Optimal management decisions are robust to unknown dynamics in an amphibian metapopulation plagued by disease

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Abstract

Identifying conservation actions to recover threatened species can be challenging due to many ecological uncertainties. For example, major threats to a species' conservation are commonly known or suspected, but the specific impacts on population or metapopulation dynamics can be uncertain. This is frequently the case with emerging infectious diseases, including chytridiomycosis, a global driver of amphibian population declines caused by the fungal pathogens Batrachochytrium dendrobatidis (Bd) and Batrachochytrium salamandrivorans. While these diseases are known to cause amphibian declines and extirpations, the mechanisms of their landscape-scale spread are still largely unknown. Such uncertainty can lead to inaction which may jeopardize timely recovery of a species. Decision analysis is a pragmatic approach to making transparent and defensible decisions while dealing with uncertainties. We investigated whether optimal actions aimed at recovering boreal toad (Anaxyrus boreas boreas) metapopulations in the southern Rocky Mountains are robust to the unknown dynamics of Bd spread using value of information and regret analyses. Value of information is a decision-analytic tool for calculating the value of new information in terms of performance on management objectives, while regret measures the cost of acting under incorrect information. We further conducted a stochastic sensitivity analysis to identify the relative effects of metapopulation parameters on system dynamics. We found optimal actions were robust to the unknown dynamics of Bd spread. While boreal toad breeding occurrence is highly sensitive to Bd distribution, the optimal decision is not. Resolving the unknown dynamics of Bd spread would lead to a minimal gain of less than one breeding toad subpopulation at the end of 50 years, given the currently available management actions. Applying a decision-analytic framework coupled with value of information and regret analyses can help frame how uncertainties affect decisions in a way that empowers decision makers.

Introduction

Management decisions in animal conservation can be challenging due to a lack of understanding about both ecological processes and the effects of potential actions. This is generally the case with threatened species facing novel stressors (Moore *et al.*, 2012; Cohen *et al.*, 2016). Decision analysis improves decisions by integrating expert and empirical knowledge in predictive models that are explicitly tied to management objectives and alternative management actions. Models are used to evaluate actions while dealing with a multitude of uncertainties (Gregory *et al.*, 2012). Common uncertainties include: (1) uncertainty about the effects of management actions on system dynamics (Gerber *et al.*, 2018), (2) uncertainty about other drivers of system dynamics (Servanty, Converse, & Bailey, 2014; Nichols et al., 2015; Converse et al., 2017), and (3) uncertainty about the state of the system (Lyons et al., 2008; Fuller, Linden, & Royle, 2016; Gerber & Kendall, 2018). For many endangered and declining animal species, key threats are known or strongly suspected, but the effect of those threats on population dynamics are poorly understood; this type of uncertainty is a known-unknown (Snowden & Boone, 2007). From a research perspective, there is often a desire to invest resources to better understand the mechanisms governing the threat. From a decision-making perspective, however, there is a need to determine if resolving known-unknown uncertainty will improve discrimination among alternative management actions and facilitate the selection of the best action to achieve management objectives (e.g. species recovery). Understanding the value of resolving uncertainty is especially critical for rapidly declining species when time spent on additional research may come at a cost to species' persistence (Martin et al., 2012a).

Decision analysis, also known as structured decisionmaking, is a formal process for decomposing decisions into their component parts and using the resulting insights to identify and address impediments to a decision, so that decisions can be made transparently and robustly (Gregory et al., 2012; Runge et al., 2020; Hemming et al., 2022). A powerful decision-analytic tool for understanding the importance of uncertainty as an impediment to decision-making is value of information, which estimates the expected management gain if uncertainties were resolved (Runge, Converse, & Lyons, 2011; Moore et al., 2012; Canessa et al., 2015; Bolam et al., 2018). Value of information can be useful for both one-time and repeated decisions. For repeated decisions, an adaptive management framework can be used for resolving incomplete knowledge of system dynamics while concurrently managing the system (Johnson et al., 2015). Evaluating the value of information for competing biological hypotheses ahead of initiating adaptive management is sensible because it informs whether the value of resolving uncertainties is large or negligible. An estimate of the value of information can be especially beneficial when monitoring is expensive, when biological mechanisms are almost completely unknown (e.g. pathogen movement across a landscape), or when declines are happening rapidly. In these cases, dedicating time or resources to resolving the uncertainty necessitates strong justification that it will improve management outcomes.

Management decisions targeting the reversal of population declines due to emerging infectious diseases (EIDs) is one situation where known-unknown uncertainties are common (Grant *et al.*, 2017). An EID that has caused rapid declines of global amphibian populations is chytridiomycosis, a disease caused by the fungal pathogens *Batrachochytrium dendrobatidis* (Bd) and *Batrachochytrium salamandrivorans* (Bsal; Scheele *et al.*, 2019). A key limitation to conserving amphibian populations challenged by these diseases is the lack of understanding of landscape dispersal mechanisms (Venesky *et al.*, 2014; Garner *et al.*, 2016). Few studies have investigated landscape-level Bd dynamics (see Daversa *et al.*, 2017, 2018; Mosher, Huyvaert, & Bailey, 2018a), but

B. D. Gerber et al.

it is reasonable to suspect that Bd-free wetlands that are near or hydrologically connected to Bd-positive wetlands would be more likely to be colonized by Bd than isolated Bd-free wetlands. However, this relationship does not explain observations where seemingly isolated amphibian populations become infected by Bd (Mosher *et al.*, 2018a; Crockett, pers. obs.).

The boreal toad (Anaxyrus boreas boreas) is a subspecies of the western toad (A. boreas) that has undergone declines associated with Bd (Muths et al., 2003) and where the mechanism of Bd wetland colonization is unknown. Gerber et al. (2018) used a host-pathogen metapopulation model to make predictions in this system and considered two mechanisms of Bd colonization. First, Gerber et al. (2018) considered a spatially explicit process where the probability of Bd colonization of a Bd-free wetland was related to the distance other Bd-positive wetlands (see also Converse to et al., 2017). The parameters of this process were estimated via detection/non-detection data. They also considered an additional colonization probability (ξ) that was spatially independent and thus was not determined by the distance to Bdpositive wetlands. This spatially independent baseline probability was estimated through expert elicitation and was intended to characterize all unknown mechanisms that could lead to Bd colonization of seemingly isolated amphibian populations. However, whether these spatially independent mechanisms exist is unknown, and the value of ξ is highly uncertain.

Some findings suggest that Bd may disperse via attire and equipment of hikers, fishers, and researchers (Johnson et al., 2003; Kolby et al., 2015), aquatic birds (Wimsatt et al., 2014; Burrowes & De la Riva, 2017), rainwater (Kolby et al., 2015), and general factors associated with anthropogenic disturbance (Pauza, Driessen, & Skerratt, 2010). Lacking empirical data, Gerber et al. (2018) used elicitation (Martin et al., 2012b) from researchers and resource managers who had experience with boreal toads and Bd to parameterize the spatially independent colonization probability. Including both spatially explicit and independent Bd colonization processes resulted in a joint Bd colonization probability distribution (Fig. 1). This distribution was used to predict the dynamics of boreal toads and Bd among wetlands under 36 management strategies (combinations of actions; Tables S1 and S2) to determine which strategy performed best relative to management objectives. However, the question remains whether the optimal decision is sensitive to the assumption that there is a spatially independent Bd colonization process and the parameter value used to quantify this process. Bd presence within a wetland in one year increases the odds (thirteen-fold) that boreal toad reproduction will not occur in the following year (Gerber et al., 2018). Given Bd's importance to boreal toad breeding occurrence, strategies identified under potentially incorrect assumptions about Bd colonization could lead to suboptimal decisions that reduce the likelihood of meeting management objectives.

Additionally, to better understand the relative effectiveness of targeted management actions, it is important to understand



Joint spatially explicit and independent colonization probabilities



Expert elicited spatially independent colonization

Colonization Probability

Figure 1 Joint spatially explicit and independent colonization probabilities for *Batrachochytrium dendrobatidis* (Bd) as a function of distance from nearest source site (top) and the probability density for the spatially independent component of colonization probability elicited from experts (ξ ; bottom) used in Gerber *et al.* (2018) and here. The dotted lines in the top panel represent the uncertainty in the spatially independent process as represented in the bottom panel.

the sensitivity of long-term outcomes (e.g. persistence of boreal toads) to system dynamics (e.g. site colonization and extirpation of Bd and hosts, such as the boreal toad) that can be influenced through management (Converse *et al.*, 2017). Identifying the amphibian-Bd dynamic metapopulation parameters to which management outcomes are most sensitive would facilitate the development of actions targeted at those parameters, such as increasing the colonization of boreal toads (e.g. via translocation) or decreasing the persistence of Bd (e.g. via habitat management to reduce the ability of Bd to persist in a host amphibian).

Our objectives were to evaluate (1) the robustness of optimal decisions to assumptions about the Bd colonization process and (2) the sensitivity of long-term boreal toad breeding occurrence to the colonization and extirpation processes of boreal toads and Bd. We accomplish the first objective by calculating regret, a measure of the cost of acting under incorrect information, and by calculating the expected value of perfect information (EVPI), a measure of the management value of resolving uncertainty (e.g. via adaptive management). We do this for two management objectives related to boreal toad persistence separately and for a combined multi14691795, 0, Downloaded from https://zslpublic

objective value that includes toad persistence objectives and financial costs. We accomplish the second objective using a stochastic sensitivity analysis where we vary dynamic metapopulation parameters to evaluate changes in long-term boreal toad persistence. Understanding which parameters exert the largest change on boreal toad persistence can be used to identify priority areas for management intervention, research, and development and to highlight actions that are less likely to be fruitful. This analysis can also be used to understand how persistence may be influenced by new threats to populations that cause colonization and extirpation processes to change.

Materials and methods

Species background and status

The boreal toad is native to western North America and was once common in the southern Rocky Mountains (SRM, southeastern Wyoming, Colorado, and northern New Mexico). Populations in the SRM began to decline noticeably in the late 1970s (Carey et al., 2005), with local extirpations and population declines linked to the presence of Bd (Muths et al., 2003; Scherer et al., 2005; Mosher et al., 2018b). Boreal toads are protected as a state-endangered species in Colorado and New Mexico and are of special concern in Wyoming. The United States Fish and Wildlife Service recently considered listing toad populations in the Eastern portion of the species' range, including the SRM, under the Endangered Species Act, but found that despite past and expected future declines the populations did not warrant federal protection at the time (U.S. Fish and Wildlife Service, 2017).

The Boreal Toad Conservation Team, made up of state and federal wildlife and land management agencies, is reframing their conservation plan to follow a decisionanalytic framework. The conservation plan outlines the problem and potential actions, and identifies objectives, namely to maximize the persistence and number of boreal toad breeding populations across the historical range over a 50-year time horizon, while considering financial costs (Converse *et al.*, 2017; Gerber *et al.*, 2018; Crockett, 2022).

Data and modeling framework

We evaluated the robustness of decisions to uncertainty about a spatially independent Bd colonization process using a dynamic two-species occupancy model to predict measured objectives under each proposed management strategy (Gerber *et al.*, 2018). The model assumes that in any year, any wetland is in one of four mutually exclusive states defined by the presence or absence of boreal toad breeding activity (i.e. eggs laid; condition A) and Bd (condition B). The states include: boreal toad breeding present and Bd absent (state A0), Bd present and no boreal toad breeding (state 0B), both boreal toad breeding and Bd absent (state A0), and both boreal toad breeding and Bd present (state AB; Fig. 2). Wetlands can transition from one state to another from year *t* to t+1 depending on state-dependent site-level colonization (γ) and extirpation (?) probabilities (Fig. 2), as well as the state of the site at time t. For example, γ^B is a generalized probability that Bd will colonize a site at time t + 1, and this may occur either if toad breeding occurred at time t (γ^{BA}). or if toad breeding did not occur at time t, (γ^{B0}) . Gerber et al. (2018) used empirical vital rates, estimated from 10 years of monitoring data (2001-2010) at a subset of 82 wetlands, and elicited effects of actions to predict boreal toad and Bd dynamics. The observation process of the estimation model considered state-dependent detection parameters, which are not used as part of the predictive modeling. Of particular interest here is the state-dependent colonization probability for Bd, which was assumed to be the same for sites with and without boreal toads (i.e. $\gamma^{BA} = \gamma^{B0}$; hereafter, γ^{B}). This parameter was modeled for site s and year t as,

$$\gamma_{s,t}^{B} = 1 - \alpha + \xi^{\left(\frac{1}{\alpha}\right)}, \tag{1}$$
$$\alpha = \prod_{j=1}^{J, j \neq s} 1 - e^{\frac{-d^{2}}{2\sigma^{2}}},$$

where *d* is the distance to occupied sites in the set *J* (all sites that could contribute to colonization of site *s*) in year *t*, scaled by the Bd-specific spatially explicit colonization parameter (σ), estimated from empirical data, and the spatially independent colonization parameter (ξ), which was derived using expert elicitation (Fig. 1).

The Boreal Toad Conservation Team developed 36 distinct management strategies, including a no-action strategy (status quo) and 35 strategies consisting of combinations of actions pertaining to disease mitigation, habitat management, or boreal toad reintroductions (Gerber et al., 2018). Using a panel of experts, the authors of Gerber et al. (2018) elicited the likely effects of each action (and associated uncertainty) on model parameters using a modified 4-point Delphi process (Speirs-Bridge et al., 2010). Some strategies contained actions thought to affect the spatially explicit Bd colonization probability, but no action was expected to directly influence the spatially independent Bd colonization probability, ξ . All strategies were evaluated under variable objective weights and the strategy that performed best over the largest range of objective weights (assuming the cost objective was weighted <0.55) was identified as optimal (see Gerber et al., 2018 for details).

Value functions

Using the predictive metapopulation model, we modified ξ to either be zero (only spatially explicit colonization of Bd), the expert-elicited spatially independent probability (mode of 0.03; Fig. 1), or a much higher value of 0.1, 0.2 or 0.3. We treat these ξ values as 5 competing biological hypotheses. We predicted toad and Bd dynamics for 50 years under each of the 36 management strategies using each hypothesized ξ (4000 simulations for each strategy and hypothesis combination). To evaluate outcomes, we considered the value produced (*V*), conditional on the strategy (*ST*) and hypothesis



State at <i>t</i> :	State at $t + 1$:			
	A0	0B	00	AB
A0	1: $(1 - \varepsilon^{A0})(1 - \gamma^{BA})$	2: $\varepsilon^{A0}\gamma^{BA}$	$3:\varepsilon^{A0}(1-\gamma^{BA})$	4: $(1 - \varepsilon^{A0})\gamma^{BA}$
0B	5: $\gamma^{AB}\varepsilon^{B0}$	$6: (1 - \gamma^{AB})(1 - \varepsilon^{B0})$	$7: (1 - \gamma^{AB})\varepsilon^{B0}$	8: $\gamma^{AB}(1-\varepsilon^{B0})$
00	9: $\gamma^{A0}(1-\gamma^{B0})$	10: $(1 - \gamma^{A0})\gamma^{B0}$	11: $(1 - \gamma^{A0})(1 - \gamma^{B0})$	12: $\gamma^{A0}\gamma^{B0}$
AB	13: $(1 - \varepsilon^{AB})\varepsilon^{BA}$	14: $\varepsilon^{AB}(1-\varepsilon^{BA})$	15: $\varepsilon^{AB}\varepsilon^{BA}$	16: $(1 - \varepsilon^{AB})(1 - \varepsilon^{BA})$

Figure 2 State transition diagram (top) and matrix (bottom) for a two-species dynamic occupancy model for boreal toads breeding (condition A) and *Batrachochytrium dendrobatidis* presence (Bd; condition B). In a given year, sites are in one of four mutually exclusive states: both boreal toad breeding and Bd presence (state AB), boreal toad breeding only (state A0), Bd presence only (state 0B), or neither boreal toad breeding nor Bd presence (state 00). Arrows represent annual transitions among states, where transitions are products of state-dependent colonization (γ) and extirpation (?) parameters as defined in the matrix.

(H) about ξ using three value functions. We considered two separate measures of boreal toad outcomes, the expected number of active toad breeding sites ($V_1 = ToadSites$) and the expected number of occupied mountain ranges $(V_2 = OccMtns)$ in 50 years. We also considered a multiobjective value function that combined ToadSites and OccMtns with a measure of financial costs (FinCost; defined in Gerber et al., 2018), such that $V_3 = W_1 * ToadSites +$ $W_2*OccMtns + W_3*$ -FinCost. The negative sign for FinCost indicates that lower financial costs are preferred and the weights, W_i (i = 1:3), are objective weights indicating decision-maker preferences. To ensure each attribute had the same relative impact on the value, we scaled ToadSites, OccMtns, and FinCosts to the interval 0-1, that is, $\frac{x-\min(x)}{\max(x)-\min(x)}$ where $\min(x)$ and $\max(x)$ are the predicted minimum and maximum values, respectively, for the attribute xover the set of management alternatives.

Regret

For each value function, V_f (f = 1:3), we first quantified regret. For any correct hypothesis h and any incorrect hypothesis h', regret is the difference between the value that would be obtained if a decision maker acted under the correct assumption that hypothesis h was correct and the value that would be obtained if a decision maker acted under the incorrect assumption that h' was correct. For any value function V, we calculate regret (R), as.

$$R_{h,h'} = \max_{ST} \{ V(ST, H = h) \} - V(ST_{h'}, H = h).$$

where $ST_{h'}$ is the strategy that maximizes V under h' and $V(ST_{h'}, H = h)$ is the value produced under h when implementing $ST_{h'}$. Regret has been used to inform robust decision-making under uncertainty, wherein decision makers select

actions that minimize the maximum regret (Loomes & Sugden, 1982). Here, we use regret simply to quantify the costs of making a decision assuming an incorrect hypothesis; thus, across all pairs of our 5 hypotheses, we gain an understanding of the range of those costs. As an illustrative example, assume that we hypothesize $\xi = 0.03$, while it truly is $\xi = 0.30$. Using our hypothesis would lead to believing the optimal strategy is C.7 for the single-attribute value function ToadSites, while the optimal strategy under the true value is C.5. Regret is the difference between the outcome we get under C.5 and C.7 (in this case, the value is 20.5-20.4 = 0.1 ToadSites). If the regret is zero, there is no difference in the outcome, and as such, we have no regrets about being wrong about our hypothesis. As regret increases, the importance of specifying the correct hypothesis increases. When calculating regret under the third value function, V_3 , we weighted each attribute (*ToadSites*, OccMtns, and FinCosts) in two ways: equally, and under all possible combinations of potential weights (which sum to 1) at increments of 0.05 to identify circumstances that would lead to a high-level of regret. Weights reflect the proportional value placed on each attribute; for example, a 0.4 weight on OccMtns and ToadSites, and 0.2 on FinCosts would convey equal value of OccMtns and ToadSites, at twice the importance of FinCosts. To understand regret under all possible combinations of weights, we calculate the maximum regret across all hypothesis comparisons for each combination of weights. We also divide the maximum regret by the expected value produced under uncertainty (see next section) for each combination of weights; smaller values indicate that more value is expected than regret.

Value of information

We estimated the value of resolving our uncertainty about ξ using each value function by calculating the EVPI (Runge *et al.*, 2011; Canessa *et al.*, 2015), which is the difference between the expected value under certainty and uncertainty, respectively. For a value function with a single attribute (V_1 and V_2), we calculate,

$$EVPI_{certainty} = \sum_{h=1}^{5} \left[\max_{ST} \{ V(ST, h) \} \times p_h \right],$$
$$EVPI_{uncertainty} = \max_{ST} \left[\sum_{h=1}^{5} \{ V(ST, h) \times p_h \} \right],$$
$$EVPI = EV_{certainty} - EV_{uncertainty},$$

where p_h is the probability of hypothesis *h*. We set $p_h = 0.2$ for all five hypotheses about ξ , as all are equally plausible, given current understanding of this system. We also calculated the EVPI for the multi-objective value function (V_3), where we weighted each attribute equally and under all possible combinations of potential attribute weights (as in the regret analysis).

Sensitivity analysis

We assessed the sensitivity of boreal toad outcomes (*Toad-Sites*, *OccMtns*) to model parameters using a stochastic

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sensitivity analysis. Starting with all empirical metapopulation parameters (i.e. under the status quo strategy: $\epsilon^{AB} = 0.34$, $\epsilon^{A0} = 0.04$, $\epsilon^{BA} = \epsilon^{B0} = 0.04$, $\gamma^{A0} = 0.51$, $\gamma^{AB} = 0.12$, $\gamma^{B} = 0.07$), we changed each parameter one at a time from 0–1 at intervals of 0.05 and estimated *ToadSites* and *OccMtns* after 50 years using 4000 simulations. We did this using both the mode of the elicited probability distribution of ξ (Fig. 1) and assuming ξ was zero.

Results

We found that the expected number of active boreal toad breeding sites that persisted after 50 years varied by management strategy and among the five hypothesized spatially independent colonization values, ξ (Fig. 3). As ξ increased, *ToadSites* decreased from 68.2 sites when $\xi = 0$ to 20.5 sites when $\xi = 0.3$. This pattern of decreasing expected value was true regardless of whether single objectives (Fig. 3) or multiple objectives (Fig. 4) were considered. Considering value functions V_1 and V_2 , we found regret (R) was relatively small, always ≤ 5 sites or ≤ 0.13 mountain ranges, respectively (Fig. 5). This generally occurred when the true spatially independent colonization probability was $\xi = 0$ but was assumed to be larger (Fig. 5). The two largest values of Rfor the multi-objective value function, V_3 , with equal weighting among the attributes, occurred when the spatially independent colonization probability was assumed to be $\xi = 0$ but was in truth $\xi = 0.03$, or when it was assumed to be 0.03 but was in truth 0.1 (Fig. 4). However, these values (~ 0.06) are relatively small considering the average value produced from all hypotheses and actions is 0.39, representing only a 15% proportional loss in value. In considering all possible attribute weights, the maximum R across weights ranged from 0 to 0.12 with a median of 0.02. Again, these values are relatively small, as indicated by being on average 5% of the expected value produced under uncertainty. Overall, these findings indicate that the strategies identified as optimal under any hypothesis about ξ will perform well relative to other strategies in mitigating the effects of Bd and reducing landscape-level toad declines regardless of the true spatially independent Bd colonization probability.

These findings are corroborated by the EVPI analysis. For value function V_1 , aimed at maximizing *ToadSites*, the EVPI was 0.407, or less than 1 site at 50 years in the future. For value function V2, aimed at maximizing OccMtns, the EVPI was 0.026, far less than one-tenth of one mountain range. For value function V_3 , aimed at maximizing toad persistence while minimizing costs, EVPI was 0.005 when using equal weights on the three attributes. This suggests negligible value in resolving uncertainty about ξ given that the expected value of V_3 under uncertainty was 0.505, such that the increase in value from eliminating uncertainty about the spatially independent colonization probability was just an increase of 0.01% of the value under uncertainty. Across all combinations of attribute weights that were considered, the maximum EVPI was 0.022 (weights: ToadSites 75%, Fin-Costs 25% and OccMtns 0%; Table S1).

Chytrid value of information



Figure 3 Expected number of boreal toad breeding sites (left subplot) and occupied mountain ranges in 50 years under each strategy (right subplot), assuming different true values for the spatially independent colonization probability of *Batrachochytrium dendrobatidis* (ξ). The optimal strategy for each ξ value is indicated with a black box and the worst strategy is indicated with a white box (bottom row), along with the associated expected number of sites or mountain ranges. Management strategies include 'SQ' for status quo (no additional action), and other strategies consisting of different combinations of management actions focused on habitat, translocation, or disease mitigation (Tables S1 and S2). Note that the scales vary between subplots.

Our sensitivity analysis revealed nonlinear relationships between changes in dynamic parameters and boreal toad outcomes (ToadSites or OccMtns; Fig. 6). Toad outcomes differed in some parts of the parameter space when comparing $\xi = 0.03$ with $\xi = 0$, although there was little proportional change when dynamic parameters were near the empirical values. This was expected, given that the strategies in Gerber et al. (2018) resulted in relatively modest changes in boreal toad outcomes; for example, ToadSites ranged from 22 to 37 and OccMtns from 2.8 to 6.5 among the 36 management strategies assuming the expert-elicited value of $\xi = 0.03$ (Fig. 3). Considering that management strategies are likely to yield moderate changes relative to empirical values, actions that increase local Bd extirpation (ϵ^{B}) are expected to yield the largest gains in ToadSites and OccMtns. However, once Bd extirpation probability exceeds 0.20, the proportional gains would be minimal (Fig. 6). The parameters to which *ToadSites* and *OccMtns* were next most sensitive were γ^{A0} and γ^{AB} , respectively; furthermore, these parameters had consistent linear relationships with both measures of toad outcomes, thus increases in boreal toad colonization probabilities will produce consistent gains toward recovering boreal toad populations across the landscape.

Discussion

Our findings illustrate that the optimal decisions in the boreal toad-Bd case study are robust to uncertainty about the Bd colonization process. While knowing the true spatially independent colonization probability could change the optimal conservation strategy, subsequent effects on the management outcomes would be minimal. The suite of optimal strategies identified across the various Bd colonization hypotheses all perform much better than the status quo strategy and most other alternative strategies. For example, when considering the value function V_1 (*ToadSites*), the difference between the optimal and worst strategy (the status quo strategy) for each Bd colonization hypothesis was always >11.4 active breeding sites, which is twice as large as the maximum observed regret associated with this value function (4.6 active breeding sites, Fig. 5). Similarly, the difference between the multiobjective value, V_3 , using equal attribute weights for the best and worst management strategy (i.e. range) for any Bd colonization hypothesis was always >0.24 (Fig. 4), which is four times higher than the highest observed R value. As such, regret will always be lower when using an optimal decision, regardless of hypotheses about Bd colonization. Therefore,



Figure 4 Multi-objective expected value (left subplot) and expected regret (R; right subplot) as a function of the assumption made about the independent colonization probability of *Batrachochytrium dendrobatidis* (ξ). Regret is the cost of acting under an incorrect assumption. For the left subplot, the optimal strategy for each true ξ value is indicated with a black box and the worst strategy is indicated with a white box, along with the associated multi-objective expected value with equal weights across the three attributes. Note that the diagonal values of R in the right subplot are zero, as these represent cases where the assumed hypothesis was the true hypothesis. Individual measurable attributes in the multi-objective value function were scaled between 0 and 1.

choosing an optimal decision under any hypotheses will lead to improving outcomes and lowering regret.

It is somewhat unsurprising that we found little value in resolving uncertainty about the true value of ξ in this system, because none of the management actions considered by the Boreal Toad Conservation Team were thought to affect the spatially independent Bd colonization process. As a generality, uncertainty about a parameter that is unaffected by management actions will be irrelevant to the overall decision, even if the parameter is biologically relevant and important. While this finding may be intuitive, we expect that the 'trap' of becoming paralyzed by an ultimately irrelevant uncertainty is common.

In our system, those strategies that Gerber *et al.* (2018) grouped into category 'C' were often optimal for either *ToadSites* or *OccMtns* individually, as well as for the multi-objective value, regardless of the hypothesized ξ value (Figs 3 and 4). These strategies typically included the maximum number (4) of toad translocations per year; required all agency employees, researchers, and fire-fighting operations to adhere to disinfection protocols; restricted ground-disturbing

activities (e.g. road construction, logging); and limited recreational use near active toad breeding sites on public lands. Collectively, these actions aimed to increase boreal toad colonization (i.e. translocations), reduce spatially explicit Bd colonization (i.e. disinfection requirements), and decrease toad extirpation probabilities (i.e. restrict ground-disturbing activities). Other opportunistic actions that have been employed by land management agencies since 2010 include reducing toad reproductive failure by temporarily adding water or moving eggs and tadpoles when breeding ponds show signs of drying before individuals could metamorphose. These opportunistic actions can reduce toad extirpation probabilities and increase translocation success, with resulting benefits to toad persistence.

Predicted outcomes and the management actions that are optimal are conditional on the set of actions that are considered. Development of new actions could change the outlook for toads and could inspire additional value of information analyses if they lead to the recognition of new sources of uncertainty. Actions aimed at influencing Bd extirpation probability (ϵ^{B} , the parameter to which *ToadSites* and

Chytrid value of information



Figure 5 Regret (*R*), or the cost of acting under an incorrect assumption about the independent colonization probability of *Batrachochytrium dendrobatidis* (ξ) in terms of the expected number of active boreal toad breeding sites (left subplot) and occupied mountain ranges in 50 years (right subplot). Note that the diagonal values are zero, as these represent cases where the assumed hypothesis was the true hypothesis.



Figure 6 Parameter sensitivity analysis of the expected number of active boreal toad breeding sites (top row) and occupied mountain ranges (bottom row) in 50 years under the status quo strategy where the spatially independent colonization probability of *Batrachochytrium dendrobatidis* is modeled using values from expert elicitation (left column) or assumed to be zero (right column). The empirical value for each parameter is identified by a colored circle. Note that listed colonization probabilities (γ) were used to derive spatially explicit values implemented in the metapopulation model. Parameters are superscripted by state: boreal toad breeding present and Bd absent (state A0), Bd present regardless of boreal toad breeding (state B), and both boreal toad breeding and Bd present (state AB).

OccMtns were most sensitive) are difficult to develop and implement (Garner et al., 2016; Brannelly et al., 2021) except in unique natural settings (e.g. Bosch et al., 2015). Instead, research efforts have focused on detecting or improving resistance or tolerance of boreal toad populations to Bd (i.e. minimizing ε^{AB}) and improving translocation outcomes (i.e. maximizing γ^{A0} and γ^{AB}). Ongoing genomic studies are investigating the potential for resistance or tolerance in the southern Rocky Mountains and the Eastern portion of the species' range. Results from these studies will be important because if there is a genetic basis for resistance or tolerance within the species and translocation cohorts were sourced from these populations, the number of active breeding sites is predicted to increase (Converse et al., 2017). Augmenting the skin microbiota of Bd hosts has also been field tested for use in concert with other management actions (Kueneman et al., 2016, Langlois, 2016; Vogrin, 2020, T. Korpita personal communication). Collectively, these actions may reduce toad extirpation probabilities at Bd-positive wetlands (ε^{AB}) and improve toad translocation success, leading to increased probabilities of toad colonization (γ^{A0} and γ^{AB}) and higher numbers of active breeding sites and occupied mountain ranges (Fig. 6).

During the decision-making process, members of the Boreal Toad Conservation Team identified a suite of research questions they would like to see resolved, including the identification of probable non-amphibian transmission vectors and pathways, and quantifying the associated rates of colonization of Bd. However, our results indicate that while boreal toad breeding persistence attributes are highly sensitive to Bd colonization (and extirpation) processes, the optimal decision is not. Therefore, limited research and development funding would likely be better spent resolving uncertainties regarding the existence of resistance or tolerance within the species range (Converse et al., 2017; Brannelly et al., 2021) and/or testing the effectiveness of management strategies within an adaptive management framework (Runge et al., 2011) as these uncertainties are more likely to be relevant to decision-making.

Our findings are dependent on the objective metrics and actions we considered, and results might be different if these elements of the decision framing changed. There would likely be substantially greater value in resolving uncertainty about Bd colonization if resources to manage boreal toads were contingent on obtaining a given level of success. This implies a value function that does not scale linearly with outcomes (e.g. ToadSites). For example, suppose a decision maker defined success as >60 persistent boreal toad breeding sites after 50 years, such that all outcomes at or above this level were valued equally, and all outcomes below this level were not valued. Under this value function, there would be considerable value in resolving uncertainty about Bd colonization, as this level of success can only be achieved by management strategies if there is no spatially independent Bd colonization (i.e. $\xi = 0$; Fig. 3). However, because of the logistical and financial challenges of collecting empirical field data on the spread of Bd across the landscape, we would predict the expected value of sample information (Runge *et al.*, 2011; Canessa *et al.*, 2015) to be very small, that is, data collection challenges would curtail the value of learning.

We believe adoption of value of information approaches (Runge et al., 2011, Canessa et al., 2015) by other conservation teams entrusted with managing threatened and declining species with known-unknown uncertainties can help ensure that research and monitoring efforts are focused on resolving uncertainties and could lead to the greatest gains in desired management outcomes. Here, we used a quantitative approach, the expected value of perfect information, to understand the value of information. Additional quantitative approaches, including the expected value of sample information or the expected value of partial perfect information (Runge et al., 2011, Canessa et al., 2015), may be useful in particular contexts to better understand the value of addressing portions of the total uncertainty. However, when predictive models are not available, perhaps due to early-stage development of a decision problem, qualitative approaches to value of information can be used (Rushing et al., 2020; Lawson et al., 2022). Our case study illustrates that when management actions are not available to address a process about which there is uncertainty, there will typically be little to no value in resolving that uncertainty until additional management actions are available. Recognition of this fact by managers has the potential to reduce the management paralysis that is sometimes associated with high levels of uncertainty about system function (Converse & Grant, 2019). In addition, the process of characterizing uncertainty clearly, which is a necessary precursor to either quantitative or qualitative value of information analysis, can bring tremendous insight to teams that believe their uncertainty is substantial but have never attempted to describe it explicitly. This process alone can begin to alleviate the management paralysis that uncertainty can inflict.

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Authors' contributions

BDG and BAM conceived the ideas. BDG, BAM, SJC, EM, and LLB designed the methodology. BDG analyzed the data. BDG, BAM, and SJC led the writing of the paper. All authors contributed critically to the drafts and gave final approval for publication.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Description of the management strategies (combined actions) evaluated using the metapopulation projection model. Strategies consist of combinations of disease management, habitat management, and reintroduction actions. Strategies with common disease and habitat management actions are given the same letter and are combined with different reintroduction actions that vary based on the number of

Chytrid value of information

reintroduction sites and the manner in which sites are selected. When multiple actions are implemented, we assume that the combined effect is the maximum potential effect from any of the singular actions. For example, all strategies include the implementation of disinfection requirements (actions 1, 2, and 3; See Table S2), which we assume produces the maximum elicited reduction in Bd colonization (i.e. no additive effects). Initially, reintroduction sites are occupied by neither Bd nor breeding toads and can be selected via the following methods: randomly (Random method), to maximize toad colonization potential (Isolated method) or chosen from the mountain range with the

lowest proportion of toad occupied breeding sites (MtRange method).

Table S2. All considered management actions and elicited proportional mean changes in model parameters. Bolded actions were used in management strategies. Positive effects indicate a change intended to improve conditions for boreal toad persistence, while negative values indicate an unintended effect that reduces conditions for toad persistence. Highlighted cells indicate the most influential action for each model parameter.

Table S3. Attribute weighting and expected value of perfect information (EVPI). The maximum EVPI value is highlighted in yellow.