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Chris Sutherland, *University of Massachusetts - Amherst*

D. A. Elston

X. Lambin

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A demographic, spatially explicit patch occupancy model of metapopulation dynamics and persistence

C. S. SUTHERLAND,^{1,3,4} D. A. ELSTON,² AND X. LAMBIN¹

¹*School of Biological Sciences, University of Aberdeen, Aberdeen AB24 2TZ United Kingdom*

²*Biomathematics and Statistics Scotland, Craigiebuckler, Aberdeen AB15 8QH United Kingdom*

³*New York Cooperative Fish and Wildlife Research Unit, Department of Natural Resources, Cornell University, Ithaca, New York 14853 USA*

Abstract. Patch occupancy models are extremely important and popular tools for understanding the dynamics, and predicting the persistence, of spatially structured populations. Typically this endeavor is facilitated either by models from classic metapopulation theory focused on spatially explicit, dispersal-driven colonization–extinction dynamics and generally assuming perfect detection, or by more recent hierarchical site occupancy models that account for imperfect detection but rarely include spatial effects, such as dispersal, explicitly. Neither approach explicitly considers local demographics in a way that can be used for future projections. However, despite being arguably of equal importance, dispersal and connectivity, local demography, and imperfect detection are rarely modeled explicitly and simultaneously. Understanding the spatiotemporal occurrence patterns of spatially structured populations and making biologically realistic long-term predictions of persistence would benefit from the simultaneous treatment of space, demography, and detectability. We integrated these key ideas in a tractable and intuitive way to develop a demographic and spatially realistic patch occupancy model that incorporates components of dispersal, local demographic stage-structure, and detectability. By explicitly relating stage-specific abundances to measurable patch properties, biologically realistic projections of long-term metapopulation dynamics could be made. We applied our model to data from a naturally fragmented population of water voles *Arvicola amphibius* to describe observed patch occupancy dynamics and to investigate long-term persistence under scenarios of elevated stage-specific local extinction. Accounting for biases induced by imperfect detection, we were able to estimate: stable, and higher than observed metapopulation occupancy; high rates of patch turnover and stage-specific colonization and extinction rates (juvenile and adult, respectively); and juvenile dispersal distances (average 2.10 km). We found that metapopulation persistence in the presence of elevated extinction risk differed depending on which life stage was exposed, and was more sensitive to elevated juvenile rather than adult extinction risk. Predictions of persistence when dynamics are stage-specific suggest that metapopulations may be more resilient to changes in the environment than predicted when relationships are based on patch size approximations rather than population sizes. Our approach allows explicit consideration of local dynamics and dispersal in spatially structured and stage-structured populations, provides a more detailed mechanistic understanding of metapopulation functioning, and can be used to investigate future extinction risk under biologically meaningful scenarios.

Key words: abundance; *Arvicola amphibius*; false negative; fragmentation; hierarchical model; migration; site occupancy; spatially realistic metapopulation theory; state-space modeling; stochastic patch occupancy model; water vole.

INTRODUCTION

Understanding observed, short-term metapopulation dynamics and translating them into useful, long-term predictions of persistence remains an important challenge for managing fragmented populations (Hanski

1998, Akçakaya and Sjögren-Gulve 2000, Etienne et al. 2004). For decades, this endeavor has been facilitated by various formulations of so-called “patch occupancy models” (Hanski 1994, Harding and McNamara 2002, MacKenzie et al. 2003). Of these, arguably the most commonly applied are stochastic patch occupancy models, SPOMs (Hanski 1994, Moilanen 1999, Ovaskainen and Hanski 2004), the core tool of spatially realistic metapopulation theory, and more recently developed detection-based occupancy models that account for imperfect detection (“detectability” models, hereafter; MacKenzie et al. 2002, 2003). Yet, despite

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⁴Present address: New York Cooperative Fish and Wildlife Research Unit, Department of Natural Resources, Cornell University, Ithaca, New York 14853 USA.
 E-mail: cs922@cornell.edu

their conceptual similarities, i.e., both model colonization–extinction dynamics conditional on patch occupancy states, the two approaches differ importantly in their inference objectives. Specifically, SPOMs consider colonization to be a function of distance-dependent dispersal from extant patches and are thus spatially explicit, whereas occupancy dynamics in detectability models rarely consider the spatial arrangement of patches between which dispersal takes place (Bled et al. 2011, Risk et al. 2011). Although both approaches have proven extremely useful to ecologists and conservation managers, there has been surprisingly little effort to formally integrate these key ideas of spatiotemporal dynamics.

SPOMs provide a formal description of how colonization–extinction dynamics are explicit functions of patch size and dispersal-driven spatial connectivity (Hanski 1994, Moilanen 1999). Major benefits of the model are that dispersal distances can be estimated from spatiotemporal patterns of patch occupancy (Risk et al. 2011, Sutherland et al. 2012), and that by using patch size as a surrogate of population size, long-term predictions of metapopulation persistence can be made without explicitly modeling demography (Hanski 1999, Moilanen 2004, Ovaskainen and Hanski 2004). However, Moilanen (2002) demonstrated that imperfect detection (false negatives) and missing data can result in overestimation of dispersal ability, connectivity, and extinction risk, and may induce large biases in subsequent predictions of metapopulation persistence. Additionally, empirical examinations of the patch size–population size assumption suggest that observed dynamics are better described by local population size (Pellet et al. 2007, Robles and Ciudad 2012) and/or structure (Franken and Hik 2004, Sutherland et al. 2012). Investigating the sensitivity to perturbations via alterations to the physical properties of the metapopulation, such as the size, number, or configuration of patches, fails to account for spatiotemporal variation in population structure and abundance; this, too, can bias predictions of metapopulation persistence. For example, demographic rates can be more sensitive than habitat quality to shifts in environment conditions (Walther et al. 2002, Gaillard and Yoccoz 2003, Ozgul et al. 2010) and are often insufficient to track environmental changes that do not affect all life stages equally (Visser and Both 2005). If responses are stage specific, or are more sensitive to perturbations than to patch quality, area-based projections may mask the true extent of extinction risk in nonstationary environments (Clinchy et al. 2002). Thus, while facilitating an intuitive understanding of metapopulation functioning, there is agreement that patch occupancy models may benefit from an explicit treatment of demography (Clinchy et al. 2002, Baguette and Schtickzelle 2003, Ozgul et al. 2009) and the errors associated with empirical data (MacKenzie et al. 2002, Moilanen 2002, Risk et al. 2011).

Royle and Kéry (2007) described a Bayesian formulation of a hierarchical patch occupancy composed of two components, a submodel for the observations that are conditional on the occupancy state, and another for the underlying occupancy state itself, which is only partially observed. The key features of the Bayesian implementation are that the latent patch occupancy states are estimated and retained (Royle and Kéry 2007 vs. MacKenzie et al. 2003) and missing data can be treated as parameters to be estimated (O'Hara et al. 2002, ter Braak and Etienne 2003). Crucially, this enables spatial effects such as distance-dependent connectivity and dispersal distances to be estimated (Risk et al. 2011) and used in subsequent projections of spatially explicit metapopulation dynamics, free from the biases previously described (Moilanen 2002). We suspect that, despite well-developed theory (Ovaskainen and Hanski 2001, 2004, Hanski and Ovaskainen 2003), the application of spatial occupancy models to empirical data has been impeded by the inability to adequately estimate spatial effects without bias when patch states are unknown and/or when data are missing.

Occupancy data are often supplemented with some form of site-level counts of individuals that are triggered by a positive detection of the focal species (e.g., two-phase sampling; Conroy et al. 2008, 2011). Because hierarchical models can be expressed as a sequence of conditional statements (Royle and Dorazio 2008), demographic information can be formally incorporated as an additional model component and used to simultaneously estimate local population size and structure. For example, the patch size–population size relationship, as well as fecundity, can be estimated directly rather than be assumed (Bender et al. 1998) by modeling the relationship between adult females and juveniles (Tavecchia et al. 2009). If these counts are formally related to site-level covariates, abundance can be estimated across all sites of interest based on these modeled relationships (*sensu* Conroy et al. 2008). Estimating such relationships within a single, hierarchical model makes it possible to use patch-level characteristics to augment/predict missing data when no demographic information was collected. Moreover, demographic influences on transition probabilities can be modeled directly despite data being incomplete, and importantly, this provides a predictive framework for including demography explicitly into projections of future metapopulation dynamics.

Here, using the flexibility of Bayesian hierarchical modeling, we integrate key components of spatially realistic metapopulation theory (dispersal and connectivity), and detectability models (accounting formally for imperfect detection). We then extend the biological realism of the general metapopulation model to allow explicitly for stage-specific contributions to both extinction and colonization transition probabilities. We apply our model to long-term data collected from a naturally fragmented population of water voles *Arvicola amph-*

bius. Our aim is to demonstrate that a demographically and spatially realistic patch occupancy model that accounts for imperfect detection of both the occupancy state and demographic data provides a flexible and general tool for testing important assumptions of metapopulation theory, and provides far greater insights into metapopulation functioning, including: the roles of dispersal and demography on colonization–extinction dynamics, the relationship between population size and patch size, demographic rates such as effective fecundity, and detectability biases.

MATERIALS AND METHODS

Water vole metapopulation and data collection

The study system is a water vole metapopulation located within a 140-km² area of Assynt, North West Scotland. Water voles are large, microtine rodents that grow up to 300 g, live in small and discrete colonies, and require slow-flowing water with vegetated banks suitable for burrowing. As a result, water voles typically have a highly fragmented metapopulation structure. In Assynt, we monitored 98 such suitable habitat patches (mean length 0.71 km, range 0.10–2.50 km), which are well distributed throughout the study area (mean distance to nearest discrete patch is 0.526 km, range 0.088–1.856 km) and make up only 8% (69.58 km) of the available 860-km waterway network. In 1998, the waterway network within the study area was comprehensively surveyed and water vole habitat patches were mapped based on the presence of suitable habitat and burrow entrances (Aars et al. 2001). In each year from 1999 to 2012, patches were visited in the breeding season (July and August) and were extensively surveyed to determine the presence or absence of water voles based on the detection, or not, of water vole latrines (fecal deposits used for territory marking). In the years 1999–2008, patches were visited only once, but in subsequent years patches were visited more often. The maximum number of visits to any site in years 2009–2012 was four, four, three, and three, respectively, and all sites, if visited at all, were visited more than once.

Where possible, live-trapping was carried out at sites where water vole signs were found during the surveys; trapping sessions lasted 3–5 days, during which individuals were marked and their sex and age (adult or juvenile based on body mass) were recorded. Patches were occupied, on average, by one family group consisting of an adult female (median number of females = 1, range = 1–7 females) and associated juveniles (median = 3, range = 1–27 juveniles). The estimated probability of a resident vole being captured at least once in four trapping occasions exceeded 0.95 (Sutherland et al. 2012) and we therefore assumed that simple enumeration of individuals trapped was representative of true colony size and structure (N^{ad} and N^{juv}). In this study, we consider juveniles of both sexes, but only females for the adult life stage.

Of the 98 patches, not all were visited in every year due to logistic and/or time constraints, or the discovery of new sites throughout the duration of the study (number of sites visited in 1999–2012, respectively: 84, 81, 76, 82, 84, 91, 89, 75, 89, 91, 93, 94, 97, 98; there were 14 sites discovered after 1999). In addition to zero trapping effort at these sites, and also due to weather constraints, not all sites with positive detections were trapped. Without a formal mechanism to account for such missing data, Sutherland et al. (2012) used a restricted data set from 1999 to 2007 to investigate metapopulation dynamics. We will describe a method to overcome the problem of missing data.

Bayesian formulation of the stochastic patch occupancy model

It has long been recognized that studies of patch occupancy are often prone to data quality issues, most notably imperfect detection and missing data (Moilanen 2002, MacKenzie and Royle 2005). To address these issues, we adopted a Bayesian approach, which provides a natural treatment of (1) missing data (failure to visit all patches in each census), by treating those data as parameters to be estimated (O'Hara et al. 2002, ter Braak and Etienne 2003, Risk et al. 2011); and (2) imperfect detection of the occupancy state (false absences), by explicitly modeling the observation process using the hierarchical model structure (Royle and Kéry 2007, Risk et al. 2011). Moreover, we propose the use of a hierarchy of submodels for colonization, extinction, and connectivity (see *Metapopulation process model*) that are conditional on models for both juvenile and adult population size (see *Basic model for N*), and finally, an observation model that accounts for imperfect detection and is specified conditional on the process model (see *Observation model*). Bayesian inference permits the joint estimation of all the parameters associated with each of these submodels and avoids the need for separate analysis and subsequent integration of each model component.

We will outline each of these model components that, when integrated, give rise to a demographically and spatially explicit dynamic patch occupancy model allowing for false negative observation errors and missing data (Royle and Kéry 2007, Risk et al. 2011).

Demographic, spatially explicit metapopulation process model

We follow the SPOM formulation described in Sutherland et al. (2012), which models transition probabilities as a function of abundance directly, relaxing the assumption that population size scales with patch size. The SPOM allows estimation of $\psi_{i,t}$, the probability that patch i is occupied in time t . No information is available regarding the occupancy states prior to the initial sampling period, so occupancy states in the initial year, $z_{i,1}$, are modeled as Bernoulli random variables governed by parameter ψ_1 :

$$z_{i,1} \sim \text{Bernoulli}(\psi_1). \quad (1)$$

The probability of occupancy in all subsequent periods, $\psi_{i,t}$ for $t > 1$, is conditional on the occupancy state in the previous period, $z_{i,t-1}$ ($z_{i,t-1} = 1$ if occupied and $z_{i,t-1} = 0$ otherwise), and the transition probabilities extinction, $\varepsilon_{i,t}$, when occupied, and colonization, $\gamma_{i,t}$, when empty:

$$z_{i,t} | z_{i,t-1} \sim \text{Bernoulli}(\psi_{i,t}) \quad (2)$$

where

$$\psi_{i,t} = (1 - z_{i,t-1})\gamma_{i,t} + z_{i,t-1}(1 - \varepsilon_{i,t-1}). \quad (3)$$

Specifically, colonization is assumed to be caused by immigrating individuals and is modeled as an asymptotically increasing function of spatial connectivity to extant patches in the previous year (Hanski 1994, Moilanen 2004):

$$\gamma_{i,t} = 1 - \exp(-S_{i,t}). \quad (4)$$

The term $S_{i,t}$ is the measure of connectivity describing the distance-dependent influence of all neighboring source populations (occupied patches) via a negative exponential dispersal kernel (Hanski 1994, Moilanen and Nieminen 2002) such that

$$S_{i,t} = \delta \sum_{j \neq i} N_{j,t-1}^* e^{-\alpha d_{i,j}}. \quad (5)$$

Here, $d_{i,j}$ is the Euclidean distance (km) between patch i and j , the term $e^{-\alpha d_{i,j}}$ describes the dispersal kernel with an estimated scaling parameter α related to the average dispersal distance, and $N_{j,t-1}^*$ is the stage-specific abundance of neighboring patch j . Following Sutherland et al. (2012), connectivity is calculated based on the number of juveniles occupying a neighboring site, e.g., $N_{j,t-1}^{\text{juv}}$. When a patch is unoccupied, $N_{j,t-1}^* = 0$ and therefore does not contribute to connectivity. Parameter δ is the population-level per capita effective dispersal rate. It is the parameter α that makes this model spatially explicit and allows for inference to be made about dispersal; taking $d' = \log(2)/\alpha$ gives the halving distance of colonization pressure from dispersal from neighboring extant patches, in the sense that a population of size $N_{j,t-1}^*$ occupying patch j at a distance $d_{i,j}$ from the focal patch i makes the same contribution to $S_{i,t}$ in Eq. 5 as would a population size of $2N_{j,t-1}^*$ occupying a patch at a distance $d_{i,j} + d'$ from patch i .

The probability of extinction, $\varepsilon_{i,t}$, is related to local abundance and too can be stage specific:

$$\text{logit}(\varepsilon_{i,t}) = \varepsilon_0 + \varepsilon_1 N_{i,t}^*. \quad (6)$$

The parameter ε_0 is the intercept, and ε_1 is the slope that relates extinction probability to abundance; again we follow Sutherland et al. (2012) and model the probability of extinction as a function of adult female population size, $N_{i,t}^{\text{ad}}$. A rescue effect can also be incorporated into the SPOM via an adjustment of the extinction probability (to

$\varepsilon_{i,t}^*$) that allows for reduced extinction risk due to migration: $\varepsilon_{i,t}^* = \varepsilon_{i,t}(1 - \gamma_{i,t})$ (Moilanen 2004, Sutherland et al. 2012).

Basic model for stage-specific abundance

Here the model departs from that specified by Sutherland et al. (2012), which uses stage-specific counts as covariate information to explain transition probabilities γ and ε in the restricted (7-year) data. Their approach precludes investigation of metapopulation persistence because future population sizes, which are required to project the model forward in time, are neither modeled nor observed. Moreover, population size and structure are unknown at sites that were not visited or for which occupancy states were falsely observed as unoccupied. Here, to enable projections of future dynamics and persistence using the demographic SPOM, we include a model for population size. We define a basic model for adult female population size that is consistent with, but flexible enough to test, the assumption that the number of individuals scales to patch size (or for water voles that occupy linear riparian habitat, patch length, $L_{i,t}$):

$$N_{i,t}^{\text{ad}} \sim \text{Poisson}(\lambda_{\text{ad}}) \quad (7)$$

where

$$\log(\lambda_{\text{ad}}) = \beta_0^{\text{ad}} + \beta_1^{\text{ad}} l_i. \quad (8)$$

Parameter β_0^{ad} is the intercept and, because we define $l_i = ([x_i - \bar{x}]/\sigma_x)$ i.e., the standardized patch length where x_i is the length of patch i and $\bar{x}$ is the average patch length, $e^{\beta_0^{\text{ad}}}$ is the expected number of adult female voles in a patch of average length. Parameter β_1^{ad} is the slope relating the number of adults to the length of the patch. Notably, this allows for a formal assessment of the assumption that patch size and population size are correlated (i.e., does the posterior distribution of β_1^{ad} include 0). The number of juveniles is then modeled as a function of the number of adult females:

$$N_{i,t}^{\text{juv}} \sim \text{Poisson}(\lambda_{\text{juv}}) \quad (9)$$

where

$$\lambda_{\text{juv}} = \beta_1^{\text{juv}} N_{i,t}^{\text{ad}}. \quad (10)$$

This assumes that the number of juveniles is proportional to the number of adults measured by the parameter β_1^{juv} , which has the convenient and intuitive interpretation as the estimated number of juveniles surviving to dispersal age or “effective fecundity.”

Because our inference is focused on patch occupancy dynamics, population size is modeled conditional on occupancy, and so the Poisson distributions previously described (Eqs. 7 and 9) are zero truncated. The parameters β_0^{ad} , β_1^{ad} , and β_1^{juv} are estimated using observed data collected during live-trapping, and these modeled relationships are used to augment population size where data are missing.

Observation model

The data $y_{i,j,t}$ denote whether the species was detected ($y = 1$) or not ($y = 0$) during the j th visit to i th patch at time t , and are related to the true patch states, $z_{i,t}$, to estimate p , the probability of detecting the species, given that it is present at a site. If a site is truly occupied at time t ($z_{i,t} = 1$), the data are Bernoulli trials with success probability p_t , whereas if a site is unoccupied ($z_{i,t} = 0$), the data are Bernoulli trials with success probability $p_t = 0$:

$$y_{i,j,t} | z_{i,t} \sim \text{Bernoulli}(z_{i,t} p_t). \quad (11)$$

In addition, we model p_t as coming from a common distribution, i.e., as a random effect:

$$\text{logit}(p_t) \sim \text{Normal}(\mu_p, \sigma_p) \quad (12)$$

which has the beneficial effect of allowing data from years in which p_t is best estimated (those with multiple site visits; year 2009 onward) to contribute to the estimation of p_t in years with a single visit (years prior to 2009). We note that extending the observation model to include covariates affecting detection probabilities poses no technical difficulty (MacKenzie et al. 2002, Royle and Kéry 2007).

Simulating metapopulation persistence

To demonstrate the benefits of modeling demographic stage structure directly, we assessed the long-term viability of the Assynt water vole metapopulation by repeatedly simulating 50-year projections of metapopulation dynamics initialized using estimates of patch occupancy states, adult population sizes, and juvenile population sizes from the final year of the study. The initial states and parameters used to simulate metapopulation dynamics were drawn from the joint posterior parameter distribution: $\theta = [\delta, \gamma, \epsilon_0, \epsilon_1, \beta_0^{\text{ad}}, \beta_1^{\text{ad}}, \beta_1^{\text{juv}}, N_{i,2012}^{\text{ad}}, N_{i,2012}^{\text{juv}}]$.

The first 20 years were simulated based on current conditions, i.e., using the fitted model (see *Methods*). This was followed by 30 years in which extinction risk was elevated according to three stage-specific extinction scenarios: (1) *Entire patch*; adults and juveniles both experience elevated extinction risk, e.g., temporary random catastrophes that induce local extinction of all inhabitants rather than destroy the habitat (Casagrandi and Gatto 2002). (2) *Juvenile only*; elevated juvenile extinction risk but adults are unaffected, e.g., high juvenile mortality due to harsh winter conditions, although adult survival and reproduction are unaffected (asp vipers *Vipera aspis*; Altwegg et al. 2005). (3) *Adult only*; adults experience elevated extinction and juveniles are unaffected, e.g., predation directed at adults because juveniles exhibit non-adult (inconspicuous) coloring early in life (marine rock crabs *Cancer irroratus*; Palma and Steneck 2001). Elevated extinction events were simulated independently in each year by assigning each patch a value, $\tau_{i,t}$, drawn randomly from a standard

normal distribution (mean = 0 and unit variance). Patches, or the stage exposed to elevated extinction, went extinct if $\tau_{i,t} < x$, where x is the value of the cumulative distribution function of a standard normal distribution corresponding to a given baseline extinction probability π , which we set to 0.25. For each of 3000 simulations, we monitored patch occupancy over time and whether or not the metapopulation went extinct.

Model-fitting was implemented using JAGS (Plummer 2003) from R 3.0.2 (R Development Core Team 2012) using the R package R2jags (Su and Yajima 2012). All simulations and the post processing of model outputs were carried out using R 3.0.2. JAGS model code and R code for the simulations are available in the Supplement. Model parameters were not sensitive to modest perturbations to the priors used, and convergence was assumed to be reached based on adequate visual diagnostics of three Markov chains. All parameter estimates are reported as posterior modes with 95% Bayesian credible intervals (BCIs) denoted as [0.025–0.975%].

RESULTS

Observed metapopulation dynamics

The Assynt water vole metapopulation appeared stable; the estimated yearly patch occupancy fluctuated between 37% and 86%, with a 14-year average of 55% (Fig. 1a), and functioned via a balancing of extinction (Fig. 1b) and colonization (Fig. 1c) events. Moreover, transition probabilities conformed to predictions from metapopulation theory that dispersal is distance dependent (Fig. 2a), that colonization probabilities increase with increasing connectivity to source populations (Fig. 2b), and that extinction probabilities increase with declining population size (Fig. 2c).

Connectivity was a function of juvenile dispersal; the halving of per juvenile colonization pressure, commonly referred to as average dispersal distance, was $\log(2)/\alpha = 2.10$ km ($\alpha = 0.33$ [0.22–0.49]; Table 1, Fig. 2a). The estimated population-level per juvenile effective dispersal rate δ was 0.015 [0.009–0.026] (Table 1). The estimated intercept and slope of the relationship between extinction probability and adult female population size, on the linear predictor scale, were $\epsilon_0 = 1.44$ [0.54–3.20] and $\epsilon_1 = -1.09$ [−2.63 to −0.47], respectively (Table 1). In the absence of a rescue effect, this translates to an extinction probability for a patch with a single adult female (the median) of 0.59, which reduces to 0.32 and 0.14 with an increase to two and three adult female voles, respectively (Fig. 2c).

Modeling abundance and accounting for imperfect detection

There was a positive relationship between the number of adult females and patch length; the regression coefficients on the linear predictor scale were $\beta_0^{\text{ad}} = -0.81$ [−1.05 to −0.64] and $\beta_1^{\text{ad}} = 0.48$ [0.38–0.58] (Table 1, Fig. 3a). For visualization, realizations from the zero-

FIG. 1. The Bayesian state-space framework allows for the estimation of true, underlying occupancy states of patches when there are missing data and observation errors. Thus, it allows estimation of the corrected predicted number of colonization and extinction events, here shown for the water vole (*Arvicola amphibius*) for the years 1999 to 2012. (a) The naïve/observed number of occupied sites (open circles) compared with the predicted number of occupied sites using the stochastic patch occupancy model, SPOM (solid circles). (b) The predicted number of extinction events (solid circles), and (c) the predicted number of colonization events (solid circles). All point estimates are modal values and error bars are the associated 95% Bayesian credible intervals.

truncated Poisson distribution were simulated using random paired draws of the linear predictors β_0^{ad} and β_1^{ad} from the joint posterior distribution (Fig. 3a). Because standardized patch lengths were used, the expected number of adult females in an average-sized patch (0.710 km long) is $\exp(\beta_0^{\text{ad}})$ and, simulating from the zero-truncated Poisson distribution, was 1.23 (bootstrapped CI: 1–3; Fig. 3a). The expected number of juveniles per adult female in a patch (effective fecundity) was $\beta_1^{\text{juv}} = 3.25$ [3.09–3.41] (Table 1, Fig. 3b).

Estimated detection probabilities per visit ranged from 0.55 in 2009 to 0.98 in years 2002, 2004, and 2006 (Table 2). To account for the variable number of site visits in each year ($j = 1, 2, 3$, or 4 visits), we also calculated the probability of a positive detection during any of the j visits at an occupied site, $p_i^* = 1 - (1 - p_i)^j$, which ranged from 0.65 in 2001 to greater than 0.99 in years 2002, 2006, 2007, 2010, and 2011 (per-visit estimates and associated BCIs are shown in Table 2). We also monitored the number of sites that, despite observing no sign, were predicted to be occupied, i.e., that were false negatives (median number of false negatives in years 1999 to 2012: 9, 15, 26, 8, 11, 5, 8, 16, 6, 8, 7, 3, 1, and 5, respectively).

Simulated metapopulation persistence

We simulated 50-year projections of patch occupancy dynamics for the water vole metapopulation using parameters from the demographic SPOM. Simulation years 1–20 were carried out using current conditions, i.e., using the fitted model (Fig. 4, section II). The metapopulation was predicted to be stable during these years, fluctuating around 56 occupied sites, which was higher than the median number of occupied sites observed between 1999 and 2012 (projected vs. observed median: 56 vs. 50 sites; Fig. 4 section II vs. I). Projected patch occupancy over the two periods, however, was more variable (projected vs. observed minimum–maximum values: 13–82 vs. 30–88 sites; Fig. 4).

Next, in simulation years 21 to 50, we simulated elevated extinction scenarios in which mean extinction rate in each year was elevated by 25% (Fig. 4, section III). To compare the sensitivity of metapopulation persistence to the different scenarios, we monitored the proportion of simulations ($n/3000$) in which the metapopulation went extinct (Fig. 4; dashed black line), and, where the metapopulation remained extant, we also recorded the number of occupied sites (Fig. 4; mean of all extant patches denoted by the solid black line). When extinctions affected both adult and juvenile life stages (i.e., when whole patches experienced elevated extinction risk), mean patch occupancy was reduced from 0.55 to 0.11 and the metapopulation went globally extinct with probability 0.28 (Fig. 4a). When elevated extinction risk affected adults only (i.e., juveniles from affected patches were not affected), mean occupancy reduced from 0.55 to 0.49 and there were no instances of metapopulation extinction (Fig. 4b). When only juveniles experience elevated extinction (i.e., adults were unaffected), the reduction in mean occupancy was more pronounced, dropping from 0.55 to 0.34, and metapopulation extinction occurred with probability 0.01 (Fig. 4c). In summary, the predicted persistence of this metapopulation changed depending on the life stage experiencing increased extinction pressure (Fig. 4); global metapopulation extinction is only likely when both life stages (complete patch) are exposed to increased extinction risk.

FIG. 2. Modeled relationships for the water vole (*Arvicola amphibius*) from the metapopulation model (SPOM) based on 25 000 simulations from the joint posterior distribution of parameters. (a) The scale of connectivity was computed from Eq. 5 using the median number of juveniles ($N = 3$); the black line represents the mean of the simulations and shaded areas are 95% intervals associated with uncertainty in parameters α and δ . Contribution to connectivity is the distance-weighted, patch-specific contribution to focal patch connectivity; focal patch connectivity is calculated as the sum of all contributions from surrounding patches (Eq. 5). (b) Colonization probability is an increasing function of proximity to juveniles, which is a deterministic function (Eq. 4); hence, there is no uncertainty. (c) The modeled relationship between extinction probability and the number of adult females in the focal patch in the absence of a rescue effect. Solid circles and vertical lines represent the simulated mean and 95% intervals associated with uncertainty in parameters ε_0 and ε_1 based on discrete values; the dashed line with shaded area is a continuous representation of the relationship.

DISCUSSION

In our analysis, we simultaneously addressed three important emerging issues associated with modeling metapopulation dynamics and species distribution; the importance of dispersal and connectivity (Hansson 1991, Hanski 1998), the need to account for imperfect detection (Moilanen 2002, MacKenzie et al. 2003, Risk et al. 2011), and the need to consider local demography (Baguette and Schtickzelle 2003, Ozgul et al. 2009).

Until now, no methods existed that integrate all of these in a tractable and intuitive way. In this paper, we developed a novel, and general, patch occupancy model that can accommodate demographic data, spatial effects, and detection error. Our model allows for the simultaneous modeling of stage-specific colonization–extinction dynamics, estimation of local population size and structure, and correcting for false negative detections and missing data. Moreover, explicitly estimating

TABLE 1. Parameter estimates from the stochastic patch occupancy model (SPOM) parameterized using stage-specific water vole (*Arvicola amphibius*) counts.

Parameter	Description	Estimate	Prior
α	Dispersal scale parameter that, when converted to $d' = \log(2)/\alpha$, gives the additional dispersal distance that exactly counterbalances the increase in colonization pressure associated with a doubling of population size.	0.33 (0.22 to 0.49)	$U(-10,10)$
ε_0	Intercept for the relationship between the probability of patch extinction and the number of adult females.	1.44 (0.54 to 3.2)	$U(-10,10)$
ε_1	Slope for the relationship between the probability of patch extinction and the number of adult females.	-1.09 (-2.63 to -0.47)	$U(-10,10)$
δ	Population-level per capita effective dispersal rate.	0.015 (0.009 to 0.026)	$U(-10,10)$
ψ_1	Expected proportion of patches occupied in the initial year.	0.85 (0.58 to 1.49)	$U(-10,10)$
β_0^{ad}	Intercept for the relationship between the number of adult females and patch length.	-0.82 (-1.05 to -0.64)	$U(-10,10)$
β_1^{ad}	Slope relating number of adult females to the length of a patch.	0.48 (0.38 to 0.58)	$U(-10,10)$
β_1^{juv}	Slope for the relationship between the number of juveniles and the number of adult females.	3.25 (3.09 to 3.41)	$U(-10,10)$
$\mu_p^\dagger$	Mean of the common distribution for year specific detection probabilities.	1.85 (1.20 to 3.03)	$U(-10,10)$
$\sigma_p^\dagger$	Standard deviation of the common distribution for year specific detection probabilities.	0.55 (0.18 to 2.53)	$U(0,5)$

Notes: All estimates are posterior modes with, in parentheses, 95% Bayesian credible intervals. Projections of metapopulation dynamics were simulated by sampling from the joint posterior distribution of $\theta = [\alpha, \varepsilon_0, \varepsilon_1, \delta, \beta_0^{\text{ad}}, \beta_1^{\text{ad}}, \beta_1^{\text{juv}}]$. U denotes the use of Uniform priors.

† Hyper-parameters are outside the bounds of 0 and 1 because year-specific detection probabilities are transformed using a logit link function.

FIG. 3. Modeled relationships from the metapopulation model (SPOM) based on 50 000 simulations from the posterior distribution of parameters from the model for adult and juvenile population sizes. Adult and juvenile population sizes are conditional on occupancy and are thus realizations from a zero truncated Poisson distribution. (a) The modeled relationship between the number of adult females and patch length; the black line shows simulated means and the shaded areas are bootstrapped 95% intervals associated with uncertainty in parameters β_0^{ad} and β_1^{ad} . The dashed line represents the (non-truncated) relationship using the estimated parameters (Eq. 6). (b) The modeled relationship between the number of juveniles and adult females; the black line shows simulated means and the shaded areas are 95% intervals associated with uncertainty in parameters β_1^{juv} . The observed data are represented by the “plus” symbols.

the relationship between abundance and measurable patch properties, the model can be used to incorporate demographic stage structure when making long-term projections of metapopulation dynamics and investigating persistence. Given the increased interest in, and application of, patch occupancy models, and the importance of understanding future extinction risk under biologically meaningful scenarios, our methodological developments should be of wide interest.

We extend the classic formulation of a SPOM to include an observation model to account for imperfect detection using repeated site visits to estimate a detection probability (MacKenzie et al. 2002, Royle and Kéry 2007). The Bayesian treatment of latent patch occupancy state variables as parameters allows underlying patch occupancy, and hence the metapopulation state, to be estimated free from the biases induced by false negatives (Moilanen 2002, MacKenzie et al. 2003). However, many long-term monitoring studies do not have multiple site visits in each year. Here we provide a means to overcome this challenge by treating year-specific detection probabilities as random effects with a common distribution with parameters informed mostly by the years with multiple site visits (here post-2008), so that imperfect detection can be accounted for even in years without multiple surveys (here, pre-2009). Our solution hinges on the assumption that detectability in years with multiple visits comes from the same distribution as in years with single visits. Here, we have no reason to believe that any such difference exists. Detection probabilities could also be modeled as functions of covariates when relevant data are available, allowing for a more mechanistic model for detectability in years with only single visits. In fact, the use of spatial effects (dispersal/connectivity) provides information

about the expected occupancy state and therefore also informs the estimation of detectability in the absence of repeated visits. The ability to correct for imperfect detection at all sites in all years, and not just those with multiple site visits, precludes discarding data from the early years of occupancy time series (Lele et al. 2012), and greatly increases the value of long-term monitoring studies in which data were not always collected using contemporary best practices (MacKenzie and Royle 2005, MacKenzie et al. 2006). This is particularly important, given that temporal stochasticity in parameter values can result in estimates of turnover and the resulting predictions of long-term metapopulation dynamics being considerably underestimated when based

TABLE 2. Year-specific detection probabilities, p_{yr} , which are random effects coming from a common distribution with a mean and standard deviation (μ_p and σ_p ; Table 1) that are estimated hyper-priors.

Year	Detection probability, p	
	Estimate	95% BCI
1999	0.97	(0.80–1.00)
2000	0.87	(0.69–0.97)
2001	0.60	(0.42–0.82)
2002	0.98	(0.85–1.00)
2003	0.91	(0.71–0.99)
2004	0.98	(0.83–1.00)
2005	0.97	(0.79–1.00)
2006	0.98	(0.85–1.00)
2007	0.93	(0.88–0.97)
2008	0.83	(0.71–0.90)
2009	0.55	(0.47–0.64)
2010	0.76	(0.68–0.82)
2011	0.8	(0.74–0.84)
2012	0.62	(0.52–0.71)

Note: All estimates are posterior modes with, in parentheses, 95% Bayesian credible intervals (BCI).

on short-term patch occupancy studies (Moilanen 1999, Thomas 2002).

An appealing, yet underutilized, feature of the Bayesian stochastic patch occupancy model is the ability to estimate effective dispersal distances rather than use known or published values (O'Hara et al. 2002, Risk et al. 2011), and to make subsequent inference about effective dispersal rates and dispersal costs (Hanski 1994, Sutherland et al. 2012; but see Eaton et al. [2014] for an example using maximum likelihood). However, inference about both based on patch occupancy patterns is biased if detectability is imperfect (Moilanen 2002). Here we empirically support the prediction that overlooking sources of dispersers through false negatives leads to assuming that dispersers originate from farther than they do in reality, which leads to overestimates of dispersal (Moilanen 2002). Given that imperfect data are the norm rather than an exception, overlooking this might have major consequences for predictive performance. Interestingly, however, models that do account for imperfect detection very rarely incorporate spatial effects such as dispersal (but see Bled et al. 2011, Harrison et al. 2011, Risk et al. 2011). The key feature of our Bayesian model, and of those just noted, which allows dispersal to be explicitly incorporated into the analysis, is the simultaneous treatment of the true occupancy states of all sites as latent variables to be estimated, in this manner allowing spatial effects to be modeled despite detection error. For example, to characterize the large-scale spread of Eurasian Collared-Dove *Streptopelia decaocto*, Bled et al. (2011) developed a spatial occupancy model in which space was discretized into units with areas over 100 km² and colonization was influenced by the (estimated) occupancy status of cells in a predefined neighborhood (first two surrounding rows; see also Eaton et al. 2014). Our approach differs in that we consider the effects of all extant patches in the patch network according to an estimated dispersal kernel in continuous space (see also Risk et al. 2011), which allows connectivity to be estimated and predicted across the entire landscape. The major difference here is that, unlike the more phenomenological conditional autoregressive (CAR) or autologistic models that represent implicit processes (Bled et al. 2011, Broms et al. 2014), we are able to model metapopulation (or patch occupancy) dynamics using an explicit process model, a model of dispersal, which could be further generalized for example through introduction of stage-, age-, or group-specific dispersal coefficients. Dispersal is arguably the most fundamental process driving spatial dynamics in fragmented populations (Hanski and Gaggiotti 2004); our model allows population stage structure and abundance to be considered explicitly when estimating dispersal rates and distances and provides an important tool for investigating the causes and consequence of dispersal (Clobert et al. 2004). We hope that our intuitive model development (and accessible model code) will address

FIG. 4. Projections over 50 years of stage-specific and dispersal-driven metapopulation dynamics. The vertical gray lines separate Section I (years 1–14; observed occupancy dynamics based on data collected from 1999 to 2012); Section II (years 14–34; 20-year projections of metapopulation dynamics based on the model described in *Methods*, i.e., under current-conditions); and Section III (years 34–64; additional 30-year projection), but under scenarios of elevated extinction. We explored the effects of three extinction scenarios in which (a) both life stages, (b) adults only, or (c) juveniles only experienced increased extinction risk. The bold black line denotes the mean occupancy of extant metapopulations, and the dashed black line denotes the cumulative proportion of the 3000 simulations in which the metapopulation went globally extinct. Gray lines represent 25 randomly selected realizations of the 3000 metapopulation projections.

the issue that, despite being arguably the most important determinant of colonization in fragmented populations, dispersal is rarely, if ever, estimated using current and popular occupancy models.

Our estimate of the scale of juvenile water vole dispersal was dramatically reduced when compared with our earlier estimate based on a subset of years in the same site, but that assumed perfect data ($d' = 2.10$ km vs. 12.40 km; Sutherland et al. 2012). Encouragingly, our improved estimate of dispersal is now remarkably similar to mean natal dispersal distances reported in a

genetic-based parentage assignment study of the same metapopulation (1.97 km; Lambin et al. 2012), and a shorter-term radiotelemetry study of dispersal behavior during the dispersal period in another water vole metapopulation in northeastern Scotland (1.8 km; Fisher et al. 2009). In addition, our adjusted estimate of the effective dispersal rate per juvenile is also much lower (0.015 [0.009–0.026] vs. 0.37 [0.28–0.46]) than that reported in Sutherland et al. (2012). This parameter, while conflating many processes (i.e., the probability of initially leaving a site and successfully dispersing, settling, and surviving to reproduction), provides valuable information about the frequency of successful, effective dispersal, but also a mechanism to investigate spatiotemporal variation in dispersal propensity. Interestingly, the parameters relating extinction probabilities to adult population size were relatively unchanged (current vs. Sutherland et al. 2012): $\varepsilon_0 = 1.62$ [0.39–3.41] vs. $\varepsilon_0 = 1.44$ [0.54–3.20], and $\varepsilon_0 = -0.75$ [–1.48 to –0.42] vs. $\varepsilon_0 = -1.09$ [–2.63 to –0.47]). This suggests that relating extinction probabilities to local population size (demographic stochasticity) is more robust to changes in model parameterization and data quality issues than are colonization probabilities and dispersal rates.

Stage-specific metapopulation dynamics have been widely reported, although rarely have such studies accounted for detectability (Crone et al. 2001, Ozgul et al. 2009, Sutherland et al. 2012). Modeling population size and stage structure explicitly in metapopulations is impaired in practice when there is uncertainty in patch occupancy states, because imperfect detection implies unknown population size and structure for those false negative observations. Although approximating demography with patch size circumvents this issue while remaining spatially realistic, it may not be sufficiently demographically realistic (Crone et al. 2001, Pellet et al. 2007, Sutherland et al. 2012). Instead, using data collected at a subset of patches and the hierarchical structure of our model, here we integrated a simple population model for jointly estimating metapopulation dynamics and stage-specific local population sizes. Doing so, the relationship between abundance and patch size was formally estimated rather than being assumed, and colonization–extinction dynamics could be modeled directly as a function of stage-specific abundance. In our water vole application, we were able to estimate the scale of juvenile dispersal, to confirm the assumed positive relationship between adult females and patch length, but also, by conditionally modeling a form of fecundity, to then estimate the number of juveniles per adult female in a patch. Interestingly, our estimate of effective fecundity was 3.25 juvenile voles surviving to dispersal age per adult female, and is similar to that described in other studies of a lowland metapopulations of water voles (Stoddart 1971). Our simple, local population model reflects the life history of water voles; individuals are born, disperse to a breeding site where they reproduce, and are very rarely captured in a third

year (hence, approximate nonoverlapping breeding generations; see Sutherland et al. 2012). However, our approach is flexible enough that our model for population size (Eqs. 7–10) can easily be substituted for a population dynamic model suited to other study systems. The great benefit of incorporating the demographic submodel is that providing an explicit description of local population dynamics provides a mechanism for predicting local population size when detection of the occupancy state is imperfect and data are missing (Conroy et al. 2008, Bled et al. 2011).

A further important advance of this paper is the ability to make forward projections of spatially and demographically realistic metapopulation dynamics, vastly increasing the range of ecologically realistic scenarios that can be investigated. For example, trophic mismatching between the timing of reproduction and peak resource availability by caribou *Rangifer tarandus* causes declines in both calf production and survival with apparently no effect on adult mortality (Post and Forchhammer 2004), and extreme winter temperatures (below -35.5°C) cause mass egg mortality in the autumn moth *Epirrita autumnata*, but adults active in other seasons are not affected (Virtanen et al. 1998). This novel feature of our model is demonstrated by simulating future water vole metapopulation dynamics and monitoring the effect of stage-specific perturbations on metapopulation persistence. We show that persistence of a water vole-like metapopulation is more sensitive to reductions in the successful colonization by the dispersive life stage (i.e., juvenile extinction) than to variation in the survival of resident life stage (i.e., adult extinction). Assuming that patch size adequately reflects population size also implicitly assumes that all life stages are affected equally and simultaneously, and precludes such inference. Indeed, it is far more likely that a species' response to perturbations depends on the particular life stage affected and that, in such circumstances, predictions of long-term metapopulation persistence may look very different to area-based projections. In fact, our simulations predict that stage-structured metapopulations should be more resilient to changes in the environment than predictions based on patch size approximations might suggest. This has extremely important management implications, because failing to acknowledge stage-specific demography can both mask (Clinchy et al. 2002) and exaggerate (Fig. 4) the true extent of extinction risk in nonstationary environments and can substantially influence whether to focus conservation effort on increasing the quality of existing patches or on increasing connectivity to facilitate dispersal (Hodgson et al. 2011).

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