

Original Contribution

A Model to Inform Management Actions as a Response to Chytridiomycosis-Associated Decline

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Abstract: Decision-analytic models provide forecasts of how systems of interest will respond to management. These models can be parameterized using empirical data, but sometimes require information elicited from experts. When evaluating the effects of disease in species translocation programs, expert judgment is likely to play a role because complete empirical information will rarely be available. We illustrate development of a decision-analytic model built to inform decision-making regarding translocations and other management actions for the boreal toad (*Anaxyrus boreas boreas*), a species with declines linked to chytridiomycosis caused by *Batrachochytrium dendrobatidis* (*Bd*). Using the model, we explored the management implications of major uncertainties in this system, including whether there is a genetic basis for resistance to pathogenic infection by *Bd*, how translocation can best be implemented, and the effectiveness of efforts to reduce the spread of *Bd*. Our modeling exercise suggested that while selection for resistance to pathogenic infection by *Bd* could increase numbers of sites occupied by toads, and translocations could increase the rate of toad recovery, efforts to reduce the spread of *Bd* may have little effect. We emphasize the need to continue developing and parameterizing models necessary to assess management actions for combating chytridiomycosis-associated declines.

keywords: *Anaxyrus boreas boreas*, boreal toads, decision analysis, disease resistance, evolutionary rescue, translocation

INTRODUCTION

One of the obstacles that managers face in arresting the decline of threatened species is choosing between available management actions given an imperfect understanding of how the system of interest functions. Decision analysis, the process of deconstructing and analyzing decisions to

achieve decision outcomes that are transparent and more likely to meet objectives (Gregory et al. 2012), has been advocated for improving the choices managers make under uncertainty (e.g., Runge 2011; Moore and Runge 2012; Converse et al. 2013a). Decision-analytic processes involve the recognition that all decisions are composed of a common set of components: a definition of the decision to be made, management objectives, the alternative management actions under consideration, models for predicting how alternative actions will perform in terms of objectives, and

an optimization algorithm for identifying the best action to take.

In decision-analytic frameworks, models forecast how alternatives will perform in terms of the management objectives. Inclusion of uncertainty is critical, because it allows for robust predictions of management effects. Uncertainty can include spatial, temporal, and demographic stochasticity as well as uncertainty about model forms and parameter values (Regan et al. 2002). A model built within a decision-analytic framework should be seen as a tool to improve understanding of the system relevant to a specific decision, rather than an accurate representation of the system (Starfield 1997). Empirical data can be used to parameterize models, but empirical data are not always available. In these cases, judgments elicited from experts are useful (Burgman 2005; Kuhnert et al. 2010; Martin et al. 2011; Runge et al. 2011).

Conservation reintroductions and supplementations (generally, translocations; IUCN/SSC 2013) are important tools in the management of declining species. When deciding to translocate species, managers must consider disease risks throughout the translocation process (Sainsbury and Vaughan-Higgins 2012; Ewen et al. 2015) as well as the disease threats that prompted translocations. A decision-analytic framework is ideal for this, but the models necessary to make predictions are unlikely to be parameterized completely with empirical data; expert input will be important for evaluating disease risks within the context of translocations (Sainsbury and Vaughan-Higgins 2012).

The amphibian chytrid fungus *Batrachochytrium dendrobatidis* (*Bd*) is a newly emerged pathogen (Berger et al. 1998; Longcore et al. 1999; Skerratt et al. 2007; Fisher et al. 2009) linked to declines of amphibians worldwide (Muths et al. 2003; Rachowicz et al. 2006; Skerratt et al. 2007; Lips 2008). *Bd* affects the epidermis of amphibians, causing thickening and resulting in the disease chytridiomycosis. There is some evidence indicating a genetic basis for resistance to pathogenic infection in a number of species which show a heterogeneous response to the pathogen, and of selection in favor of resistance-conferring alleles (Savage and Zamudio 2011; Bataille et al. 2015). Genetically-based resistance to a disease that exerts a strong selective pressure can lead to rapid evolution and, potentially, recovery when resistant individuals begin to dominate (evolutionary rescue; Gonzalez et al. 2013; Maslo and Fefferman 2015). However, substantial questions remain about genetic

resistance and whether evolutionary rescue can contribute to the conservation of *Bd*-affected species. Therefore, managers making decisions to conserve *Bd*-affected species, including translocation decisions, are faced with uncertainty about the existence of genetic resistance and the potential for evolutionary rescue. Modeling frameworks are necessary to determine the implications of competing hypotheses about genetic resistance, and other uncertainties, for decision making. Though the body of research on *Bd* and chytridiomycosis is substantial, little has been done to produce the synthetic models necessary to support decision makers considering various management actions to respond to the threat posed by *Bd*.

Boreal toads (*Anaxyrus boreas boreas*) are a subspecies of the North American western toad. An evolutionarily significant clade of boreal toads exists in the Southern Rocky Mountains (SRM), in Colorado, south-central Wyoming, and (prior to recent extirpations) New Mexico. Documented declines attributed to *Bd* occurred as early as the mid-1990s in the SRM (Muths et al. 2003). Boreal toads are protected as a state endangered species in Colorado and New Mexico, and are candidates for listing under the US Endangered Species Act (US Fish and Wildlife Service 2012). Several conservation plans have been developed in the past 20 years, the last in 2001.

In 2014, a boreal toad conservation plan revision was initiated by the SRM Recovery Team. During the planning process, major sources of uncertainty were identified, including the effectiveness of methods to minimize the spread of *Bd*, how best to conduct translocations, and whether there is a genetic basis for *Bd* resistance in boreal toads. Our purpose was to construct a model integrating the dynamics of this system and use it to test the effectiveness of potential management actions, while accounting for major uncertainties. In building the model, we integrated empirical data with expert judgement, where empirical data were lacking, to make predictions about management outcomes. An expanded form of this model will be used in a decision-analytic process that will include consideration of multiple management objectives (Converse et al. 2013b) and a wide variety of potential management actions in the development of a conservation plan for boreal toads in the SRM. Our approach demonstrates how models are useful, and in fact necessary, for assessing the range of management actions available to managers tasked with recovering amphibians affected by *Bd*.

METHODS

Model Overview

Our model is based on a dynamic multi-species occupancy framework for the meta-population comprising 105 historical boreal toad breeding sites in Colorado (2500–3500 m elevation). The occupancy framework is ideal because it reflects ongoing monitoring efforts, using methods that account for imperfect detection of both toads and *Bd*. At any (annual) time step, a given site can be occupied by toads and/or by *Bd*, resulting in four potential occupancy states: *AB* (toads and *Bd*), *A0* (toads only), *B0* (*Bd* only), and *00* (neither toads nor *Bd*). Parameters that control transitions between states include extinction probabilities (ε) and colonization probabilities (γ). These parameters are dependent on the state of the site at the previous time step. For example, $\varepsilon_{s,t}^{AB}$ is the probability that toads (*A*) will go locally extinct at site *s* between time $t - 1$ and t when *Bd* (*B*) is present, while $\gamma_{s,t}^{B0}$ is the probability that *Bd* colonizes a site *s* between $t - 1$ and t when toads are absent, and so on (Table 1).

We built two structural forms of the model representing two competing hypotheses: one in which *Bd* resistance exists and one in which it does not. Conditional on its occupancy state, each site at each time has a parameter for the proportion of resistant-type individuals at that site ($p_{s,t}$). When resistance does not exist, this parameter is set to 0 across all sites. When resistance exists, we assume that toads can belong to one of two groups: resistant-type or wild-type (Maslo and Fefferman 2015). Resistant-type individuals are resistant to pathogenic infection by *Bd*, and therefore are favored by selection at sites where *Bd* is present. Change in the proportion $p_{s,t}$ over time is a function of the occupancy state of the site at time $t - 1$ and t (Table 2). We posit the existence of resistant-type indi-

viduals (sensu Savage and Zamudio 2011) to examine how this would influence dynamics in this meta-population; we have no direct empirical evidence that such individuals exist in this species, although there are localized differences in boreal toad survival that are potentially attributable to differences in innate resistance (Murphy et al. 2009).

We used empirical information derived from a dynamic conditional two-species occupancy model (Mosher unpublished; Richmond et al. 2010) and expert judgment to parameterize the predictive model. The data used to generate the occupancy estimates were collected at 83 sites in Colorado (a subset of the 105 in this model) monitored over 10 years (2001–2010). The occupancy model structure assumes that the presence of toads does not influence the colonization or extinction probability of *Bd*; the presence of *Bd* does not influence the colonization of toads but does influence toad extinction, and all parameters are time constant, i.e., $\gamma^{BA}(\cdot) = \gamma^{B0}(\cdot)$, $\varepsilon^{BA}(\cdot) = \varepsilon^{B0}(\cdot)$, $\gamma^{AB}(\cdot) = \gamma^{A0}(\cdot)$, $\varepsilon^{AB}(\cdot) \neq \varepsilon^{A0}(\cdot)$. *Bd* detection in this dataset occurs only via swabbing boreal toads, and is therefore dependent on toad occupancy and subsequent detection. This dependency creates parameter redundancy issues that precluded the use of a more general estimation model.

Where empirical information was lacking, we used an expert elicitation process. Four experts (the authors except BDG and SJC) were led through the elicitation process by SJC. Each of the four experts has research expertise in boreal toad ecology, population ecology, and evolutionary ecology, and in *Bd* impacts on boreal toads. The development of methods for selecting and working with experts to develop high-quality judgments is a field of study in itself (e.g., Meyer and Booker 1990; MacMillan and Marshall 2006; Kuhnert et al. 2010; Burgman et al. 2011; Martin et al. 2011; McBride et al. 2012). Ideally, inclusion of more than four experts—which was precluded by time and budget constraints—would be desir-

Table 1. State Transition Probabilities for the Dynamic Two-Species Occupancy Model (MacKenzie et al. 2006; Richmond et al. 2010), as a Function of Extinction (ε) and Colonization (γ) Parameters, Used to Model Dynamics of Boreal Toads (*A*) and *Batrachochytrium dendrobatidis* (*B*).

State at	t			
	<i>AB</i>	<i>A0</i>	<i>B0</i>	<i>00</i>
$t - 1$				
<i>AB</i>	$(1 - \varepsilon^{AB}) * (1 - \varepsilon^{BA})$	$(1 - \varepsilon^{AB}) * \varepsilon^{BA}$	$\varepsilon^{AB} * (1 - \varepsilon^{BA})$	$\varepsilon^{AB} * \varepsilon^{BA}$
<i>A0</i>	$(1 - \varepsilon^{A0}) * \gamma^{BA}$	$(1 - \varepsilon^{A0}) * (1 - \gamma^{BA})$	$\varepsilon^{A0} * \gamma^{BA}$	$\varepsilon^{A0} * (1 - \gamma^{BA})$
<i>B0</i>	$\gamma^{AB} * (1 - \varepsilon^{B0})$	$\gamma^{AB} * \varepsilon^{B0}$	$(1 - \gamma^{AB}) * (1 - \varepsilon^{B0})$	$(1 - \gamma^{AB}) * \varepsilon^{B0}$
<i>00</i>	$\gamma^{A0} * \gamma^{B0}$	$\gamma^{A0} * (1 - \gamma^{B0})$	$(1 - \gamma^{A0}) * \gamma^{B0}$	$(1 - \gamma^{A0}) * (1 - \gamma^{B0})$

Table 2. Transitions for the Proportion of Individual Toads at Time t at Site s ($p_{s,t}$) that are Resistant-Type (Versus Wild-Type).

State at	t			
	AB	$A0$	$B0$	00
$t - 1$				
AB	Eq. 6	Eq. 6	0	0
$A0$	$p_{s,t-1}$	$p_{s,t-1}$	0	0
$B0$	Eq. 9	Eq. 9	0	0
00	Eq. 9	Eq. 9	0	0

Transitions are a function of the occupancy state at the time of the transition t (i.e., a site where toads do not exist at time t cannot have resistant-type individuals) and state in the previous time step $t - 1$ (i.e., if toads co-occurred with Bd in the previous time step, selection pressure will favor an increase in the proportion of individuals that are resistant-type).

able. Therefore, the judgments of experts in our case should be treated as preliminary. More comprehensive elicitation of expert judgment will be conducted in the development of future iterations of our model. We used a 4-point elicitation procedure (Speirs-Bridge et al. 2010) wherein experts were asked to provide their best estimate for parameters of interest, their lowest and highest estimate, and their confidence that the truth was between their lowest and highest estimates. The first round of elicitation was completed by each expert independently; the results were displayed for the panel, and the panel members were given an opportunity to discuss results prior to a second round of elicitation in which experts could revise their estimates (Martin et al. 2011). We fit the resulting output to distributions, as described below, for use in the model.

Modeling Extinction Parameters

We modeled site-specific toad extinction parameters as a function of both the presence of Bd and the proportion of resistant-type individuals at a site. In our formulation, we assumed that resistant-type individuals at sites where Bd is present have survival rates equivalent to individuals at sites where Bd is absent. This assumption implies that, as $p_{s,t-1} \rightarrow 1$, $\epsilon_{s,t}^{AB} \rightarrow \epsilon_{s,t}^{A0}$. This is a strong assumption, but is useful for assessing the potential for evolutionary rescue within this system (see “Discussion” section). From the empirical data (Mosher unpublished), we obtained estimates of $\widehat{\epsilon}_{s,t}^{A0} = 0$ ($\widehat{SE} = 0$) and $\widehat{\epsilon}_{s,t}^{AB} = 0.175$ ($\widehat{SE} = 0.042$); a caret above a parameter indicates it was estimated from data, simulation model parameters do not include a caret. Therefore, we used

$$\epsilon_{s,t}^{A0} = 0 \quad (1)$$

and

$$\epsilon_{s,t}^{AB} = \text{expit}(\widehat{\theta}_0) - \text{expit}(\widehat{\theta}_0) * p_{s,t-1}. \quad (2)$$

where $\widehat{\theta}_0$ is the logit-scale parameter for the estimate of $\widehat{\epsilon}_{s,t}^{AB}$ (Table 3). Under this model, when $p_{s,t-1} = 1$, $\epsilon_{s,t}^{AB} = 0$, and when $p_{s,t-1} = 0$, $E(\epsilon_{s,t}^{AB}) = 0.175$. Our calculations assume that the proportion of resistant-type individuals in the meta-population that produced the estimate of $\widehat{\epsilon}_{s,t}^{AB} = 0.175$ was 0.

For Bd extinction parameters, we assume that

$$\epsilon_{s,t}^{BA} = \epsilon_{s,t}^{B0} = \text{expit}(\widehat{\theta}_1) \quad (3)$$

where $\widehat{\theta}_1$ (Table 3) is the logit-scale parameter for the estimate of $\widehat{\epsilon}_{s,t}^{BA} = \widehat{\epsilon}_{s,t}^{B0} = 0.064$ ($\widehat{SE} = 0.030$). Equal extinction probability of Bd regardless of the presence of toads is presumably reasonable if other hosts are available, suggesting that including the dynamics of alternative Bd hosts may be valuable. However, in the absence of empirical support for this, and to preserve model simplicity, we did not include alternative hosts in the model.

Modeling Colonization Parameters

We modeled toad colonization probability as invariant to Bd occurrence but dependent on the distance to potential source sites:

$$\gamma_{s,t}^{AB} = \gamma_{s,t}^{A0} = 1 - \prod_{j=1}^{J, j \neq s} \left(1 - e^{\frac{-d_{s,j}^2}{(2\sigma^A)^2}} * I_{j,t-1}^A \right) \quad (4)$$

where $d_{s,j}$ is the distance (in km) from any site of interest s to a site j that could provide colonists, σ^A is a parameter controlling distance-weighted dispersal by potential colonists,

Table 3. Required Parameters for the Multi-species Dynamic Occupancy Model for Boreal Toads and *Bd*.

Primary parameter	Sub-parameter	Description	Equations	Value
$e_{s,t}^{A0}$		Probability of extinction of toads in absence of <i>Bd</i>	1	0
$e_{s,t}^{AB}$	θ_0	Logit-scale parameter for relationship of $e_{s,t}^{AB}$ with $p_{s,t-1}$	2	-1.548
$e_{s,t}^{AB}$	SE(θ_0)	Standard error of θ_0	2	0.294
$e_{s,t}^{BA} = e_{s,t}^{B0}$	θ_1	Logit-scale parameter for extinction probability of <i>Bd</i>	3	-2.689
$e_{s,t}^{BA} = e_{s,t}^{B0}$	SE(θ_1)	Standard error of θ_1	3	0.507
$\gamma_{s,t}^{AB} = \gamma_{s,t}^{A0}$	σ^A	Parameter from distance-weighted Gaussian dispersal model for toads	4, 9	1.246
$\gamma_{s,t}^{AB} = \gamma_{s,t}^{A0}$	SE(σ^A)	Standard error of σ^A	4, 9	0.248
$\gamma_{s,t}^{BA} = \gamma_{s,t}^{B0}$	σ^B	Parameter from distance-weighted Gaussian dispersal model for <i>Bd</i>	5	1.066
$\gamma_{s,t}^{BA} = \gamma_{s,t}^{B0}$	SE(σ^B)	Standard error of σ^B	5	0.111
$\gamma_{s,t}^{BA} = \gamma_{s,t}^{B0}$	$\tau^{DM}(\alpha)$	Beta distribution α parameter for effect of disease management on <i>Bd</i> colonization (values for experts 1–4, respectively)	5	4.461, 3.460, 4.118, 3.003
$\gamma_{s,t}^{BA} = \gamma_{s,t}^{B0}$	$\tau^{DM}(\beta)$	Beta distribution β parameter for effect of disease management (π) on <i>Bd</i> colonization (values for experts 1–4, respectively)	5	14.84, 5.370, 15.806, 9.518
$p_{s,t}$	π_0	Logit-scale intercept from Pilliod et al. (2010) for calculation of S^R and S^W	6–8	1.178
$p_{s,t}$	SE(π_0)	SE for π_0	6–8	0.199
$p_{s,t}$	π_1	Logit-scale effect of being <i>Bd</i> -positive from Pilliod et al. (2010) for calculation of S^W	6, 8	-1.468
$p_{s,t}$	SE(π_1)	SE for π_1	6, 8	0.564
$p_{s,t}$	K	Sample size for demographic stochasticity	6, 9, 11, 12	100
$\psi_{t=1}^{AB}$		Initial probability of being in state <i>AB</i>	10	0.333
$\psi_{t=1}^{A0}$		Initial probability of being in state <i>A0</i>	10	0.392
$\psi_{t=1}^{B0}$		Initial probability of being in state <i>B0</i>	10	0.224
$\psi_{t=1}^{00}$		Initial probability of being in state <i>00</i>	10	0.051
$p_{s,t=1}$	p.init (α)	Beta distribution α parameter for initial proportion resistant-type (values for experts 1–4, respectively)	11	1.033, 5.877, 10.259, 3.065
$p_{s,t=1}$	p.init (β)	Beta distribution β parameter for initial proportion resistant-type (values for experts 1–4, respectively)	11	6.300, 26.693, 104.939, 44.625

The derivation of parameters is described in detail in the text. The primary parameters include extinction, $e_{s,t}^{XY}$, and colonization, $\gamma_{s,t}^{XY}$, parameters for a given site s and year t for species where X is the species whose extinction or colonization parameter is described ($A =$ toads, $B = Bd$), and the value of the parameter may be a function of whether the other species is present (A or B) or not (i.e., 0). The relationship between sub-parameters and primary parameters are given in the text by the listed equations. Values are given for the described sub-parameter: note that in many cases sub-parameters are not on the real scale but on a transformed scale (e.g., logit). Standard errors of parameters were used to generate values for each simulation to account for parametric uncertainty.

and $I_{j,t-1}^A$ is an indicator for whether site j is occupied by toads at time $t - 1$. The exponentiated term in Eq. 4 is a standard Gaussian dispersal function (Clobert et al. 2012; Chandler et al. 2015). Because the empirical parameter estimates for

colonization probability were not fit using a distance-weighted function, we estimated σ^A by first calculating the average probability of occupancy for toads (either in state *AB* or *A0*) over the 10-year dataset, $\widehat{\psi}_{s,t}^A = 0.793$. Considering the

empirical estimate $\widehat{\gamma}_{s,t}^{AB} = \widehat{\gamma}_{s,t}^{A0} = 0.174$ (SE = 0.050), we calculated the value of σ^A that would produce the observed colonization probability via simulation. Specifically, we randomly selected a target site and then randomly selected $\widehat{\psi}_s^A = 0.793 \times 105 = 83$ occupied sites as potential sources for the target site. We simulated that process over a range of possible values of σ^A until we located a value for which the average $\gamma_{s,t}^{AB} = \gamma_{s,t}^{A0} = 0.174$, according to Eq. 4. We repeated this procedure for the estimated upper and lower 95% confidence limits of $\widehat{\gamma}_{s,t}^{AB} = \widehat{\gamma}_{s,t}^{A0}$ and calculated a SE by dividing the difference between those values by 1.96×2 (to approximate a normal confidence interval length; Table 3).

We modeled colonization for *Bd* using a function similar to Eq. 4:

$$\gamma_{s,t}^{BA} = \gamma_{s,t}^{B0} = \left(1 - \prod_{j=1}^{J_{j \neq s}} \left(1 - \frac{-d_{sj}^2}{e^{(2\sigma^B)^2}} * I_{j,t-1}^B \right) \right) * (1 - \tau^{\text{DM}}) * a(\text{DM})_{s,t} \quad (5)$$

where the difference between Eqs. 4 and 5 is the effect associated with disease management. The disease management action—denoted $a(\text{DM})_{s,t}$ —represents a set of activities designed to reduce colonization by *Bd*. We followed the same procedure as described above to estimate σ^B (Table 3). We used expert elicitation to estimate the effect of disease management on *Bd* colonization (τ^{DM}). Experts were asked to consider a suite of activities designed to reduce *Bd* colonization, including disinfection requirements for agency employees, limitations on visitor use, guidelines to reduce contamination during forest management efforts, and education programs to encourage visitors to practice disinfection. Experts were asked for their judgment on the expected decrease in colonization rate at a given site if disease management was implemented, using the 4-point elicitation method. We then fit beta distributions for each expert (Table 3). The resulting effect of disease management used in the model was 0.267 (SD = 0.137), i.e., the expected probability of colonization by *Bd* was only 73.3% as high with disease management implemented as without.

Modeling Proportion Resistant-Type

Transitions for the proportion of a local population that is resistant-type (Table 2) include the simple case when the proportion at a site goes to 0 if toads go locally extinct, or stays at the same level if *Bd* is not present, or if only 1 allele

(resistant-type or wild-type) is found at the site. In addition, we allow natural selection (Eq. 6) or colonization of sites by resistant-type individuals (Eq. 7). However, changes to resistance at occupied sites are not allowed due to migration.

Natural selection for resistant-type individuals is given by

$$\text{if } 0 < p_{s,t-1} < 1 : p_{s,t} \sim \frac{\text{Bin}\left(K, \frac{p_{s,t-1} \times S^R}{p_{s,t-1} \times S^R + (1-p_{s,t-1}) \times S^W}\right)}{K} \quad (6)$$

else: $p_{s,t} = p_{s,t-1}$

where S^R and S^W are the survival rates for resistant-type and wild-type individuals, respectively, at a *Bd*-infected site. We use a binomial distribution to introduce process variation into the model, i.e., demographic stochasticity. While individuals are not being tracked in the model, this allows us to model the change in resistance based on individual-level parameters. The parameter K provides an order-of-magnitude approximation of abundance at a site, but its only function is to control process variation, so the variance of $p_{s,t}$ declines as K increases (only 1 value for K exists in the model, and is applied to all sites). To obtain S^R and S^W values for our model, we used estimates from Pilliod et al. (2010). The authors used mark-recapture methods to estimate the effect of *Bd* test outcome on survival of boreal toads at three Rocky Mountain sites (Table 3 from Pilliod et al. 2010). Based on our assumption that resistant-type individuals survive in the presence of *Bd* at similar rates to individuals not exposed to *Bd*, we assume that S^R is equal to the survival observed for uninfected individuals from Pilliod et al. (2010) i.e., $S^R = \widehat{S}^U = 0.76$ and S^W is equal to the survival observed for infected individuals $S^W = \widehat{S}^I = 0.43$. We obtained these rates using

$$S^R = \text{expit}(\widehat{\pi}_0) \quad (7)$$

and

$$S^W = \text{expit}(\widehat{\pi}_0 + \widehat{\pi}_1) \quad (8)$$

where $\widehat{\pi}_0$ is the intercept of survival from the top-ranked model from Pilliod et al. (2010) and $\widehat{\pi}_1$ is the effect of being *Bd*-positive (Table 3). We have ignored the effects of Mendelian inheritance and dominance, and assume reproduction produces offspring that are resistant-type in the same proportion as the previous generation. For the binomial sample size K , we conducted sensitivity analysis, varying K by orders of magnitude from 10 to 1000. We found that it made little difference in the final number of

sites in different occupancy states, and used a value of $K = 100$ for subsequent analyses.

We calculated the proportion resistant-type in newly colonized sites from:

$$p_{s,t} \sim \frac{\text{Bin}\left(K, \frac{\sum_{j=1}^J \frac{e^{-d^2_{sj}}}{e^{(2\sigma^A)^2}} \times I_{j,t-1}^A \times p_{j,t-1}}{\sum_{j=1}^J \frac{e^{-d^2_{sj}}}{e^{(2\sigma^A)^2}} \times I_{j,t-1}^A \times p_{j,t-1} + \sum_{j=1}^J \frac{e^{-d^2_{sj}}}{e^{(2\sigma^A)^2}} \times I_{j,t-1}^A \times (1-p_{j,t-1})}\right)}{K} \quad (9)$$

in which we used the distance-weighted colonization function in Eq. 4 to calculate the ratio of resistant-type colonists to total colonists. We also applied demographic stochasticity based on the binomial distribution as in Eq. 6 (Table 3).

Model Initialization

To initialize the model, we assigned each site to an initial state, and provided an initial proportion of resistant-type individuals to each occupied site. State-dependent occupancy probability estimates from the dataset were used in a deterministic projection of the system, and we initialized the model using estimates from the first year of the projection (i.e., 2011; Mosher unpublished), $\widehat{\psi}_{t=1}^{AB} = 0.333$, $\widehat{\psi}_{t=1}^{A0} = 0.392$, $\widehat{\psi}_{t=1}^{B0} = 0.224$, $\widehat{\psi}_{t=1}^{00} = 0.051$ (Table 3). We then assigned initial state to each site with a multinomial process:

$$\text{state}_{s,t=1} \sim \text{MN}(1, (\widehat{\psi}_{t=1}^{AB}, \widehat{\psi}_{t=1}^{A0}, \widehat{\psi}_{t=1}^{B0}, \widehat{\psi}_{t=1}^{00})). \quad (10)$$

We used expert judgment to parameterize the initial proportion resistant-type. We followed the described elicitation procedure and fit beta distributions for each of the 4 experts, from which we sampled $p.\text{init}$ for each model simulation (Table 3). The mean proportion resistant-type used in the model was $p.\text{init} = 0.1184$ (SD = 0.0854). We applied a binomial distribution to simulate stochasticity, where the number of trials is equal to K (Table 3)

$$p_{s,t=1} \sim \frac{\text{Bin}(K, p.\text{init})}{K} \quad (11)$$

Management Actions

We considered two types of translocations, both of which involved moving toads to unoccupied sites, i.e., reintroductions (IUCN/SSC 2013). In all translocations, we as-

sumed success in establishing a local population (see “Discussion” section). The first translocation type was a standard translocation to 1 site each year (years 1: $T - 1$). The sites to receive translocations were selected randomly from those without toads (i.e., state $B0$ or 00). The second type of translocation was a translocation to 1 site each year where Bd does not occur. The sites for releases in this case are selected randomly from among those that are Bd -free (i.e., state 00). In both cases, the proportion resistant-type at the new site s arises from the mean proportion in the meta-population at the time of translocation:

$$p_{s,t} \sim \frac{\text{Bin}\left(K, \frac{\sum_{j=1}^J p_{j,t}}{J}\right)}{K} \quad (12)$$

where J in this case are the set of sites that were occupied by toads in year t (and so can act as a source).

We also considered disease management, in which we assume that a suite of management actions are applied to reduce the probability of colonization by Bd , as in Eq. 5. Finally, we considered combinations of disease management with the two translocation strategies.

Model Execution

We implemented our model in the R programming language (R Development Core Team 2012; any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government). We considered 12 different scenarios including scenarios with and without resistant-type individuals crossed with various combinations of management actions: with and without translocation, and with and without disease management (Table 4). We conducted 500 simulations of each scenario, with a 50-year time frame for each. In the simulations, we applied parametric uncertainty at the level of the simulation loop and applied process uncertainty (i.e., demographic stochasticity) in annual time loops nested within the simulation loop, to properly separate these forms of uncertainty (White 2000; McGowan et al. 2011). An interactive version of the model is available at https://boraltoad.shinyapps.io/Converse_et_al_EcoHealth.

RESULTS

Scenarios including no management actions resulted in a mean of 82 toad-occupied sites after 50 years when genetic

Table 4. Results from Simulations Carried Out with the Boreal Toad and *Bd* System Model, with Scenarios Comprised of Whether a Genetic Basis for *Bd* Resistance Exists in the Meta-Population, Whether Management Actions to Reduce the Spread of *Bd* are Applied, and Whether and What Type of Translocations are Carried Out (Standard = Translocations at Any Site Without Toads, *Bd* Free = Translocations Only to Sites Without Toads and Without *Bd*).

Scenario	<i>Bd</i> Resistance	<i>Bd</i> Mgmt.	Transloc.	Count AB	Count A0	Count B0	Count 00	Count A.	$p_{t=50}$
1	Yes	No	None	22 (7,39)	60 (38,79)	3 (0,15)	21 (10,35)	82 (61,93)	0.49 (0.13,0.66)
2	No	No	None	11 (2,20)	47 (28,71)	12 (1,31)	34 (21,50)	58 (34,79)	0
3	Yes	Yes	None	17 (3,32)	59 (35,80)	4 (0,21)	25 (11,42)	76 (51,92)	0.38 (0.05,0.62)
4	No	Yes	None	10 (1,19)	50 (31,70)	11 (0,31)	33 (21,47)	60 (39,79)	0
5	Yes	No	Standard	24 (8,44)	81 (60,96)	0 (0,1)	0 (0,1)	104 (104,105)	0.69 (0.56,0.82)
6	No	No	Standard	15 (5,27)	72 (44,96)	9 (0,28)	9 (0,23)	86 (60,104)	0
7	Yes	No	<i>Bd</i> free	24 (8,45)	80 (59,96)	1 (0,5)	0 (0,1)	104 (99,105)	0.62 (0.20,0.79)
8	No	No	<i>Bd</i> free	16 (4,32)	80 (62,97)	8 (1,27)	1 (0,7)	95 (74,104)	0
9	Yes	Yes	Standard	21 (4,42)	83 (62,101)	0 (0,1)	1 (0,1)	104 (104,105)	0.64 (0.39,0.80)
10	No	Yes	Standard	13 (4,25)	74 (47,99)	9 (0,26)	9 (0,23)	88 (60,105)	0
11	Yes	Yes	<i>Bd</i> free	20 (5,38)	84 (64,99)	1 (0,6)	0 (0,2)	104 (98,105)	0.58 (0.13,0.77)
12	No	Yes	<i>Bd</i> free	15 (2,30)	82 (63,99)	7 (0,23)	1 (0,7)	97 (79,105)	0

Results, for year = 50, include the number of sites in each of the four system states (occupied by toads and *Bd*, AB; toads only, A0; *Bd* only, B0; or neither species, 00), the total number of “successes” (i.e., toad-occupied sites; A.), and the mean proportion of toads that are resistant-type over all sites, including 95% confidence intervals for each result.

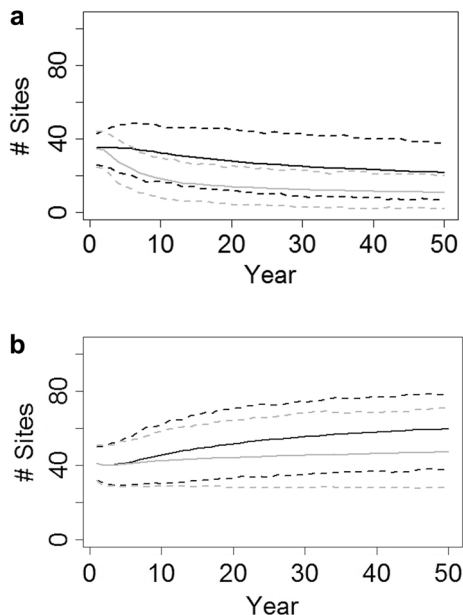


Fig. 1. The number of sites occupied by both toads and *Bd* (state AB; **a**) and by toads alone (state A0, **b**) when genetic resistance exists (black line; with dotted lines representing 95% CI) and when genetic resistance does not exist (gray line; with dotted lines representing 95% CI) over 50 years when no management actions are applied (Scenarios 1 and 2, Table 4, respectively)

resistance was assumed to exist (95% CI 61, 93; Scenario 1, Table 4) versus 58 when resistance was not assumed to exist (95% CI 34, 79; Scenario 2, Table 4). The higher expected

number of toad-occupied sites when resistance-type individuals exist demonstrates the evolutionary rescue effect (though we note that the confidence intervals for Scenarios 1 and 2 overlap). In fact, the effect of parametric uncertainty was substantial throughout our scenarios; we therefore focus on the patterns revealed from expected (mean) outcomes. In Scenario 1, where resistant-type individuals exist, the expected number of sites occupied by both boreal toads and *Bd* (state AB, black line; Fig. 1a) was slower to decline over the 50-year time period than in Scenario 2 (gray line, Fig. 1a), where no resistance exists. This is indicative of the expected greater ability of a meta-population including resistant-type individuals to coexist with *Bd*. Also, the expected number of sites occupied by toads alone (state A0) increased more quickly over the 50-year time period when resistance exists (black line; Fig. 1b) than when it does not (gray line; Fig. 1b).

The application of disease management had relatively little effect on the outcomes with only marginally greater expected numbers of toad-occupied sites after 50 years of effort to reduce *Bd* colonization, and then only in scenarios where *Bd* resistance did not occur [60 (95% CI = 39, 79; Scenario 4) vs. 58 (95% CI = 34, 79; Scenario 2)]. When *Bd* resistance did occur, disease management actually resulted in slightly lower expected numbers of toad-occupied sites [76 (95% CI = 51, 92; Scenario 3) vs. 82 (95% CI 61, 93; Scenario 1)].

By contrast, translocation programs resulted in high expected numbers of toad-occupied sites, especially when resistant-type individuals were present (104 expected toad-occupied sites with translocations and *Bd* resistance; Scenarios 5, 7, 9, and 11; Table 4). The expected 104 toad-occupied sites for these scenarios was nearly equal to the total number of sites (105) thus none of the additional management actions (such as efforts to translocate only to *Bd*-free sites) had any effect. However, without *Bd* resistance, translocating to *Bd*-free sites was more effective than translocating to any site [95 (95% CI 74, 104; Scenario 8) vs. 86 (95% CI 60, 104; Scenario 6); also see Scenario 12 versus Scenario 10; Table 4] presumably due to the high probability of local extinction when toads were translocated to *Bd*-positive sites.

DISCUSSION

Decision analysis is values-focused (Keeney 1992): objectives are determined first, and drive the rest of the process. Draft objectives of the updated boreal toad conservation plan include both toad persistence probability and toad distribution, and so models must make predictions relevant to those objectives. Thus, the numbers and distribution of *AB* and *A0* sites in our model can serve as measures of success. Note that toads in state *AB*, where *Bd* is extant, can still reasonably be counted towards persistence. In fact, *Bd* resistance, if it did exist, should increase the toads' persistence in the presence of *Bd*.

A major challenge with the modeling framework we developed was reconciling what is inherently an individual-based trait, disease resistance, with the site-level occupancy framework. Our solution was to develop a site-specific characteristic, proportion of resistant-type individuals. We assumed two genetic types—wild and resistant—though genetically conferred variation in survival of animals exposed to *Bd* may be expected to be more complex. However, this simplification was valuable for the purpose of exploring the potential for evolutionary rescue, and in the absence of additional information we judged it to be a useful first step in model development. A 2-type system has also been employed to evaluate the potential for evolutionary rescue from another emerging fungal disease: white-nose syndrome in bats (Maslo and Fefferman 2015).

We assumed that resistant-type individuals do not exhibit increased mortality in the presence of *Bd*. This strong assumption will maximize the effects of any genetic

resistance, though the assumption may not be unreasonable. For example, individuals of *Lithobates yavapaiensis* with putative genetic resistance had substantially higher survival than individuals without (Savage and Zamudio 2011). The presence of resistance is an important source of uncertainty, and therefore we explored the management implications of two competing hypotheses, i.e., resistance exists vs. resistance does not exist in boreal toads. We found that resistance changes the expected effectiveness of management actions. For example, we found that if genetic resistance exists, there is no difference in the expected number of toad-occupied sites if translocations occur at any site vs. only at *Bd*-free sites. This is not the case, however, in the absence of resistance, where translocations to *Bd*-free sites only resulted in greater expected numbers of toad-occupied sites. Management implications of this type suggest that there would be value in investigating disease resistance in boreal toads, because the choice of management action is sensitive to this uncertainty (Runge et al. 2011).

The presence of genetically conferred disease resistance in boreal toads has not been explored in any depth. However, Murphy et al. (2009) speculated that variation in mortality rates in laboratory experiments from boreal toads in different parts of the species' range (Wyoming vs. Colorado) could be due to differences in innate resistance. If *Bd* resistance did exist, it might be beneficial to make use of animals that have survived *Bd* exposure in reintroduction programs, thus presumably using individuals with greater resistance to spearhead recovery efforts (Woodhams et al. 2011; Scheele et al. 2014; Brannelly et al. 2015). It is important that the intriguing possibility of *Bd* resistance not be confused with the reality of resistance, however, and that management plans are made fully recognizing the speculative nature of genetic resistance in boreal toads at this time. An approach to decision-making in the face of uncertainty of this type is to use model-averaged predictions of the outcomes of competing management alternatives to guide decision-making, where model weights can be generated based on expert judgment (Converse et al. 2013b).

In our model, we assumed that translocations always resulted in success, thus ignoring the establishment period of reintroductions (Sarrazin and Barbault 1996; Armstrong and Seddon 2008; Converse et al. 2013a). Relaxing that assumption will be a focus of future work. If *Bd* infection influences establishment success at translocated sites, then targeting *Bd*-negative sites for translocations may be more

beneficial than our current results suggest. We also did not consider the impacts of translocations on the viability of source populations, but instead assumed that adequate numbers of propagules would be available to support a translocation program without affecting local populations. We did not consider captive boreal toads as a source for translocations, though propagules are available from a captive facility in Colorado. Although this is not precluded by our framework, inclusion of a captive source would necessitate different predictions about the proportion of resistant-type individuals at translocation sites. There are at least four concerns regarding the use of captive animals for translocations: the challenge of producing adequate numbers of individuals in captivity, the potential for selection of traits in captivity that are non-optimal post-release, detrimental physiological effects of captivity (Lanier 2015) and the cost of maintaining captive populations (Canessa et al. 2015). Here we demonstrate an additional potential benefit of wild-to-wild translocations: the ability to translocate individuals from local populations that have been subjected to selective pressures for *Bd* resistance in the wild (Woodhams et al. 2011; Scheele et al. 2014; Brannelly et al. 2015).

Monitoring is critical to management in this framework: either monitoring for the presence of toads or monitoring for *Bd* (in each case, to know whether the site is a candidate for translocations). Both monitoring actions, but especially the second, have significant costs that must be considered in decision-making. Monitoring to reduce uncertainty about system function is also likely to be valuable for boreal toads and other *Bd*-sensitive species. There remains substantial uncertainty about aspects of the modeling framework we have presented, as well as the effectiveness of other potential management actions that were not modeled. Uncertainty, coupled with the ability to make decisions repeatedly over time, produces the conditions necessary for adaptive management (Walters 1986; Runge 2011; McCarthy et al. 2012). Perhaps one of the greatest uncertainties is whether there is a genetic basis for *Bd* resistance in boreal toads, and if so, the survival benefit it confers.

Our framework can be expanded to include a wide variety of management actions. Each action must be coupled with predictions of how it will impact extinction and/or colonization parameters. We anticipate further use of expert elicitation to parameterize the effects of management actions in this system. Management actions under consideration include habitat manipulations to reduce *Bd*

pathogenicity to hosts (e.g., increasing basking sites; Puschendorf et al. 2011; Roznik et al. 2015), increasing the use of reintroduction and supplementation, head-starting programs, and management actions to reduce stressors that are coincident with *Bd* (Scheele et al. 2014). One intriguing but speculative alternative is whether reintroductions using individuals from *Bd*-exposed populations could improve success, perhaps due to selection in those populations for resistance (Scheele et al. 2014; Brannelly et al. 2015). The approach we have taken here, using empirical information coupled with expert judgement to build an initial model of system function, is easily transferrable and relevant to other species that are subject to *Bd*-mediated declines.

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