Category count models for adaptive management of metapopulations: Case study of an imperiled salamander

Katherine M. O'Donnell1 | Paul L. Fackler2 | Fred A. Johnson1 | Mathieu N. Bonneau3 | Julien Martin1,4 | Susan C. Walls1

1Wetland and Aquatic Research Center, United States Geological Survey, Gainesville, Florida
2Department of Agricultural and Resource Economics, North Carolina State University, Raleigh, North Carolina
3Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, Florida
4St Petersburg Coastal and Marine Science Center, United States Geological Survey, St. Petersburg, Florida

Correspondence
Katherine M. O'Donnell, Wetland and Aquatic Research Center, United States Geological Survey, 7920 NW 71st Street, Gainesville, FL 32653.
Email: kmodonnell@usgs.gov

Present address
Mathieu N. Bonneau, Unité de Recherches Zootechnique (URZ), INRA, 97170 Petit-Bourg (Guadeloupe), France.

Funding information
U.S. Geological Survey

Abstract
Managing spatially structured populations of imperiled species presents many challenges. Spatial structure can make it difficult to predict population responses to potential recovery activities, and learning through experimentation may not be advised if it could harm threatened populations. Adaptive management provides an appealing framework when experimentation is considered too risky or time consuming; we used such an approach for imperiled flatwoods salamanders at a Florida wildlife refuge. We represented this metapopulation with category count models and used stochastic dynamic programming to identify optimal decision policies that weighed trade-offs between metapopulation persistence and management costs. We defined possible wetland categories in terms of habitat suitability and occupancy, specified category-specific management actions, and identified transition probabilities via expert elicitation for two management strategies: “future” status quo (FSQ; frequent growing-season burns) and extra management actions (EMA; restoration, translocation, head-starting). We simulated metapopulation dynamics using the resulting optimal management policy and found that under model FSQ, occupancy steadily declined over time, indicating that populations would rapidly become extirpated; with model EMA, occupancy remained stable, suggesting that populations would persist only if additional actions are applied and are effective. This approach can be used to identify optimal solutions while accounting for uncertainty and considering both habitat and population dynamics, and to help managers make conservation decisions for populations at imminent risk of extinction.

KEYWORDS
adaptive management, Ambystoma, amphibian, decision analysis, endangered species, flatwoods salamander, Markov decision process, stochastic dynamic programming
1 | INTRODUCTION

Natural resource management decisions often involve high levels of uncertainty, but the management of spatially structured populations can add substantial complexity to decision problems. Some complications can be simplified by ignoring the spatial structure of a system, but, in other cases, accounting for spatial dynamics can significantly improve decision outcomes. Metapopulation models are useful approximations to explore the dynamics of many spatially structured populations and they have been used in the context of decision analyses (Bogich & Shea, 2008; Westphal, Pickett, Getz, & Possingham, 2003). One appeal of applying these models to decision making is that they can approximate complex systems with very simple models and therefore reduce computational problems caused by the “curse of dimensionality” (Fackler, Pacifici, Martin, & McIntyre, 2014; Marescot et al., 2013; Wilson, McBride, Bode, & Possingham, 2006).

As anthropogenic pressures on ecosystems increase, many metapopulations are facing greater risks of extinctions (Ceballos et al., 2015). Management of imperiled species involves added challenges, including difficulties in monitoring rare and elusive species, legal and practical constraints on experimentation (which reduce the ability to learn quickly), and the reality that extinction corresponds to an irreversible “absorbing state” that adds risk to management decisions. Decision-analytic models, like the one we will present here, can address issues of spatially structured populations, absorbing states, and uncertainty. For recurrent decisions, adaptive management can be used to systematically reduce uncertainty over time (Walters & Holling, 1990; Williams, 2011a). There is a misconception that adaptive management is inherently too risky in cases involving threatened or endangered species (Allen & Gunderson, 2011); however, formal decision-analytic approaches integrate decision makers’ attitudes about risk, ensuring that a chosen course of action will account for the value of learning relative to that risk (Runge, 2011).

Individuals within many imperiled populations are elusive and hard to detect, which makes rigorous monitoring difficult to implement and often results in a lack of key demographic parameters. One management option is to maintain status quo or postpone new recovery actions until necessary data have been collected and then develop rigorous models that link actions to predicted outcomes. However, such an approach may lead to lost opportunities for recovery (Martin et al., 2012). As noted by others, “doing nothing” is in fact a decision, though it is often a poor one (Maguire & Albright, 2005; Samuelson & Zeckhauser, 1988). An alternative is to use a decision science approach (e.g., structured decision making [SDM]; Conroy & Peterson, 2013), construct models based on best available information, and use expert elicitation to fill information gaps (Martin et al., 2012). This approach can help managers to (a) think more clearly about the decision problem, (b) identify actions that would potentially perform better than status quo, and (c) recognize important sources of uncertainty and prioritize data collection for the most critical model parameters. This strategy can also stimulate the set-up of a rigorous framework that ties management objectives, potential actions, scientific models, optimization, and targeted monitoring in a transparent way, which can be updated as new data become available.

Conservation decision-makers are often faced with management problems that do not have obvious solutions. They may be uncertain about the relative effectiveness of the various actions that have been proposed to solve the problem. In a decision science approach, the manager would evaluate the predicted success of potential alternative actions, consider trade-offs, and choose the action that they expect to have the best outcome. When decisions are recurrent and system dynamics are complex and uncertain, we can frame the problem as a Markov decision process (MDP), in which future states depend only on the current system state and the action taken. At each time step, a decision-maker determines the current system state, chooses among the possible actions, and implements an action; the system then transitions between states (Marescot et al., 2013). The value of the system in the next time step is known as the “reward.” The optimal solution to an MDP (referred to as a “policy”) tells the decision-maker the best action to take for each system state. One way to generate that optimal management policy is through the optimization method of stochastic dynamic programming (SDP; Chadès et al., 2017; Marescot et al., 2013). The SDP approach has been applied in a range of conservation decisions, including those about managing imperiled species (Johnson et al., 2011; Martin et al., 2011; McDonald-Madden et al., 2010), fire management practices (Richards, Possingham, & Tizard, 1999), and controlling invasive species (Bogich & Shea, 2008; Shea & Possingham, 2000).

Some of the key features of this framework are: (a) that it allows for the consideration of sequential decisions (i.e., a decision made today has consequences for future decisions), which remains too uncommon in conservation decision making; (b) it can be used to discriminate among alternative hypotheses without using formal experimentation; (c) it is well suited for applications related to spatially structured systems such as metapopulations; and (d) it accounts for the dynamics of habitat suitability. Several studies (e.g., African elephants, Martin et al., 2010;
amphibians, Miller, Brehme, Hines, Nichols, & Fisher, 2012; Florida scrub jays, Johnson et al., 2011) have demonstrated the usefulness of modeling occupancy and habitat simultaneously, yet, few have incorporated these models into dynamic optimization models.

We used SDP to develop an optimal policy for adaptive management of frosted flatwoods salamanders (Ambystoma cingulatum; federally threatened). These pond-breeding salamanders inhabit wetlands embedded in the pine-wiregrass ecosystem of the southeastern United States. Flatwoods salamanders have complex life cycles (i.e., larvae are aquatic, postmetamorphic salamanders are terrestrial). Their decline is thought to be driven by widespread destruction of longleaf pine environments (Means, Palis, & Baggett, 1996) and degradation of remaining habitat due to fire suppression (Bishop & Haas, 2005). Land managers are attempting to restore flatwoods salamander habitat, but uncertainty remains about the ideal course of action. To help resolve uncertainty regarding system dynamics and treatment effectiveness, we used a structured decision-making process to set up an adaptive management framework for one of the last strongholds for A. cingulatum—St. Marks National Wildlife Refuge (SMNWR; O’Donnell et al., 2017). Our study objective was to identify the best sequence of potential management actions with respect to our management objectives (flatwood salamanders’ persistence and cost) and to our understanding of the system. We considered two alternative models that represented alternative hypotheses about how salamanders would respond to management actions. The adaptive management framework would allow us to discriminate among these hypotheses over time by monitoring the effects of management actions. Here, we give a brief overview of our decision approach, and we illustrate how we used an SDP-based category count model (Fackler, 2012) to address epistemic uncertainty about our system.

2 | METHODS

2.1 | Decision context

We held a 4-day decision-making workshop in February 2015 to address habitat and population management of frosted flatwoods salamanders at SMNWR. We sought to define management objectives, develop possible actions, and assess how to best meet management goals given limited resources. Representatives from federal agencies (U.S. Fish and Wildlife Service, U.S. Geological Survey), nongovernmental organizations, and university scientists participated in the workshop. We continued developing the decision model after the workshop, which we describe here in terms of the key elements of SDP: Objectives, states, actions, transition probabilities, costs, and optimization (Marescot et al., 2013).

2.2 | Objectives

At the workshop, we defined two primary fundamental objectives: (a) maximizing the likelihood of population persistence and (b) minimizing costs. In the model presented here, we used the number of occupied wetlands as a proxy for population persistence.

2.3 | States

We recognized that management actions would depend on both habitat suitability (suitable or unsuitable) and occupancy (occupied or not occupied). We defined four possible categories: Suitable/occupied (S/O), suitable/not occupied (S/N), unsuitable/occupied (U/O), and unsuitable/not occupied (U/N).

An ideal modeling framework for this case would be spatially explicit, with site characteristics correlated by distance (e.g., closer sites are more likely to be in the same category). However, optimizing a spatially explicit management policy is often computationally intractable for problems of realistic size (Fackler, 2012; Nicol & Chadès, 2011; Schapaugh & Tyre, 2012). Category count models are useful alternatives that ignore direct interactions between sites (Fackler, 2012; Tyre et al., 2011); each site is assigned to a category (here, S/O, S/N, U/O, or U/N) at time step t, and the site’s future category (t + 1) depends on its current category, the action applied at time t and, possibly, other factors that are common across all sites. When multiple sites are managed, we define the system state $S_t$ as a vector of length 4, where $S_t(i)$ represents the number of sites in category i at time t (i.e., [{#S/O, #S/N, #U/O, #U/N}]). We delineated wetland clusters based on management unit boundaries (Figure 1).

2.4 | Actions

During the workshop, the group quickly reached consensus that the existing management strategy was not sufficient to restore habitat. We agreed on a new management status quo for SMNWR consisting of more frequent (every 1–2 years) prescribed burns within the growing season (April–August; Knapp, Estes, & Skinner, 2009)—a strategy we named the “future status quo” (O’Donnell et al., 2017)—that would more closely align with historic fire patterns of the region (Noss, 2018).
Previously, prescribed burns were conducted less frequently, typically during the dormant season (November–March) when fires would not penetrate wetland basins. In addition, we generated a list of extra management actions intended to either speed up habitat restoration or bolster salamander populations, and we defined category-dependent actions as follows.

1. **Head-starting (at S/O and U/O sites):** (a) Collecting eggs and/or larvae, (b) putting them into predator-free mesocosms (cattle tanks; Semlitsch & Boone, 2009) to increase survival to metamorphosis, (c) checking tanks nightly to remove salamanders as they reach metamorphosis, and (d) releasing metamorphs at their natal wetlands.

2. **Restoration (at U/O and U/N sites):** Restoring wetland basins through targeted prescribed burns and/or mechanical/herbicidal removal of woody vegetation at unsuitable sites.

3. **Translocation (at S/N sites):** Soft-releasing (keeping salamanders in enclosed area for acclimatization period) head-started salamanders at suitable, unoccupied sites.

Thus, we specified two alternative strategies: (a) the future status quo (FSQ), in which the same management action (frequent growing-season burns) would be applied to each wetland, and (b) an “all-of-the-above” strategy, in which all applicable extra management actions (EMA) would be taken at each wetland (i.e., head-starting, restoration, translocation), in addition to FSQ burning.

The set of actions taken at time \( t \) can be denoted by a \( 4 \times 2 \) matrix \( A_t \), with element \( A_{ij} \) representing the number of sites currently in category \( i \) that receive treatment \( j \) (\( j = 1 \) for FSQ and \( j = 2 \) for EMA). A set of actions is feasible if \( A_{i1} + A_{i2} = S(i) \) (i.e., the number of sites in category \( i \) allocated to both treatments must equal the total number of sites currently in category \( i \)). The set of feasible actions also depends on the system state (e.g., translocation can only be applied at S/N sites). A management policy, denoted \( d \), is a decision rule or function that returns a feasible set of actions \( A_t \) depending on the sites’ state \( S_t \):

\[
d(S_t) \rightarrow A_t.
\]

### 2.5 Transitions

As with many other endangered species, we lacked empirical data necessary to define transition probabilities.
between categories. Therefore, we specified transition probabilities using expert elicitation, which can generate reliable outcomes when proper elicitation methods are used (Gustafson, Shukla, Delbecq, & Walster, 1973; Hemming, Burgman, Hanea, McBride, & Wintle, 2017; MacMillan & Marshall, 2006; Martin, Burgman, et al., 2012; Morgan, 2014; Runge, Converse, & Lyons, 2011). We elicited all possible transition probabilities under the two alternative management strategies defined above (FSQ, EMA). Ten experts first completed the elicitation survey independently, attempting to estimate joint probabilities (e.g., probability of a site transitioning from unsuitable and not occupied [U/N] to suitable and occupied [S/O]). However, participants found it unwieldy to consider habitat and occupancy transitions simultaneously. Experts could estimate marginal transition probabilities more intuitively (e.g., probability of a site transitioning from unsuitable to suitable, regardless of occupancy status). Thus, we elicited marginal transition probabilities from the group, and recorded the group consensus for the lowest reasonable value, highest reasonable value, and best guess value for each possible transition (see Table S1; MacMillan & Marshall, 2006).

The high and low values were elicited with a confidence level of 95% (Johnson et al., 2017). We then calculated joint probabilities as products of the appropriate marginal probabilities. Results presented here are based on best guess estimates (Table 1).

We made two key assumptions about transition probabilities. First, we assumed that future habitat suitability depends only on the current suitability and the restoration action, but not on occupancy. As the EMA action restoration is never performed on already-suitable sites, the three probabilities that a site is suitable at time $t + 1$ are:

$$P(\text{Suitable}_{t+1} | \text{Unsuitable}_t, A_t = \text{FSQ}) = 0.3$$

For the occupancy probabilities, the key assumption was that next period’s occupancy is conditionally dependent on current suitability, current occupancy, and action taken, but not conditional on future suitability. These occupancy probabilities are summarized in the final row of Table 1.

To account for potential metapopulation (cluster) extinction, we included an absorbing state in the transition probability matrices. If no sites within a metapopulation are occupied at time $t$, there is zero chance for any sites within this metapopulation to become occupied in future time steps. Thus, once a metapopulation enters the absorbing state, it cannot leave that state.

### 2.6 Costs

We used field data, published information, previous work, and expert judgement to estimate annual per-site costs for all management actions (Table 2; see Supporting Information for calculation details, Appendix S2. For the results presented here, we specified that the ecological “damage” costs $D$ were proportional to the number of sites occupied ($D_{\text{Not occupied}} = 1$, $D_{\text{Occupied}} = 0$); this amounts to a “penalty” when a site is not occupied. We can represent the per-site per-period utility function with a $4 \times 2$ matrix

$$U = wD + (1-w)C$$

where $w$ is a utility weight that represents the trade-off between ecological damage costs ($D$) and treatment costs

### Table 1

| Future category | Current category |
|-----------------|-----------------|
|                 | FSQ             | EMA             |
| S/O             | S/N             | U/O             | U/N |
| S/O             | 70.7            | 11.7            | 17.0 | 2.3 | 78.0 | 50.1 | 57.8 | 7.6 | 86.7 | 55.7 | 82.6 | 19.4 |
| S/N             | 19.3            | 78.3            | 13.0 | 27.7 | 12.0 | 39.9 | 12.2 | 56.4 |
| U/O             | 7.9             | 1.3             | 39.8 | 5.3  | 8.7  | 5.6  | 24.8 | 5.8 |
| U/N             | 2.1             | 8.7             | 30.2 | 64.7 | 1.3  | 4.4  | 5.2  | 24.2 |
| Total occupied  | 78.6            | 13.0            | 56.8 | 7.6  | 86.7 | 55.7 | 82.6 | 19.4 |

Note: Extra management actions are category-dependent (i.e., S/O, head-starting; S/N, translocation; U/O, head-starting + restoration; U/N, restoration). Bottom row indicates the overall probability of a site being occupied in the next time step (given current category and current action).

Abbreviations: S/O, suitable/occupied; S/N, suitable/not occupied; U/O, unsuitable/occupied; U/N, unsuitable/not occupied.
An optimal management policy \( d^* \) will minimize the total cost for any possible state (i.e., maximizing the number of occupied sites less the enhanced management cost). We used the “catcountP” function in the MATLAB-based MDPSolve package (Fackler, 2011) to compute the optimal management strategy for each cluster of sites.

In this problem, the primary uncertainty about system dynamics was whether extra management actions are more effective than the FSQ for maximizing the number of occupied sites. We considered two alternative transition models \( P_{FSQ}(\cdot) \) and \( P_{EMA}(\cdot) \) to reflect the different hypotheses. Under transition model \( P_{FSQ}(\cdot) \), we assume that the extra management actions do not have significant impact; thus, the sites’ transition probabilities are not influenced when extra management action are used. \( P_{FSQ}(\cdot) \) is simply the transition probability elicited for the case where only FSQ actions are used. Conversely, under transition model \( P_{EMA}(\cdot) \), we assume that the extra management actions are effective. For example, under this model, the head-starting action increases the probability that a site will remain suitable and occupied from 70.7% under model \( P_{FSQ} \) to 78% under model \( P_{EMA} \).

Because we are uncertain about which one of these transition models is true, the management policy \( d \) should also consider the current belief in these two models. We denote the belief in model EMA at time \( t \) as \( b_t \). (Note that because we only have two models, the belief in model FSQ is equal to \( 1 - b_t \)). If \( b_t = 0 \) (i.e., the extra management actions are believed to be ineffective), then there is no advantage in using any extra management actions—doing so would increase the management cost without increasing our chance to improve the population status. Thus, our management policy \( d \) is a function of both the current state of the sites \( S_t \) and the belief in the EMA model \( b_t \):

\[
d(S_t, b_t) \rightarrow A_t. \tag{5}
\]

This approach is a type of active adaptive management (Williams, 2001), because the beliefs (model weights) are updated at each step in the optimization using Bayes’ rule:
This is in contrast with passive adaptive management, in which model weights are updated outside of the optimization procedure (Williams, 2001). The resulting optimal policy reflects a balance between short-term outcomes based on current knowledge and future rewards due to updated beliefs. Because we discretized $b$ (in intervals of 0.01), the policy itself consists of a look-up table containing management prescriptions (number of sites per category to treat) for each possible system-state/belief-state combination.

### 2.8 | Simulations

To illustrate the efficacy of the optimal management strategy $d^*$, we simulated the state of wetland clusters over a 25-year time frame using the MDPSolve function “xpomdpsim.” For each cluster, we specified an initial state $S_0$ that we believe approximates the actual landscape (i.e., based on annual occupancy surveys; see Table S2). We set the initial belief in the EMA model $b_0 = 0.5$, meaning that we are completely uncertain whether extra management actions are effective. In each time step, a management action was selected using the optimal strategy, and site transitions were simulated using the corresponding transition probability model (Figure 2). Observations of new system states permit updating of the belief state, again based on Bayes rule (Equation 6).

Based on the new belief and the current system state, the policy determined a new management action (Figure 2). We simulated 50,000 trajectories for each scenario and used per-year means in results presented here.

We explored how cluster size (i.e., number of wetlands in a metapopulation $[N]$) and initial state $S_0$ (i.e., number of sites per category; $[#S/O, #S/N, #U/O, #U/N]$) affected the speed of learning (i.e., rate of change in $b$, which shows how quickly we discriminate between competing models) by varying these two parameters in additional simulations. First, we varied the number of wetlands ($N = 4, 8, 10$), but kept initial state $S_0$ constant (50% S/O, 50% U/O). Next, we kept cluster size constant ($N = 8$) and compared five initial states $S_0$: $\{8,0,0,0\}$, $\{0,8,0,0\}$, $\{0,0,8,0\}$, $\{0,0,0,8\}$, and $\{2,2,2,2\}$. We report results from these simulations below, as they effectively illustrate general properties of the policy (but see Figures S1–S6 for SMNWR results).

\[
b_{t+1} = \frac{b_t P_{EMA}(S_{t+1} | S_t, A_t)}{b_t P_{EMA}(S_{t+1} | S_t, A_t) + (1 - b_t) P_{FSQ}(S_{t+1} | S_t, A_t)}.
\]

### 2.9 | Expected value of perfect information

We calculated the expected value of perfect information (EVPI), which represents the increase in expected management performance (measured on the scale of $U$) if model uncertainty could be eliminated (Runge et al., 2011; Williams, 2001). We used a scenario with few sites ($N = 4$) to explore patterns in EVPI, resulting in 35 possible system states $s_t$ to evaluate. Each of the 35 states had a set of belief-dependent expected values. We calculated EVPI for the optimal policy $d^*$ using the formula

\[
EVPI(s, b) = \sum_m b_m V_m(s) - V(s, b)
\]

where $m$ denotes a transition model ($P_{FSQ}$ or $P_{EMA}$), $b_m$ is the probability (belief) in model $m$, $V_m(s)$ is the value function when model $m$ is known to be true, and $V(s, b)$ is the optimal value for the average model (Williams & Johnson, 2015). The first term in the EVPI calculation denotes the expected value under perfect information (i.e., $b_t = 0$ or 1); the second term represents the best performance under continued uncertainty.

### 3 | RESULTS

#### 3.1 | Elicited transition probabilities

We found several notable differences between the FSQ and EMA transition probabilities we elicited from experts...
Experts deemed that a suitable site was more likely to remain suitable (0.9) than an unsuitable site was to become suitable without restoration (0.3), but restoring an unsuitable site made it more likely to become suitable in the next period (0.7). Taking extra management actions always improved the probability of occupancy relative to FSQ actions (i.e., in bottom row of Table 1, last four values > first four values). Under FSQ actions, future occupancy probability was deemed highest for currently suitable/occupied (S/O) sites and lowest for currently unsuitable/uncleaned (U/N) sites (Table 1). Restored unsuitable sites (U/O or U/N) had higher chances of future occupancy than untreated suitable sites with the same current occupancy status (19.4% > 13.0% and 82.6% > 76.6%; Table 1).

For sites currently U/O, the probability of remaining occupied (S/O or U/O) in the next time step increased from 56.8% using P_{FSQ} to 82.6% using the P_{EMA} model. These probabilities were greater than probabilities of current S/N sites becoming occupied (13.0% under P_{FSQ}, 55.7% under P_{EMA}), which indicates that experts were more optimistic about keeping occupied sites occupied (even if habitat conditions are not ideal) than about unoccupied sites becoming occupied (even if habitat is ideal). For U/N sites, the greatest difference between strategies was the probability of a site becoming suitable (S/O or S/N), which increased from 30.0% under P_{FSQ} to 70.0% under P_{EMA}. Experts judged the probability of a U/N site becoming occupied to be low under both models (7.6% under P_{FSQ}, 19.4% under P_{EMA}).

### 3.2 | Optimization

It is difficult to succinctly summarize the optimal policy, but some general patterns emerged (Figures S7–S10). Nearly all unsuitable sites (both U/O and U/N) were prescribed extra management actions (EMA) when the belief that extra management actions were effective was 0.3 or greater (b ≥ 0.3; Figures S8 and S9). When b < 0.3, more unsuitable sites were prescribed EMA as the number of occupied sites decreased. The number of S/N sites prescribed EMA was not affected by b, except that no sites were treated when b = 0 (Figure S8). The number of treated S/N sites never exceeded the number of occupied (S/O + U/O) sites, as the treatment (translocation) requires a source of head-started animals from occupied sites. One site would not provide enough animals for translocations to multiple sites. Belief in model EMA (b) had the strongest effect on the number of S/O sites assigned treatment; only when b > 0.7 would all S/O sites be treated (Figure S7).

Intuition for these results can be gained by considering the impact of enhanced treatments on the occupancy goal. The combination of treated U/O and S/N sites results in a relatively large increase in the probability of occupancy at both site types (25.8 and 42.7%, respectively). Treating S/O sites, on the other hand, resulted in only an 8.1% increase in occupancy probability in the next period (Table 1). Although the treatment costs for U/O sites are high (Table 2), in combination with treating an S/N site it provides a relatively cost-effective way to increase the number of occupied sites—especially if there are few S/O sites available to treat. If we examine the cost per expected increase in the number of occupied sites, it would cost $13,354 to ensure a S/O site remains occupied, whereas ensuring subsequent occupancy of one S/N site and one U/O site would cost $16,424, which is comparable.

### 3.3 | Simulations

At t = 25, we found large differences between model EMA and model FSQ in expected number of sites per category (Figures 3 and 4). Under model FSQ, the number of occupied sites steadily declined over time, indicating that populations would become extirpated. Initial system state S_0 did not strongly affect the amount of time to reach a steady state (Figure 3 vs. Figure 4), but the two models differed greatly in convergence time; under model EMA, steady state was reached in ~5 years; under model FSQ, it took >25 years (Figures 3 and 4). These results were obtained using a utility weight of w = 0.75 in the objective function; with less weight on population persistence (e.g., w = 0.50), there were fewer sites occupied (Figure S11a) and treated (Figure S11b).

Our simulations indicated that both cluster size (total number of sites) and initial system state S_0 (sites per category) affected learning speed (i.e., how quickly we discriminate between competing models; Figure 5). Assuming model EMA is true (i.e., extra management actions are effective), b increased fastest when N = 10, and slowest when N = 4 (Figure 5a). When the initial state S_0 was all U/O sites (i.e., \{0,0,8,0\}), learning speed was most rapid (Figure 5b). Initial states S_0 of \{0,8,0,0\} (all S/N) and \{0,0,0,8\} (all U/N) represent the absorbing state in which no actions are taken, so no learning is possible (i.e., b did not change over time; Figure 5b).

### 3.4 | Expected value of perfect information

For the N = 4 case that we evaluated, five of the 35 states had no occupied sites (\{0,4,0,0\}, \{0,3,0,1\}, \{0,2,0,2\}, \{0,1,0,3\}, and \{0,0,0,4\}); because these represent the
**FIGURE 3** Simulated number of sites per category (top row) and number of sites treated (bottom row) under “extra management” (left column) and “status quo” (right column) scenarios. Initial system state $S_0$ for this simulation = 8 sites, all suitable/occupied [8,0,0,0]. S/O, suitable/occupied; S/N, suitable/not occupied; U/O, unsuitable/occupied; U/N, unsuitable/not occupied

**FIGURE 4** Simulated number of sites per category (top row) and number of sites treated (bottom row) under “extra management” (left column) and “status quo” (right column) scenarios. Initial system state $S_0$ for this simulation = 8 sites, 2 per category [2,2,2,2]. S/O, suitable/occupied; S/N, suitable/not occupied; U/O, unsuitable/occupied; U/N, unsuitable/not occupied
absorbing state in which no actions are taken, their EVPI = 0, regardless of \( b \) (Figure 6). For the other 30 states, EVPI was relatively small (<1.5%). Absolute EVPI peaked at a mean \( b \) of 0.82 (range: 0.71–0.87; Figure 6). Thus, EVPI is not maximized when uncertainty is maximized \((b = 0.5)\), but at the point of greatest ambiguity about the optimal action. The belief in EMA must be quite high before one is willing to consider the additional, costly management actions.

4 | DISCUSSION

We used a category count model to generate a preliminary optimal decision policy for flatwoods salamander habitat restoration and population management. We included an absorbing state to account for scenarios of local (metapopulation) extirpation; if all sites within a cluster become unoccupied, there is no chance to reestablish that metapopulation within our model. This constraint reflects our belief that natural recolonization from another metapopulation is extremely unlikely. If extirpated, restoration efforts and cost could far exceed costs associated with preventing the metapopulation from becoming extirpated in the first place. When we generated an optimal policy without an absorbing state, our simulations showed the number of occupied wetlands remaining stable over time under the FSQ model (Figure S12). Such a policy could give managers a false sense of security due to a lower perceived risk of extirpation.

Overall, we found that experts thought extra management actions would substantially improve chances of salamanders persisting at SMNWR. Differences between transition models \( P_{FSQ} \) and \( P_{EMA} \) revealed some hypotheses that experts used in their reasoning. First, experts indicated that, regardless of habitat quality, they were more optimistic about maintaining occupancy \((O \rightarrow O)\) than repatriating unoccupied sites \((N \rightarrow O)\). This finding could reflect a hidden assumption that occupied sites are inherently more suitable for salamanders, even if we cannot detect a difference in habitat suitability or identify an explanation. Second, experts were more optimistic that extra management actions would successfully restore habitat \((U \rightarrow S)\) than occupancy \((N \rightarrow O)\) within one time step. For \( U/N \) sites, the probability of becoming \( S/O \) was low under both strategies, but there was a moderate chance of improving the habitat component in a single time step \((30\% \text{ with } P_{FSQ}, 70\% \text{ with } P_{EMA})\). This result suggests that experts anticipated a \( U/N \rightarrow S/O \) transition taking more than 1 year, with habitat restoration occurring before repatriation of salamanders.

Under simulations when additional management actions were not effective, the proportion of occupied wetlands declined rapidly (Right columns in Figures 3 and 4). Only when additional management actions were
effective did the proportion of occupied wetlands stabilize (Left columns in Figures 3 and 4). While our simulations project that the $P_{\text{EMA}}$ model would lead to persistence of salamander populations in this system, it is important to note that those extra management actions represent substantial efforts that would not necessarily be implemented at other properties with remaining flatwoods salamander populations. We caution that these results may be optimistic, as even the “do nothing” action (FSQ) involves increased management efforts relative to previous practices. Our simulation results show that even this improved management strategy (“future status quo” of frequent, growing-season burns) is likely not sufficient for flatwoods salamander persistence. Additional actions, such as targeted prescribed burns within wetland basins, will likely be necessary. These findings underscore the urgent need to restore flatwoods salamander habitat across the species’ ranges.

Our finding that EVPI peaked around $b = 0.8$ indicates that it is most advantageous to resolve our uncertainty when we are fairly confident that $P_{\text{EMA}}$ is the correct model. According to the optimal policy, we would treat most sites with extra management actions when $b \geq 0.8$ (Figures S7–S10), with the nature of the extra actions dependent on the category (e.g., head-starting is done at S/O sites). Thus, our management costs would be high, yet we would not be completely confident in the actions’ effectiveness. At that point, our results suggest a potential benefit in spending a bit more in the short-term to increase learning in exchange for long-term benefits from resolving uncertainty.

Several points concerning assumptions in our modeling framework are noteworthy. First, use of a multi-attribute utility function such as ours requires that all objectives be in the same “currency.” In our case, it was quite difficult to assign a monetary damage cost (in dollars) for unoccupied sites, so we simply assigned quite difficult to assign a monetary damage cost. Our assumption about utility weight, our assumption of risk neutrality is for illustrative purposes only.

A general utility of this modeling framework is the ease of updating transition probabilities based on monitoring efforts following the initial management actions. This is especially useful in situations with high model uncertainty because it allows managers to test hypotheses about how the species and habitat will respond to actions. In our flatwoods salamander case study, we are uncertain about how successful our proposed actions will be—that is, how close the true transition probabilities will be to the elicited values. This framework will also enable us to easily update cost estimates based on actual expenses, which could have a large impact on the optimal policy. We also conducted some exploratory analyses that quantified the rate of learning as a function of the number of sites considered (Figure 5). Not surprisingly, the pace of learning is much slower with fewer sites, which is another “curse” associated with the management of small metapopulations.

There are numerous ways to extend this framework to other situations. In some management scenarios, there may be actions that differentially affect occupancy and habitat. For instance, a prescribed burn applied during breeding migrations could significantly improve salamander habitat but directly harm the migrating animals. This model could be modified to include these types of tradeoffs; that would be a means to incorporate risks associated with managing threatened and endangered species (Runge, 2011). One could also extend this model to explicitly investigate the effect of transition probability uncertainty (e.g., by using a Dirichlet distribution). In cases where imperfect detection is a major concern, one could employ a partially observable Markov decision process (POMDP) to account for the inability to perfectly observe the status of a site (e.g., occupancy status; Williams, 2011b, Fackler et al., 2014). This approach would enable updated beliefs to incorporate the observational uncertainty and therefore to ultimately discriminate among alternative models (i.e., to learn).

Although there are ways to extend the approach we outline here, the fundamental structure allows us to initiate well-informed conservation actions, even in the face of great uncertainty. Importantly, our results highlight the concerted efforts that will likely be needed to fully recover flatwoods salamander populations—even in relative “stronghold” locations like SMNWR. Some management actions have been implemented since the workshop, and some (e.g., head-starting) have even been adopted by managers of other flatwoods salamander...
populations. However, some actions, including growing-season burns, have proven more difficult to implement than expected. Further development of the model (prior to full implementation) could assess the effect of this partial controllability. The flexibility of the modeling approach we have presented will enable us to continue refining our decision policy as new information becomes available.

ACKNOWLEDGMENTS
This work began with the 2015 SDM workshop described above; we sincerely thank all workshop participants for their expertise and input. We thank W. J. Barichivich for assistance with designating wetland categories and calculating management costs. We thank A. J. Tyre, I. Chadès, and two anonymous reviewers for comments that improved this manuscript. This study was partially funded by the USGS Ecosystems Mission Area through the DOI Status & Trends Program. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government. The authors have no conflicts of interest to declare.

AUTHOR CONTRIBUTIONS
S.C.W. convened the 2015 SDM workshop, which F.A.J. and J.M. facilitated and K.M.O. attended. P.L.F. developed the model framework; K.M.O., P.L.F., F.A.J., M.N.B., and J.M. ran models and interpreted results. K.M.O. wrote the manuscript with input from all authors.

DATA AVAILABILITY STATEMENT
Data associated with the research described herein is available in tables of this manuscript and in a data release at https://doi.org/10.5066/P9K3ZA2D

ORCID
Katherine M. O’Donnell https://orcid.org/0000-0001-9023-174X

REFERENCES
Allen, C. R., & Gunderson, L. H. (2011). Pathology and failure in the design and implementation of adaptive management. Journal of Environmental Management, 92, 1379–1384.
Bishop, D. C., & Haas, C. A. (2005). Burning trends and potential negative effects of suppressing wetland fires on Flatwoods salamanders. Natural Areas Journal, 25, 290–294.
Bogich, T., & Shea, K. (2008). A state-dependent model for the optimal management of an invasive metapopulation. Ecological Applications, 18, 748–761.
Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human-induced species losses: Entering the sixth mass extinction. Science Advances, 1, e1400253.
Chadès, I., Nicol, S., Rout, T. M., Peron, M., Dujardin, Y., Pichancourt, J., ... Hauser, C. E. (2017). Optimization methods to solve adaptive management problems. Theoretical Ecology, 10, 1–20.
Conroy, M. J., & Peterson, J. T. (2013). Decision making in natural resource management: A structured, adaptive approach. Hoboken, NJ: John Wiley & Sons.
Fackler, P. L. (2011). MDPSOLVE User’s Guide. Retrieved from: https://sites.google.com/site/mdpsolve/
Fackler, P. L. (2012). Category count models for resource management. Methods in Ecology and Evolution, 3, 555–563.
Fackler, P. L., Pacifici, K., Martin, J., & McIntyre, C. (2014). Efficient use of information in adaptive management with an application to managing recreation near golden eagle nesting sites. PLoS One, 9(5), e102434.
Gustafson, D. H., Shukla, R. K., Delbecq, A., & Walster, G. W. (1973). A comparative study of differences in subjective likelihood estimates made by individuals, interacting groups, Delphi groups, and nominal groups. Organizational Behavior and Human Performance, 9, 280–291.
Hemming, V., Burgman, M. A., Hanea, A. M., McBride, M. F., & Wintle, B. C. (2017). A practical guide to structured expert elicitation using the IDEA protocol. Methods in Ecology and Evolution, 9, 169–180.
Johnson, F. A., Breininger, D. R., Duncan, B. W., Nichols, J. D., Runge, M. C., & Williams, B. K. (2011). A Markov decision process for managing habitat for Florida scrub-jays. Journal of Fish and Wildlife Management, 2, 234–246.
Johnson, F. A., Smith, B. J., Bonneau, M., Martin, J., Romigosa, C., Mazzotti, F., ... Vitt, L. J. (2017). Expert elicitation, uncertainty, and the value of information in controlling invasive species. Ecological Economics, 137, 83–90.
Knapp, E. E., Estes, B. L., & Skinner, C. N. (2009). Ecological effects of prescribed fire season: A literature review and synthesis for managers. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station.
MacMillan, D. C., & Marshall, K. (2006). The Delphi process: An expert-based approach to ecological modelling in data-poor environments. Animal Conservation, 9, 11–19.
Maguire, L. A., & Albright, E. A. (2005). Can behavioral decision theory explain risk-averse fire management decisions? Forest Ecology and Management, 211, 47–58.
Marescot, L., Chapron, G., Chadès, I., Fackler, P. L., Duchamp, C., Marboutin, E., & Gimenez, O. (2013). Complex decisions made simple: A primer on stochastic dynamic programming. Methods in Ecology and Evolution, 4, 872–884.
Martin, J., Chamaille-Jammes, S., Nichols, J. D., Fritz, H., Hines, J. E., Fonnesbeck, C. J., ... Bailey, L. L. (2010). Simultaneous modeling of habitat suitability, occupancy, and relative abundance: African elephants in Zimbabwe. Ecological Applications, 20, 1173–1182.
Martin, J., Fackler, P. L., Nichols, J. D., Runge, M. C., McIntyre, C. L., Lubow, B. L., ... Schmutz, J. A. (2011). An adaptive-management framework for optimal control of hiking near golden eagle nests in Denali National Park. Conservation Biology, 25, 316–323.
Martin, T. G., Burgman, M. A., Fidler, F., Kuhnert, P. M., Low Choy, S., Mebride, M., & Mengersen, K. (2012). Eliciting expert knowledge in conservation science. Conservation Biology, 26, 29–38.
Martin, T. G., Nally, S., Burbidge, A. A., Arnall, S., Garnett, S. T., Hayward, M. W., ... Possingham, H. P. (2012). Acting fast helps avoid extinction. Conservation Letters, 5, 274–280.

McDonald-Madden, E., Probert, W. J. M., Hauser, C. E., Runge, M. C., Possingham, H. P., Jones, M. E., ... Wintle, B. A. (2010). Active adaptive conservation of threatened species in the face of uncertainty. Ecological Applications, 20, 1476–1489.

Means, D. B., Palis, J. G., & Baggett, M. (1996). Effects of slash pine silviculture on a Florida population of Flatwoods salamander. Conservation Biology, 10, 426–437.

Miller, D. A. W., Brehme, C. S., Hines, J. E., Nichols, J. D., & Fisher, R. N. (2012). Joint estimation of habitat dynamics and species interactions: Disturbance reduces co-occurrence of non-native predators with an endangered toad. Journal of Animal Ecology, 81, 1288–1297.

Morgan, M. G. (2014). Use (and abuse) of expert elicitation in support of decision making for public policy. Proceedings of the National Academy of Sciences of the United States of America, 111, 7176–7184.

Nicol, S., & Chadès, I. (2011). Beyond stochastic dynamic programming: A heuristic sampling method for optimizing conservation decisions in very large state spaces. Methods in Ecology and Evolution, 2, 221–228.

Noss, R. F. (2018). Fire ecology of Florida and the southeastern coastal plain. Gainesville, FL: University Press of Florida.

O’Donnell, K. M., Messermer, A. F., Barichivich, W. J., Semlitsch, R. D., Gorman, T. A., Mitchell, H. G., ... Walls, S. C. (2017). Structured decision making as a conservation tool for recovery planning of two endangered salamanders. Journal for Nature Conservation, 37, 66–72.

Richards, S., Possingham, H. P., & Tizard, J. (1999). Optimal fire management for maintaining community diversity. Ecological Applications, 9, 880–892.

Runge, M. C. (2011). An introduction to adaptive management for threatened and endangered species. Journal of Fish and Wildlife Management, 2, 220–233.

Runge, M. C., Converse, S. J., & Lyons, J. E. (2011). Which uncertainty? Using expert elicitation and expected value of information to design an adaptive program. Biological Conservation, 144, 1214–1223.

Samuelson, W., & Zeckhauser, R. (1988). Status quo bias in decision making. Journal of Risk and Uncertainty, 1, 7–59.

Schapaughe, A. W., & Tyre, A. J. (2012). A simple method for dealing with large state spaces. Methods in Ecology and Evolution, 3, 949–957.

Semlitsch, R. D., & Boone, M. D. (2009). Aquatic mesocosms. In C. K. Dodd (Ed.), Amphibian ecology and conservation: A handbook of techniques (pp. 87–104). Oxford: Oxford University Press.

Shea, K., & Possingham, H. P. (2000). Optimal release strategies for biological control agents: An application of stochastic dynamic programming to population management. Journal of Applied Ecology, 37, 77–86.

Tyre, A. J., Peterson, J. T., Converse, S. J., Bogich, T., Miller, D., Post van der Burg, M., ... Runge, M. C. (2011). Adaptive management of bull trout populations in the Lemhi Basin. Journal of Fish and Wildlife Management, 2, 262–281.

Walters, C. J., & Holling, C. S. (1990). Large-scale management experiments and learning by doing. Ecology, 71, 2060–2068.

Westphal, M. I., Pickett, M., Getz, W. M., & Possingham, H. P. (2003). The use of stochastic dynamic programming in optimal landscape reconstruction for metapopulations. Ecological Applications, 13, 543–555.

Williams, B. K. (2001). Uncertainty, learning, and the optimal management of wildlife. Environmental and Ecological Statistics, 8, 269–288.

Williams, B. K. (2011a). Adaptive management of natural resources—Framework and issues. Journal of Environmental Management, 92, 1346–1353.

Williams, B. K. (2011b). Resolving structural uncertainty in natural resources management using POMDP approaches. Ecological Modelling, 222, 1092–1102.

Williams, B. K., & Johnson, F. A. (2015). Value of information in natural resource management: Technical developments and application to pink-footed geese. Ecology and Evolution, 5, 466–474.

Wilson, K. A., McBride, M. F., Bode, M., & Possingham, H. P. (2006). Prioritizing global conservation efforts. Nature, 440, 337–340.

SUPPORTING INFORMATION

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

How to cite this article: O’Donnell KM, Fackler PL, Johnson FA, Bonneau MN, Martin J, Walls SC. Category count models for adaptive management of metapopulations: Case study of an imperiled salamander. Conservation Science and Practice. 2020;2:e180. https://doi.org/10.1111/csp2.180