application of spatial metapopulation models is that, even if all sites are surveyed, imperfect detection introduces uncertainty about the true occupancy state. Consequently, naive estimates of the proportion of sites occupied will be too low (MacKenzie *et al.* 2006), and estimates of extinction probability will be too high (Alpizar-Jara *et al.* 2004; Kéry *et al.* 2006). This problem has motivated the development of models that allow for inference about both occupancy and detection parameters (MacKenzie *et al.* 2003; Tyre *et al.* 2003; Royle & Kéry 2007). Although applied widely, these dynamic occupancy models are not spatially explicit and hence share some of the limitations of early metapopulation models.

Recent efforts have begun to fuse dynamic occupancy models with spatial metapopulation models so that metapopulation theory can be applied in the typical situation in which not all sites are surveyed and observation error prohibits perfect knowledge of occupancy status (Harrison, Hanski & Ovaskainen 2011; Risk, De Valpine & Beissinger 2011; Heard *et al.* 2013; Sutherland, Elston & Lambin 2014). While these spatial occupancy models have increased the utility of spatial metapopulation theory, existing models require either demographic data that may be too expensive to collect or assumptions about how abundance scales with area, which may not hold in many systems.

The purposes of this paper are to (i) present a spatial occupancy model suitable for standard binary detection data that arise from many metapopulation monitoring studies and (ii) demonstrate how the model can be used to assess metapopulation viability, connectivity and spatial spread following reintroduction of a declining species into an area where it had gone extinct. We analyse 6 years of post-reintroduction data collected on the US

federally threatened Chiricahua leopard frog *Lithobates chiricahuensis* (USFWS, 2007) and evaluate the extent to which leopard frog metapopulation dynamics are governed by initial release conditions, site configuration and hydrological conditions.

Materials and methods

SAMPLING DESIGN AND DATA

Lithobates chiricahuensis is restricted to portions of Arizona, New Mexico and northern Mexico (Fig. 1), where it occurs as a set of metapopulations. In 2001, the metapopulation in the Altar Valley of southern Arizona went extinct, presumably as a result of drought and predation by the invasive American bullfrog *Lithobates catesbeiana*. However, following the implementation of predator control, *L. chiricahuensis* was reintroduced as larvae to three sites in the Buenos Aires National Wildlife Refuge (BANWR) in 2003 (Jarchow *et al.*, 2015). Sites here are defined as any wetland potentially suitable for reproduction. Due to extensive destruction of the natural habitat, most sites in the

region are constructed wetlands built to provide water for livestock.

Our work was restricted to the Altar Valley of southern Arizona that includes portions of BANWR as well as public and private land used primarily for grazing (Fig. 1). Within this region, we used aerial photographs, topographic maps and ground searches to locate all possible breeding locations. Although it is possible that a few small sites were not found, for our purposes, we regard the 273 discovered sites as the entire set of sites available to this metapopulation. From this collection of sites, we randomly selected 41 at which we conducted occupancy surveys in June, immediately prior to reproduction and the onset of the monsoon season. Each site was surveyed as many as three times per year, for up to 6 years (2007–2012; Jarchow *et al.*, 2015).

Surveys were conducted between 21:00 h and 02:00 h, and observers recorded $y_{i,jk} = 1$ if they detected at least one leopard frog or $y_{i,jk} = 0$ if no detections were made at site i in $1, \dots, R$ on occasion j in $1, \dots, J$ during year k in $1, \dots, K$. All detections were of juveniles and adults, made during night-time visual encounter surveys (Fellers & Kleeman 2006). It is important to note that no data were collected during the 3 years following reintroduction. In addition, we recorded the spatial coordinates

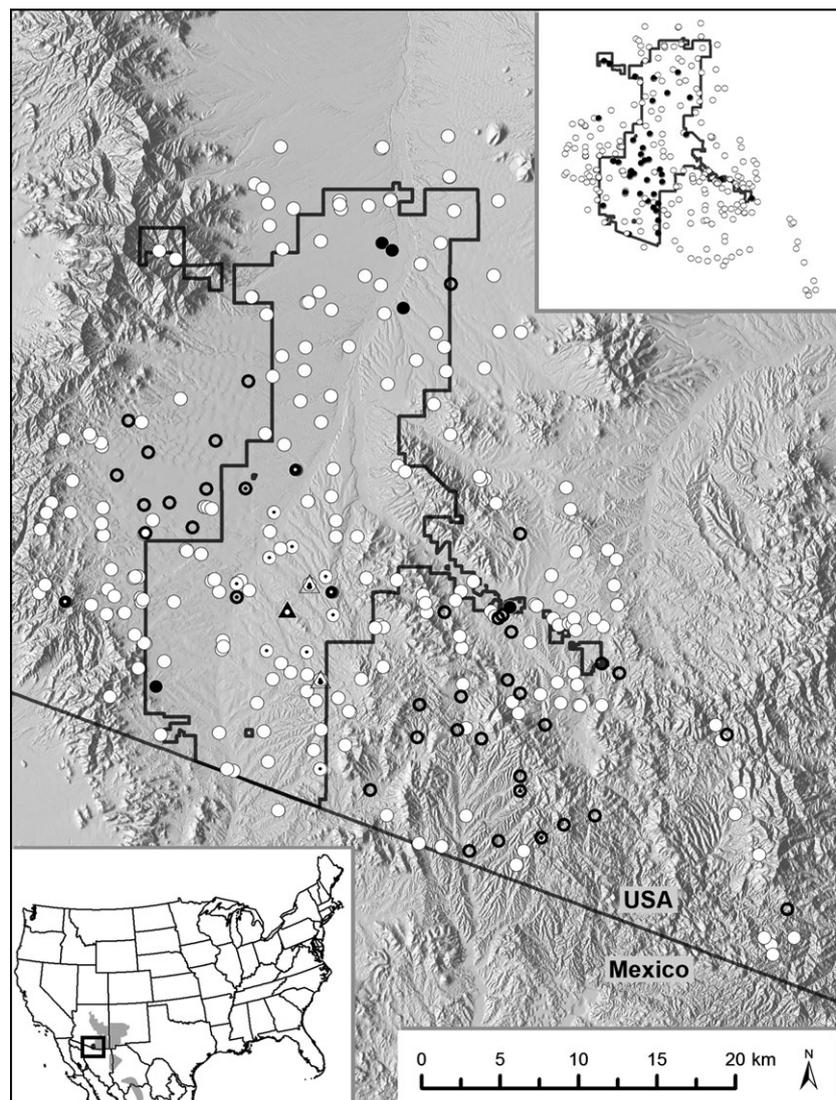


Fig. 1. Locations of all sites in the metapopulation network in the Altar Valley, Arizona. White circles are sites with intermittent water availability, open black circles are semi-permanent sites, and filled black circles represent sites with permanent water. The three release sites are shown as triangles. Dots inside circles are sites where at least one frog was detected. The polygon is the refuge boundary. Filled circles in the upper inset indicate the 41 sites that were sampled at least once. The lower inset indicates the known range of the species and the location of the study area.

and a hydroperiod variable indicating whether the site held water permanently (40 sites), semi-permanently (nine sites) or intermittently (224 sites) at all 273 sites. The hydroperiod variable was recorded during field surveys conducted as part of the bullfrog eradication effort. We also recorded temperature and an index of wind speed on each survey occasion because we expected that these variables might influence activity patterns and detection probability.

SPATIAL OCCUPANCY MODEL

We developed a spatial occupancy model that can be used to predict the dynamics and viability of reintroduced metapopulations while accounting for the observation error associated with binary detection data. From a statistical perspective, our model is a spatially explicit first-order hidden Markov model with components describing (i) the initial occupancy state at time $k = 1$, (ii) the occupancy state in subsequent time periods as determined by colonization and extinction processes and (iii) the detection process. The key distinction between our model and standard dynamic occupancy models (MacKenzie *et al.* 2003; Royle & Kéry 2007) is that we directly account for the reintroduction process and we treat colonization and extinction as stochastic spatial processes based on spatially realistic metapopulation theory (Hanski 1999).

Let z denote the true occupancy state, such that $z_{i,k} = 1$ if site i was occupied by at least one individual during year k , and $z_{i,k} = 0$ if the site was unoccupied. In standard dynamic occupancy models, the expected value of occupancy in the first time period (ψ) is usually modelled as a logit-linear function site-specific covariates; however, in the context of species reintroductions, the true initial occupancy state is determined by the reintroduction design, and thus, $\{z_{i,1}\}$ are data, not latent variables. If for some reason, the release locations were not recorded, one could estimate the initial occupancy state, but this would introduce additional uncertainty into the model and should be avoided if possible.

We model occupancy dynamics in subsequent years as:

$$z_{i,k} \sim \text{Bernoulli}(\gamma_{i,k-1}(1 - z_{i,k-1}) + \phi_{i,k-1}z_{i,k-1}) \quad \text{eqn 1}$$

such that an unoccupied site at time $k-1$ is colonized with probability $\gamma_{i,k-1}$, and an occupied site remains occupied with probability $\phi_{i,k-1}$. In spatial metapopulation models, colonization is defined as the successful dispersal of at least one individual to an unoccupied site from at least one neighbouring site that was occupied in the previous year. Thus, colonization is a function of the dispersal ability of the species, the occupancy status of all other sites in the metapopulation network and the spatial arrangement of the sites. We therefore used a distance-based dispersal model as the basis for each pairwise colonization probability. We chose a model based on the Gaussian kernel for this purpose because it is a standard model used to describe a gradual decrease in dispersal probability with distance (Clobert *et al.* 2012). Under the Gaussian model, the probability that site i is colonized by at least one individual from site j is:

$$\rho_{i,j,k} = \rho_0 \exp(-d_{i,j}^2/(2\sigma^2))z_{j,k-1} \quad \text{eqn 2}$$

where ρ_0 is the baseline colonization probability for coincident sites, $d_{i,j}$ is the Euclidean distance between sites, and σ is the scale parameter determining the rate of decay in colonization

probability as a function of distance. This parameterization enforces the condition that site i cannot be colonized by site j if $z_{j,k-1} = 0$.

Having defined each pairwise colonization probability, the cumulative probability of a colonization event is given by:

$$\gamma_{i,k} = 1 - \left\{ \prod_{j=1}^M (1 - \rho_{i,j,k}) \right\} \quad \text{eqn 3}$$

where M is the total number of sites in the metapopulation network. Equation 3 can be viewed as a measure of site-level connectivity because sites with low values of $\gamma_{i,k}$ are functionally isolated from occupied sites. Summing eqn 3 over all sites in the network results in a measure of landscape-level connectivity (Tischendorf & Fahrig 2001). Equation 3 can be used to create connectivity maps by evaluating it at all locations within the study area. In practice,

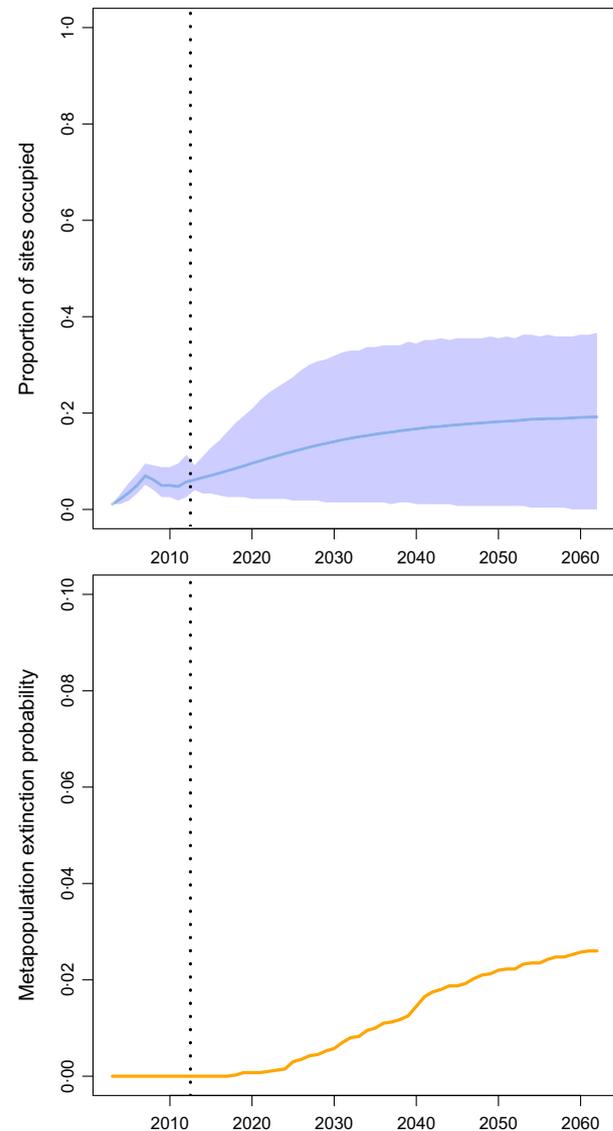


Fig. 2. Proportion of sites occupied and metapopulation extinction probability for the 9 years following reintroduction of the Chiricahua leopard frog and the 50-year projection. Estimates are posterior means and 95% credible intervals. The vertical lines represent the final year with data.

the evaluations can be made at points defined by a regular grid imposed over the region. The resulting connectivity maps represent the probability that a hypothetical new site would be colonized if placed anywhere in the study area. Such maps could be used by managers to identify locations for creating new sites to enhance metapopulation viability following reintroduction.

Equation 3 differs from colonization functions used in many metapopulation models in that it does not assume that the number of emigrants scales linearly with patch area (Hanski 1998). We did not use an area-based formulation because area is not a reliable proxy of abundance for pond-breeding amphibians, and hydroperiod is expected to exert much stronger influence over metapopulation dynamics (Prugh *et al.* 2008; Gould *et al.* 2012). To account for variation in hydroperiod among sites, we estimated local extinction probability (ϵ) for each of the three hydroperiod classes: intermittent, semi-permanent and permanent. We also allowed for the rescue effect, in which extinction events are less likely to be observed at highly connected sites than at isolated sites, because the former sites have a greater chance of being colonized immediately after extinction. Hanski (1999, p. 60) calls this the pseudo-rescue effect to distinguish it from the effects of connectivity on actual extinction risk (Brown & Kodric-Brown 1977). We modelled the pseudo-rescue effect as: $\phi_{i,k-1} = 1 - \epsilon_i (1 - \gamma_{i,k-1})$, indicating that the probability that an occupied site remains occupied is one minus the probability it goes extinct and is not recolonized.

The final component of our model describes the detection process. As with many species, Chiricahua leopard frogs are not always detected during surveys when they are present, and hence, the true occupancy state of a site is often unknown. In our study, there were only two situations in which the actual occupancy state was known with certainty: in the initial release year, and in survey years at sites where frogs were detected. To account for the fact that sites may have been occupied even when no detections were recorded, we modelled the observed data conditional on the latent occupancy state and as a function of detection probability $p = \Pr(y = 1|z = 1)$. We allowed for the possibility that detection probability might be influenced by temperature and wind, and included these effects in a logit-linear model:

$$y_{i,j,k} \sim \text{Bernoulli}(z_{i,k} \times p_{i,j,k}) \quad \text{eqn 4}$$

$$\text{logit}(p_{i,j,k}) = \beta_0 + \beta_1 \text{TEMP}_{i,j,k} + \beta_2 \text{PRECIP}_{i,j,k} \quad \text{eqn 5}$$

where the β parameters are regression coefficients to be estimated.

We analysed our model using Bayesian methods because standard likelihood-based approaches would be challenging to implement given the high number of conditionally related discrete

random variables. Moreover, a Bayesian analysis using MCMC allowed us to make metapopulation projections and thereby forecast metapopulation viability while accounting for parameter uncertainty. Forecasts were made by using each posterior draw to project the metapopulation forward over a 50-year time horizon. For each year of the projection, we computed the number of sites occupied: $N_k = \sum_{i=1}^M z_{i,k}$ and the metapopulation extinction risk (ζ_k), defined as the proportion of MCMC projections in which the metapopulation went extinct before or during year k . An alternative and equivalent way to present extinction risk would be in terms of time to extinction (T_e) because ζ_k is the cumulative distribution of this random variable.

We used vague priors for all parameters. Specifically, we used logit-transformed Uniform(0,1) priors for the three hydroperiod-specific extinction parameters ϵ_1 , ϵ_2 , ϵ_3 and β_0 , β_1 , β_2 . We used a Uniform(0,1) prior for ρ_0 , and a Gamma(1,0.1) prior for σ . We sampled posterior distributions using four Markov chains each of length 50 000 after discarding the initial 5000 samples as burn-in. Point estimates are reported as posterior means and 95% credible intervals. MCMC sampling was conducted using JAGS-3.3.0 run from R with the rjags package (Plummer 2013; R Core Team, 2013). Convergence was assessed using the Gelman-Rubin diagnostic. JAGS code and convergence diagnostics are presented in Appendix S1 (Supporting information).

Results

The proportion of sites occupied grew steadily following the 2003 reintroduction except for a 2-year period of retraction in 2008 and 2009 (Fig. 2). Model projections indicate that the proportion of sites occupied will continue to increase to approximately 20% site occupancy by year 2060 (Fig. 2). However, in each future year, there is a non-negligible probability that each of the occupied sites will go extinct, and as a result, the extinction risk for the entire metapopulation is predicted to increase slightly each year to nearly 3% by the end of the 50-year forecast horizon (Fig. 2).

Our results suggest two reasons why metapopulation extinction risk is so low. First, the dispersal capabilities of leopard frogs appear sufficient to colonize new sites given the spatial arrangement of existing sites. This is true even though the probability that an unoccupied site was colonized by an adjacent occupied neighbour was only 0.060 (CI: 0.019–0.132) and decreased to <0.001 for neighbours beyond 5 km (Table 1, Fig. 3). The high density of sites compensated for the low pairwise colonization prob-

Table 1. Posterior mean, SD and percentiles for parameters of the spatial occupancy model

Parameter	Description	Mean	SD	2.5%	50%	97.5%
ρ_0	Baseline colonization probability	0.060	0.030	0.019	0.054	0.132
σ	Scale parameter of colonization function	2.939	0.841	1.743	2.796	4.972
ϵ_1	Extinction prob. for intermittent sites	0.882	0.090	0.652	0.905	0.989
ϵ_2	Extinction prob. for semi-permanent sites	0.195	0.125	0.031	0.169	0.504
ϵ_3	Extinction prob. for permanent sites	0.092	0.060	0.014	0.079	0.242
β_0	Intercept of logit-linear detection model	0.835	0.225	0.403	0.830	1.288
β_1	Effect of temperature on logit(p)	0.112	0.266	-0.413	0.114	0.630
β_2	Effect of wind on logit(p)	0.442	0.338	-0.140	0.413	1.177

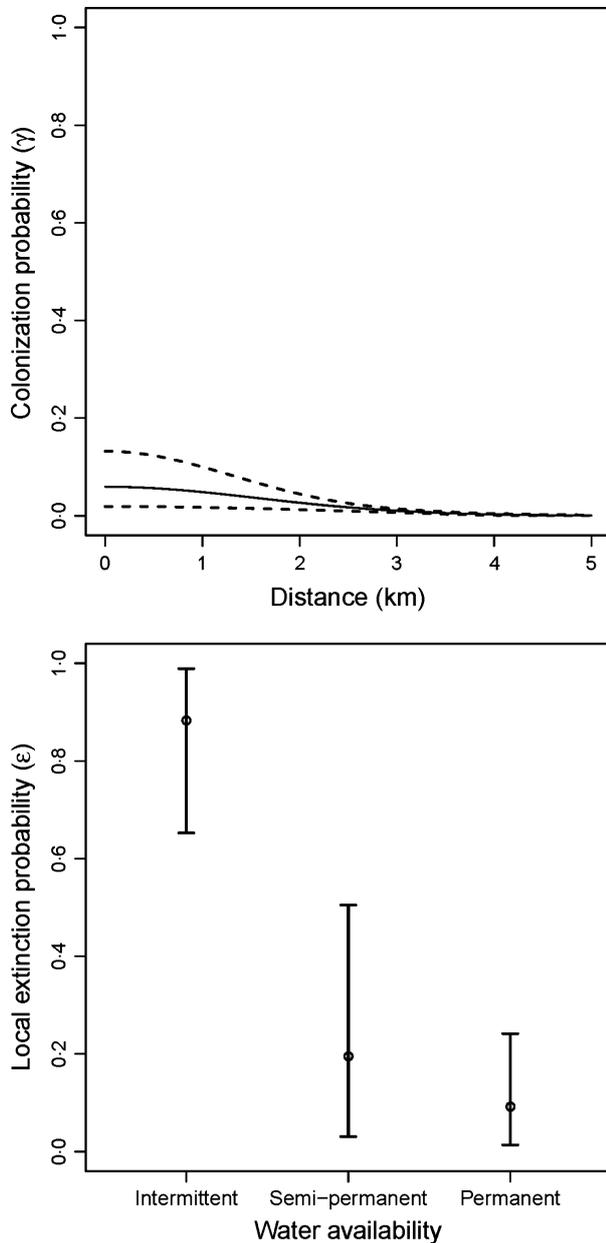


Fig. 3. Colonization probability for Chiricahua leopard frogs as a function of distance to an occupied site, and local extinction probability in the three water availability classes. Estimates represent posterior means and 95% credible intervals.

abilities, resulting in an overall colonization probability >0.15 for many sites in the core of the study area (Fig. 4). However, many other sites were effectively isolated, and colonization dynamics varied considerably over time as the metapopulation expanded and contracted (Fig. 4).

The second reason why overall metapopulation extinction risk is low is because local extinction probabilities were <0.1 at the 40 sites with permanent water (Table 1, Fig. 3). As a result, our projections indicate that, once colonized, these sites are likely to remain occupied for numerous consecutive seasons (Table 1, Fig. 3). Given the relatively high local extinction probabilities at the other

sites, and the fact that 82% (224/273) of the sites only held water intermittently, the permanent water sites are critical to the viability of this metapopulation.

All of our results account for observation error due to imperfect detection. However, we determined that detection probability was not affected strongly by either wind or temperature as evidenced by 95% credible intervals that included 0 for both β_1 and β_2 (Table 1). The overall probability of detecting the species during a survey, given that it was present, was 0.69 (95% CI: 0.60–0.78) and was >0.97 after just three surveys, suggesting that two visits per year would be sufficient for sampling this metapopulation.

Discussion

Spatial metapopulation theory represents one of the most coherent and potentially useful frameworks for assessing the viability of fragmented populations linked by dispersal, but until now it had not been used for statistical inference in the context of metapopulation reintroduction programmes. One reason for this is the fact that most spatial metapopulation models require abundance data or data free of observation error, which can be cost prohibitive or impossible to acquire. We developed and applied a spatially explicit model that combines recent developments in metapopulation theory with innovations in occupancy modelling and only requires standard binary detection data from surveys of a subset of sites.

Our model can be viewed as a spatially explicit extension of occupancy models that account for imperfect detection (MacKenzie *et al.* 2006). Several other spatially explicit extensions of these models exist, all of which account for spatial correlation in colonization and extinction dynamics using autologistic or conditional autoregressive (CAR) models (Besag 1974; Bled, Royle & Cam 2011; Yackulic *et al.* 2012; Bled, Nichols & Altwegg 2013; Broms *et al.* 2013; Eaton *et al.* 2014). These models apply to systems in which the ‘neighbourhood’ of sites (i.e. the set of sites that might influence the occupancy dynamics of a focal site) is defined *a priori*, typically as adjacent cells on a grid or neighbouring polygons. Our approach differs in that we use a colonization model based on a dispersal function to estimate the spatial correlation between all pairs of sites. This avoids the need to make subjective decisions about spatial neighbourhoods. The models of Risk, De Valpine & Beissinger (2011), Heard *et al.* (2013) and Sutherland, Elston & Lambin (2014) are similar to the one developed here, but our application is unique in that we had data on the reintroduction locations and we were able to account for all of the sites in the metapopulation network, not just those that were sampled.

We demonstrated the utility of the model to assess the viability of the Chiricahua leopard frog metapopulation that was reintroduced in 2003. Our results indicate that the species colonized new sites rapidly following reintroduction, suggesting that Allee effects (Deredec & Courchamp 2007), if present, were minimal. Although our

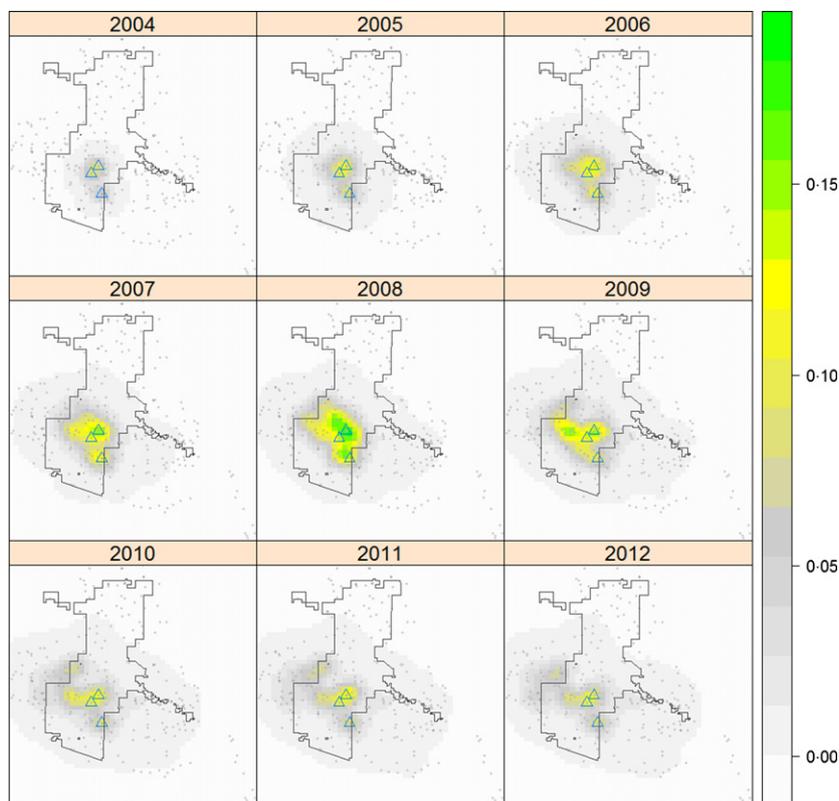


Fig. 4. Colonization probability surfaces (posterior means) for the 9 years following reintroduction. The colour of the surface depicts the probability that a hypothetical site would be occupied at any location in the region, conditional on the estimated occupancy states of all sites in the previous year. Triangles represent the three reintroduction sites.

model predicts that metapopulation extinction risk is low over the next 50 years, our estimate may be optimistic because we did not have enough data to model the possibility of catastrophic events such as extreme drought or the invasion of new exotic predators. In addition, most sites are isolated by distance and hold water only intermittently. Of the sites that do hold permanent water and are highly connected, many lie off the refuge and therefore are not easily managed.

Our findings suggest several management actions that could increase viability. One potential management action would be to increase the hydroperiod of sites that currently hold water only intermittently. This could ameliorate potential effects of high annual variation in precipitation delivered by summer monsoons. However, in addition to providing habitat for Chiricahua leopard frogs, permanent water attracts predators such as the American bullfrog and other invasive species that compete with or prey upon the Chiricahua leopard frog (USFWS, 2007). Because bullfrogs are present at sites near the refuge, the persistence of Chiricahua leopard frogs in the Altar Valley is likely conditional upon the continued management of bullfrogs. Another management action that could increase metapopulation viability is the construction of new sites to improve connectivity and increase the potential for colonization.

Unlike many studies that have used expert opinion and *ad hoc* connectivity metrics, we directly estimated the connectivity. Our results suggest that sites >4 km from an occupied site have very little chance of being colonized.

This finding suggests that amendments are needed to the 5-year review of the recovery plan USFWS (2011) that recommends 3–5 km spacing. In addition to allowing for recommendations about site spacing, the estimated colonization probability surfaces from our model can be used to select optimal locations for establishing new sites (*sensu* van Teeffelen, Cabeza & Moilanen 2006), ideally as part of a formal decision analysis process accounting for financial and logistical constraints (Drechsler *et al.* 2003; Runge 2011; Converse *et al.* 2013).

One challenge to fitting spatial metapopulation models is deciding how much model complexity to allow (Harrison, Hanski & Ovaskainen 2011). Although it is useful to make inferences about metapopulation dynamics using simple binary data, we did not feel that our data from just 41 sites and 6 years were sufficient for modelling complex processes such as spatially correlated extinction (Sutherland, Elston & Lambin 2012), or abundance-induced heterogeneity in dispersal (Sutherland, Elston & Lambin 2014). Such trade-offs are common in ecological research, and researchers and managers need to consider the importance of these processes when deciding how much sampling effort is needed and what state variable is to be monitored.

Our work demonstrates that many of the obstacles preventing the application of metapopulation theory in reintroduction contexts can be overcome using spatial occupancy models. These tools allow for inference about spatial and temporal metapopulation dynamics without sampling all sites in the metapopulation and without

ignoring observation error, thereby increasing the opportunities for making science-based conservation decisions founded on well-established theory.

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Data accessibility

The data in the present study have not been archived because the data contain sensitive information about a protected species listed as threatened under the U. S. Endangered Species Act.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. JAGS model statement, MCMC traceplots, and posterior densities.