# RETHINKING RARE: NOVEL APPROACHES TO RARE SPECIES MONITORING AND CONSERVATION 

Jessie Deanne Golding

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## AND CONSERVATION

By

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Rethinking rare: novel approaches to rare species monitoring and conservation

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Conservation of rare species is widely valued and important for ecosystems. Unfortunately, many of the approaches to conserve rare species have been developed with common species (e.g., harvested species) which have larger populations and targeted objectives. Conservation of rare species is difficult in part because of problems created by scarcity and low information. With low information, learning leads to new questions and the utility of information in decisions can quickly become obsolete. Therefore, monitoring strategies that can adapt as well as provide information tailored to relevant decisions are needed. To address rare species monitoring, I developed a long-term monitoring approach for rare species called goal efficient monitoring (GEM). GEM allows monitoring questions to evolve as we obtain information. GEM includes sampling rules connected to a Bayesian integrated population model (IPM), which allows for changing questions and data collection while maintaining long-term inference. For example, GEM sampling rules work when populations are small (less than 10 individuals) and provide guidance to adjust monitoring observations if the population gets large (over 100 individuals), all while maintaining the same long-term inference because of the IPM structure. I outline the GEM approach using Canada lynx (Lynx canadensis), which is Threatened under the Endangered Species Act. To test GEM, I simulated 100 small populations with constant demographic rates for 11 years, applied GEM sampling rules to simulate observations, and predicted population values with the GEM model. On average, the predicted range of values from the GEM model contained the true values $97.1 \%$ of the time. These and other results contained within demonstrate how a GEM approach can provide long-term inference for rare species while addressing changing information needs. To address the problem of rare species information that is tailored to decisions made with rare species information, I propose the use of processes from the professional field of Design to reframe the user needs of the rare species information. I provide an overview of how some Design methods are already in use in conservation and how adopting Design processes more formally through the creation of the field of conservation design may aid in rare species conservation.

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## INTRODUCTION: Why rethink rare?

For as much as individuals and societies around the world value rare species and therefore care about and protect them (e.g., Gaston 1994, Angulo \& Courchamp 2009), there often appear to be a limited number of avenues to achieve actionable conservation of rare species. Here I define rare species as those that have low abundance or limited ranges (Gaston 1994), in contrast to common species which have high abundance and broad ranges. Rare species conservation is frequently hindered by lack of funding, but this explanation hides a more complex truth about the way we think about rare species and for just how long we have been struggling to understand why they exist. As applied conservation disciplines are drifting farther from basic ecology (Hintzen et al. 2020), understanding why so many species are rare may be moving farther out of reach. In addition, because so frequently rare species populations are small and isolated, they defy our systems of monitoring that are built for common species. How does one even begin to approach conserving rare species with so many potential difficulties and continued rare species declines while we attempt to solve questions of knowledge? These are not simply theoretical questions, but questions that we are facing in our lifetimes. In 2021, the U.S. proposed to remove 23 species from protection under the U.S. Endangered Species Act (ESA) due to extinction, some of which have not been seen since the 1940s, some as recently as 1990 (FR 2021). Some species have become rare over just the past two decades, like the world's smallest porpoise, the vaquita (Phocoena sinus), which stands the brink of extinction with an estimated 10 individuals left (Sonne et al. 2021). The time for actionable rare species conservation is now.

Therefore, my goal in this dissertation research was to advance our abilities to conserve rare species, guided by two overarching questions: 1) how can we meaningfully monitor rare
species in small and isolated populations, where population dynamics are irregular and stochastic? and 2) how can we turn rare species monitoring information into meaningful conservation action? I used two main fields of study to answer that question, each seemingly very different, but each providing an integral part to the answer: quantitative ecology and Design. Quantitative ecology is the application of mathematical and statistical modeling to understand dynamics in ecological systems. Design, denoted throughout this document with a capital "D" to distinguish it from the common use of the word, is the professional field of research and practice that studies the process of changing existing conditions into preferred ones (Simon 2019). While quantitative ecology guided the exploration of understanding rare species population dynamics, Design provided a new way to think about how to turn information from quantitative ecology into action.

The first two chapters of this dissertation present the development of a population monitoring approach that was built to provide biologically meaningful information on rare species: goal efficient monitoring (GEM). The monitoring approach was built on the fundamental premise that once people learn new information, they will have new questions. This principle dominates rare species monitoring because the stochastic population changes that appear as irregular dynamics cause constant changes in knowledge and questions. Therefore, a monitoring system built to detect a trend over time, which asks the same question over time (e.g., for occupancy trend monitoring asking "is the species present?" or for abundance trend monitoring asking "how many are present?") works well for common species, would be unsatisfying to those conducting the monitoring and result in limited learning about the stochastic dynamics driving the population. I therefore created the GEM system (model and field monitoring approach) that includes the appropriate dynamics for small or isolated populations of
rare species, possible using the flexible Bayesian hierarchical integrative population modeling structure, and an ability to change questions within a set of five rules based on what is known to allow people flexibility (Chapter 1). I also extended the GEM system to reflect more biological reality and provided a new monitoring metric that can be used for frequent predictions for small populations, which can be used to guide direct management action (Chapter 2).

However, in thinking about how to move GEM from a theoretical monitoring system to on the ground conservation that accomplished a specific goal, I realized there was seemingly no guidance on what field to even look to accomplish that. I found Design and quickly realized that Design, as a discipline that is about how to turn ideas into plans and processes, was generally absent from our growing list of partnerships in conservation biology and practice, despite its tremendous potential and widespread used in other fields like technology (Thomke \& Feinberg 2019), business (Liedtka 2018) and healthcare (Bazzano et al. 2017). I recognized the need to provide a broad overview of how Design could turn conservation biology into effective conservation practice and proposed the idea that we work towards developing a field of Conservation Design, combining conservation biology and Design (Chapter 3). I used this idea to frame some of how I envision GEM being applied, but I hope that is just a small preview of what is to come from this idea.

I am optimistic that with this work that I have moved the field of rare species conservation even the smallest step forward and that this gives future conservation designers a reason to envision a different future for rare species.

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Chapter 1: Goal efficient monitoring: an approach to monitoring as information changes ${ }^{1}$


#### Abstract

Long-term monitoring is important for understanding wildlife ecology and management. Unfortunately, long-term wildlife monitoring typically focuses on specific questions and can be inflexible. In rare species monitoring our questions evolve as we obtain more information. For example, we often start with: 1) is a species present? If so, subsequent questions often are: 2) are multiple individuals present? and 3) are both females and males present? To make long term monitoring programs more flexible, such programs should be able to change questions while still providing a long-term data stream. We propose Goal Efficient Monitoring (GEM) as an approach to monitoring that includes sampling rules connected to a Bayesian integrated population model, which allows for changing data collection and questions while maintaining long-term inference. To test GEM, we simulated 100 small populations with constant demographic rates that were for 11 years, applied our sampling rules to simulate observations, and predicted population values with an integrated population model. On average across all simulations, the predicted range of values from the model contained the true population values $97.5 \%$ of the time. These results demonstrate how a GEM approach can guide data collection and provide long-term inference for rare species while being responsive to immediate information needs.


## INTRODUCTION

Long-term monitoring of wildlife populations is essential for understanding and effectively managing wildlife populations (Holling 1978; Yocozz et al. 2001; Manley et al. 2004; Lyons et al. 2008; Conroy et al. 2011; Grant et al. 2013; Ellis et al. 2014; Buckland and Johnson 2017).

[^1]Monitoring can inform tasks ranging from local wildlife management (Cook et al. 2010; Cook et al. 2013) to achieving large global conservation targets, such as those recommended by the Convention on Biological Diversity (Laikre et al. 2010; Buckland and Johnson 2017). Monitoring can be defined as "the process of gathering information about some state variables at different points of time for the purpose of assessing system state and drawing inferences about change in state over time" (Yoccoz et al. 2001, p. 446). In addition, given the significant logistic and financial investment required for wildlife monitoring (Field et al. 2004; Reynolds et al. 2016), it is important that monitoring is as useful as possible across many different species and time scales. However, ensuring information generated from long-term monitoring programs is relevant and meaningful has been consistently raised as an issue (Legg and Nagy 2006; Nichols and Williams 2006). Authors have acknowledged that long-term monitoring often does not answer questions that it was originally designed to address (Legg and Nagy 2006), nor is it built with the specificity necessary to address questions beyond broad "surveillance" monitoring (Nichols and Williams 2006). In addition, authors acknowledge that information needs change relative to hypotheses, particularly in the face of rapid environmental change (Conroy et al. 2011).

The proposed solutions to make monitoring more relevant or useful rely heavily on the idea that defining goals a priori can solve many of the relevancy problems. For instance, to ensure that monitoring addresses the question of interest appropriately, Legg and Nagy (2006) recommend identifying a hypothesis and conducting a power analysis before a long-term monitoring program proceeds. Similarly, "targeted" monitoring, which targets a specific question, suggested by Nichols and Williams (2006) requires practitioners to define the monitoring of question of interest ahead of time, rather than assume that questions that emerge
from patterns in "surveillance" monitoring, or broad monitoring that is not question driven, can be answered effectively by a monitoring program. The proposed solutions to creating relevant information with long-term monitoring do not address two fundamental problems with knowledge acquisition over time; 1) questions change once information is learned; and 2) as questions change, the previous data stream is often abandoned and answering a new question requires a new investment in a different monitoring program (Magurran et al. 2010).

No single question, regardless of how carefully it is framed, will satisfy all information needs about populations over time because questions change as knowledge is gained. Thus, changes in questions that arise during long-term monitoring often occur irregularly and in an unplanned manner. This pattern of is particularly evident in rare species. For example, consider a protected species that is so locally rare that it is generally absent through much of an area of interest: the Canada lynx (Lynx canadensis) in the U. S. northern Rocky Mountain Region of the contiguous U. S. provides an example. For this species, the first question is typically: are there any present (Golding et al. 2018)? Because the organism is absent in many locations throughout the Northern Rocky Mountain region, it is critical that a monitoring effort answer the question of presence as efficiently as possible. Once the organism is found, the question of presence is immediately of less interest than other questions and a monitoring design that exclusively asks this presence question will be almost instantly irrelevant. Knowledge of the species presence leads to a logical next question conditioned on its established presence: is more than one individual present? Once this is known, there are a series of additional questions that logically follow as knowledge is gained, such as are both sexes present, is reproduction occurring, or how many of each sex are present? Although it is difficult to predict where questions may stop, the initial gathering of information proceeds through multiple predictably changing questions of 1 ) is
the species present? 2) Is more than one individual present? 3) Are both sexes present? (Golding et al. 2018).

In wildlife management literature there is little guidance on if or how to use information from different monitoring efforts, while the statistical literature suggests that it results in uncertain inference (e.g., Magurran et al. 2010), both of which can result in abandoned data streams and investments. For example, populations of the western snowy plover (Charadrius nivosus nivosus) in the United States have been monitored since the 1970s as a rare species; they were federally listed under the ESA in 1993 (58 FR 12864:12874). Recently, managers have found that recovering populations are now so abundant that changes in number have become non-informative and too expensive to obtain (Marcot 2019). Although monitoring information that was once relevant has become uninformative, pivoting monitoring strategies means abandoning a long-term data stream for the species that was a large financial investment. Additional funding to complete more monitoring is often difficult to obtain because funding requires continued societal support and therefore interest over long periods of time.

There is, however, a growing body of literature that shows that Bayesian integrated population models (IPMs) (Schaub and Abadi 2011) are a promising method for integrating multiple data streams (Zipkin and Saunders 2018). Although IPMs can be sensitive to underlying model assumptions (e.g., Riecke et al. 2019), they are effective tools for combining different data streams about a single population and have been shown to facilitate effective conservation decisions through improved ecological understanding (Arnold et al. 2018). As a result, IPMs are more frequently being used for species monitoring (e.g., Tempel et al. 2014, Ahrestani et al. 2017). However, the use of the IPM structure in these cases is focused on improving population
parameter estimates, which was one of the original benefits noted from the creation of IPMs (Schaub and Abadi 2011).

Rather than approach wildlife monitoring as the process of defining a single, targeted question asked repeatedly over time or different questions with disconnected data streams, we propose that knowledge acquired through wildlife monitoring can be designed to include changing questions collected as a continuous stream over time with multiple data types. Further, we suggest that a Bayesian IPM structure provides a statistical model framework that can accommodate changing observation needs and questions in a monitoring structure. We therefore propose Goal Efficient Monitoring (GEM) as a monitoring approach, that includes a population model for the species of interest, a set of sampling rules based on current knowledge (GEM sampling rules) and an IPM model that links changing observations to the population. In addition to the GEM the sampling rules, the IPM structure allows questions to shift to any parameter of the population that is outlined in the IPM, and thus can address the problem of allowing for changing questions as knowledge is gained and populations change over time. We consider GEM "goal efficient" because it is designed to be responsive to information goals for rare species, including the common rare species observation goals of answering the three questions about a small or isolated population of 1) is the species present? 2) Is more than one individual present? 3) Are both sexes present? Additionally, it is designed to be efficient by maximizing information gain through changing questions based on what is known from previously collected data using a flexible modeling and data structure.

We use a simulation study to test if the GEM sampling rules, which are field sampling rules based on the prior season's knowledge (explained in further detail in the Methods section below), and GEM model can provide reliable population information and if long-term
monitoring can be built to be flexible to changing questions while providing continual inference. We use the Canada lynx (Lynx canadensis) in the contiguous U.S. as an example species for the simulations because in much of its range within the U.S. it is in very small populations. In addition, Canada lynx have been listed as threatened under the ESA since 2000 (FR 2000). They are useful model organisms for GEM because there are specific regulations related to nested questions about presence of different population states on the landscape. If a National Forest is occupied by Canada lynx, the presence of a single individual or a female with kittens determines which land management regulations occur on National Forest landscapes across large areas of the Rocky Mountains (USDA 2007). In addition, surveys for Canada lynx typically employ noninvasive methods that provide a nested information structure which lends itself to different resolutions of information: they include winter track surveys (Squires et al. 2004) that provide individual, sex, and species identification through traditional non-invasive sign like scat, obtained through backtracking (Squires et al. 2004) or species identification through eDNA in the snow tracks (Franklin et al. 2019). Finally, as a rare species in the U. S. northern Rocky Mountain region, questions about Canada lynx are likely to change frequently. For example, in the Garnet Mountain Range of Montana, the small population of Canada lynx, estimated to be 7 to 10 individuals, became locally extinct sometime between 2011 and 2015. After that loss, the question about Canada lynx in the Garnet Mountains changed to presence of the species in the mountain range, which was verified in 2016 (USFWS 2017).

To provide a model for the GEM approach, we propose for our Canada lynx example a combined multistate and IPM formulation to: 1) incorporate population dynamics for the species that are relevant to population changes, including unobserved demographic parameters that may be of interest in the future (Zipkin et al. 2018); 2) provide probability metrics to describe
immediate (next season) changes that may occur in very small populations, such as the probability to retain breeding potential, which can provide immediately relevant information in the context of longer term trends and guide changes in monitoring questions over time; 3 ) shift between very small population and larger population dynamics, to maximize relevancy across a longer time period for wildlife species.

To incorporate population dynamics, we build the IPM of a hypothetical Canada lynx population at the southern edge of its range with a simple population formulation that includes survival of adult females and males, the ability to breed (indicated by the presence of females and males), and the birth, survival, and maturation of new individuals. Because we use an IPM framework, multiple data types can be used in the model and all variables outlined in the IPM, whether they are observed directly or not, can be predicted. We define multistate transition probability metrics for small populations based on GEM population states (breeding potential $=$ GEM state 4 ; isolated individuals of single sex $=$ GEM state 3 ; isolated individual $=$ GEM state 2; and not present = GEM state 1 ). We connect the IPM population predictions to the GEM population states to provide probabilities that the populations change GEM states in the next season, while still providing traditional long-term population monitoring information, such abundance over time. To test whether the GEM approach can provide reliable long-term monitoring information for a rare species, we simulate 100 populations with constant demographic rates for 11 years, simulate observations of the populations with the GEM sampling, and use the IPM to generate population predictions, which we compare to the original simulated population. In addition, to illustrate how GEM can be used to track two questions of "How does the probability of retaining breeding potential over time change?" and "how does the
abundance of females over time change?", we simulate an example of a manager monitoring Canada lynx in two different population conditions, established population and a new population.

## METHODS

To develop the basic model structure of GEM, we created an extension of an integrated population model to include a multistate model with the four GEM states: not present, single individual present, multiple individuals of a single sex present, and multiple individuals and both sexes present. We use a Bayesian hierarchical modeling approach because this allows flexibility with scarce data, which is typical of rare species and very small populations, as well as a continual, consistent way to incorporate multiple data streams to produce reliable estimates of a population (Zipkin and Saunders 2018; Sanderlin et al. 2018; Guillera-Arrotia 2017; Kéry and Schaub 2012). This extension is based on the previous Bayesian hierarchical multistate dynamic occupancy models of Royle (2004), Royle and Link (2005), Nichols et al. (2007), MacKenzie et al. (2009), and Kéry and Schaub (2012), as well as the integrated population model. Because we are using a Bayesian structure, the parts of the models are explained below with typical Bayesian terminology, where the term "biological process" refers to the dynamics of the population of interest (i.e., states, abundance, and transitions between states over time driven by population dynamics) occurring on the landscape and "observation process" refers to the process of attempts by surveyors to observe (i.e., surveys to detect individuals, sexes, or states) the biological process. The biological process represents a rare species or small population categorized by four population states (Figure 1-1): breeding potential (multiple individuals, both sexes); isolated individuals (multiple individuals, single sex); isolated individual; and locally extinct. We first describe the Bayesian structure of the hierarchical GEM model and then describe the
simulations, including the basis for the population simulation values and the performance metrics, run using R (version 4.0.2; R Development Core Team 2020) and JAGS (http://mcmcjags.sourceforge.net) to build and test the GEM model.

## GEM Model

## Biological Process

Because both female and male abundance are important in very small populations and can lead to reproduction in a small population (i.e., 12 individual wolverines that created a reproducing population in a mountain range in Montana [Squires et al. 2007]), we modeled male and female abundance separately. We modeled female, $N_{f, t}$, and male, $N_{m, t}$, abundance for a population at initial time $t=1$ (noted as t throughout the manuscript) as Poisson random variables with a mean average group size, $\lambda$, of 7 . Total individuals, $N_{t}$, were a derived parameter that was the sum of $N_{f, t}$ and $N_{m, t}$ (equation 3). We derived a population occupancy term for time $t=1, z 1_{t}$, and assigned occupancy if $N_{t}>0$, or unoccupied if $N_{t}=0$ (equations 4 and 5). Additionally, we derived the GEM population state for time $t=1, z 2_{t}$, from the composition of females and males and only allowed it to take on values of $4,3,2$, or 1 to represent the GEM states (4=breeding potential, $3=$ isolated individuals, $2=$ isolated individual, and $1=$ locally extinct) (equations 6 through 9). Because of the starting numbers of each sex, the populations were likely to start in state 4 (multiple individuals and both sexes):

1) $N_{f, t} \sim$ Poisson ( $\lambda$ )
2) $N_{m, t} \sim$ Poisson ( $\lambda$ )
3) $N_{t}=N_{f, t}+N_{m, t}$
4) $N_{t}>0 \rightarrow z 1_{t}=1$
5) $N_{t}>0 \rightarrow z 1_{t}=0$
6) $N_{f, t}=0$ and $N_{m, t}=0 \rightarrow z 2_{1}=1$
7) $N_{f, t}=1$ and $N_{m, t}=0$ or $N_{f, t}=0$ and $N_{m, t}=1 \rightarrow z 2_{t}=2$
8) $N_{f, t} \geq 2$ and $N_{m, t}=0$ or $N_{f, t}=0$ and $N_{m, t} \geq 1 \rightarrow z 2_{t}=3$
9) $N_{f, t} \geq 1$ and $N_{m, t} \geq 1 \rightarrow z 2_{t}=4$

We assumed that all juveniles could breed at 1 year of age, which is consistent with Canada lynx population dynamics when snowshoe hare (Lepus americanus) are abundant (Mowat et al. 2000). New individuals entered the population in time $t=1$ through a process that was function of three events: 1) the population being able to produce a litter, $l_{t}$, which was dependent on if the GEM population state, $z 2_{t}$, was breeding potential (GEM state 4), and the probability of litter production, p.litter, which we assumed was constant over time and populations (equations 10 and 11); 2) birth events, $B_{t}$, occurring, which were modeled as a Poisson random variable with the probability of success $l_{t}$ with $N_{f, t}$ trials (equation 12); 3) and new individuals born, $W_{t}$, which was modeled as a Poisson random variable with a mean that was a function of birth events, $B_{t}$, and a litter size, litter size, set as constant at 2 (equation 13) to include demographic stochasticity, which plays a large role in small populations (Lande 1993). The number of new females from the birth events, $W_{f, t}$, were derived as a binomial random variable with the probability of success set by a sex ratio, $s r$, of 0.5 out of the $W_{t}$ trials. The number of males $W_{m, t}$ were then derived from the difference between the total $W_{t}$ and number of females $W_{f, t}$ added to the population in time $t=1$ (equations 13a and 13b):
10) $z 2_{t}=4 \rightarrow l_{t}=p$. litter
11) $z 2_{t}=3$ or $z 2_{t}=2$ or $z 2_{t}=1 \rightarrow l_{t}=0$
12) $B_{t} \sim \operatorname{Binomial}\left(N_{f, t}, l_{t}\right)$
13) $W_{t}=$ litter size $* B_{t}$
a. $W_{f, t} \sim \operatorname{Binomial}\left(W_{t}, s r\right)$
b. $W_{m, t}=W_{t}-W_{f, t}$

For time $\mathrm{t}=2$ (noted as $t+1$ throughout the manuscript) and beyond (noted as $t+1 \ldots$ throughout the manuscript), we modeled these same population dynamics and incorporated survival to the next time step (breeding season). We modeled the total number of females and males alive at the next time step, $N_{f, t+1}$ and $N_{m, t+1}$, as the total of adults in time $t=1$ surviving to time $t+1, S_{f, t+1}$ and $S_{m, t+1}$, (equations 14 and 15) plus newly added individuals from births, $W_{f, t}$ and $W_{m, t}$, surviving to $t+1$ (equations 16 and 17), all of which were modeled as binomial random variables with a probability of success $s$, survival, which we kept as constant over time and age classes, and number of trials based on total individuals in that class. Total surviving individuals for each sex were derived as sums of the number of individuals that survived in both classes (equations 18 and 19):

$$
\begin{aligned}
& \text { 14) } S_{f, t+1} \sim \operatorname{Binomial}\left(N_{f, t}, s\right) \\
& \text { 15) } S_{m t+1} \sim \operatorname{Binomial}\left(N_{m, t}, s\right) \\
& \text { 16) } W_{f t+1} \sim \operatorname{Binomial}\left(W_{f, t}, s\right) \\
& \text { 17) } W_{m t+1} \sim \operatorname{Binomial}\left(W_{m, t,}, s\right) \\
& \text { 18) } N_{f t+1}=S_{f, t+1}+W_{f, t+1} \\
& \text { 19) } N_{m t+1}=S_{m, t+1}+W_{m, t+1}
\end{aligned}
$$

We linked the transition probabilities of the GEM population states, $z 2_{t}$, to the population dynamics of each time $t$ by deriving them from the abundance values at each time step. Thus, the likelihood of a population transitioning between the end of a time step and the next time step was a derived probability vector $\boldsymbol{\Psi}_{\boldsymbol{t}}$ that was formulated to track dynamics relevant to small populations. To keep the simulation simple and representative of small, isolated
populations, we only allowed transitions based on internal dynamics of birth and death, and not immigration and emigration, so that once a population had only isolated individuals (GEM state 3 or lower) it could only persist or decline, not transition back to include more individuals through breeding (which required GEM state 4) (Figure 1-2). Thus, the vector $\boldsymbol{\Psi}_{t}$ for transitioning to the GEM states in the next time step ( $\mathrm{t}+1$ ) was modeled as a four-by-four matrix, with the rows representing the GEM state in the previous time step and the columns representing the probability of the GEM state in the current time step as follows:

$$
\boldsymbol{\Psi}_{\boldsymbol{t}}=\left[\begin{array}{cccc}
1 & 0 & 0 & 0 \\
\psi_{t+1,21} & 1-\psi_{t+1,21} & 0 & 0 \\
\psi_{t+1,31} & \psi_{t+1,32} & 1-\psi_{t+1,32}-\psi_{t+1,31} & 0 \\
\psi_{t+1,41} & \psi_{t+1,42} & \psi_{t+1,43} & 1-\psi_{t+1,43}-\psi_{t+1,42}-\psi_{t+1,41}
\end{array}\right]
$$

The transition probabilities in the matrix above are dependent each population's GEM state at time $t$, such that only a single row is relevant at each time $t$. The probability of transition given population is in a state at time $t$ is dependent on the number of females, $N_{t}$ or $N_{f, t}$, males, $N_{t}$ or $N_{m, t}$, and survival, $s$, and death, $1-s$, probabilities at time $t$. The only exception was if a population was not present at time $t$, in which case it could not be present at time $t+1$ because we did not include immigration, so the probability of it remaining not present (GEM state 1 ) was 1 and all other probabilities of transition from not present were 0 .

Because the probabilities involve multiple classes, we provide the full binomial formulations for each transition that was possible below. Note that for each time $t$, a population can only be in a single state so only one row of the matrix is relevant. Thus if a population was in breeding potential (GEM state 4 ) it could: transition at time $t+1$ to locally extinct (GEM state 1 ) based on the probability that all individuals die (equation 20); transition to an isolated individual (GEM state 2) based on the probability that all individuals but one die (equation 21); transition to isolated individuals (GEM state 3 ) based on the probability that all individuals of a single sex die
and at least 2 individuals of the remaining sex live (equation 22); or stay in breeding potential (GEM state 4), which is the probability of the previously described probabilities not occurring (equation 23) (Figure 1-2a).

$$
\begin{aligned}
& \text { 20) } \begin{aligned}
& P\left(z 2_{t+1}=1\right)=\binom{N_{t}}{N_{t}}(1-s)^{N_{t}} *(s)^{N_{t}-N_{t}} \\
& \text { 21) } P\left(z 2_{t+1}=2\right)=\binom{N_{t}}{1}(1-s)^{N_{t}-1} *(s)^{1} \\
& \text { 22) } P\left(z 2_{t+1}=3\right)=\left(1-\left(\binom{N_{f, t}}{1}(1-s)^{N_{f, t}-1} *(s)^{1}\right) *\binom{N_{m, t}}{N_{m, t}}(1-s)^{N_{m, t}} *\right. \\
&\left.(s)^{N_{m, t}-N_{m, t}}\right)+\left(1-\left(\binom{N_{m, t}}{1}(1-s)^{N_{m, t}-1} *(s)^{1}\right) *\binom{N_{f, t}}{N_{f, t}}(1-s)^{N_{f, t}} *(s)^{N_{f, t}-N_{f, t}}\right) \\
& \text { 23) } P\left(z 2_{t+1}=4\right)=1-\left(\left(\left(1-\left(\binom{N_{f, t}}{1}(1-s)^{N_{f, t}-1} *(s)^{1}\right) *\binom{N_{m, t}}{N_{m, t}}(1-s)^{N_{m, t}} *\right.\right.\right. \\
&\left.(s)^{N_{m, t}-N_{m, t}}\right)+\left(1-\left(\binom{N_{m, t}}{1}(1-s)^{N_{m, t}-1} *(s)^{1}\right) *\binom{N_{f, t}}{N_{f, t}}(1-s)^{N_{f, t}} *\right. \\
&\left.\left.(s)^{N_{f, t}-N_{f, t}}\right)\right)+\left(\binom{N_{t} t}{1}(1-s)^{N_{t}-1} *(s)^{1}\right)+\left(\binom{N_{t}}{N_{t}}(1-s)^{N_{t}} *(s)^{\left.\left.N_{t}-N_{t}\right)\right)}\right.
\end{aligned}
\end{aligned}
$$

There are multiples ways a population can exist with breeding potential, which means that in some cases it can only transition to state 2 or 1 or stay in state 4 (Figure 1-2c). If this is the case equation 22 still accommodates this and can be calculated as 0 if that is the case.

If a population contained isolated individuals and only a single sex (GEM state 3 ) it could transition to locally extinct (GEM state 1) based on the probability that all individuals die (equation 20), transition to isolated individual (GEM state 2) based on the probability that all but one die (equation 21), or not transition out of isolated individuals (GEM state 3) (equation 24) (Figure 1-2c).

$$
\text { 24) } P\left(z 2_{t+1}=3\right)=1-\left(\left(\binom{N_{t}}{1}(1-s)^{N_{t}-1} *(s)^{1}\right)+\left(\binom{N_{t}}{N_{t}}(1-s)^{N_{t}} *(s)^{N_{t}-N_{t}}\right)\right)
$$

Finally, if a population contained an isolated individual (GEM state 2) it could transition at time $t+1$ to not present based on the probability that that individual died (equation 20), or stay as an isolated individual (equation 25) (Figure 1-2d).

$$
\text { 25) } P\left(z 2_{t+1}=2\right)=1-\left(\binom{N_{t}}{N_{t}}(1-s)^{N_{t}} *(s)^{N_{t}-N_{t}}\right)
$$

Note that for these formulations we assumed that the number of females surviving is independent of the number of males surviving each time step.

## Observation Process

To accommodate changing questions related to knowledge, the observation process of GEM must include the ability to adjust methods based on knowledge and select the appropriate detection method to gather information relevant to what is known and unknown. We therefore modeled the observation process as three hierarchical processes: observing the presence of a species, observing the number of individuals within a population, and observing the distribution of females and males within that sample of individuals from the population. We modeled these processes based on a series of GEM sampling rules as follows:
a) GEM sampling rule 1 If nothing is known, obtain confirmation of presence only.
b) GEM sampling rule 2

If presence has been confirmed in the previous season, obtain information on whether multiple individuals are present via counts.
c) GEM sampling rule 3

If counts are $>2$ across a single visit in a season (not $>2$ in total across repeat visits in a single season), obtain information on whether females and males are
present via collection of sex identifying information (e.g., genetic material) during counts.
d) GEM sampling rule 4

If multiple individuals and only a single sex were confirmed in the previous season, obtain information on whether multiple individuals are present via counts.
e) GEM sampling rule 5

If multiple individuals and both sexes were confirmed in the previous season, obtain information on whether females and males are present via collection of sex identifying information (e.g., genetic material) during counts.

Table 1-1 shows an example of these rules applied over four time steps (survey seasons) when nothing is known prior to the start of the first time step other than that the species may be present. Note that which of these sampling rules to apply will change based on what is known, but that will also change based on how the population is changing.

We considered the observation of the presence of the species as during a repeat visit $j$ at time $t$ or beyond, $y_{z, j, t}$, to be a Bernoulli random variable that represented the observation of $z 1_{t}$ with a probability of detection that depended on an individual detection probability, $p$, and the total number of individuals presents per the Royle and Nichols (2003) formulation: $1-(1-p)^{N_{t}}$ (equation 26). We modeled the observation of counts of individuals, $y_{c, j, t}$, as a Binomial random variable with probability of detection $p$ out of the total that were present, $N_{t}$ (equation 27). We modeled counts of females and males as a subset of counts based on backtracking methods for Canada lynx, where a track is encountered and can be verified with an eDNA track collection (Franklin et al. 2018) and backtracked to genetic material (i.e., scat or hair) that can be analyzed to individual and sex, which can typically be found within 2 km (McKelvey et al. 2006).

However, because genetic material is not always detected in backtracking efforts, we modeled the number of individuals with available genetic material, $y_{g, j, t}$, as a Binomial random variable which was a subset of those counted for that year determined by a probability of leaving genetic material, $p_{g}$ (equation 28). We then modeled the number of females in the individuals observed during backtracking in visit $j$ at time $t$ or beyond, $y_{f, j, t}$, as a hypergeometric random variable that was a function of the total population at time $t, N_{t}$, number of females at time $t, N_{f, t}$, and number of females counted with genetic identification after collection, which were a subset of genetically identified individuals, $y_{g, j, t}$ (equation 28a). The number of males counted with genetic identification after collection, $y_{m, j, t}$, were the remainder of the genetically identified individuals not identified as females (equation 28b):

$$
\begin{aligned}
& \text { 26) } y_{z, j, t} \sim \operatorname{Bernouli}\left(1-(1-p)^{N_{t}}\right) \\
& \text { 27) } y_{c, j, t} \sim \operatorname{Binomial}\left(N_{t}, p\right) \\
& \text { 28) } y_{g, j, t} \sim \operatorname{Binomial}\left(y_{c, j, t}, p_{g}\right)
\end{aligned}
$$

a. $y_{f, j, t} \sim$ Hypergeometric $\left(N_{t}, N_{f, t}, y_{g, j, t}\right)$
b. $y_{m, j, t}=y_{g, j, t}-y_{f, j, t}$

In this formulation, the detection of females and males is dependent on a probability determined by p , the probability of detecting an individual, and the proportion of the class of interest relative to the total population size (i.e., for females it is $\frac{N_{f, t}}{N_{t}}$. Because the population states defined in this paper depend on female and male composition, we derived population occupancy state in a population at time $t, z 2_{t}$, from the counts of females and males. This formulation relies on the relationship between detection probability and abundance (Royle and Nichols 2003). We assumed that no false positives (misidentifications) occurred and that only false negatives (missed detections) occurred. We also assumed a pre-breeding survey, so only adults were
observed. Figure 1-3 shows an overview of the integrated population model structure, which includes both the biological and observation processes, and the relationship of the processes in time.

## Simulations

We simulated 100 replicates to assess the performance of the GEM model that each contained three parts: 1) a simulated population for 11 time steps; 2) observation of the simulated population with the GEM sampling rules for 11 time steps; and 3) the GEM model run with the simulated observation data and posterior distribution predictions from the GEM model. In the following section we describe the process for each part of a single simulation replicate in the order presented above.

To create the simulated populations in each replicate we simulated the biological process described above (equations 1-19) with the following values. Each population was started in breeding potential at time $\mathrm{t}=1$ (GEM state $\left.4, z 2_{t}=4\right)$ and abundance of females, $N_{f, t}$, and males, $N_{m, t}$, was drawn from a Poisson distribution with a mean of $7(\lambda=7)$. The probability of litter if the population was in breeding potential, p . litter, was set as constant at 0.5 , which was the lower end of the empirically measured probability of lynx having a litter in mature forest in the same region as the study used for detection probability (Kosterman et al. 2018). We modeled birth events according to equations 10-13 and set litter size at a constant of 2 and sex ratio as a constant and equal at 0.5 . We used 0.7 for survival, which is equivalent to the highest rates of adult lynx survival when snowshoe hare densities are high (Mowat et al. 2000). For each time step in a replicate we also calculated the GEM state transition probability according to equations 20-25.

To create the observation data of the simulated population in each replicate, we simulated the observation process (equations 26-28) of following the GEM sampling rules. We assumed that the first time step of observation in every replicate started with no knowledge of the species. Thus, the first observation process was always attempting to observe presence (equation 26). This was simulated with 3 repeat visits within the season that generated detection/non-detection data. To simplify the simulations and compare across replicates, we set detection probability of an individual, $p$, set as a constant at 0.63 , which was based on research that showed that was the lower end of the cumulative probability of detecting one or more lynx in an area with known males and females (Squires et al. 2012). For time steps 2 through 11, we followed the GEM sampling rules and changed observation based on what was observed in the previous time step. Thus, following the GEM sampling rules, if the question changed to the presence of multiple individuals, a count with 3 repeat visits was simulated (equation 27). If multiple individuals were detected (at least 2 individuals within a single visit the previous time step), the question changed to presence of both sexes, a count with 3 repeat visits and collection of genetic material with a detection probability of $p_{g}$, set at 0.50 , which was based on the probability of detection of lynx genetic sign with 1 kilometer of snow tracking effort (McKelvey et al. 2006) (equation 28). The order of the questions was only set according to the sampling rules. Thus, with the knowledge gained each time step, the survey methods (detection/non-detection, counts of individuals, counts of females and males and state observation) adjusted based on what was known. For all detection, count, and genetic observations we assumed that there were no false positives (i.e., individuals that were double counted or misidentified).

Finally, to assess GEM model performance in each replicate we ran the GEM model with the observed population data as the model input to predict the following biological process
parameters of the simulated population at each time step: adult female $\left(N_{f, t, t+1 . . .}\right)$ and male $\left(N_{m, t, t+1 \ldots}\right)$ abundance, birth events $\left(B_{t, t+1 \ldots}\right)$, new individuals $\left(W_{t, t+1}\right)$, new females $\left(W_{f, t, t+1 \ldots}\right)$ and males $\left(W_{m, t, t+1 \ldots}\right)$, total individuals $\left(N_{t, t+1 \ldots}\right)$, survival $(s)$, and GEM transition probabilities. In addition, for each replicate the GEM model also provided predictions of individual detection probability $(p)$ and detection probability of genetic sign ( $p_{\text {genetic }}$ ). We used the following uninformative prior distributions: for survival (s) we used a uniform distribution constrained between 0.1 and 1 ; for litter probability (p.litter) we used a uniform distribution constrained between 0 and 1 ; and for both detection probabilities ( p and $p_{\text {genetic }}$ ) we used uniform distributions constrained between 0 and 1 . For each GEM model run we ran 3 MCMC chains each for 400,000 iterations, discarding the first 10,000 as a burn-in, and included thinning at a rate of 10 to reduce the size of data stored for each replicate. All simulations were conducted in program R (version 4.0.2; R Development Core Team 2020) and JAGS (http://mcmcjags.sourceforge.net). Code to generate simulated data, observation, and execute the GEM model is included in Appendix A.

## Model Performance

To assess the GEM model performance, we first assessed model convergence. To assess model convergence, we visually examined the trace plots (King et al. 2010) and used the $\hat{R}$ statistic which is a ratio estimator of how variable each chain was compared to how variable all chains were and should be around 1.0 (Brooks and Gelman 1998). For a given replicate if the average $\hat{R}$ across all GEM model predictions was at or below 1.05 we assumed the model had converged for that replicate. If the average $\hat{R}$ was higher than 1.05 , we discarded the replicate. This process was done until we had 100 replicates that converged.

We used four metrics to assess the GEM model performance, or the ability of the model to recover the true parameter values for the following biological and observation parameters: adult female, $N_{f, t, t+1 \ldots}$, and male, $N_{m, t, t+1 \ldots}$, abundance, birth events, $B_{t, t+1 \ldots . .}$, new females, $W_{f, t, t+1 \ldots .}$, new males, $W_{m, t, t+1 \ldots,}$, total individuals, $N_{t, t+1 \ldots,}$, survival, $s$, and GEM transition probabilities. For each replicate, all true parameters were known based on the simulated population in that replicate and all predicted parameters were from the GEM model posterior predictions, which were estimated using only the simulated observation data. First, we measured coverage, which is the percent of time out of all of the simulations that the $95 \%$ Bayesian credible interval (CRI) contained the true value of the simulated population. Next, we calculated mean absolute percent error of GEM model estimates, which is the absolute value of the difference between the true simulated population parameter value and predicted GEM model value, divided by the true simulated population parameter value, multiplied by 100. In addition, we added a measure we called mean absolute individual error to assist in interpretation of the mean absolute percent error metric. We felt that mean absolute percent error is difficult to interpret with very small populations because each individual makes up such a large percentage of the population (i.e., one individual makes up $25 \%$ of a population of 4 ), so mean absolute individual error is the absolute value of the total individuals that the abundance estimates deviated by. To determine the accuracy of the GEM model estimates, we calculated relative root mean square error (RRMSE) for each estimated parameter using the following equation:
29) $R R M S E=\frac{\sqrt{\frac{1}{r \sum_{i=1}^{n}\left(\hat{\theta}_{k}-\theta_{k}\right)^{2}}}}{\bar{\theta}}$
where $r$ was the number of replicates, $\hat{\theta}_{k}$ is the predicted parameter value and $\theta_{k}$ is the true value at replicate $k$ and $\bar{\theta}$ is the mean true value of the parameter over all replicates. We used RRMSE so that accuracy was comparable across all of the parameters in the GEM model and replicates.

## Management Example

We ran an additional 200 replicates with the same process described above with two different starting conditions in breeding potential (GEM state 4). Rather than a draw from a Poisson with a mean of $\lambda$, we set the starting conditions for 100 replicates to be 2 individuals (a female and a male) to represent a new population and 100 replicates to be 8 individuals (4 females and 4 males) to represent an established population. We only tracked the probability to retain breeding potential, $\psi_{t+1,44}$, and adult female abundance adult female ( $N_{f, t, t+1 . . .}$ ) over the 11 time steps. All other processes were conducted as described in the methods section above. In addition, Appendix B contains further explorations of these simulations and how the GEM model performs with lower starting GEM states.

## RESULTS

GEM model convergence was achieved for all parameters during the simulation. Visual inspection of MCMC chain plots all showed visual signs of adequate mixing. In addition, the $\hat{R}$ statistics for each parameter, were all around 1. All results presented in this section are summarized over all simulations, including all time steps within each simulation replicate, and the notation for each variable below has been simplified with $t$ and $j$ subscripts to represent the values of time and visits over the simulations. Results described below are summarized in Table 1-2.

## Biological Process

The GEM model estimated biological process variables well. For female adult abundance, $N_{f, t, t+1 \ldots . .}$, coverage was $98.1 \%$, mean absolute percent error was $74.5 \%$, mean absolute individual error was 6.61 , and RRMSE was 0.587 . For male adult abundance, $N_{m, t, t+1 \ldots,}$,
coverage was $87.9 \%$, mean absolute percent error was $74.5 \%$, mean absolute individual error was 7.25 , and RRMSE was 0.676 . For birth events, $B_{t, t+1 \ldots,}$, coverage was $99.9 \%$, mean absolute percent error was $71.0 \%$, mean absolute individual error (in this case representing events) was 1.18, and RRMSE was 0.583 . For new females, $W_{f, t, t+1 \ldots,}$, coverage was $99.7 \%$, mean absolute percent error was $88.0 \%$, mean absolute individual error was 3.68 , and RRMSE was 0.646 . For new males, $W_{m, t, t+1 \ldots}$, coverage was $99.7 \%$, mean absolute percent error was $91.2 \%$, mean absolute individual error was 3.71 , and RRMSE was 0.653 . For total individuals, $N_{t, t+1}$, coverage was $98.5 \%$, mean absolute percent error was $54.4 \%$, mean absolute individual error was 18.37, and RRMSE was 0.551 . For survival, $s$, coverage was $100 \%$, mean absolute percent error was $8.10 \%$, and RRMSE was 0.0767 . In addition, GEM population state, $z 2_{t}$, coverage was high with an overall coverage of $100 \%$.

The GEM model predicted only transition probabilities that occurred. In all replicates, the populations stayed in breeding potential, so the GEM model only provided predictions for transitions from breeding potential (GEM state 4) with an average coverage of $99.0 \%$ (Table 12). Overall coverage was high for all possible transitions; coverage of the probability of staying in breeding potential $\left(\psi_{t+1,44}\right)$ was $100 \%$; coverage of the probability of transitioning from breeding potential to isolated individuals $\left(\psi_{t+143}\right)$ was $100 \%$; coverage of the probability of transitioning from breeding potential to a single isolated individual $\left(\psi_{t+1,42}\right)$ was $95.9 \%$; coverage of the probability of transitioning from breeding potential to locally extinct ( $\psi_{t+1,41}$ ) was $100 \%$. Overall, the error of the transition probabilities was higher than the biological variables. For the probability of staying in breeding potential $\left(\psi_{t+1,44}\right)$ or going transitioning to locally extinct $\left(\psi_{t+1,41}\right)$, the mean absolute percent error was low ( $22.0 \%$ for both), whereas the mean absolute percent error for the other transitions from breeding potential to isolated
individuals $\left(\psi_{t+1,43}\right)$ and a single isolated individual $\left(\psi_{t+1,42}\right)$ was much higher at $1.60 \times 107 \%$ and $2.33 \times 10^{25 \%}$, respectively. In addition, the RRMSE showed a similar pattern, with .

## Observation Process

For the 100 simulations each with 11 time steps, a total of 1,100 simulation time steps (GEM questions remained constant across visits within a time step), GEM sampling rules resulted in the 100 simulation time steps $(9.1 \%)$ where the observation question was "Is the species present?" with detection data collected, 200 simulation time steps ( $18.2 \%$ ) where the observation question was "Are multiple individuals present?" with count data collected, and 900 simulation time steps (72.7\%) where the observation question was "Are females and males present?" with count and genetic data collected. Individual detection probability, p , was well estimated across scenarios. Coverage was $96.0 \%$, mean absolute percent error was $16.9 \%$, and RRMSE was 0.191 . Genetic sign detection probability, $p_{\text {genetic }}$, was estimated with less error: coverage was $96.0 \%$, mean absolute percent error was $4.96 \%$, and RRMSE was 0.050 .

## Management Example

For the 100 simulations for a new population ( 2 starting individuals), the GEM model estimated female adult abundance, $N_{f, t, t+1 \ldots}$, well: coverage was $94.1 \%$, mean absolute percent error was $31.0 \%$, mean absolute individual error was 1.17 , and RRMSE was 0.235 . The probability of retaining breeding potential, $\psi_{t+1,44}$, was also estimated well: coverage was $94.2 \%$, mean absolute percent error was $4.46 \%$, and RRMSE was 0.0381 .

For the 100 simulations for an established population (8 starting individuals), the GEM model estimated female adult abundance, $N_{f, t, t+1 . . .}$, well: coverage was $93.63 \%$, mean absolute percent error was $65.5 \%$, mean absolute individual error was 2.91 , and RRMSE was 0.521 . The
probability of retaining breeding potential, $\psi_{t+1,44}$, was also estimated well: coverage was $94.5 \%$, mean absolute percent error was $2.32 \%$, and RRMSE was 0.0206 .

## DISCUSSION

We demonstrate that the ability to change questions within a pre-defined suite of questions is an approach to monitoring that can provide relevant information so knowledge is continually built upon and that it can be accomplished with the GEM framework, combining hierarchical integrated population models and multistate model frameworks. We present an example of those combined model frameworks and demonstrate that not only does the GEM model and sampling approach consistently predict biological variables accurately, but that it can do so while accommodating changing questions based on what is known. Rather than assume that the key to relevant and effective monitoring is careful upfront planning to determine a single question of interest, the GEM framework provides a way one can outline the dynamics fundamental to a population of interest through the GEM IPM portion, adjust sampling in a predictable way with GEM sampling rules based on what is currently known about the population, and augment at various points additional monitoring variables are of interest to improve monitoring estimates. In addition, by providing a quantitative link between observation and the population through GEM population state transitions, time-relevant information (i.e., predictions for the next season) that is biologically meaningful, such as the probability of breeding capacity persisting in the next year, can be produced without losing a long-term monitoring data stream. In addition, the sampling rules allow for a series of changing questions (Figure 1-4) that are common for rare wildlife and small populations (Golding et al. 2018), but they are flexible enough to still work once a population is large.

The ability of the GEM model to reliably predict both observed and unobserved population parameters from a changing set of sampling approaches, including different field methods and data types, is due largely to the underlying IPM structure. Abundance or occupancy values that were directly "observed" in the simulation through detection of adults were predicted with similar credible interval coverage as those that were not directly "observed", such as birth events per season and new individuals. Although error rates, as measured by mean absolute percent error and RRMSE, were lower for the directly "observed" parameters, the high coverage for all parameters and the ability to quantify the uncertainty around predictions suggests high power to perform in real world settings for small populations. In fact, in many small populations, stochastic fluctuations make predictions difficult, and one may therefore not even expect high amounts of predictability. However, having a range of possibility expressed through uncertainty may be useful for decisions or ecological models, which is something that other single-question monitoring approaches do not provide well or at all for small populations. In addition, with the prediction of unobserved variables, data that is difficult to obtain for small populations, such as survival, does not have to be directly observed to be estimated. Having unobserved variables as part of the long-term data stream also means that future monitoring can shift again to focus on a previously unobserved parameter and still have a consistent data stream for that parameter from the start of monitoring. More potential mechanistic understandings are available with this full knowledge than with monitoring confined to a single, repeated question.

The GEM state structure and transition probabilities are designed to allow for tracking population conditions through various phases of small population dynamics: starting with individual colonists and progressing through the generation of a small population containing males and females and through its decay toward extinction. It can effectively track these
dynamics because each of the states and transition probabilities are derived from the observed field efforts that contain nested information: in monitoring to determine multiple sexes you can detect the states of occupancy or in looking for both sexes you can individuals you count individuals. As such, it provides information on small population dynamics that are absent when focusing on a single metric. In addition, the transition probabilities of the states are biologically relevant and provide time-relevant information (for the next season) in a long-term program, which may be more meaningful than long-term trend for a small population. For instance, the probability of transitioning out of the multiple individuals and both sexes present (GEM state 4) reflects the probability of losing breeding capacity between the end of a survey season and the next year. If that probability is predicted to be high, or even highly uncertain, action such as limiting access to certain areas can be taken prior to the next year to attempt to bolster reproductive success or survival of a litter. Thus, the multistate structure provides the ability to produce meaningful information for the immediate future as part of, rather than detracting efforts from, the long-term data stream, a key advantage for any long-term monitoring system to remain relevant through societal or environmental changes.

We also show how the GEM state structure and transition probabilities can allow for tracking different population metrics such as female abundance and the probability to retain breeding potential if question change through the management example. In both a new and established population the GEM model and sampling structure provided reliable estimates of changing probabilities and abundance. This is important because if the desired type of information changes between these metrics, or even to other metrics that are outline in the population model portion of the IPM and linked to the multistate structure, this shift can be accommodated seamlessly. In addition, if an information goal shifted to a vital rate, such as
survival, not only is that variable tracked but because of the IPM structure additional survival observation data can be collected and integrated with the existing data stream.

The GEM structure is also very flexible on the type of data and field methods that can be used. The nested nature of the questions also leads to operational efficiencies. In the initial state of asking whether the species is present, methods can be designed to detect unmarked individuals using flexible and inexpensive methods such as camera sets (Steenweg et al. 2017) or snow-print based DNA samples (Franklin et al. 2019). Once an organism has been detected, sampling is augmented to more demanding methods: examples include more rigorous camera-based detections that allow the application of space to detection models (Moeller et al. 2018) or obtaining individual identifications through the collection of forensic DNA (e.g., using scat dogs [Wasser et al. 2004] or snow backtracking [McKelvey et al. 2006]) that allows both individual and sex identifications. Because the implementation of more intensive non-invasive sample collection methods are only undertaken once there is knowledge that the area is occupied (using the GEM sampling rules), they are only applied in areas where they are add information to what is currently known, leading to an effort that is targeted towards maximizing information gain. We are aware that this progression is often applied ad-hoc in occupancy designs. The multistate design, however, formalizes its application into a coherent long-term monitoring program.

There are a few important limitations to consider for the execution of the GEM framework as presented. One limitation for small populations is the difficulty of initial values: the Bayesian GEM structure at low population values is sensitive to initial values and at very low abundance numbers (which may reflect realities) may fail repeatedly due to the stochastic nature of such populations. In addition, as with many multistate and IPM models, the model is computationally intensive and often can become cumbersome to track because of the large
number of dimensions calculated in each iteration. This computational load will increase for any parameters that are expected to vary, like survival with different age classes, although there are methods to speed up processing (e.g., Yackulic et al. 2020).

We present a general format for the GEM biological process to show its utility and acknowledge that many possible extensions or iterations can be built based on the principles provided here. We suggest that further iterations include different or additional biological parameters, such as emigration and immigration, to reflect the population of interest, as well as different observation processes. We suggest that further simulation and empirical research be conducted to provide guidance on how to most effectively use the quantitative metrics in the GEM framework, such as transition probabilities or associated uncertainty, to formally guide field work, as the structure provides many potential benefits for field operational efficiencies. We further suggest future research into sampling approaches with GEM. To illustrate the GEM concept and model, we assumed distinct and closed populations and annual sampling with three repeat visits within the season, although this is not always reflective of reality. There are practical benefits associated with tracking small populations rather than individuals in the GEM framework. In conventional occupancy modeling, the ideal spatial area to associate with occupancy is generally considered to be defined by a single home range. However, for a variety of reasons but most fundamentally because a grid will not line up precisely with the underlying home range structure, individual organisms are detected in multiple cells, a fundamental violation of model closure assumptions (MacKenzie et al. 2017). The cells associated with a multistate model can be larger: they can be delineated to fit a small population and can be more closely aligned with topographic features that define populations. For example, Squires et al. (2007) estimated the population of wolverines across 3 disjunct mountain ranges to $\sim 12$
individuals. Applying the multistate model to wolverines in this area, each mountain range would provide an appropriate cell. In addition, we see many opportunities for further exploration of the use of GEM under different monitoring scenarios, including understanding the effects of different monitoring time intervals, variation in biological parameters, and the use of additional non-invasive data streams to observe some of the latent variables in the model.

We believe the GEM framework is an important step forward in rethinking the approach to monitoring wildlife populations. Although we highlight its utility for rare species, where information gains are often rapid and questions change frequently, we see this approach as an important concept for all wildlife monitoring. As we face unprecedented and unpredictable change in the climate and environment, there is no doubt that many of our static monitoring systems of repeated questions over long periods of time will become obsolete, as they will increasingly not reflect current conditions and therefore questions. As such, we see the need to re-envision monitoring from a static, repeated process, to a flexible, dynamic, GEM process that can be adapted relative the information we are interested in acquiring. We have demonstrated that the flexible quantitative Bayesian tools available today can provide the modeling structures to accomplish a GEM process, including the ability to have a continuous data stream as questions change or species change from rare to common or common to rare. But more importantly, we see the need for a shift in thinking about what wildlife monitoring is and should accomplish. Ultimately, we believe that we must build evolutionary monitoring systems; otherwise monitoring programs, and the information that they provide that once seemed relevant, will go extinct.

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## TABLES

Table 1-1) The Goal Efficient Monitoring (GEM) sampling rules applied across four time steps (survey seasons). The process outlined below is based on a hypothetical example for a mountain range thought to contain Canada lynx (Lynx canadensis) that has no recent (within the previous year) confirmation of that. Although the methods listed are specific to this example, these are not intended to represent the only methods available to obtain that type of data. Note that in time step 4, the females and males question is asked again, but in this case it represents the question if females and males continue to be present because it follows a year where they were detected.

| Time step | Knowledge from previous season's sampling | GEM question | GEM sampling rule | Data to collect this season | Field method | Season outcome |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | GEM sampling rule 1: |  |  |  |
| 1 | None | Is the species present? | If nothing is known, obtain confirmation of presence only | Detection/nondetection | Snow tracking | Presence confirmed |
|  |  |  | GEM sampling rule 2 : |  |  |  |
| 2 | Presence | Are multiple individuals present? | If presence has been confirmed in the previous season, obtain information on whether multiple individuals are present via counts | Count <br> Derived: <br> Detection/nondetection | Snow tracking | Count $>2$ on a single visit |
|  |  |  | GEM sampling rule 3: | Count |  |  |
| 3 | Multiple individuals | Are females and males present? | If counts are >2 across a single visit last season, obtain information on whether females and males are present via collection of sex identifying information (e.g., genetic material) during counts | Count of females and males <br> Derived: <br> Detection/nondetection, GEM state | Snow tracking plus backtracking to genetic material | Females and males confirmed <br> Derived: <br> GEM state 4 |


| 4 | Females and males | Are females and males present? | GEM sampling rule 5: Count |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | If multiple individuals and both sexes were confirmed through counts and sex id last season, obtain information on whether | Count of females and males | Snow tracking plus backtracking | Females and males confirmed |
|  |  |  | females and males are present via collection of sex identifying information (e.g., genetic material) during counts | Derived: <br> Detection/nondetection, GEM state | to genetic material | Derived: <br> GEM state 4 |

Table 1-2) The parameters of the GEM model and performance metrics across 100 replicate simulations, each with 3 MCMC chains, 50,000 iterations, 5,000 burn-in period and no thinning, with the full observation scenario (counts of males and females with 3 visits and one independent observation of GEM population state every time step). $\mathrm{RRMSE}=$ relative root mean square error.
$\left.\begin{array}{ccccc}\text { Parameter } & \text { Description } & \begin{array}{c}\text { Mean } \\ \text { absolute } \\ \text { percent } \\ \text { error }\end{array} & \text { Coverage } & \text { RRMSE }\end{array} \begin{array}{c}\text { Mean } \\ \text { absolute } \\ \text { individual } \\ \text { error }\end{array}\right]$

## FIGURES

Figure 1-1) An example of four GEM population states of interest for Canada lynx (Lynx canadensis): 1) locally extinct (not present shown as gray); 2) single isolated individual; 3 ) isolated individuals (single sex shown as blue); and 4) breeding potential (males represented as blue and females represented as orange).


Figure 1-2) An example of four GEM population states of interest for Canada lynx (Lynx canadensis), locally extinct (not present shown as gray), single isolated individual (either sex is represented as black), isolated individuals (single sex shown as blue), and breeding potential (males represented as blue and females represented as orange), and their transition probabilities within a closed population (i.e., only births and deaths lead to population change). Transition are shown by the state in which they start: $a=$ transitions from breeding potential (GEM state 4 ), $b=$ transitions from isolated individuals (GEM state 3), $\mathrm{c}=$ transitions from isolated individual (GEM state 2). The not present state is not shown because once a population is in the not present state it stays in that state with a probability of one (as there are only births and deaths shown in this example). Note that transition probabilities, $\psi$, are simplified for display and exclude time subscripts and use the number for the GEM states.
A)

B)


Figure 1-3) The integrated population model framework for a hypothetical population of Canada lynx (Lynx canadensis) over a single time step. The time scale included shows a single calendar year divided by months, including notations of $t$ and $t+1$ relative to the model. The biological process and equations are represented on the top of the timeline and observation process and equations are shown on the bottom. Note that all possible parts of a GEM observation approach is shown in the observation process.

| $z 1_{t}$ | $B_{t} \sim$ Binomail $\left(N_{f, t}\right.$, litterp $\left.{ }_{t}\right)$ | $S_{f, t+1} \sim$ Binomial $\left(N_{f, t}, s\right)$ |
| :--- | :--- | :--- |
| $z 2_{t}$ | $W_{t}=B_{t} *$ litter size | $S_{m, t+1} \sim \operatorname{Binomial}\left(N_{m, t} s\right)$ |
| $N_{t}=N f_{t}+N m_{t}$ |  | $W_{f, t+1} \sim \operatorname{Binomial}\left(W_{f, t}, s\right)$ |
|  | $W_{f, t} \sim$ Binomail $\left(W_{t}\right.$, sex ratio $)$ | $W_{m, t+1} \sim \operatorname{Binomial}\left(W_{m, t}, s\right)$ |
|  | $W_{m, t}=W_{t}-W_{f, t}$ | $N_{f, t+1}=S_{f, t+1}+W_{f, t+1}$ |
|  |  | $N_{m, t+1}=S_{m, t+1}+W_{m, t+1}$ |



Figure 1-4) Example results from a simulation replicate. The total abundance predicted by the GEM model (black), uncertainty associated with the prediction (gray ribbon), and true value of the simulation (blue) is shown on top. GEM questions, knowledge, field methods and per-visit data generated with GEM sampling rules, with detection/non-detection first, count of track encounters second, and females and males third, are shown on the bottom. $\mathrm{MI}=$ multiple individuals, $\mathrm{MIB}=$ multiple individuals, both sexes.


## APPENDIX A: R CODE

R code for creating the simulations, including packages needed to run the code and:

1) A function to simulate the biological process (gem_sim_bio)
2) A function observation process (gem_sim_obs)
3) A function to run the GEM model using JAGS (gem_run_mode1)
\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\# packages = c("jagsuI", "reshape2", "dp1yr", "rlist")
package.check <- lapply(packages, FUN = function(x) \{ if (!require(x, character.only = TRUE)) \{ install. packages ( $x$, dependencies $=$ TRUE) library(x, character.on7y = TRUE) \}\})
```
########################################################################
# 1. GEM_SIM_BIO
#######################################################################
# Name: gem_sim_bio
# Description: function to simulate biological process of one or multiple small
populations with four GEM states (not present, single individual present, multiple
individuals of a single sex present, and multiple individuals with both sexes present)
#######################################################################
# Arguments
#######################################################################
# n.group: number of groups (populations), whole number
# s.group: group size (for one sex), whole number
# n.timestep: number of time steps, whole number
# n.states: number of GEM population states, whole number
# s.surv: survival probability, probability between 0 and 1
# p.litter: probability of having a litter, probability between 0 and 1
# n.litter: number of individuals per litter, whole number
# sr.litter: sex ratio of females to females per litter, number between 0 and 1
#######################################################################
# Function outputs
#######################################################################
```

\# Biodata: a list written to the global environment containing simulated population
\# data
\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#
\# Function
\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#
gem_sim_bio <- function(n.group, s.group, n.timestep, n.states, s.surv, p.litter,
n. 1 itter, sr.1itter) \{
\#\#\# Create matrices/arrays to hold data
\# Start abundance
$n \mathrm{~m}<-\operatorname{ar} r a y(d a t a=N A, \operatorname{dim}=c(1, n$. timestep,$n$. group $)$,
dimnames = 1ist(c("nm"),
c(1:n.tímestep),
c(1:n.group)))
$\mathrm{nf}<-\operatorname{array}($ data $=N A, \operatorname{dim}=c(1, n$, timestep, n . group $)$,
dimnames = 1ist(c("nf"),
c(1:n.timestep),
c(1:n.group))
\# Birth events
be <-array (data $=N A, \operatorname{dim}=c(1, n . t i m e s t e p, n . g r o u p)$,
dimnames = 1ist(c("be") ,
c(1:n.timestep),
c(1:n.group)) )

```
# New individuals
ni <-array(data = NA, dim=c(1,n.timestep,n.group),
    dimnames = 1ist(c("ni"),
                        c(1:n.timestep),
                        c(1:n.group)))
# New males
wm <-array(data = NA, dim = c(1,n.timestep,n.group),
    dimnames = 1ist(c("wm"),
    c(1:n.timestep),
    c(1:n.group)))
# New females
wf <-array(data = NA, dim = c(1,n.timestep,n.group),
    dimnames = 1ist(c("wf"),
                                    c(1:n.timestep),
                        c(1:n.group)))
# End abundance
wnm <-array(data = NA, dim = c(1,n.timestep,n.group),
        dimnames = list(c("wnm"),
                                    c(1:n.timestep),
                                    c(1:n.group)))
wnf <-array(data = NA, dim = c(1,n.timestep,n.group),
    dimnames = list(c("wnf"),
                        c(1:n.timestep),
                        c(1:n.group)))
wtot <-array(data = NA, dim=c(1,n.timestep,n.group),
        dimnames = list(c("wtot"),
                    c(1:n.timestep),
                        c(1:n.group)))
# Lambda
7am <-array(data = NA, dim = c(1,n.timestep,n.group),
    dimnames = 1ist(c("1"),
                        c(1:n.timestep),
                        c(1:n.group)))
# Z - states
z <-array(data = NA, dim = c(1,n.timestep,n.group),
    dimnames = list(c("z"),
                                    c(1:n.timestep),
                                    c(1:n.group)))
nfa1 <-NULL
nma1 <-NULL
# Reproduction
1itter_prob<-matrix(NA,n.timestep,n.group)
state_breed <-matrix(NA,n.timestep,n.group)
# Survival
S <-matrix(NA,n.group,n.timestep)
# Probability of litter
L <-matrix(NA,n.group,n.timestep)
# Fill in survival and probability of litter
for (1 in 1:n.group){
for (k in 1:n.timestep){
    S[1,k] <-s.surv
    L[1,k] <-p.1itter
}
############################ Initial time 1 values ##############################
## Initial states for time 1
# Initial population size at time 1
for (i in 1:n.group){
    nfa1[i] <- rpois(1,s.group) # females
    nma1[i] <- rpois(1,s.group) # males
```

```
}
######################### Loop to generate population ##########################
# Population
for (i in 1:n.group){
    for(j in 2:n.timestep){
## Time 1
# Entering individuals/state
    nm[1,1,i] <- as.numeric(nma1[i])
    nf[1,1,i] <- as.numeric(nfa1[i])
    z[1,1,i] <-ifelse(nm[1,1,i] >= 1 & nf[1,1,i] >=1, 4,
                            ifelse(nm[1,1,i] > 1 & nf[1,1,i] == 0 nf[1,1,i] > 1 & nm[1,1,i] == 0, 3,
                            ife1se(nm[1,1,i] == 0 & nf[2,1,i] == 0,1,NA))))
# Breeding possible
    state_breed[1,i] <-as.numeric(ife]se(z[1,1,i]==4,1,0))
    litter_prob[1,i] <-state_breed[1,i]*L[i,i]
# Births
    be[1,1,i] <- rbinom(1,nf[1,1,i],1itter_prob[1,i])
# New individuals
    ni[1,1,i] <- be[1,1,i]*n.1itter
    wm[1,1,i] <- rbinom(1,ni[1,1,i], sr.1itter) # new males
    wf[1,1,i] <- ni[1,1,i] - wm[1,1,i] # new females
# Totals
    wnm[1,1,i] <- wm[1,1,i] + nm[1,1,i] # total males at time 1
    wnf[1,1,i] <- wf[1,1,i] + nf[1,1,i] # total females at time 1
    wtot[1,1,i] <-wnm[1,1,i] + wnf[1,1,i] # total at time 1
# Lambda
    1am[1,1,i] <- NA
## Time 2 and beyond
## Entering individuals/state
    nm[1,j,i] <- rbinom(1,wnm[1,j-1,i], s[i,j])
    nf[1,j,i] <- rbinom(1,wnf[1,j-1,i],s[i,j])
    z[1,j,i] <-ife]se(nm[1,j,i] >= 1 & nf[1,j,i] >=1, 4,
                                    ifelsennm[1,j,i] >1 & nf[1,j,i] == 0|nf[1,j,i] > 1 & nm[1,j,i] == 0, 3,
                                    ifelse(nm[1,j,i] == 1 & nf[1,j,i] == 0 | nf[1,j,i] ==1 & nm[1,j,i] == 0, 2,
                                    ifelse(nm[1,j,i] == 0 & nf[1,j,i] == 0,1,NA))'))
# Breeding possible
    state_breed[j,i] <-as.numeric(ifelse(z[1,j,i]==4,1,0))
    litter_prob[j,i] <-state_breed[j,i]*L[i,j]
# Births
    be[1,j,i] <- rbinom(1, nf[1,j,i], litter_prob[j,i])
# New individuals
    ni[1,j,i] <- be[1,j,i]*n.litter
    wm[1,j,i] <- rbinom(1,ni[1,j,i],sr.1itter) # new males
    wf[1,j,i] <- ni[1,j,i] - wm[1,j,i] # new females
# Totals
    wnm[1,j,i] <- wm[1,j,i] + nm[1,j,i] # total males
    wnf[1,j,i] <- wf[1,j,i] + nf[1,j,i] # total females
    wtot[1,j,i] <- wnm[1,j,i] + wnf[1,j,i] # tota1
    # Lambda
    7am[1,j,i] <- wtot[1,j,i]/wtot[1,j-1,i]
}
#################################################################################
### Create long data frames for plotting and result/diagnostic comparisons
    nm2 <-as.data.frame(me7t(nm))
```

```
    colnames(nm2) <-c("variable","time","group","value")
    nf2 <-as.data.frame(me1t(nf))
    colnames(nf2) <-c("variable","time","group","value")
    z2 <-as.data.frame(me7t(z))
    colnames(z2) <-c("variable","time","group","value")
    be2 <-as.data.frame(me7t(be))
    colnames(be2) <-c("variable","time", "group", "value")
    ni2 <-as.data.frame(melt(ni))
    colnames(ni2) <-c("variable","time","group","value")
    wm2 <-as.data.frame(me7t(wm))
    colnames(wm2) <-c("variable","time","group","value")
    wf2 <-as.data.frame(melt(wf))
    colnames(wf2) <-c("variable","time","group","value")
    wnm2 <-as.data.frame(me1t(wnm))
    colnames(wnm2) <-c("variable","time", "group", "value")
wnf2 <-as.data.frame(me7t(wnf))
colnames(wnf2) <-c("variable","time","group","value")
wtot2 <-as.data.frame(me7t(wtot))
colnames(wtot2) <-c("variable","time","group", "value")
1am2 <-as.data.frame(me1t(lam))
colnames(1am2) <-c("variable","time", "group", "value")
n2 <-rbind(nm2,nf2,z2,be2,ni2,wm2,wf2,wnm2,wnf2,wtot2,1am2)
```

\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\# write data to global environment \#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#
biodata <- list("n.group"= n.group, "s.group"= s.group,"n.timestep"=n.timestep,
"n.states"= n.states, "s.surv" = s.surv, "s"=s,
"p.litter"= p.litter, "L"=L, "n.litter"= n.litter,
"sr. 1 itter" = sr.litter, "N_long" = n2, "breed"= state_breed,
"nf.init" = nfa1, "nm.init"= nma1, "nf" = nf, "nm" = nm,"z" = z,
"be" = be, "ni" = ni, "wm" = wm, "wf" = wf, "wnm" = wnm,
"wnf" = wnf,"wtot" = wtot, "1am" = 1am)
1ist2env(biodata,.Globa1Env)
\}
\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#
\# 2. GEM_SIM_OBS
\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#
\# Name: gem_sim_obs
\# Description: function to simulate observation process with GEM sampling rules
outlined in this manuscript for one or multiple small populations with four GEM states
(not present, single individual present, multiple individuals of a single sex present,
and multiple individuals with both sexes present)
\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#
\# Arguments
\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#
\# p: detection probability of an individual, probability between 0 and 1
\# nf: abundance of females from gem_sim_bio function
\# nm: abundance of males from gem_sim_bio function
\# n.visits: number of repeat visits to a population during a survey season
\# n.timestep: number of time steps
\# n.states: number of GEM population states
\# z: data frame of occupancy of the population from gem_sim_bio function
\# pgenetic: detection probability of genetic sign, probability between 0 and 1
\# obsdata: a list written to the global environment containing observation data

```
#######################################################################
# Function
########################################################################
gem_sim_obs <- function(p, nf, nm, n.visits, n.group, n.timestep, n.states, z,
pgenetic){
### Create matrices/arrays to hold data
    # Present, counts, genetic sign, females genetic sign, males genetic sign
    yp <- yc <- yg <- ygf <- ygm <-array(data = NA, dim = c(n.visits, n.timestep,
n.group))
for (k in 1:n.visits){
    for (i in 1:n.group){
        for(j in 2:n.timestep){
        ## Time 1
        ## Is the species present?
            yp[k,1,i] <- rbinom(1,ifelse(z[1,1,i]>1,1,0),1-((1-p)^(nf[1,1,i]+nm[1,1,i])))
        ## Time 2 and beyond
        ## Is the species present?
            yp[k,j,i] <- rbinom(1,ifelse(z[1,j,i]>1,1,0),1-((1-p)^(nf[1,j,i]+nm[1,j,i])))
        ## Are multiple individuals present?
            yc[k,j,i] <- ifelse(any(yp[,j-1,i]==1), rbinom(1,nf[1,j,i]+nm[1,j,i],p),NA)
        ## Are females and males present?
            yg[k,j,i] <- ifelse(any(yc[,j-1,i]>1),rbinom(1,yc[1,j,i],pgenetic),NA)
            ygf[k,j,i] <-rhyper(1,nf[1,j,i],nf[1,j,i],yg[k,j,i])
            ygm[k,j,i] <-yg[k,j,i]-ygf[k,j,i]
        }
    }
}
##################################################################################
    obsdata <- list("p"= p, "yp"= yp,"yc"= yc, "yg"= yg, "ygf"=ygf, "ygm" = ygm,
                            "pgenetic" = pgenetic, "n.visits" = n.visits)
    1ist2env(obsdata ,.Globa1Env)
}
```

```
########################################################################
# 3. GEM_RUN_MODEL
#########################################################################
# Name: gem_run_mode1
# Description: function to run the GEM model using R and JAGS
#########################################################################
# Arguments
#########################################################################
# yp: a data frame of the observed presence data
# yc: a data frame of the observed count data
# yg: a data frame of the observed genetic sign data
# ygf: a data frame of the observed genetic sign from females data
# params: parameters to keep track of in the model (example: params = c("N","p","z3"))
# n.group: number of groups (populations)
# s.group: mean group size (for one sex)
# n.timestep: number of time steps
# n.visits: number of visits in observation season
# n.litter: number of individuals per litter
# sr: sex ratio of females to females per litter
# n.iter: number of JAGS model iterations to run
# n.burnin: number of burn-in iterations to discard
# s.surv.init: mean of diffuse normal distribution initial survival value
#######################################################################
# Function outputs
#######################################################################
# out: a list written to the global environment of the JAGS model output for the
parameters that are
# being tracked
#######################################################################
# Function
#######################################################################
gem_run_mode1 <- function(yp, yc, yg, ygf, params, n.group, s.group, n.timestep,
                                    n.visits, n.litter, sr, n.iter, n.burnin, s.surv.init){
sink("Mode1.txt")
cat(''
    mode1{
    ## Priors
    # Detection
    p ~ dunif(0, 1)
    s.surv ~ dunif(0.1,1)
    p.1itter ~ dunif(0,1)
    pgenetic ~ dunif(0,1)
    1ambda ~ dgamma(0.001,0.001)
        for(i in 1:n.group){
        for(j in 1:n.timestep){
                S[i,j] <- s.surv
                L[i,j] <- p.litter
                sexratio[i,j] <- sr
                n7[i,j] <-n.1itter
    }
        }
    for(i in 1:n.group){
        nfi[i] ~ dpois(lambda)
            nmi[i] ~ dpois(lambda)
    }
    ## Biological mode1
    for(i in 1:n.group){
    ## Time 1
    # Entering individuals/state
                nf[1,1,i] <-nfi[i]
```

```
        nm[1,1,i] <-nmi[i]
        z[1,1,i] <- ifelse(nm[1,1,i] >= 1 && nf[1,1,i] >=1,4,
            ifelse(nm[1,1,i] > 1 && nf[1,1,i] == 0 || nf[1,1,i] > 1 && nm[1,1,i]
== 0,3,
            ifelse(nm[1,1,i] == 1 && nf[1,1,i] == 0 || nf[1,1,i] == 1 &&
nm[1,1,i] == 0,2, lfelse(nm[1,1,i] == 1 && nf[1,1,i] == 0 nfelse(nm[1,1,i] == 0 && nf[1,1,i] == 0,1,99))))
    z2[1,1,i] <- ifelse(z[1,1,i] > 1,1,0)
        # Breeding possible
    state_breed[1,i] <-ife1se(z[1,1,i]==4,1,0)
    1itter_prob[1,i] <-inprod(state_breed[1,i],L[i,1])
    # Births
    be[1,1,i] ~ dbin(1itter_prob[1,i], nf[1,1,i])
    # New individuals
    ni[1,1,i] <- inprod(be[1,1,i],n1[i,1])
    wm[1,1,i] ~ dbin(sexratio[i,1], ni[1,1,i])
    wf[1,1,i] <- ni[1,1,i] - wm[1,1,i]
    # Totals
    wnf[1,1,i] <- wf[1,1,i] + nf[1,1,i]
    wnm[1,1,i] <- wm[1,1,i] + nm[1,1,i]
    wtot[1,i,i] <- wnm[1,1,i] + wnf[1,1,i]
    for(j in 2:n.timestep){
        ## Time 2+
        # Entering individuals/state
            nf[1,j,i] ~ dbin(S[i,j], wnf[1,j-1,i])
            nm[1,j,i] ~- ifelse(nm[1,j,i] >= 1 && nf[1,j,i] >=1,4,
malelse(nm[1,j,i]> 1 && nf[1,j,i] == 0 || nf[1,j,i] > 1 &&
nm[1,j,i] == 0,3, ife1se(nm[1,j,i] == 1 && nf[1,j,i] == 0 || nf[1,j,i] == 1 &&
nm[1,j,i] == 0,2, ifelse(nm[1,j,i] == 0 && nf[1,j,i] == 0,1,99))))
    z2[1,j,i] <- ifelse(z[1,j,i] > 1,1,0)
        # Breeding possible
    state_breed[j,i] <-ife1se(z[1,j,i]==4,1,0)
    litter_prob[j,i] <-inprod(state_breed[j,i],L[i,j])
    # Births
    be[1,j,i] ~ dbin(litter_prob[j,i], nf[1,j,i])
    # New individuals
    ni[1,j,i] <- inprod(be[1,j,i],n1[i,j])
    wm[1,j,i] ~ dbin(sexratio[i,j], ni[1,j,i])
    wf[1,j,i] <- ni[1,j,i] - wm[1,j,i]
    # Totals
    wnf[1,j,i] <- wf[1,j,i] + nf[1,j,i]
    wnm[1,j,i] <- wm[1,j,i] + nm[1,j,i]
    wtot[i,j,i] <- wnm[1,j,i] + wnf[i,j,i]
    # Lambda
    1am[j,i] <- (wtot[1,j,i])/(wtot[1,j-1,i])
}
## Observation mode1
for (k in 1:n.visits){
for(i in 1:n.group){
## Time 1
```

```
    # Is the species present?
        yp[k,1,i] ~ dbin((1-((1-p)^(nf[1,1,i]+nm[1,1,i]))), z2[1,1,i])
    for(j in 2:n.timestep){
    ## Time 2 +
    # Is the species present?
        yp[k,j,i] ~ dbin((1-((1-p)^(nf[1,j,i]+nm[1,j,i]))), z2[1,j,i])
    # Are multiple individuals present?
        yc[k,j,i] ~ dbin(p, nf[1,j,i]+nm[1,j,i])
    # Are females and males present?
        yg[k,j,i] ~ dbin(pgenetic, yc[k,j,i])
        ygf[k,j,i] ~ dhyper(nf[1,j,i],nm[i,j,i],yg[k,j,i],1)
        }
    }
}
sink(O, fil1 = TRUE)
# Main data
data <- list(n.group = n.group, s.group = s.group, n.timestep = n.timestep,
                                    n.litter = n.litter, sr = sr, n.visits = n.visits,
                                    yp = yp, yc = yc, yg = yg, ygf = ygf)
# Initial value data
inits <- function() {
    list(nfi = nf.init, nmi = nm.init, s.surv = rtruncnorm(1, a=0, b=1, mean =
s.surv.init, sd = 0.15))
}
# Run mode1 and save output as object out
out<- jags(data=data, inits=inits, parameters.to.save = params, "Mode1.txt",
                        n.chains=3, n.thin=10, n.iter=n.iter, n.burnin=n.burnin, n.adapt=5000,
                            paralle1 = TRUE)
modeldata <- list("out"= out)
list2env(modeldata ,.GlobalEnv)
}
```


## APPENDIX B: ADDITIONAL SIMULATIONS

## Additional simulations

To explore how the GEM model predicts downward transitions, the following additional simulations were conducted:
A. 100 simulations starting in state 2 ( 1 individual, sex selected randomly)
B. 100 simulations starting in state 3 ( 3 individuals, single sex selected randomly)
C. 100 simulations starting in state 4 low ( 2 individuals -1 male, 1 female)
D. 100 simulations starting in state 4 high ( 8 individuals -4 males, 4 females)

For all simulations, the following variables were used to simulate the true populations in all simulations.

| Biological variable | Value |
| :--- | :--- |
| Survival | 0.7 (Mowat et al. 2000) |
| Probability of litter | 0.5 (Kosterman et al. 2018) |
| Number of kittens per litter | 2 (Mowat et al. 2000) |
| Sex ratio | 0.5 (Burstahler et al. 2016) |


| Observation variable | Value |
| :--- | :--- |
| Detection probability of <br> lynx | 0.63 (Squires et al. 2012) |
| Detection probability of <br> genetic sign | 0.50 (McKelvey et al. <br> 2006) - probability for 1 <br> km search |
| Repeat visits | 3 |
| Detection target each year | GEM sampling rules <br> applied |

All simulations were run for 400,000 iterations, with a burn-in period of 10,000 iterations and thinning at a rate of 10 due to the large amount of simulation data. Only simulations that converged (Rhat values at or below 1.05) were used for analysis. All priors were set as uninformative. The survival prior was set as a uniform distribution between 0.1 and 1 and given an initial value of a diffuse normal distribution with a mean set to 0.7 . All simulations were run using the GEM model structure described in Chapter 1.

## Results

| Variable |  | $\begin{gathered} \text { Scenario A } \\ \text { (state 2) } \\ \hline \end{gathered}$ | $\begin{gathered} \text { Scenario B } \\ \text { (state 3) } \\ \hline \end{gathered}$ | $\begin{aligned} & \text { Scenario C } \\ & \text { (state } 4 \text { low) } \\ & \hline \end{aligned}$ | Scenario D (state 4 high) |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  | Metric |  |  |  |  |
| Total individuals | Mean absolute percent error | 3.07\% | 9.66\% | 22.48\% | 59.56\% |
|  | Mean absolute individual error | 0.03 | 0.15 | 2.69 | 9.13 |
|  | Coverage | 100\% | 99.91\% | 97.82\% | 96.73\% |
|  | RRMSE | 0.03 | 0.12 | 0.18 | 0.55 |
| Adult females | Mean absolute percent error | 4.31\% | 10.17\% | 31.00\% | 65.46\% |
|  | Mean absolute individual error | 0.04 | 0.16 | 1.18 | 2.91 |
|  | Coverage | 100\% | 100\% | 94.15\% | 93.64\% |
|  | RRMSE | 0.05 | 0.13 | 0.23 | 0.52 |
| Adult males | Mean absolute percent error | 2.66\% | 9.49\% | 41.65\% | 69.78\% |
|  | Mean absolute individual error | 0.03 | 0.15 | 1.40 | 2.95 |
|  | Coverage | 100\% | 99.88\% | 90.52\% | 91.73\% |
|  | RRMSE | 0.03 | 0.12 | 0.31 | 0.54 |
| New and adult females | Mean absolute percent error | NA | NA | 38.84\% | 94.00\% |
|  | Mean absolute individual error |  |  | 1.99 | 1.73 |
|  | Coverage |  |  | 95.61\% | 94.00\% |
|  | RRMSE |  |  | 0.26 | 0.61 |


| New and adult males | Mean absolute percent error | NA | NA | 36.68\% | 69.28\% |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  | Mean absolute individual error |  |  | 1.97 | 4.85 |
|  | Coverage |  |  | 93.44\% | 95.27\% |
|  | RRMSE |  |  | 0.27 | 0.59 |
| Birth events | Mean absolute percent error | NA | NA | 41.14\% | 105.68\% |
|  | Mean absolute individual error |  |  | 0.97 | 8.00 |
|  | Coverage |  |  | 99.08\% | 98.55\% |
|  | RRMSE |  |  | 0.37 | 0.84 |
| State | Coverage | 100.00\% | 100.00\% | 99.64\% | 100.00\% |
| Survival | Mean absolute percent error | 27.16\% | 16.47\% | 5.74\% | 8.15\% |
|  | Coverage | 48.00\% | 100.00\% | 100.00\% | 100.00\% |
|  | RRMSE | 0.21 | 0.14 | 0.06 | 0.09 |
| Detection probability | Mean absolute percent error | 8.06\% | 8.99\% | 9.98\% | 15.85\% |
|  | Coverage | 96.00\% | 98.00\% | 100.00\% | 96.00\% |
|  | RRMSE | 0.08 | 0.09 | 0.10 | 0.17 |
| Detection probability of genetic sign | Mean absolute percent error | 0.07\% | 0.07\% | 11.37\% | 7.81\% |
|  | Coverage | 61.00\% | 69.00\% | 71.00\% | 86.00\% |
|  | RRMSE | 0 | 0 | 0.12 | 0.08 |

## Transition probabilities

| Variable |  | Scenario A (state 2) | $\begin{gathered} \text { Scenario } \\ \text { B } \\ \text { (state 3) } \end{gathered}$ | Scenario C <br> (state 4 low) | Scenario <br> D <br> (state 4 <br> high) |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  | Metric |  |  |  |  |
| Retain breeding potential (state 4 to state 4 ) | Mean absolute percent error | NA | NA | 4.46\% | 2.32\% |
|  | Coverage |  |  | 94.18\% | 94.51\% |
|  | RRMSE |  |  | 0.04 | 0.02 |
| Lose all of one sex and breeding potential (state 4 to state 3) | Mean absolute percent error | NA | NA | $\begin{gathered} 1.49 \times 10^{4} \\ \% \end{gathered}$ | $\begin{gathered} 9.72 \times 10^{6} \\ \% \end{gathered}$ |
|  | Coverage |  |  | 94.09\% | 93.48\% |
|  | RRMSE |  |  | 0.77 | 0.89 |
| Lose breeding potential and retain only a single individual (state 4 to state 2) | Mean absolute percent error | NA | NA | $\begin{gathered} 4.79 \times 10^{12} \\ \% \end{gathered}$ | $\begin{gathered} 6.08 \times 10^{16} \\ \% \end{gathered}$ |
|  | Coverage |  |  | 95.27\% | 95.90\% |
|  | RRMSE |  |  | 1.05 | 1.30 |
| Lose breeding potential and go locally extinct (state 4 to state 1 ) | Mean absolute percent error | NA | NA | 4.46\% | 2.32\% |
|  | Coverage |  |  | 94.18\% | 94.51\% |
|  | RRMSE |  |  | 0.04 | 0.02 |
| Stay as isolated individuals of a single sex (state 3 to state 3) | Mean absolute percent error | NA | 25.22\% | 78.95\% | 26.27\% |
|  | Coverage |  | 100.00\% | 98.18\% | 80.00\% |
|  | RRMSE |  | 0.24 | 41.24 | 0.48 |
| Lose individuals and retain only a single individual (state 3 to state 2) | Mean absolute percent error | NA | 54.72\% | 79.08\% | 63.12\% |
|  | Coverage |  | 94.12\% | 98.09\% | 60.00\% |
|  | RRMSE |  | 1.71 | 35.88 | 0.76 |
| Lose individuals and go locally extinct (state 3 to state 1) | Mean absolute percent error | NA | 64.92\% | 87.30\% | 235.21\% |
|  | Coverage |  | 94.12\% | 98.09\% | 60.00\% |
|  | RRMSE |  | 14.62 | 41.56 | 2.88 |
| Stay as isolated individual (state 2 to state 2) | Mean absolute percent error | 27.80\% | 17.88\% | 9.84\% | 13.14\% |
|  | Coverage | 43.98\% | 96.37\% | 99.91\% | 100.00\% |


|  | RRMSE | 0.28 | 1.22 | 2.58 | 0.13 |
| :---: | :--- | :---: | :---: | :---: | :---: |
| Lose isolated individual <br> and go locally extinct <br> (state 2 to state 1) | Mean <br> absolute <br> percent error | $64.87 \%$ | $41.71 \%$ | $22.96 \%$ | $30.65 \%$ |
|  | Coverage | $43.98 \%$ | $96.37 \%$ | $99.91 \%$ | $100.00 \%$ |
|  | RRMSE | 1.98 | 0.60 | 6.01 | 0.31 |

Chapter 2: Goal efficient monitoring for small and isolated populations ${ }^{2}$


#### Abstract

The need to manage small or isolated populations in an evidence-based conservation world requires robust information to inform decisions. Monitoring with associated thresholds or trigger points is the current gold standard for evidence-based conservation, but there has been little development of ecological thresholds that apply across species, particularly for small or isolated populations. The recently proposed goal efficient monitoring (GEM) approach provides a quantitative framework connected to population dynamics relevant for small or isolated populations that can potentially be used to set ecological thresholds for small or isolated populations. However, there are three main limitations of using GEM in this way as it was originally proposed. The first is that small or isolated populations are sensitive to movement and the GEM model did not include immigration or emigration. The second is that the spatial scale of GEM states was not defined, which is necessary for application of GEM to real populations. The third is that current monitoring methods for small and isolated populations focus on a single monitoring question often because of the scarcity of data, so it is unclear if changing questions for the GEM observation approach provide an advantage over a single question in a data scarce environment. To address these limitations we conducted a series of simulations parametrized with Canada lynx (Lynx canadensis) life history information. Using an expanded GEM IPM structure, we explored the spatial scale at which GEM states should be measured to most effectively describe GEM state changes. In addition, we compared a single occupancy question to GEM questions for a small and isolated population of lynx. Our results showed that a spatial scale of 9 home range sizes is the optimal size measuring changes in the GEM breeding state. In


[^2]addition, changing questions with GEM provided an advantage over a single question. Thus, the GEM structure can be extended to provide novel advances in monitoring thresholds for small and isolated populations.

## INTRODUCTION

Small or isolated populations are important for conservation. Often, small or isolated populations are rare species, which are valued and protected by individuals and societies around the world (Angulo \& Courchamp 2009), and often contribute disproportionately to biodiversity and for ecosystem functioning (e.g., Lyons et al. 2005; Mouillot et al. 2013; Loiseau et al. 2020). In addition, although conservation objectives may reflect goals for an entire species, on-the-ground management often occurs in small parcels of land which contain isolated populations, such as on private lands where voluntary conservation occurs or land is acquired by non-profits for conservation (Gooden et al. 2020). Beyond a legal requirement for protection, as in the Endangered Species Act of 1973, conserving small or isolated populations is important for a variety of reasons. For example, conserving small or isolated populations can show success of conservation spending, often the prerequisite for additional conservation funding (Baier \& Segal 2020). Maintaining populations that appear isolated can also be important for metapopulation connectivity for an entire population. For example, Moilanen et al. (1998) showed that what appeared to be an isolated group of populations that consistently showed low occupancy in the American pika (Ochotona princeps) in Mono County, California, was responsible for the pika's persistence across a larger scale. Finally, conserving small or isolated populations can be the entire basis for preservation of a species, such as the Dixie Valley toad (Anaxyrus williamsi), which was given emergency protection under the Endangered Species Act on April 7 due to the
immediate threat of a geothermal energy development project in the Dixie Meadows, Nevada, the only location the species is known to exist (FR 2022).

Population monitoring, often coupled with vegetation or other environmental variable monitoring, is one of the main tools for understanding and managing small and isolated populations (McDonald-Madden et al. 2010). The often legally required and scientificallysupported push for evidence-based conservation (Sutherland et al. 2004), requires that information is known about populations through monitoring. However, many have pointed out that for an evidence-based conservation and management monitoring system to be effective, decision triggers related to monitoring need to be clearly defined (Schultz et al. 2013; Cook et al. 2016). Here, we use the definition of decision triggers provided by Cook et al. (2016), and describe decision triggers as pre-defined events that when detected in monitoring data are linked to a pre-defined management action. Ecological thresholds, which are points that represent biological consequences for a population (Martin et al. 2009), are one of the most important factors for setting decision triggers (Lindemeyer et al. 2013; Cook et al. 2016), particularly for small or isolated populations. Although there has been some effort to define what makes effective ecological thresholds (e.g., Samhouri et al. 2010) and these concepts have been applied in marine and freshwater aquatic environments (Dodds et al. 2010), ecological thresholds that are generalizable across species or ecosystems have been difficult to define (Johnson 2013). Not only have effective thresholds been difficult to define, but finding thresholds that are relevant for conservation, detectable with monitoring, and connectable to decisions remains a challenge (Cook et al. 2016).

One of the reasons ecological thresholds for small or isolated populations are difficult to define are that small populations dynamics are characterized by stochastic events (Fauvergue et
al. 2012), which are difficult to predict with traditional monitoring metrics such as trend. Stochastic dynamics result in what often appears as sudden population changes, making them more appropriately thought of as state changes. We define "state" in this manuscript as a description of a condition at a specific time of an individual (e.g., alive or dead), area such as a home range (e.g., occupied or unoccupied), or population (e.g., breeding or non-breeding). Indeed, one reason occupancy modeling (MacKenzie et al. 2002), which has grown to become the primary rare species monitoring tool since it was introduced, was promoted for rare species monitoring is because it can be effectively accomplished with state-based metrics. State descriptions like occupancy of a home range (occupied or not occupied), however, often provide little insight on mechanism of population change because they fail to capture demographic information that can explain causes (Schaub et al. 2010). State models have been expanded to be more descriptive of population processes by including multiple (three or more) states, also known as multistate models, and can include additional population descriptions such as a breeding state (MacKenzie et al. 2009). These multistate models work best in systems where the state describes a discrete entity that is discrete and therefore closed, such a bird's nest. As state descriptions are scaled up to less definably discrete entities, such as home ranges or populations, the semi- or complete openness of the entity means that the likelihood of a state like breeding occurring can change based on multiple individuals present in the entity. In most multistate models, similar to occupancy, this is addressed with the assumption of closure or a definition of discreteness of the unit rather than accounting for the possibility of multiple individuals. However, for small or isolated populations, particularly when Allee effects are strong and individuals group together, the composition of a small number of individuals can drastically alter the likelihood of different states being present, particularly as they relate to breeding.

To provide state definitions appropriate for small and isolated individuals, Golding et al. (Chapter 1), proposed four state descriptions for small or isolated populations that account for individuals as part of goal efficient monitoring (GEM) approach (Table 2-1): breeding potential (multiple individuals and both sexes, GEM state 4); isolated individuals (multiple individuals of a single sex, GEM state 3 ); isolated individual (single individual, GEM state 2 ); and locally extinct (not present, GEM state 1). GEM is a monitoring system designed for small or isolated populations that tracks changes using an integrated population model (IPM) structure, where the biological process includes an age-based population model linked to the states listed above. It is important to note that while these states vary in their importance for persistence of a small or isolated population, with breeding potential representing the most important state, all are important for conservation and management of a small or isolated population for a number of reasons. For example, if a species is protected under the ESA, such as the Dixie Valley toad, all states of the isolated population are important to know. Similarly, if a private landowner wants to provide habitat for elk on their conservation easement property near a reintroduction site, dynamics of a few individuals that might move in and breed are essential to know.

In addition to describing states that are important for management, GEM population states can also be used to look at patterns over time of state changes, or transitions. Here we use the term state change to describe changes, or no change, in the GEM population state between time $t$ and $t+1$. Each time period, the probability of a state change, including which changes are possible, depend on the current state of the population. We focus on breeding population potential (GEM state 4 ), although all changes and states are possible, and the changes available from that state for the remainder of the manuscript. Figure 2-1 shows the potential state changes, which can be described as probabilities (shown as arrows to the other states), from a breeding
potential population at time $t$. The arrow highlighted in yellow represents the probability that the population will retain breeding potential (i.e., the probability that the yellow arrow occurs and gray arrows do not occur). This change is important for conservation and management because it provides a near-term description of the likelihood of persistence, as it is relevant to a time period between 2 time steps, which is much shorter than the trend time periods necessary for most trend monitoring programs (e.g., Ellis et al. 2014).

The short time period over which the state change is relevant, combined with the IPM structure of GEM means that population predictions, in the form of the probability of retaining breeding potential (e.g., staying in GEM state 4), can be made concurrently with the gathering of long-term monitoring data. These short-term predictions of GEM state changes can also provide a practical, quantifiable, and biologically meaningful way to define decision trigger. For example, a threshold on the probability of retaining breeding can be set at $90 \%$ based on a species biology. However, a variety of additional factors, such as legal protections and a riskaverse management approach, can be considered to adjust the threshold to $95 \%$. With this threshold determined prior to the start of monitoring, a practitioner or conservation agency can then use the GEM monitoring approach and state change predictions each time step to make decisions about conservation actions each year. Figure 2-2 provides a hypothetical example of how this can be accomplished for a simulated population of Canada lynx (Lynx canadensis), which was the model organism used for the illustration of the GEM system. There are a number of ways in which actions can be linked to the threshold as well, depending on the conservation actions that are possible. Importantly, because this is conducted within an IPM structure, longterm monitoring data collection is not compromised or sacrificed for the threshold data collection effort: in fact, the long-term population data is the basis of the state change metrics.

However, GEM was originally proposed as a conceptual model under simplified conditions and did not include immigration and emigration in the population simulations or the state change probabilities. Immigration can be an important dynamic for small and isolated populations. In fact, immigration can be one of the main dynamics that allows small or isolated populations to persist (With \& King 2008) and retain enough occupied territories for breeding (Lande 1987). For example, Stacey and Taper (1992) showed that in the southwestern US the acorn woodpecker (Melanerpes formicivorus) in small, isolated populations only with immigration, but that for populations to persist for over 1000 years in simulations, only 5 migrants per year were needed. Thus, to use GEM to monitor for ecological thresholds with GEM state changes effectively for small or isolated populations, which are often the populations most in need of monitoring and conservation action, it is essential that the dynamics of immigration and emigration are captured in the GEM states and underlying population model structure in the GEM IPM. In addition, the GEM observation process has five sampling rules (Table 2-2), designed to address the fact that changing questions arise rapidly in rare species systems because populations change frequently. These sampling rules were developed to optimize the original simplified format of GEM which did not include immigration and emigration.

We therefore had three main objectives in this study to explore the benefits of the GEM approach and the use of GEM state changes for real-world small or isolated population monitoring. The first was to capture the important dynamics for small and isolated populations and expand the underlying GEM IPM structure and state change probabilities to include immigration and emigration. Second, we set out to determine the most relevant spatial scale at which the probability of small or isolated populations retaining or losing breeding capability
(staying in or changing from GEM state 4) should be measured. Finally, our third goal was to determine if the GEM observation structure of changing questions based on the GEM sampling rules provided a benefit over traditional state-based presence monitoring given the potentially high amount of variability introduced with both immigration and emigration in the biological systems and changing observation. We predicted that because of the large amount of population change in small populations that would occur when immigration and emigration were added, compared to a single question, changing questions would provide more efficient information relative to the information goal for the population, which was the basis of the GEM system development, and lead to improved GEM state change metrics. After extending the model and state change probabilities to include immigration and emigration, we used a series of population simulations, parameterized with lynx information as the model organism, to accomplish the second and third goals, described below.

## METHODS

We provide a series of model expansions and simulations to further the GEM model structure and accomplish the goals outlined above. We first describe the GEM model structure and expansion for immigration and emigration. We then describe the simulations to determine the appropriate scale, which we define as a GEM grid cell, for GEM state change monitoring. Finally, we describe our simulations to examine if changing questions according to the GEM sampling rules provided improved GEM state change estimation over simple presence absence observation. All data simulation and analysis described below was run using R (version 4.0.2; R Development Core Team 2020) and JAGS (http://mcmc-jags.sourceforge.net).

We use lynx as our example organism for a number of reasons. Lynx have been listed as Threatened in the US under the ESA since 2000. In the US northern Rocky Mountain area, lynx
are at the southern periphery of their range and therefore are rare and subject to fluctuating metapopulation dynamics (Ruggiero et al. 2000; Schwartz et al. 2002). In addition, under the Northern Rockies Lynx Management Direction (NRLMD) (USDA Forest Service 2007), there are different regulations and considerations applied to $8,282,000$ acres of Forest Service land when no lynx are present, a single lynx is present, a female with kittens is present, or a population is present. Thus, GEM states are relevant and parallel to the NRLMD lynx states. However, we emphasize that the GEM approach, as well as the approach for including immigration and emigration extensions, and cell size simulations are potentially applicable to a wide variety of species other than lynx.

For all simulations we simulated a 10 -season survey period (11 time steps total: 1 baseline survey year and 10 monitoring periods after) across a small lynx population. We set survival, $s$, constant at 0.7 , based on the highest rates of adult lynx survival when snowshoe hare densities are high (Mowat et al. 2000). We set the probability of having a litter, p.litter, constant at 0.5 , based on the lower end of measured probability of lynx having a litter in mature forest in a study area in the northern Rocky Mountains (Kosterman et al. 2018). We set the number in each litter equal to 2, which is the low end of number per litter in normal years for lynx (Mowat et al. 2000) and the sex ratio as constant and equal at 0.5 , which is close to the ratio observe in real lynx population (Burstahler et al. 2016).

## GEM biological process model

To construct the biological process of the IPM, we modeled female, $N_{f, t}$, and male, $N_{m, t}$, abundance for a population at initial time $t$ as ) as Poisson random variables with a mean average group size, $\lambda$, of 7 (equations 1 and 2 ). Total individuals, $N_{t}$, were a derived parameter that was the sum of $N_{f, t}$ and $N_{m, t}$ (equation 3). Population occupancy at time $t, z 1_{t}$, was derived $z 1_{t}$ and
assigned as occupied if 1 if $N_{t}>0$ (equations 4 and 5). GEM state for each time $t, z 2_{t}$, was also derived from $N_{f t}$ and $N_{m t}$ (composition of females and males at time $t$ ) and assigned a 4, 3, 2, or 1 to represent the GEM states (equations 6-9):

1) $N_{f, t} \sim$ Poisson ( $\lambda$ )
2) $N_{m, t} \sim$ Poisson ( $\lambda$ )
3) $N_{t}=N_{f, t}+N_{m, t}$
4) $N_{t}>0 \rightarrow z 1_{t}=1$
5) $N_{t}>0 \rightarrow z 1_{t}=0$
6) $N_{f, t}=0$ and $N_{m, t}=0 \rightarrow z 2_{1}=1$
7) $N_{f, t}=1$ and $N_{m, t}=0$ or $N_{f, t}=0$ and $N_{m, t}=1 \rightarrow z 2_{t}=2$
8) $N_{f, t} \geq 2$ and $N_{m, t}=0$ or $N_{f, t}=0$ and $N_{m, t} \geq 1 \rightarrow z 2_{t}=3$
9) $N_{f, t} \geq 1$ and $N_{m, t} \geq 1 \rightarrow z 2_{t}=4$

We then modeled the abundance of new females $W_{f, t}$ and males $W_{m, t}$ in time t . New individuals entered the population in based on a combination of the following processes: 1) a probability of the population producing a litter at time $t, l_{t}$, which was a function of the probability of litter production, $p$. litter, based on if the GEM state, $z 2_{t}$, at time $t$ was in breeding potential (GEM state 4 ) (equations 10 and 11); 2) birth events, $B_{t}$, which were modeled as a binomial random variable with the probability of success, $l_{t}$, with $N_{f, t}$ trials (equation 12); 3) and new individuals born, $W_{t}$, which was modeled as a function of birth events, $B_{t}$, multiplied by a litter size, which we set as constant at 2 (equation 13). New females from the birth events, $W_{f, t}$, were were derived as a binomial random variable with the probability of success set by a sex ratio, sr, of 0.5 out of $W_{t}$ trials (equation 13a) and new males from the birth event, $W_{m, t}$, were derived from the difference of $W_{t}$ and $W_{f, t}$ (equation 13b):
10) $z 2_{t}=4 \rightarrow l_{t}=p$.litter
11) $z 2_{t}=3$ or $z 2_{t}=2$ or $z 2_{t}=1 \rightarrow l_{t}=0$
12) $B_{t} \sim \operatorname{Binomial}\left(N_{f, t}, l_{t}\right)$
13) $W_{t} \sim \operatorname{Poisson}\left(B_{t} *\right.$ litter size $)$
a. $W_{f, t} \sim \operatorname{Binomial}\left(W_{t}, s r\right)$
b. $W_{m, t}=W_{t}-W_{f, t}$

We assumed juveniles bred at 1 year of age, so could breed in the next time step and were counted as part of the adult population if they survived. Survival for all classes to time $t=2$ (noted as $t+1$ throughout the manuscript) and beyond (noted as $t+1 \ldots$ throughout the manuscript), was modeled as a binomial random variable with a probability of success of survival probability $s$, which we kept constant at 0.7 , out of the number of trials in the class of interest (adult females, $N_{f, t} ;$ adult males, $N_{m, t} ;$ new females from the previous time step, $W_{f, t} ;$ new males from the previous time step, $W_{m, t}$ (equations 14-17). We derived the total adult abundance at the next time step as the combination of the existing adults and new individuals added from breeding events (equations 18-19).
14) $S_{f, t+1} \sim \operatorname{Binomial}\left(N_{f, t}, s\right)$
15) $S_{m, t+1} \sim \operatorname{Binomial}\left(N_{m, t}, s\right)$
16) $S_{f, t+1} \sim \operatorname{Binomial}\left(W_{f, t}, s\right)$
17) $S_{m, t+1} \sim \operatorname{Binomial}\left(W_{m, t}, s\right)$
18) $N_{f, t+1}=S_{f, t+1}+S_{f, t+1}$
19) $N_{m, t+1}=S_{m, t+1}+S_{m, t+1}$

Immigration and emigration extension

To incorporate more biological reality for small and isolated populations into the GEM model, we extended the original GEM model from Chapter 1 to include a parameter for emigration, or leaving population $i$, and immigration, or new individuals entering population $i$ through movement (not birth processes). We then modified the GEM biological process described above with the following considerations: first, lynx kittens remain with females in their first year and do not disperse until April or May of the following year (Slough et al. 1997); second, because we considered juveniles capable of breeding at 1 year of age, by the time lynx move they will be considered adults, so we considered processes of immigration and emigration only for adult individuals in a population and one that occurred in late spring and early summer. Because female and male lynx often exhibit different movement behavior, we modeled each sex separately. Thus, we modeled the total females who emigrated from a population at time $t, E_{f, i, t}$, as a binomial random variable with a probability of success of a migration probability of females, $m p_{f}$, which we kept constant at 0.05 , and the number of trials as the total number of females in the population at time $t, N_{f, i, t}$ (equation 20). Adult males who emigrated at time $t$, $E_{m, i, t}$, were similarly modeled as a binomial random variable with a probability of success of a migration probability of males, $m p_{m}$, which we kept constant at 0.10 , and the number of trials as the total number of males in the population at time $t, N_{m, i, t}$ (equation 21). These probabilities were based on observed low rates of movements among adult lynx (Mowat et al. 2000; Kolbe and Squires 2006).
20) $E_{f, i, t} \sim \operatorname{Binomial}\left(N_{f, i, t}, m p_{f}\right)$
21) $E_{m, i, t} \sim \operatorname{Binomial}\left(N_{m, i, t}, m p_{m}\right)$

We modeled the process of survival during movement and assumed only a subset of those who moved would survive with probability $s$, which we kept as the same survival probability as
for the other processes at 0.7 (equations 22 and 23). To make this model implicitly spatial, we modeled 3 populations that were set in a vertical row as follows: population 1, population 2, population 3. To represent that, we set the distance between the populations with colonization probabilities, with the populations farthest from each (populations 1 and 3 ) other having the lowest colonization probability. Colonization probability was represented as a matrix, $C p_{i}$, where rows represent the population $i$ that the individuals were coming from and columns represented the population that the individuals were going to. We kept the colonization probabilities as constant throughout the simulations (equation 24). We assumed that all individuals who survived colonized another population, but not their own. Finally, the number of females, $C_{f, i, t}$, and males,, $C_{m, i, t}$, that colonized an adjacent GEM population $i$ were modeled as a binomial random variable with probability of success as a colonization probability out of the total surviving individuals that left population $i, S E_{m, i, t}$ and $S E_{f, i, t}$, trials (equations 22 and 23).

$$
\begin{aligned}
& \text { 22) } S E_{f, i, t+1} \sim \operatorname{Binomial}\left(E_{f, i, t}, s\right) \\
& \text { 23) } S E_{m, i, t+1} \sim \operatorname{Binomial}\left(E_{m, i, t}, s\right) \\
& \text { 24) } C p_{i}=\left[\begin{array}{ccc}
0 & 0.3 & 0.4 \\
0.3 & 0 & 0.6 \\
0.4 & 0.6 & 0
\end{array}\right] \\
& \text { 25) } C_{f, i, t+1} \sim \operatorname{Binomial}\left(S E_{f, i, t+1}, C p_{i}\right) \\
& \text { 26) } C_{m, i, t+1} \sim \operatorname{Binomial}\left(S E_{m, i, t+1}, C p_{i}\right)
\end{aligned}
$$

Finally, we modified the total number of individuals at the end of time $t+1$ to include losses of adults due to emigration from population $i$ (subtraction of $E_{f, i, t}$ and $E_{m, i, t}$ from $N_{f, i, t}$ and $N_{f i t}$ before the next time step $t+1 \ldots$ ) an additions of new colonizing individuals, $C_{f, i, t}$ and $C_{m, i, t}$, starting in the next time step $t+1$. Figure 2-3 shows an overview of this extended model structure.

We also modified the GEM population state change probabilities. We linked the GEM states, $z 2_{t}$, to the population dynamics of each time $t$ by deriving the state from the abundance values at each time step. Thus, the likelihood of a population changing between the end of a time step and the next time step was a derived probability matrix $\Psi_{t}$. Because we expanded the population dynamics to include birth, death, immigration, and emigration, all state changes were theoretically possible (Figure 2-4). The matrix $\Psi_{t}$ for each time step after t was modeled as a four-by-four matrix, with the rows representing the GEM state in time $t$ and the columns representing the probability of the GEM state changing in the next timestep $t+1$ as follows:

$$
\left.\begin{array}{l}
\Psi_{t} \\
=\left[\begin{array}{cccc}
1-\psi_{t, 12}-\psi_{t+1,13}-\psi_{t+1,14} & \psi_{t+1,12} & \psi_{t+1,13} & \\
\psi_{t+1,21} & 1-\psi_{t+1,21}-\psi_{t+1,23}-\psi_{t+1,33} & \psi_{t+1,23} & \psi_{t+1,14} \\
\psi_{t+1,31} & \psi_{t+1,32} & 1-\psi_{t+1,32}-\psi_{t+1,31}-\psi_{t+1,34} & \psi_{t+1,24} \\
\psi_{t+1,41} & \psi_{t+1,42} & \psi_{t+1,43} & \psi_{t+1,34} \\
\hline
\end{array} \quad \psi_{t+1,43}-\psi_{t+1,42}-\psi_{t+1,41}\right.
\end{array}\right] .
$$

Because each population can only be in a single state at one time, the state change, or transition, probabilities are conditional, so that only a single row is relevant at each time step. Appendix A provides a full written and mathematical description of the probabilities presented in the vector $\Psi_{t}$.

## GEM observation process model

We modeled the sampling process within a GEM grid cell according to the GEM sampling rules as follows:
a. If nothing is known, obtain confirmation of presence only.
b. If presence has been confirmed in the previous season, obtain information on whether multiple individuals are present via counts.
c. If counts are $>2$ across a single visit in a season (not $>2$ in total across repeat visits in a single season), obtain information on whether females and males are present via collection of sex identifying information (e.g., genetic material) during counts.
d. If multiple individuals and only a single sex were confirmed in the previous season, obtain information on whether multiple individuals are present via counts.
e. If multiple individuals and both sexes were confirmed in the previous season, obtain information on whether females and males are present via collection of sex identifying information (e.g., genetic material) during counts.

We used this sampling process to then generate the observation of one or more of the following based on whatever the GEM rule dictated: the presence of the species in population $i$ during a repeat visit $j$ at time $t$ or beyond, $y_{z, i, j, t}$, which we modeled as a Bernoulli random variable that represented the observation of $z 1_{t}$ with a probability of detection, $p$, that depended the total number of individuals present (equation 27); counts of individuals in population $i$ during a repeat visit $j$ at time $t$ or beyond, $y_{c, i, j, t}$, which we modeled as a Binomial random variable with probability of success of detection $p$ out of the total that were present, $N_{t}$, trials (equation 28); or counts of females and males as a subset of individuals counted that deposited genetic sign that was detected, $y_{g, i, j, t}$, which we modeled as a Binomial random variable with a probability of success of the probability leaving genetic material that was found, $p_{\text {genetic }}$, out of the number that were counted, $y_{c, i, i, t}$, trials (equation 29). Counts of females, $y_{f, i, j, t}$, were modeled as a hypergeometric random variable that was a subset of the number of females $N_{f, i, t}$ in the total population $N_{i, t}$, and the total number counted with genetic sign, $y_{g, i, i, t}$ (equation 29a). The number of males counted with genetic identification after collection, The number of males
counted with genetic identification after collection, $y_{m, j, t}$, were the remainder of the genetically identified individuals not identified as females (equation 29b):
27) $y_{z, i, j, t} \sim \operatorname{Bernouli}\left(1-(1-p)^{N_{t}}\right)$
28) $y_{c, i, i, t} \sim \operatorname{Binomial}\left(N_{t}, p\right)$
29) $y_{g, i, j, t} \sim \operatorname{Binomial}\left(y_{c, i, j, t}, p_{\text {genetic }}\right)$
a. $y_{f, i, j, t} \sim$ Hypergeometric $\left(N_{i, t}, N_{f, i, t}, y_{g, i, j, t}\right)$
b. $y_{m, i, j, t}=y_{g, i, j, t}-y_{f, i, j, t}$

GEM cell size
GEM was originally proposed without spatial information. However, for GEM to be used in a real-world monitoring context for small or isolated populations, the appropriate scale at which it should be used needs to be defined. We use the concept of grid cells (Mackenzie et al. 2002), which represent a home range of an individual and the scale at which detection or nondetection information is observed. Because GEM is based on four population states (breeding potential; isolated individuals; isolated; and locally extinct), the GEM grid cell size must be large enough to accommodate the largest state (breeding potential) and incorporate multiple (at least two) home ranges. However, the cell must also be at the appropriate scale to measure the change around the breeding potential state. If it is too large, the state description becomes irrelevant. For example, knowing there is breeding potential in a population of 50 individuals is not informative. However, if it is too small then the grid cell always changes out of the state, such as a cell size of 2 individuals where a female and male could represent breeding potential, but with survival and only two individuals it is unlikely that that scale would ever stay in breeding potential more than occasionally. Thus, to determine an optimal size for this grid cell, we conducted a series of simulations with different starting population sizes above the minimum needed to be in the
highest state of breeding potential within a single closed GEM grid cell using the original GEM model. We used three different starting population sizes (all with equal sex ratios of females and males):

- 4 individuals ( 2 females, 2 males)
- 8 individuals (4 females, 4 males)
- 12 individuals (6 females, 6 males)

To simulate a true "grid cell," we used a closed population without the immigration and emigration extension, so that the dynamics of the cell could accommodate internal growth through breeding or loose individuals through death but were not obscured by movement in and out of the population. We assumed that the starting population size was representative of the GEM grid cell size and refer to the grid cell sizes in the remainder of the manuscript based on number of home ranges (starting population) in each cell. We then compared probability of staying in breeding potential, $\psi_{44}$, using the original closed population GEM formulation state calculation (see Appendix B for probability equations), as the basis for cell size evaluation. For each of the three GEM grid cell sizes tested ( 4,8 , and 12 home ranges) we ran 100 simulations of the GEM model described above.

## Monitoring with a single question or GEM sampling rules to change questions

To quantify how much changing questions with the GEM observation process for monitoring small or isolated populations would provide better, and therefore potentially more valuable, information, we used two observation scenarios with the biological process as the GEM IPM structure described above: 1) a single question - is the species present - observation scenario across all time (hereafter single question scenario); and 2) a GEM sampling rule approach to ask three changing questions - is the species present, are multiple individuals
present, are males and females present - observation scenario across all time steps (hereafter GEM question scenario). Both scenarios were simulated with the same underlying biological process described in the GEM biological process model section above. The single question scenario was simulated with only the observation of presence each time step (Equation 13) and the GEM question scenario was simulated with the observation of all questions if the GEM sampling rules applies (Equations 13-27).

For each of the two question scenarios (single question and GEM question), we ran 100 simulations with the expanded GEM model and used the same biological parameters used for the grid cell size, but with the addition of two more populations and movement probabilities for females (0.05) and males (0.10), which were based on observed low rates of movements among adult lynx (Mowat et al. 2000; Kolbe and Squires 2006).

## GEM cell size and question performance metrics

For each simulation, we ran 3 MCMC chains each for 50,000 iterations, discarding the first 5,000 as a burn-in, and included a thinning rate of 1 to reduce simulation file size. We used the following uninformative prior distributions: for both detection probabilities ( p and $p_{\text {genetic }}$ ) we used uniform distributions constrained between 0 and 1 . Because there were so many complex axes of change for these simulations, we chose to provide the model with the values for survival $(\mathrm{s}=0.7)$ litter probability $(\mathrm{p} . \mathrm{litter}=0.5)$. To assess model convergence, we used the $\hat{R}$ statistic which is a ratio estimator of how variable each chain was compared to how variable all chains were and should be around 1.0 (Brooks \& Gelman 1998).

To assess how well the GEM model predicted variables under the different conditions of differing cell size and questions, including population variables and the GEM state change probabilities, we calculated mean absolute percent error (MAPE), the absolute value of the
difference between the true parameter value and GEM parameter estimate, divided by the true parameter value, multiplied by 100 , of model estimates compared to the true simulation values. To compare the accuracy of the GEM model estimates across different question scenarios, we calculated relative root mean square error (RRMSE) for $\psi_{t 44}$ each GEM grid cell size using the following equation:

$$
\text { RRMSE }=\frac{\sqrt{\frac{1}{r \sum_{k=1}^{n}\left(\hat{\theta}_{k}-\theta_{k}\right)^{2}}}}{\bar{\theta}}
$$

where $r$ was the number of replicates, $\hat{\theta}_{k}$ is the predicted parameter value and $\theta_{i}$ is the true parameter value at replicate $k$ and $\bar{\theta}$ is the mean true value of parameter over all replicates. In addition, for the GEM grid cell size simulations, we tracked the percentage of time over 100 simulations that each population spent with breeding potential (i.e., in GEM state 4), which we measured as the number of time steps across all simulations where the population was in state 4 out of the total number of time steps across all simulations $(1,100$, or 100 simulations of 11 time steps). For population parameters, we also calculated coverage, which is the percent of time the 95\% Bayesian credible interval (CRI) contained the true value for each parameter over all simulations. For abundance estimates, we also used a measure of the absolute value of the total individuals that the abundance estimates deviated by, or mean absolute individual error (MAIE), which was a metric suggested by Golding et al. (Chapter 1) to provide an additional descriptive measure of error in small or isolated populations.

## RESULTS

GEM cell size
All results presented in this section are summarized over all 100 simulations for each grid cell size $(4,8$, or 12 home ranges), including all timesteps within each simulation run. The three

GEM grid cell sizes all resulted in estimates of retaining breeding potential, $\psi_{44}$, with mean absolute percent error rates below $14 \%$. An increase in GEM grid cell size resulted in lower $\psi_{44}$ prediction error: a grid cell size of 4 home ranges resulted in a $\psi_{44}$ mean absolute percent error rate of $13.4 \%$ and an RRMSE of $0.156 ; 8$ home ranges resulted in a $\psi_{44}$ mean absolute percent error rate of $6.95 \%$ and an RRMSE of 0.104 ; and 12 home ranges resulted in a $\psi_{44}$ mean absolute percent error rate of $3.96 \%$ and an RRMSE of 0.0754. In addition, an increase in GEM grid cell size resulted in an increase in the proportion of simulations that each population spent in the state of breeding potential, with $25.9 \%$ ( 4 home ranges), $48.2 \%$ ( 8 home ranges), and $78 \%$ (12 home ranges) of time step simulations in breeding potential (GEM state 4) (Table 2-3). Monitoring with a single or changing questions: GEM state changes and population parameters

Overall, the GEM question scenario predicted the GEM state change probabilities with lower error for all state changes that occurred. We only present state changes that occurred, as they are conditional probabilities so ones that did not occur had a probability of zero and were thus predicted as zero. Therefore, we present changes from isolated individual (GEM state 2 ), isolated individuals (GEM state 3), and breeding potential (GEM state 4). For each state change probability, we calculated the MAPE and the RRMSE and information is summarized in Tables 2-4a (GEM state 2), 2-4b (GEM state 3) and 2-4c (GEM state 4).

For predicting state changes from breeding potential (GEM state 4 ), the GEM observation scenario performed better than the single question scenario for three of the four probabilities. For the probability that the population would change from breeding capable to locally extinct, $\psi_{t+1,41}$, the GEM observation scenario resulted in lower error that the single question scenario, with an RRMSE of 2.44 and 6.57, respectively, and mean MAPE of 1501 and $8.09 \mathrm{e}^{31}$, respectively. Similarly, for the probability that the potentially breeding population lost
all but a single individual, $\psi_{t+1,42}$, the GEM observation scenario again resulted in lower error than the single question scenario, with an RRMSE of 1.73 and 4.84 , respectively, and mean MAPE of 963 and $2.03 \mathrm{e}^{31}$, respectively. For the probability of losing breeding capability by dropping to only individuals of a single sex, $\psi_{t+1,43}$, the GEM observation scenario resulted in lower error than the single question scenario, with an RRMSE of 1.10 and 2.39 , respectively, and mean MAPE of 135 and $8.02 \mathrm{e}^{14}$, respectively. Finally, for the probability that the population retained breeding capability, $\psi_{t+1,44}$, the GEM observation scenario resulted in slightly higher error than the single question scenario, with an RRMSE of 0.172 and 0.106 , respectively, and mean MAPE of 14.9 and 5.82, respectively (Table 2-4c).

Overall, the prediction of the population parameters across both observation scenarios was accurate, with predictions from the GEM model in both observation scenarios well recovered by the simulations. Across all population parameters predicted from the GEM model (GEM population state, $z 2_{t}$; female and male abundance at the end of each time step $\left(N_{f, i, t}, N_{m, i, t}\right)$; female and male abundance at the beginning of each time step $\left(N_{f, i, t+1}, N_{m, i, t+1}\right)$; birth events $\left(B_{t}\right)$; and new females and males born $\left(W_{f, i, t}, W_{m, i, t}\right)$, the GEM observation scenario resulted in lower MAPE, MAIE and RRMSE than the single question observation scenario. Similarly, coverage of the predicted model values across all population variables measured from the GEM model with the GEM observation scenario was higher than the single question scenario. This information is summarized in table 2-5.

## DISCUSSION

Finding meaningful ways to monitor small or isolated populations, particularly with traceable and biological meaningful thresholds that can be linked to actions has in the past been difficult. However, the GEM approach and the state change probability that is calculated
annually along with long-term monitoring data provides a new potential solution to this problem. When immigration and emigration are included within the GEM IPM structure, the GEM model provides predictions of the GEM state transitions better than a single question in most cases. With an IPM structure, the GEM approach also provides estimates of demographic parameters that were previously unobservable (Zipkin \& Saunders 2018). In addition, changing questions results in monitoring predictions across all population parameters. However, these estimates are on model runs with a large amount of information (including known demographic parameters of survival) and thus may be unrealistic for many rare species. But the expansion of the GEM IPM structure and the results presented here suggest that many expansions of GEM are possible. Results from Chapter 1 with uninformative priors suggest that less information in these simulation will likely still results in high CRI coverage but variables predicted larger amounts of error. Optimization of parameter estimates in expanded GEM settings, including exploration of what variables are known or unknown, should be explored in species- and context-specific studies. Thus, GEM provides an important step forward for small or isolated population monitoring with a threshold that can be defined and detected annually according to state change probabilities.

Near-term, or between the time periods set by monitoring, predictions of the GEM state change probabilities offer many possible approaches to setting biologically meaningful thresholds, as suggested by many (Schultz et al. 2013; Cook et al. 2016). For example, if a GEM cell with breeding potential is in danger of losing breeding capability by the next season (probability of staying in state 4 is low or below a certain threshold that has been defined), a practitioner can decide to reduce human activity in areas that are important for connectivity or movement to that cell or attempt to increase chance of survival of individuals. Because these
thresholds can be assessed on an annual basis, they can provide the basis for much more frequent (if needed) interventions that may save a small or isolated population from extinction. This is arguably a favorable alternative to continued population monitoring as a population declines with few potential opportunities or logical points for intervention (e.g., Lindenmeyer et al. 2013).

In addition, because GEM is abundance-based and still a long-term monitoring system, it can result in a continuous monitoring approach and data stream for the species, even if the species has periods where it may become common, like lynx in the US in the 1970s (Ruggiero et al. 2000) or snowy plover (Charadrius nivosus nivosus) (Marcot et al. 2019) in the US which became common after ESA protection was given to them in 1993 (58 FR 12864:12874). In these instances, the long-term monitoring data stream provided in the GEM system from when the species was rare to when they become common would not be interrupted and still function. Although we suggest that thresholds for small and isolated populations are defined relative to breeding potential, we see the possibility for expanding this type of structure to state changes that are potentially meaningful to larger populations. For example, additional state transitions may be set for larger populations, such as skewed sex ratios, which can be early indicators of population decline in larger populations (Lehikoinen et al. 2008). Importantly, these types of extensions are feasible in the GEM framework because it is already designed to keep track of both females and males. If thresholds of interest are linked to state changes in the IPM framework as GEM provides, they can be set or adjusted according to biology, risk tolerance (Burgman 2005) and monitored with an extension of the GEM approach.

We show that when movement is incorporated in a GEM framework, changing questions using the GEM system that includes changing questions provides the best basis for estimating state changes and population metrics. Because the changing questions that arise from the GEM
sampling rules allow for targeted collection of information based on the states present, provide a way to effectively target information that is systematic and traceable. This is important because it makes the process flexible, which is a necessity for a small or isolated populations because of the large amount of change, but repeatable. Repeatable and transparent methods in monitoring systems, particularly as presented with a tie to meaningful threshold metrics, because they support one of the core elements of transparency of collaborative environmental decision making (Hemming et al. 2022).

GEM was originally proposed to address changing questions that arise due to species rarity. However, with this extension to include movement and the demonstration of the benefit that changing questions provides for effective estimation of GEM metrics, we provide a real way for GEM to advance rare species monitoring. With a basis of state-of-the-art data inference from an IPM structure and the addition of realistic metrics to predict short-term dynamics, we have begun the construction of what we hope is a new era in rare species monitoring. Many have the desire to leverage the small amounts of data that are available for rare species into as much inferences as possible. We provide a framework that potentially opens a new realm of conservation actions, guided by biological processes that govern small populations.

Although we use lynx as an example to demonstrate this, the structures provided, including the GEM state change probabilities with immigration and emigration, are flexible and can be extended or modified for many different species. We suggest that additional efforts to explore GEM in lynx and other species include empirical and simulation exploration of GEM, particularly to explore the how different thresholds related to the state of breeding potential may lead to different conservation outcomes. For broader application of GEM for small and isolated species, we encourage practitioners consider the following guidelines. The first is that the GEM
grid cell size should be scaled to 9 home ranges of the species of interest. Overall, simulations showed that the optimal cell size was approximately 8 home ranges, which is the size where the cell spent approximately half the time in GEM state 4 but still changed from that state so error on the estimates of the GEM state 4 change probability remained low. However, to put this into practice, we recognize that a group of 8 can have difficult spatial properties (i.e., it cannot be aggregated into a square cell from a grid of single-home-range-sized cells) that make it less than ideal for surveying or drawing inference. Therefore, we determined that a GEM grid cell size of 9 home ranges would still accomplish most of the estimation benefits of a GEM cell size of 8 home ranges, but provide a significant increase in real-world usability. We thus suggest a GEM grid cell size of 9 home ranges for GEM field applications. The second is that a basic understanding of the life history and population process should be known to create the IPM structure, although we highlight that demographic parameters do not have to be known. The third is that practitioners should consider the range of ways in which the basis of GEM sampling information can be collected. The three tiers of information, presence, counts (to determine multiple individuals), and counts of females and males can be determined with multiple methods, including non-invasive genetic methods (Schwartz et al. 2007), cameras (Moeller et al. 2018), even to artificial intelligence (e.g., Green et al. 2020), such that conservation practitioners may have multiple options to obtain this information.

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## TABLES

Table 2-1) The goal efficient monitoring (GEM) population states used in this manuscript.
Additional information on the biological meaning of the state, population importance, conservation and management importance, and the contribution of the state to persistence potential are also provided. Females are represented with an f and males represented with an m on the lynx figure.

|  | Goal Efficient Monitoring (GEM) for small or isolated populations |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  | Population sates |  |  |  |  |
|  | $\begin{aligned} & \text { GEM population } \\ & \text { state } \end{aligned}$ | Biological description | Population importance | Conservation/ management importance | Persistence potential |
| rexte | Multiple individuals, both sexes (GEM state 4) |  | High (may provide important connectivity or future |  | Somewhat likely (can be boosted by colonization potential, increased demographic rates) |
|  | Mutiple indiviculs singele sex <br>  | Esolitedinduducus | $\begin{aligned} & \text { Limited } \\ & \text { (but may provide } \\ & \text { important connectivity } \\ & \text { or future population } \\ & \text { potential) } \end{aligned}$ |  | Sole |
| nt | Sindeme | Bolcied indindual | $\begin{aligned} & \text { Limited } \\ & \text { (but may provide } \\ & \text { important connectivity } \\ & \text { or future population } \\ & \text { potential) } \end{aligned}$ | efforts to augment population may be undertaken) | Very limited <br> colonization potential) |
| 极 |  | Locol extiction | $\begin{aligned} & \text { Very limited } \\ & \text { (may provide important } \\ & \text { connectivity or future } \\ & \text { population potential) } \end{aligned}$ | Very high (if protected or of conservation interest, efforts to reintroduce may be undertaken) | $\begin{aligned} & \text { None } \\ & \text { (unless there is } \\ & \text { colonization potential) } \end{aligned}$ |

Table 2-2) The goal efficient monitoring (GEM) sampling rules for the GEM observation process to change questions and field methods based on what is known.

| Sampling Rule <br> $\#$ | Description |
| :--- | :--- |
| 1 | If no information about the population is known, obtain confirmation of <br> presence only. |
| 2 | If presence has been confirmed in the previous season, obtain information on <br> whether multiple individuals are present via counts. |
| 3 | If counts are $>2$ across a single visit in a season (not $>2$ in total across repeat <br> visits in a single season), obtain information on whether females and males <br> are present via collection of sex identifying information (e.g., genetic <br> material) during counts. |
| 4 | If multiple individuals and only a single sex were confirmed in the previous <br> season, obtain information on whether multiple individuals are present via <br> counts. |
| 5 | If multiple individuals and both sexes were confirmed in the previous <br> season, obtain information on whether females and males are present via <br> collection of sex identifying information (e.g., genetic material) during <br> counts. |

Table 2-3) The estimates of the GEM model for $\boldsymbol{\psi}_{\boldsymbol{t} 44}$, the probability of staying in multiple individuals of both sexes, or retaining breeding capability, across 100 replicate simulations of the GEM model, each with 3 MCMC chains, 50,000 iterations, 5,000 burn-in period and no thinning. All simulations in used the following for the biological process: different starting populations (4 individuals, 8 individuals, and 16 individuals, all with an equal sex ratio to begin with) and the same demographic parameters (survival $=0.7$, probability of litter $=0.5$, size of litter $=2$, and equal sex ratio of litter). All populations used the GEM sampling rules for the observation process, which included 3 visits each season, detection probability of individuals of $\mathrm{p}=0.63$, and probability of detection of genetic sign of pgenetic $=0.7 . \mathrm{RRMSE}=$ relative root mean square error.

|  | Percent of time steps in <br> simulations that were <br> in state 4 (total number <br> out of 1,100) | $\boldsymbol{\psi}_{\boldsymbol{t} 44}$ mean absolute <br> percent error | RRMSE |
| :---: | :---: | :---: | :---: |
| 4 (2 females, 2 males) | $25.9 \%(285)$ | $13.4 \%$ | 0.156 |
| 8 (4 females, 4 males) | $48.2 \%(531)$ | $6.95 \%$ | 0.104 |
| 16 (4 females, 4 males) | $78.0 \%(862)$ | $3.96 \%$ | 0.0754 |

Table 2-4) The population parameters of the GEM model and performance metrics across 100 replicate simulations, each with 3 MCMC chains, 50,000 iterations, 5,000 burn-in period and no thinning, with the single question observation scenario (is the species present) and the GEM question scenario (is the species present, are multiple individuals present, are males and females present). The different performance metrics of relative root mean square error (RRMSE) (a), coverage (b), average mean absolute percent error (MAPE) (c), and average mean absolute individual error (MAIE) (d) are provided below. Because not all metrics apply to all variables, only the relevant variables for each metric are included.
c. RRMSE (lower error is shown with lower numbers)

| Observation scenario | $N_{\text {ft }}$ | $\boldsymbol{N}_{\boldsymbol{m} t}$ | Birth events $_{t}$ | New $\operatorname{ind}_{f t}$ | New ind $v_{m t}$ | $N_{f t+1}$ | $N_{m t+1}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| GEM question | 0.520 | 0.453 | 1.08 | 1.51 | 1.48 | 0.407 | 0.376 |
| Single question | 0.753 | 0.653 | 0.859 | 0.970 | 0.995 | 0.727 | 0.619 |

d. Coverage (better parameter estimation is shown with higher numbers)

| Observation scenario | $N_{f t}$ | $N_{m t}$ | $\underset{\substack{\text { GEM population } \\ \text { state }}}{\mathbf{z 2}}$ | Birth events $_{t}$ | New $\boldsymbol{i n d} v_{f t}$ | New $\operatorname{ind}_{\mathrm{m}}{ }$ | $N_{f t+1}$ | $N_{m t+1}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| GEM question | 98.6 | 98.7 | 93.4 | 99.6 | 99.5 | 99.5 | 99.3 | 99.1 |
| Single question | 97.1 | 97.3 | 91.1 | 98.3 | 98.3 | 98.1 | 97.1 | 98.3 |

e. Mean MAPE (lower error is shown with lower numbers)

| Observation <br> scenario | $\boldsymbol{N}_{\boldsymbol{f t}}$ <br> Female <br> abundance | $\boldsymbol{N}_{\boldsymbol{m} \boldsymbol{t}}$ <br> male abundance | Birth <br> events $_{t}$ | New <br> indv $_{f t}$ | New <br> indv $_{m t}$ | $\boldsymbol{N}_{f t+1}$ | $\boldsymbol{N}_{\boldsymbol{m t + 1}}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| GEM question | 22.9 | 22.7 | 32.1 | 23.1 | 26.5 | 15.4 | 16.9 |
| Single question | 86.1 | 69.8 | 91.6 | 80.2 | 81.9 | 69.8 | 65.5 |

f. Mean MAIE (lower error is shown with lower numbers)

| Observation scenario | $\underset{\substack{\text { Female } \\ \text { abundance }}}{N_{f t}}$ | $\underset{\text { male abundance }}{N_{m t}}$ | Birth events $_{t}$ | New $\boldsymbol{i n d} v_{f t}$ | New $\boldsymbol{i n d} \boldsymbol{v}_{m t}$ | $\boldsymbol{N}_{\text {ft+1 }}$ | $N_{m t+1}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| GEM question | 0.514 | 0.543 | 0.562 | 0.315 | 0.378 | 0.266 | 0.324 |
| Single question | 3.28 | 2.78 | 2.62 | 1.49 | 1.52 | 2.12 | 1.84 |

Table 2-5) The relative root mean square error (RRMSE) and the mean across all simulations and groups of the mean absolute percent error (mean MAPE) of the GEM state change probabilities across 100 replicate simulations, each with 3 MCMC chains, 50,000 iterations, 5,000 burn-in period and no thinning, with the single question observation scenario (is the species present) (top) and the GEM question scenario (is the species present, are multiple individuals present, are males and females present). The description of what each of the state change probability means biologically is included below each probability.
a. State changes from single individual present (GEM state 2)

| Observation scenario | $\psi_{t 21}$ |  | $\psi_{t 22}$ |  | $\psi_{t 23}$ |  | $\psi_{t 24}$ |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Probability of local extinction (from single individual present) |  | Probability of only single individual persisting (from single individual present) |  | Probability of gaining at least one individual of the same sex (from single individual present) |  | Probability of gaining breeding capability (from single individual present) |  |
|  | RRMSE | Mean <br> MAPE | RRMSE | Mean <br> MAPE | RRMSE | Mean <br> MAPE | RRMSE | Mean <br> MAPE |
| GEM question | 0.155 | 9.72 | 0.0845 | 2.85 | Not predicted |  | Not predicted |  |
| Single question | 0.259 | 26.7 | 0.150 | 9.37 | Not predicted |  | Not predicted |  |

b. State changes from multiple individuals present of a single sex (GEM state 3 )

| Observation scenario | $\psi_{t 31}$ |  | $\psi_{t 32}$ |  | $\psi_{t 33}$ |  | $\psi_{t 34}$ |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Probability of local extinction (from multiple individuals and single sex present) |  | Probability of only single individual persisting (from multiple individuals and single sex present) |  | Probability of only persisting as multiple individuals but only a single sex (from multiple individuals and single sex present) |  | Probability of gaining breeding capability (from multiple individuals and single sex present) |  |
|  | RRMSE | Mean <br> MAPE | RRMSE | Mean <br> MAPE | RRMSE | Mean <br> MAPE | RRMSE | Mean <br> MAPE |
| GEM question | 0.551 | 50.2 | 0.411 | 34.6 | 0.300 | 22.4 | 0.591 | 48.0 |
| Single question | 0.869 | 138 | 0.724 | 85.8 | 0.539 | 52.1 | 1.01 | 92.6 |

c. State changes from multiple individuals and both sexes present (GEM state 4)

| Observation scenario | $\psi_{t 41}$ |  | $\psi_{t 42}$ |  | $\psi_{t 43}$ |  | $\psi_{t 44}$ |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Probability of local extinction (from females and males present) |  | Probability of only single individual persisting (from females and males present) |  | Probability of losing breeding capability (from females and males present) |  | Probability of retaining breeding capability (from females and males present) |  |
|  | RRMSE | Mean <br> MAPE | RRMSE | Mean <br> MAPE | RRMSE | Mean <br> MAPE | RRMSE | Mean <br> MAPE |
| GEM question | 2.44 | 1501 | 1.73 | 963 | 1.10 | 135 | 0.172 | 14.9 |
| Single question | 6.57 | $8.09 \mathrm{e}^{31}$ | 4.84 | $2.03 \mathrm{e}^{31}$ | 2.39 | $8.02 \mathrm{e}^{14}$ | 0.106 | 5.82 |

## FIGURES



Figure 2-1) The goal efficient monitoring (GEM) state change probabilities from a potential breeding population (GEM state 4) at time $t$ to the other states of isolated individuals, isolated individual, and local extinction at time $\mathrm{t}+1$. The table provides an additional explanation for the probability highlighted with the yellow arrow (probability of not changing state and retaining breeding). Additional information on the biological meaning of the state, population importance, conservation and management importance, and the ability of existing monitoring methods to detect the state change are also provided. Females are represented with an f and males represented with an $m$ on the lynx figure. Note that any of the other state changes (shown with gray arrows) are possible, but not described in the figure.


Figure 2-2) Goal efficient monitoring (GEM) data from a simulation of a single population that started with 19 individuals based on the methods presented in Chapter 1. The data presented include population predictions (shown in black and uncertainty shown in gray), state change probabilities (represented as the proportion of the yellow state filled, also listed on the state) between time steps, generated in a GEM simulation using the GEM observation approach. Below the x -axis are examples of assessments and decisions at each time step relative to a hypothetical ecological threshold (red dashed line) set prior to monitoring. After the population is assessed to see if the state change probability is below the threshold (i.e., likely to lose breeding capability),
a decision is made, and conservation actions can be taken or removed. Females are represented with an $f$ and males represented with an $m$ on the lynx figure.

Figure 2-3) The GEM integrated population model framework for Canada lynx (Lynx canadensis) with an extension for emigration and immigration. The time scale included shows a single calendar year divided by months, including notations of $t$ and $t+1$ relative to the model. The biological process and equations are represented on the top of the timeline and observation process and equations are shown on the bottom. Note that all possible parts of a GEM observation approach are shown in the observation process.


Figure 2-4) The goal efficient monitoring (GEM) state change probabilities possible with the immigration and emigration extension.


## APPENDIX A: TRANSITION PROBABILITIES

## Not present (GEM state 1 - $\Psi_{t+1}$ row 1)

1. If the population is in state 1 (locally extinct) it can:
a. Transition to state 2 (isolated individual) based on the probability that:
i. A single male immigrates into the population and exactly zero females immigrate into the population
or
ii. A single female immigrates into the population and exactly zero males immigrate into the population

$$
\begin{aligned}
P\left(z 2_{t+1}=2\right)= & \left.\left.\left(\binom{C_{m, i, t+1}}{1}\left(1-C p_{i}\right)^{C_{m, i, t+1}-1} *\left(C p_{i}\right)\right)^{1} *\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{f, i, t+1}}\right)+ \\
& \left.\left(\binom{C_{f, i, t+1}}{1}\left(1-C p_{i}\right)^{C_{f, i, t+1}-1} *\left(C p_{i}\right)\right)^{1} *\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{\left.C_{m, i, t+1} *\left(C p_{i}\right)\right)^{C_{m, i, t+1}-C_{m, i, t+1}}}\right)
\end{aligned}
$$

b. Transition to state 3 (isolated individuals) based on the probability that:
i. At least two males immigrate and exactly zero females immigrate into the population or
ii. At least two females immigrate and exactly zero males immigrate into the population

$$
\begin{aligned}
P\left(z 2_{t+1}=3\right)= & \left.\left.\left(1-\left(\binom{C_{m, i, t+1}}{1}\left(1-C p_{i}\right)^{C_{m, i, t+1}-1} *\left(C p_{i}\right)\right)^{1}\right) *\binom{C_{f, i, t+1}}{C_{f, i t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{f, i, t+1}}\right)+ \\
& \left.\left(1-\left(\binom{C_{f, i, t+1}}{1}\left(1-C p_{i}\right)^{C_{f, i, t+1}-1} *\left(C p_{i}\right)\right)^{1}\right) *\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{\left.C_{m, i t+1} *\left(C p_{i}\right)\right)^{C_{m, i, t+1}-C_{m, i, t+1}}}\right)
\end{aligned}
$$

c. Transition to state 4 (breeding potential) based on the probability that:
i. At least one male and at least one female immigrates into the population

$$
\left.\left.P\left(z 2_{t+1}=4\right)=\left(1-\left(\binom{C_{m, i, t+1}}{1}\left(1-C p_{i}\right)^{C_{m, i, t+1}-1} *\left(C p_{i}\right)\right)^{1}\right) * 1-\left(\binom{C_{f, i, t+1}}{1}\left(1-C p_{i}\right)^{C_{f, i, t+1}-1} *\left(C p_{i}\right)\right)^{1}\right)\right)
$$

d. Stay in state 1 (not present) based on the probability that none of the other transitions (1a-1c) occur

$$
\begin{aligned}
P\left(z 2_{t+1}=1\right)= & 1 \\
& \left.-\left(\left(\binom{C_{m, i, t+1}}{1}\left(1-C p_{i}\right)^{c_{m, i t+1}-1} *\left(C p_{i}\right)\right)^{1} *\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{f, i, t+1}}\right) \\
& +\left(\binom{C_{f, i, t+1}}{1}\left(1-C p_{i}\right)^{C_{f, i, t+1}-1} *\left(C p_{i}\right)\right)^{1} *\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{C_{m, i, t+1}} \\
& \left.\left.\left.*\left(C p_{i}\right)\right)^{C_{m, i, t+1}-C_{m, i, t+1}}\right)\right) \\
& -\left(\left(1-\left(\binom{C_{m, i, t+1}}{1}\left(1-C p_{i}\right)^{C_{m, i t+1}-1} *\left(C p_{i}\right)\right)^{1}\right) *\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}}\right. \\
& \left.\left.*\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{f, i, t+1}}\right) \\
& +\left(1-\left(\binom{C_{f, i, t+1}}{1}\left(1-C p_{i}\right)^{C_{f, i, t+1}-1} *\left(C p_{i}\right)\right)^{1}\right) *\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{C_{m, i, t+1}} \\
& \left.\left.\left.*\left(C p_{i}\right)\right)^{C_{m, i, t+1}-C_{m, i, t+1}}\right)\right) \\
& -\left(\left(1-\left(\binom{C_{m, i, t+1}}{1}\left(1-C p_{i}\right)^{C_{m, i, t+1}-1} *\left(C p_{i}\right)\right)^{1}\right) * 1\right. \\
& \left.\left.\left.-\left(\binom{C_{f, i, t+1}}{1}\left(1-C p_{i}\right)^{C_{f, i, t+1}-1} *\left(C p_{i}\right)\right)^{1}\right)\right)\right)
\end{aligned}
$$

## Single individual present (GEM state 2 - $\Psi_{t+1}$ row 2)

2. If the population is in state 2 (isolated individual) it can:
a. Transition to state 1 (locally extinct) based on the probability that:
i. The single individual dies and no males and no females immigrate into the population

$$
\begin{aligned}
P\left(z 2_{t+1}=1\right)= & \left.\left(\binom{N_{i, t}}{N_{i, t}}(1-s)^{N_{i, t}} *(s)^{N_{i, t}-N_{i, t}}\right) *\left(\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{f, i, t+1}}\right) \\
& \left.*\left(\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{C_{m, i, t+1}} *\left(C p_{i}\right)\right)^{C_{m, i, t+1}-C_{m, i, t+1}}\right)
\end{aligned}
$$

b. Transition to state 3 (isolated individuals) based on the probability that:
i. At least one male immigrates and the single individual present survives and exactly zero females immigrate into the population
or
ii. At least one female immigrates and the single individual present survives and exactly zero males immigrate into the population
or
iii. At least two males immigrate and exactly zero females immigrate into the population and the single individual present does not survive or
iv. At least two females immigrate and exactly zero males immigrate into the population and the single individual present does not survive

$$
\begin{aligned}
P\left(z 2_{t+1}=3\right)= & \left(\left(1-\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{C_{m, i, t+1}} *\left(C p_{i}\right)\right)^{C_{m, i, t+1}-C_{m, i, t+1}}\right) *\left(\binom{N_{i, t}}{N_{i, t}}(1-s)^{N_{i, t}} *(s)^{N_{i, t}-N_{i, t}}\right) \\
& \left.\left.*\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{f, i, t+1}}\right) \\
& +\left(\left(1-\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{f, i, t+1}}\right) *\left(\binom{N_{i, t}}{N_{i, t}}(1-s)^{N_{i, t}} *(s)^{N_{i, t}-N_{i, t}}\right) \\
& \left.+\left(\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{C_{m, i, t+1}} *\left(C p_{i}\right)\right)^{C_{m, i, t+1}-C_{m, i, t+1}}\right) \\
& +\left(\begin{array}{c}
\left.\left.\left.1-\binom{C_{m, i, t+1}}{1}\left(1-C p_{i}\right)^{C_{m, i, t+1}-1} *\left(C p_{i}\right)\right)^{1}\right) *\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{f, i, t+1}} \\
\\
\end{array}\right) \\
& \left.+\binom{N_{i, t}}{N_{i, t}}(1-s)^{N_{i, t}} *(s)^{N_{i, t}-N_{i, t}}\right) \\
& \left.*\binom{N_{i, t}}{N_{i, t}}(1-s)^{N_{i, t}} *(s)^{N_{, i, t}-N_{i, t}}\right)
\end{aligned}
$$

c. Transition to state 4 (breeding potential) based on the probability that:
i. At least one male immigrates and at least one female immigrates into the population and the single individual dies
or
ii. At least one male immigrates and at least one female immigrates into the population and the single individual lives

$$
\begin{aligned}
P\left(z 2_{t+1}=4\right)= & \left(\left(1-\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{C_{m, i, t+1}} *\left(C p_{i}\right)\right)^{C_{m, i, t+1}-C_{m, i, t+1}}\right) \\
& \left.\left.*\left(1-\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{f, i, t+1}}\right) *\left(\binom{N_{i, t}}{N_{i, t}}(1-s)^{N_{i, t}} *(s)^{N_{i, t}-N_{i, t}}\right)\right) \\
& +\left(\left(\left(1-\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{\left.\left.C_{m, i, t+1} *\left(C p_{i}\right)\right)^{c_{m, i, t+1}-C_{m, i, t+1}}\right)}\right.\right.\right. \\
& \left.\left.\left.*\left(1-\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{f, i, t+1}}\right) *\left(\binom{N_{i, t}}{1}(1-s)^{N_{i, t}-1} * s^{1}\right)\right)\right)
\end{aligned}
$$

d. Stay in state 2 (single individual present) based on the probability that none of the other transitions (2a-2c) occur

$$
\begin{aligned}
& P\left(z 2_{t+1}=2\right)=1 \\
& -\left(\left(\binom{N_{i, t}}{N_{i, t}}(1-s)^{N_{i, t}} *(s)^{N_{i, t}-N_{i, t}}\right) *\left(\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{f, i, t+1}}\right) \\
& \left.\left.*\left(\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{C_{m, i, t+1}} *\left(C p_{i}\right)\right)^{C_{m, i, t+1}-C_{m, i, t+1}}\right)\right) \\
& -\left(\left(\left(1-\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{C_{m, i, t+1}} *\left(C p_{i}\right)\right)^{C_{m, i, t+1}-C_{m, i, t+1}}\right) *\left(\binom{N_{i, t}}{N_{i, t}}(1-s)^{N_{i, t}} *(s)^{N_{i, t}-N_{i, t}}\right)\right. \\
& \left.\left.*\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{f, i, t+1}}\right) \\
& +\left(\left(1-\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{f, i, t+1}}\right) *\left(\binom{N_{i, t}}{N_{i, t}}(1-s)^{N_{i, t}} *(s)^{N_{i, t}-N_{i, t}}\right) \\
& \left.\left.*\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{C_{m, i, t+1}} *\left(C p_{i}\right)\right)^{C_{m, i, t+1}-C_{m, i, t+1}}\right) \\
& \left.+\left(\left(1-\binom{C_{m, i, t+1}}{1}\left(1-C p_{i}\right)^{C_{m, i, t+1}-1} *\left(C p_{i}\right)\right)^{1}\right) *\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{f, i, t+1}} \\
& \left.*\binom{N_{i, t}}{N_{i, t}}(1-s)^{N_{i, t}} *(s)^{N_{i, t}-N_{i, t}}\right) \\
& \left.+\left(\left(1-\binom{C_{f, i, t+1}}{1}\left(1-C p_{i}\right)^{C_{f, i, t+1}-1} *\left(C p_{i}\right)\right)^{1}\right) *\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{C_{m, i, t+1}} *\left(C p_{i}\right)\right)^{C_{m, i, t+1}-C_{m, i, t+1}} \\
& \left.\left.*\binom{N_{i, t}}{N_{i, t}}(1-s)^{N_{i, t}} *(s)^{N_{i, i, t}-N_{i, t}}\right)\right) \\
& -\left(\left(\left(1-\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{\left.\left.C_{m, i, t+1} *\left(C p_{i}\right)\right)^{C_{m, i, t+1}-C_{m, i, t+1}}\right)}\right.\right.\right. \\
& \left.\left.*\left(1-\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{f, i, t+1}}\right) *\left(\binom{N_{i, t}}{N_{i, t}}(1-s)^{N_{i, t}} *(s)^{N_{i, t}-N_{i, t}}\right)\right) \\
& +\left(\left(\left(1-\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{C_{m, i, t+1}} *\left(C p_{i}\right)\right)^{C_{m, i, t+1}-C_{m, i, t+1}}\right)\right.
\end{aligned}
$$

$$
\left.\left.\left.\left.*\left(1-\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{f, i, t+1}}\right) *\left(\binom{N_{i, t}}{1}(1-s)^{N_{i, t}-1} * s^{1}\right)\right)\right)\right)
$$

## Multiple individuals of a single sex present (GEM state 3 - $\Psi_{t+1}$ row 3)

3. If the population is in state 3 (isolated individuals) it can:
a. Transition to state 1 (not present) based on the probability that:
i. All individuals die and exactly zero males and exactly zero females immigrate into the population

$$
\begin{aligned}
P\left(z 2_{t+1}=1\right)= & \left.\left(\binom{N_{i, t}}{N_{i, t}}(1-s)^{N_{i, t}} *(s)^{N_{i, t}-N_{i, t}}\right) *\left(\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{f, i, t+1}}\right) \\
& \left.*\left(\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{C_{m, i, t+1}} *\left(C p_{i}\right)\right)^{C_{m, i, t+1}-C_{m, i, t+1}}\right)
\end{aligned}
$$

b. Transition to state 2 (isolated individuals) based on the probability that:
ii. A single individual present lives and exactly zero males and exactly zero females immigrate
or
iii. All individuals present die and a single male immigrates and exactly zero females immigrate into the population
or
iv. All individuals present die and a single female immigrates and exactly zero males immigrate into the population

$$
\left.\left.\begin{array}{rl}
P\left(z 2_{t+1}=2\right)= & \left.\left(\binom{N_{i, t}}{1}(1-s)^{N_{i, t}-1} * s^{1}\right) *\left(\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i t+1}-C_{f, i, t+1}}\right) \\
& \left.\left.*\left(\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{C_{m, i, t+1}} *\left(C p_{i}\right)\right)^{c_{m, i t+1}-C_{m, i, t+1}}\right)\right) \\
& +\left(\binom{N_{t}}{N_{t}}(1-s)^{N_{t}} *(s)^{N_{t}-N_{t}} *\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{f, i, t+1}} \\
& *\left(\binom{C_{m, i, t+1}}{1}\left(1-C p_{i}\right)^{C_{m, i, t+1}-1} *\left(C p_{i}\right)\right)^{1}
\end{array}\right)\right), ~\left(\binom{N_{t}}{N_{t}}(1-s)^{N_{t}} *(s)^{N_{t}-N_{t}} *\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{C_{m, i, t+1}} *\left(C p_{i}\right)\right)^{C_{m, i, t+1}-C_{m, i, t+1}} .
$$

c. Transition to state 4 (breeding potential) based on the probability that:
i. At least one male and at least on female immigrates and the single individual present dies
or
ii. At least one male and at least on female immigrates and the single individual present lives

$$
\begin{aligned}
P\left(z 2_{t+1}=4\right)= & \left(\left(1-\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{c_{m, i, t+1}} *\left(C p_{i}\right)\right)^{c_{m, i, t+1}-C_{m, i, t+1}}\right) \\
& \left.\left.*\left(1-\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{c_{m, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{m, i, t+1}}\right) *\left(\binom{N_{i, t}}{N_{i, t}}(1-s)^{N_{i, t}} *(s)^{N_{i, t}-N_{i, t}}\right)\right) \\
& +\left(\left(1-\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{c_{m, i, t+1}} *\left(C p_{i}\right)\right)^{c_{m, i, t+1}-C_{m, i, t+1}}\right) \\
& \left.\left.*\left(1-\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{c_{m, i t+1}} *\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{m, i, t+1}}\right) *\left(\binom{N_{i, t}}{1}(1-s)^{N_{i, t}-1} *(s)^{1}\right)\right)
\end{aligned}
$$

d. Stay in state 3 (multiple individuals of a single sex present) based on the probability that none of the other transitions (3a-3c) occur.

$$
\begin{aligned}
& P\left(z 2_{t+1}=3\right)=1 \\
& -\left(\left(\binom{N_{i, t}}{N_{i, t}}(1-s)^{N_{i, t}} *(s)^{N_{i, t}-N_{i, t}}\right) *\left(\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{f, i, t+1}}\right) \\
& \left.\left.*\left(\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{c_{m, i t+1}} *\left(C p_{i}\right)\right)^{c_{m, i t+1}-c_{m, i, t+1}}\right)\right) \\
& -\left(\left(\binom{N_{i, t}}{1}(1-s)^{N_{i, t}-1} * s^{1}\right) *\left(\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i t+1}-C_{f, i, t+1}}\right) \\
& \left.\left.*\left(\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{C_{m, i, t+1}} *\left(C p_{i}\right)\right)^{c_{m, i, t+1}-C_{m, i, t+1}}\right)\right) \\
& +\left(\binom{N_{t}}{N_{t}}(1-s)^{N_{t}} *(s)^{N_{t}-N_{t}} *\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i t+1}-C_{f, i, t+1}} \\
& \left.\left.*\left(\binom{C_{m, i, t+1}}{1}\left(1-C p_{i}\right)^{C_{m, i, t+1}-1} *\left(C p_{i}\right)\right)^{1}\right)\right) \\
& +\left(\binom{N_{t}}{N_{t}}(1-s)^{N_{t}} *(s)^{N_{t}-N_{t}} *\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{c_{m, i, t+1}} *\left(C p_{i}\right)\right)^{c_{m, i, t+1}-c_{m, i, t+1}} \\
& \left.\left.\left.*\left(\binom{C_{f, i, t+1}}{1}\left(1-C p_{i}\right)^{C_{f, i, t+1}-1} *\left(C p_{i}\right)\right)^{1}\right)\right)\right) \\
& -\left(\left(\left(1-\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{c_{m, i, t+1}} *\left(C p_{i}\right)\right)^{c_{m, i, t+1}-c_{m, i, t+1}}\right)\right. \\
& \left.*\left(1-\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{C_{m, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{m, i, t+1}}\right) \\
& \left.*\left(\binom{N_{i, t}}{N_{i, t}}(1-s)^{N_{i, t}} *(s)^{N_{i, t}-N_{i, t}}\right)\right) \\
& +\left(\left(1-\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{c_{m, i, t+1}} *\left(C p_{i}\right)\right)^{c_{m, i, t+1}-C_{m, i, t+1}}\right) \\
& \left.*\left(1-\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{C_{m, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i t+1}-C_{m, i, t+1}}\right) \\
& \left.\left.*\left(\binom{N_{i, t}}{1}(1-s)^{N_{i, t}-1} *(s)^{1}\right)\right)\right)
\end{aligned}
$$

## Multiple individuals of both sexes present (GEM state 4 - $\Psi_{t+1}$ row 4)

4. If the population is in state 4 (breeding potential) it can:
a. Transition to state 1 (locally extinct) based on the probability that:
i. All individuals die and no males and no females immigrate into the population

$$
\begin{aligned}
P\left(z 2_{t+1}=1\right)= & \left.\left(\binom{N_{i, t}}{N_{i, t}}(1-s)^{N_{i, t}} *(s)^{N_{i, t}-N_{i, t}}\right) *\left(\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{f, i, t+1}}\right) \\
& \left.*\left(\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{C_{m, i, t+1}} *\left(C p_{i}\right)\right)^{C_{m, i, t+1}-C_{m, i, t+1}}\right)
\end{aligned}
$$

b. Transition to state 2 (isolated individual) based on the probability that:
i. A single individual present lives and no males and females immigrate or
ii. All individuals present die and a single male immigrates and exactly zero females immigrate into the population
or
iii. All individuals present die and a single female immigrates and exactly zero males immigrate into the population

$$
\left.\left.\begin{array}{rl}
P\left(z 2_{t+1}=2\right)= & \left(\left(\binom{N_{i, t}}{1}(1-s)^{N_{i, t}-1} * s^{1}\right) *\left(\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i t+1}} *\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{f, i, t+1}}\right) \\
& \left.\left.*\left(\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{C_{m, i, t+1}} *\left(C p_{i}\right)\right)^{C_{m, i, t+1}-C_{m, i, t+1}}\right)\right) \\
& +\left(\binom{N_{t}}{N_{t}}(1-s)^{N_{t}} *(s)^{N_{t}-N_{t}} *\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{f, i, t+1}} \\
& *\left(\binom{C_{m, i, t+1}}{1}\left(1-C p_{i}\right)^{C_{m, i, t+1}-1} *\left(C p_{i}\right)\right)^{1}
\end{array}\right)\right), ~\left(\binom{N_{i, t}}{N_{i, t}}(1-s)^{N_{i, t}} *(s)^{N_{i, t}-N_{i, t}} *\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{C_{m, i, t+1}} *\left(C p_{i}\right)\right)^{C_{m, i, t+1}-C_{m, i, t+1}} .
$$

c. Transition to state 3 (isolated individuals) based on the probability that:
i. At least two males present live and no females live and no females immigrate or
ii. At least two females present live and no males live and no males immigrate or
iii. No females present live and no males present live and at least two females immigrate
or
iv. No females present live and no males present live and at least two males immigrate or
v. One male present lives and no females live and no females immigrate and at least one male immigrates
or
vi. One female present lives and no males live and no males immigrate and at least one female immigrates

$$
\begin{aligned}
& P\left(z 2_{t+1}=3\right)=\left(\left(1-\binom{N_{m, i, t}}{1}(1-s)^{N_{m, i t}-1} *(s)^{1}\right) *\left(\binom{N_{f, i, t}}{N_{f, i, t}}(1-s)^{N_{f, i, t}} *(s)^{N_{f, i, t}-N_{f, i, t}}\right)\right. \\
& \left.\left.*\left(\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{f, i, t+1}}\right)\right) \\
& +\left(\left(1-\binom{N_{f, i, t}}{1}(1-s)^{N_{f, i t}-1} *(s)^{1}\right) *\left(\binom{N_{m, i, t}}{N_{m, i, t}}(1-s)^{N_{m, i t}} *(s)^{N_{m, i, t}-N_{m, i t}}\right)\right. \\
& \left.\left.*\left(\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{c_{m, i, t+1}} *\left(C p_{i}\right)\right)^{c_{m, i, t+1}-C_{m, i, t+1}}\right)\right) \\
& +\left(\left(1-\binom{N_{f, i, t}}{1}(1-s)^{N_{f, i t}-1} *(s)^{1}\right) *\left(\binom{N_{m, i, t}}{N_{m, i, t}}(1-s)^{N_{m, i, t}} *(s)^{N_{m, i, t}-N_{m, i t}}\right)\right. \\
& \left.\left.*\left(1-\left(\binom{C_{m, i, t+1}}{1}\left(1-C p_{i}\right)^{C_{m, i, t+1}-1} *\left(C p_{i}\right)\right)^{1}\right)\right)\right) \\
& +\left(\binom{N_{m, i, t}}{1}(1-s)^{N_{m, i t}-1} *(s)^{1} *\binom{N_{f, i, t}}{N_{f, i, t}}(1-s)^{N_{f, i, t}} *(s)^{N_{f, i, t}-N_{f, i, t}}\right. \\
& \left.\left.*\left(1-\left(\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{C_{m, i, t+1}} *\left(C p_{i}\right)\right)^{c_{m, i, t+1}-C_{m, i, t+1}}\right)\right)\right) \\
& +\left(\binom{N_{f, i, t}}{1}(1-s)^{N_{f, i, t}-1} *(s)^{1} *\binom{N_{m, i, t}}{N_{m, i, t}}(1-s)^{N_{m, i, t}} *(s)^{N_{m, i, t}-N_{m, i t}}\right. \\
& \left.\left.*\left(1-\left(\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{f, i, t+1}}\right)\right)\right)
\end{aligned}
$$

d. Stay in state 4 (breeding potential) based on the probability that none of the other transitions (4a-4c) occur

$$
\begin{aligned}
& P\left(z 2_{t+1}=4\right)=1 \\
& -\left(\left(\binom{N_{i, t}}{N_{i, t}}(1-s)^{N_{i, t}} *(s)^{N_{i, t}-N_{i, t}}\right) *\left(\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{f, i t+1}}\right) \\
& \left.\left.*\left(\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{c_{m, i, t+1}} *\left(C p_{i}\right)\right)^{c_{m, i, t+1}-c_{m, i, t+1}}\right)\right) \\
& -\left(\left(\binom{N_{i, t}}{1}(1-s)^{N_{i, t}-1} * s^{1}\right) *\left(\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{f, i, t+1}}\right) \\
& \left.\left.*\left(\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{c_{m, i, t+1}} *\left(C p_{i}\right)\right)^{c_{m, i, t+1}-c_{m, i, t+1}}\right)\right) \\
& +\left(\binom{N_{t}}{N_{t}}(1-s)^{N_{t}} *(s)^{N_{t}-N_{t}} *\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i t+1}-C_{f, i, t+1}} \\
& \left.\left.*\left(\binom{C_{m, i, t+1}}{1}\left(1-C p_{i}\right)^{C_{m, i, t+1}-1} *\left(C p_{i}\right)\right)^{1}\right)\right) \\
& +\left(\binom{N_{t}}{N_{t}}(1-s)^{N_{t}} *(s)^{N_{t}-N_{t}} *\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{C_{m, i, t+1}} *\left(C p_{i}\right)\right)^{C_{m, i, t+1}-C_{m, i, t+1}} \\
& \left.\left.\left.*\left(\binom{C_{f, i, t+1}}{1}\left(1-C p_{i}\right)^{C_{f, i, t+1}-1} *\left(C p_{i}\right)\right)^{1}\right)\right)\right) \\
& -\left(\left(\left(1-\binom{N_{m, i, t}}{1}(1-s)^{N_{m, i t}-1} *(s)^{1}\right) *\left(\binom{N_{f, i, t}}{N_{f, i, t}}(1-s)^{N_{f, i, t}} *(s)^{N_{f, i, t}-N_{f, i, t}}\right)\right.\right. \\
& \left.\left.*\left(\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{f, i, t+1}}\right)\right) \\
& +\left(\left(1-\binom{N_{f, i, t}}{1}(1-s)^{N_{f, i t}-1} *(s)^{1}\right) *\left(\binom{N_{m, i, t}}{N_{m, i, t}}(1-s)^{N_{m, i, t}} *(s)^{N_{m, i, t}-N_{m, i, t}}\right)\right. \\
& \left.\left.*\left(\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{c_{m, i, t+1}} *\left(C p_{i}\right)\right)^{c_{m, i, t+1}-C_{m, i t+1}}\right)\right) \\
& +\left(\left(1-\binom{N_{f, i, t}}{1}(1-s)^{N_{f, i t}-1} *(s)^{1}\right) *\left(\binom{N_{m, i, t}}{N_{m, i, t}}(1-s)^{N_{m, i t}} *(s)^{N_{m, i, t}-N_{m, i t}}\right)\right. \\
& \left.\left.*\left(1-\left(\binom{C_{m, i, t+1}}{1}\left(1-C p_{i}\right)^{c_{m, i, t+1^{-1}}} *\left(C p_{i}\right)\right)^{1}\right)\right)\right) \\
& +\left(\binom{N_{m, i, t}}{1}(1-s)^{N_{m, i, t}-1} *(s)^{1} *\binom{N_{f, i, t}}{N_{f, i, t}}(1-s)^{N_{f, i, t}} *(s)^{N_{f, i, t}-N_{f, i, t}}\right.
\end{aligned}
$$

$$
\begin{aligned}
& \left.\left.*\left(1-\left(\binom{C_{m, i, t+1}}{C_{m, i, t+1}}\left(1-C p_{i}\right)^{C_{m, i, t+1}} *\left(C p_{i}\right)\right)^{C_{m, i, t+1}-C_{m, i t+1}}\right)\right)\right) \\
& +\left(\binom{N_{f, i, t}}{1}(1-s)^{N_{f, i, t}-1} *(s)^{1} *\binom{N_{m, i, t}}{N_{m, i, t}}(1-s)^{N_{m, i, t}} *(s)^{N_{m, i, t}-N_{m, i, t}}\right. \\
& \left.\left.\left.*\left(1-\left(\binom{C_{f, i, t+1}}{C_{f, i, t+1}}\left(1-C p_{i}\right)^{C_{f, i, t+1}} *\left(C p_{i}\right)\right)^{C_{f, i, t+1}-C_{f, i, t+1}}\right)\right)\right)\right)
\end{aligned}
$$

## Chapter 3: Conservation design ${ }^{3}$


#### Abstract

Conservation biology and practice currently relies on biological, social, and policy-based solutions to connect science to actions. However, processes to ensure conservation actions are effective is often ill-defined, which can lead to ineffective outcomes. To achieve effective solutions in conservation, we propose that conservation practice would benefit from the field of Design - a discipline that engages in research and practice on the plans and processes to change existing problematic conditions into preferred ones. The field is concerned with a wide range of design practices from communication, to engineering to business. In this article, we argue that the approach to problem solving known as Design Thinking will complement and improve conservation practice. Design thinking is an iterative process that guides designers and stakeholders on how to effectively build a product or process that meets the needs of the users they are intended for; it complements existing conservation practice approaches through its focus on building and testing effective solutions. We propose that combining conservation biology and Design thinking, which we call Conservation Design, could result in effective solutions and new innovations to further the field of conservation practice.


## THE STATE OF CONSERVATION PRACTICE

When Michael Soulé founded the modern field of conservation biology in 1985, he defined it as "... a new stage in the application of science to conservation problems," (Soule 1985). The use of the phrase "application" may have foreshadowed where the field was going, because today, almost 30 years later, the field of conservation biology has now grown to more broadly and

[^3]formally encompass the idea of conservation practice (Fleishman et al. 1999), or the acts taken to achieve a conservation goal. From the addition of an entire journal dedicated to practice, Conservation Science and Practice from the Society for Conservation Biology (Schwartz et al. 2019), to widely used frameworks such as the Open Standards for the Practice of Conservation for practitioners to share lessons from practice (CMP 2022), to increased research on ways to link science to decisions (e.g., Schwartz et al. 2018), practice has in many ways become a renewed frontier of conservation. Limited funding, accelerated environmental change, and increased standards for science-based conservation and management means that conservation practice has to be more efficient than it has ever been.

To make conservation practice more effective, or likely to achieve the desired conservation goal, there has been a rapid development of frameworks, processes, and tools for conservation practitioners to accomplish conservation. According to Schwartz et al. (2018): a framework is a cohesive set of guidelines and specific tools to accomplish conservation practice; a process is a set of steps to accomplish a specific activity in conservation practice, with fewer prescriptions on how to accomplish the steps and what tools to use than a framework; and a tool is an individual product (e.g., software, planning method) designed to accomplish a specific purpose. These frameworks, processes, and tools are providing theoretical advances, as well improvements for on-the-ground processes (e.g., CMP 2022). However, for these frameworks, processes, and tools to be useful on the scale and pace required for current conservation practice, they need to be usable far beyond the scientific literature. One way this can occur is through more attention into developing these as usable systems and products, including carefully defining who and what they are intended to be used by and for. To more effectively achieve conservation practice with current frameworks, processes, and tools, we need
an effective way to articulate and build the purpose of the methods at multiple levels and integrate the existing steps within the processes to work towards that purpose.

An interdisciplinary approach where Design plays a larger role in defining the system provides a promising way forward to accomplish the transformation of conservation practice into a more usable system built with existing methods. The field of Design, which we define here as the professional field of research and practice to change existing conditions into preferred ones

## Glossary

conservation biology: "a new stage in the application of science to conservation problems" (Soule 1985)
conservation practice: the acts taken to achieve a conservation goal
design: to plan how something will be created (verb); the plans and processes to achieve an idea (noun)
Design: the professional field of research and practice to change existing conditions into preferred ones
Designer: a professional in Design, either in academic or industry setting
Design thinking: a Design framework that helps people generate and quickly test a range of possible options and identify an optimal solution by iterating through five steps of empathizing, defining, ideating, prototyping, and testing
effective conservation practice: likely to achieve the desired conservation goal
empathize: the first step in Design thinking
empathy interviews: a Design method for interviewing to build empathy through an interview by observing, emerging, and engaging with users
experience prototyping: a Design method that uses a physical or visual representation of what it is like to be the user framework: cohesive set of guidelines and specific tools to accomplish conservation practice or Design
process: steps to accomplish a specific activity in conservation practice, but with fewer formal prescriptions on how to accomplish steps and what tools to use than a framework
results chain: conservation practice method to visually show the assumed links between a conservation action and the desired goals of the action
role playing: a Design method that uses acting out the role of the user by the Designer in realistic scenarios
scenario description swim lanes: a Design method to visualize the activities of multiple stakeholders through a process to visualize how a complex group may respond to a Design
stakeholder maps: a Design method that is widely used in other disciplines to visually represent the key stakeholders of a project and their connections to one another
stakeholder walk through: a Design method to bring stakeholders together with Designers to present and evaluate early prototypes
story board: a Design method to provide a visual narrative of how a user will interact with a product, specifically used to generate empathy and understand the context the user will interact with the Design
(Simon 1970), and conservation practice can both be improved when used together in novel ways. In particular, Design thinking, which is a Design framework that helps designers generate and quickly test a range of possible options and identify an optimal solution, can provide a broad and flexible framework to help at a number of scales to make these processes more effective and usable. Because the field of Design has been working for decades to hone how to most effectively turn purpose into plans, it is a new discipline to bring a structured cohesion to conservation practice. In fact, conservation practice already recognizes some value in Design; terms like "use inspired science" (Wall et al. 2017) and the description of science products produced for "users" (Fisher et al. 2019) are not just language of the discipline of Design, these are the foundation of Design activities.

In this chapter we present a review of Design and Design thinking, some of the most common frameworks and processes in conservation practice, examples of where we think Design thinking can help to improve these frameworks and processes and provide synergistic possibilities for innovations created between the fields of Design and conservation practice. We then provide an example of how we might use Design to build a monitoring implementation system for two different goals. Finally, we suggest ways in which a field that combines Design and conservation practice may develop. Although Design has not been widely used in conservation practice (a few notable examples do exist, however - see Design for Wildlife), we believe there is great potential in including Designers on the conservation practice team to build connections between conservation information and implementation.

## DESIGN, DESIGN WITH A CAPITAL "D," AND DESIGN THINKING

First, it is important that we clarify the use of the terms surrounding design, as that is often a source of confusion. As a verb, design refers to planing how something will be created, and as a noun, design refers to the plans and processes to achieve an idea. In his foundational book on design, The Science of the Artificial, Herbert Simon defined design as "The process of changing existing conditions into preferred ones" (Simon 2019). We bring these definitions up to highlight that all of


Figure 3-1) The Design thinking process (adapted from Stanford d.school 2019) us, whether in our daily life or in our professional careers, design to achieve specific purposes. Design, noted with a capital "D," in this essay is used to refer to the professional field of research (conducted in academic settings such as the Carnegie Mellon School of Design or the Rhode Island School of Design) and practice of Design (conducted throughout both academic and professional settings to accomplish service, social, or societal goals). Design is conducted for a user or target group (usually people unless stated otherwise) by a Designer, also noted with a capital "D", who is a professional in the Design field, typically either in academic or industry setting.

We focus on Design thinking for use in conservation practice because of the breadth of situations it can be applied to; as Buchanan (1992) noted, "the subject matter of design (thinking) is potentially universal in scope..." Design thinking is often explained as five stages, all of which
are meant to be iterative before the completion of the final design: empathize, define, ideate, prototype, and test (Figure 3-1). Empathize is the process of fully understanding the needs of the end users. It starts with stakeholder interviews and literature surveys with the goal of empathizing with the people and culture surrounding the problem (Kouprie \& Visser 2009) and understanding their needs. Next, information gained from the empathize step is applied to frame the Design problem from the stakeholders' perspective, using techniques such as generating "point of view" problem statements (e.g., "Local business owners need economically feasible clean water options from a municipality because they care about their livelihoods and value their community"). Then, a Designer generates ideas using this problem statement. This step, often called "ideation," involves techniques of mass idea production (e.g., brainstorming) and visual representation of those ideas (Martin \& Hanington 2012). Filtering ideas is critical in the ideation process and is conducted after ideas are generated, often using filter categories such as: 1) idea most likely to succeed; 2) idea most likely to delight; 3 ) most breakthrough idea (Stanford d.school 2019). After selecting one or a few ideas through filtering, a Designer will build prototypes-moving gradually from lower to higher fidelity prototypes, which allows for minimal investment and rapid iterative evaluation of the ideas. Prototypes are tested with interviews or users interacting directly with the prototypes (Stanford d.school 2019). These five steps are conducted repeatedly as an iterative process, with iteration often more frequently occurring in prototyping through testing.

Design thinking has been a successful framework to create some of the most important experiences in people's lives. For example, the Design firm IDEO has worked with Los Angeles County to build a prototype for new voting machines to replace the current machines from the 1960s. The machine is designed to be customizable and provide an equitable experience for
anyone voting, with adjustable options for vision impairment, reading disabilities, and audio controller available with just a few buttons (IDEO 2022). Design thinking has arguably changed our lives and societies through the products it has produced. With a goal to lead with Design and what people needed, rather than the technology that made a Design possible, Steve Jobs and others at Apple had a core value system based on Design that was responsible for the modern products today that reshaped music (iPod), communication (iPhone), and personal computing (the Macintosh computer) (Thomke \& Feinberg 2009). Design thinking in healthcare has also fundamentally changed some aspects of how healthcare is delivered. For example, in 2002 the Mayo Clinic created the See-Plan-Act-Refine-Communicate (SPARC) laboratory with Design

## Design for Wildlife: applying Design to human-wildlife conflict

Elephant crop raiding is a major human-wildlife conflict issue in Africa and Asia (MacKenzie \& Ahabyona 2012). A large body of conservation research has refined understanding of the problem (e.g., Barua et al. 2013), as well as effectiveness of natural repellent solutions to deter elephants (e.g., Hedges \& Gunaryadi 2010). Yet, there was little research to ensure that solutions to alleviate the conflict could both be built and sustained. To address this, Design for Wildlife, a collective of creative professionals focused on applying Design principles to solve human-wildlife conflicts, approached creating an economically sustainable elephant-crop raiding solution as a Design problem. They asked if disseminating information about what effectively repels elephants in a simple format (i.e., a recipe) would result in production of the repellent and sustained use of these methods and, if not, how might they ensure that happens?

In 2017-2019, Design for Wildlife conducted trials and showed that the elephant repellent made from natural ingredients grown throughout Africa reduced crop raiding by 80\%. However, Design for Wildlife also found that a recipe alone was not sufficient to encourage widespread production of the repellant because the recipe called for cash crops (crops grown for sale and not local consumption) such as chili, which are not grown unless there is a market for them. Through Design field research in Uganda, which included role playing, voting, and categorization exercises, they determined that creating a local business market for repellent would be most successful and economically sustainable (i.e., not donor dependent). However, before implementing a large, systematic solution, they evaluated it by creating full-scale local production prototypes and testing them in various markets in Uganda.

Design for Wildlife was successful. Now the repellent is widely produced through a local market created by and for local residents of Uganda. By using a Design thinking process, Design for Wildlife demonstrated a key benefit of Design in conservation: it is a way to bridge the gap between technical knowledge of a solution and the creation of a long-term, functional solution in practice (Design for Wildlife 2022).
firm IDEO (Brown 2019), as collaborative space for doctors, designers, health care
professionals, and even patients to work together on new ways to deliver care. The innovation process in the SPARC laboratory generated early prototypes of telemedicine. During an ideation phase of Design thinking, SPARC laboratory determined through the ideation process that care might also be able to be delivered via video. The prototype of the video system turned out to be successful and time saving way to access appointment (Malagrino et al. 2012). This innovation helped spur the larger development of telemedicine (Vimalananda et al. 2015). Whether it is in business (Brown 2019), education (Koh et al. 2015), public health (Bazzano et al. 2017), or government defense (US Air Force 2017), Design thinking is transforming the way fields solve problems.

## HOW DESIGN THINKING CAN IMPROVE CONSERVATION PRACTICE

## APPROACHES

Currently the theory of conservation practice is described in the scientific literature as frameworks, processes, and tools. Here, we focus on a small group of more frequently cited frameworks and processes to explore how Design thinking and adding a Designer to the teams that can lead to new innovations. While we recognize that Design thinking applied to the construction of the tools in conservation practice could greatly increase their popularity and functionality, there are so many and being produced so fast that it would likely take a book to describe them all. In addition, we feel that focusing on frameworks and processes allows for more possibilities for innovation with Design and conservation practice.

Schwartz et al. (2018) identified five major decision support frameworks in conservation practice: open standards for the practice of conservation (CMP 2022); evidence-based practice (Salafsky et al. 2019); systematic conservation planning (Margules and Pressey 2000); structured
decision making (Conroy \& Peterson 2013); and strategic foresight (Cook et al. 2014). In addition, we identified three more processes, which are less prescriptive in their tools and ways to achieve steps, which represent additional ways in which scientists are actively participating in conservation practice: impactful science (Fisher et al. 2019); coproduction of science (Beier et al. 2017); and translational ecology (Enquist et al. 2017). These frameworks and processes are the most current in broad conservation practice approaches that are in use today. We see many areas where Designers on the team using Design thinking can augment existing frameworks or processes and innovate with conservation practitioners. We describe some examples below according to the Design thinking step they correspond to and provide additional information in Table 3-1.

## Empathizing

Conservation practice is an applied science, meaning it requires us on some level to be empathetic to a stakeholder. Trends toward inclusion of stakeholders in all processes in conservation practice reflect the desire to consider stakeholder needs (e.g., Beier et al. 2017; Enquist et al. 2017). However, science itself is not designed to create a product that we can empathize with. We often conduct science to discover non-intuitive information, but not through empathy. While conservation biology and conservation practice may include empathy as part of a larger solution, the science itself actively does not use empathy. However, empathy may be a key factor in success of conservation practice. As Zimmerman et al. (2021) noted, conservation practice situations can each be very different because of the different people and socioeconomic factors involved. Having a Designer who is professionally trained and frequently uses empathy techniques such as observation studies, where a Designer observes a user in their environment,
and experience prototyping, where a Designer uses a representation of what it is like to be the user (Kouprie \& Visser 2009), who can actively work with empathy may provide solutions that were not previously considered.

An empathy approach used to understand the problem may be particularly useful in a framework such as structured decision making (SDM), which is used for making collective environmental decisions, often to meet multiple stakeholder objectives (Conroy \& Peterson 2013). The entire tone and direction of the SDM exercise is built on defining the problem as the first step. Individual problem definitions may be very different than a group definition, and may even differ if stakeholders are sharing their views with the entire group or in a one-on-one setting with a Designer who is actively working to understand their problem. Designers use empathy because of the understanding that there is frequently a difference between what people say, think, feel and do. Often what people will do is based on what they feel, so empathy is a good technique to use to understand this. However, conservation practice has been effective in using social science and measuring what people say and think more scientifically and rigorously (Bennett et al. 2016) and the SDM process attempts to quantify that so others can see it. We see the potential for Design and conservation practice to develop novel methods for groups to visualize or interact with the information about what people are saying, thinking, feeling and doing to define more inclusive collective problem statements.

## Defining

Defining the correct problem has been widely recognized as one the most important steps in most conservation practice and many aspects of conservation biology. The same is true for Design thinking. In fact, many of the methods currently in use in some of the conservation practice approaches, such as the open standards for the practice of conservation are methods
commonly used by Designers. For instance, Designers are already experts and well-practiced in many of the methods suggested in the assess step of the open standards for the practice of conservation framework, including stakeholder maps, stakeholder walk throughs, and storyboards (Martin \& Hanington 2018). Because open standards for the practice of conservation framework is meant to be very usable and accessible, Designers may not always be present to assist with these techniques. However, Designers could help to provide widely usable ways to create stakeholder maps, walkthroughs, or storyboards to include with the documents already produced by open standards for the practice of conservation. The Conservation Measures Partnership, developers of the open standards for the practice of conservation framework, already show a commitment to investing in creating more usable products, with the development of their user-friendly "cookbook" version of the framework (CMP 2022) and could greatly benefit from working with Designers to Design more user-centered material.

## Ideating

The ideation phase of Design thinking is intended to broaden the range of possible solutions through a combination of divergent thinking and a complimentary filtering process for converging on one or two ideas. Broadening the range of potential solutions through ideation has two major benefits: a larger space of potentially functional, not just optimal, solutions is explored (Munzner 2014) and the ability to produce potentially major innovations (Liedtka 2018). This ideation phase could provide new ways to approach steps of systematic conservation planning, which is a framework to systematically plan so that protected areas remain representative of the biodiversity they were designed to protect and provide for the persistence of biodiversity targets (Margules \& Pressey 2000). The second step in this framework could be setting quantitative
goals for biodiversity targets. Margules and Pressey (2000) admit these goals may be subjective, but the benefit of having a target outweighs any downside to subjectivity.

Here, Designers and conservation practitioners could create a new approach to brainstorming to set these goals. A project planning group could brainstorm possible biological targets, making sure to include area and biodiversity, purposely removing the constraints of possibility while generating ideas. This is yet another point of synergy for a Design and conservation practice approach. Whereas Designers have methods to filter such as idea most likely to succeed or idea most likely to delight (Stanford d.school 2019), conservation practice approaches lean more heavily on scientifically documented evidence. Not only can Designers in a multidisciplinary project use an additional scientific filtering criterion, such as idea with the most empirical evidence of success, but a combined filter approach could include the more traditional Design criteria. Accordingly, ideas generated in the brainstorming process could be filtered according to the criteria of biologically possible, idea most likely to delight, and most affordable. This could allow bolder ideas to be taken forward to a prototyping phase if the full process of Design thinking is in use, where new possibilities for accomplishing the ideas might be considered (importantly, before any official targets are set). In addition, the use of a scientific filtering criteria can give credibility to the Design, which is especially important in urgent conservation action.

## Prototyping and Testing

Prototyping and testing before a system is implemented to see if it would be successful is a significant departure from some of the long cycles of iteration that have been proposed in conservation practice. Long iterative cycles in conservation practice systems, such as adaptive
management, are likely to not lead to iterative improvements or changes as intended because once organizations have invested in an effort, changing that effort can be seen as an abandonment of an investment (Williams \& Brown 2014). However, Design thinking condenses much of this iteration to before the project is implemented on the ground, still retaining the important testing step to ensure feasibility, however.

There are many potential areas for innovation between Design and conservation practice when it comes to prototyping and testing. For example, theoretical ecological models and simulated data can provide environments to explore changes on multiple timelines relevant for conservation, which can be used as a form of prototyping for conservation practice that does not require any risk associated with implementation. In addition, although they are not described with the word "prototyping," there are already prototyping methods in use in conservation practice. For instance, a results chain analysis (Margoluis et al. 2013), is a prototyping method where a conservation practitioner draws a diagram of the assumed links between a conservation action and the desired goals of the action. A theory of change analysis is another prototyping approach where a conservation practitioner writes out the chain of events and assumptions that they think create a desired result to understand the assumptions and potential real-world results of the action. Results chain or theory of change analyses, as well as other prototyping methods already in use in conservation practice can be adapted to include additional testing methods from Design thinking. Finally, the simulations I present to test the goal efficient monitoring GEM system I present in Chapters 1 and 2 of this dissertation are in many ways a prototype and the different scenarios that were run are analogous to testing.

## THE POTENTIAL FOR DESIGN IN CONSERVATION PRACTICE

Access to the information of conservation practice can be further Designed. For the conservation practice frameworks and processes to be maximally effective they should have a version that is accessible and understandable for a non-scientific audience (beyond the scientific literature which is important for documentation and theoretical advances in the field). However, rather than assume what form this would best be accomplished with before the Design process, a Designer would identify a user, interview them, and create and refine a problem statement before any potential designs were created. For example, a Designer might identify a small group of government employees at a land management agency as users of conservation practice frameworks. After conducting empathy interviews with employees that represent that user group, the Designer might define the problem as follows (name used for illustrative purposes): "Team X needs a way to update their 10 -year management plan to provide and maintain for biodiversity and stay within legal requirements, but only has access to one full time staff for 3 months to accomplish that. They do not understand the difference in scope or application of the conservation practice frameworks, but would like to use them because they are scientifically defensible approaches and they are required to use the best available science." This may get further refined to: "provide a clear way to choose between conservation practice frameworks based on the applicability to biodiversity goals, the number of people required to execute it, and the ratio of planning time to implementation". The Designer then might ideate through brainstorming ways to present this information. After a brainstorming and filtering session that resulted in selection of visual Designs, the Designer would prototype a system that might look like Figure 3-2.

Open standards for the practice of conservation


Evidence-based practice


Strategic foresight


Figure 3-2) A visual design that could result from a Design thinking process used to provide a way for practitioners to decide what conservation practice frameworks to use based on the criteria important to the user. Biodiversity is represented with the symbol on the left (hypothetical qualitative comparisons among the frameworks are listed). The symbol on the right represents the team members required for the full use of the framework (hypothetical numbers are listed). The hypothetical balance of upfront planning time (shown in blue) relative to implementation time (shown in yellow) is also listed.
With a few rounds of testing this Design with Team $X$ and other employees, the Designer might
then work with the government agency, conservation practitioners, and conservation scientists to
Design this visual tool for the government agency users. This is a fictional example with fictional metrics, but it is meant to illustrate the how a Designer might help to translate complex conservation practice information into a usable format. The Designer would help to create

Designs that bring together the best available science and user needs.

## LARGE-SCALE DESIGN OF CONSERVATION PRACTICE

We see many potential avenues for Designers to use principles of Design thinking to innovate within existing conservation practice approaches. However, we also see the possibility of using Design on a larger scale to create new conservation practice systems. We illustrate this with an example for Canada lynx (Lynx canadensis) monitoring in the US Northern Rocky Mountains. We use a cycle of common steps in active rare species management for the species that involves protection, through laws or policies, monitoring, analysis, knowledge and an eventual update and recycle through the system (Figure 3-3).

The first step in applying Design thinking to this process could be to

Therefore, one might define the purpose as maintaining breeding potential of lynx in the


Figure 3-3) A simplified representation of a system of information flow for active rare species management by an agency.
area of management (using goal efficient monitoring [GEM] population state criteria presented in Chapter 2). This could then lead to an exercise of mapping stakeholders in this process, including natural resource managers, research and monitoring scientists, as well as the lynx. The next step would then be to narrow the user groups to the natural resource managers who will work most directly with this system and the research and monitoring scientists who advise or construct the population monitoring for the species. Empathy interviews with these users could
uncover key barriers in communication or understanding about how information is used or created. For example, a practitioner reading a technical monitoring report that covers the past five years of monitoring data may not know how to interpret what significant regional trends mean for their smaller area of interest. This might highlight a lack of reality in the way the system is conceived and illuminate the fact that the arrows are undefined processes that result in long timelines, confusion, and lack of the right product arriving at the next step. This could lead to the Designer identifying users at each step and previously undefined users in the interim steps represented by the arrows. This process could lead to an additional iteration through defining the problem, mapping stakeholders, and interviewing a broader group of users.

The Designer then might ideate with an interdisciplinary team in a stepwise fashion, starting with the main steps, to determine potential plans to build each step effectively. Separately, the team might ideate for how to build the steps of the connecting arrows most effectively and at the end filter them according to a mix of Design criteria, like most breakthrough idea, and criteria related to the steps, including most likely to achieve information goals for the next step. With the interim step ideas narrowed, the team could run through another round of filtering with the main steps and the filtered connecting steps. This multi-tiered ideation and filtering process could allow for creativity and flexibility in generating ideas to effectively build the entire system, without the team getting distracted in the complexity and scope of the entire system.

After the ideation phase a few ideas for the design of the entire system would move forward to the prototyping phases. These could involve a series of simulations of lynx populations, which could build on the work presented with GEM, and the monitoring data that might come from the populations. Simulating the other steps in the process, including the flow of
information but also the change of protection status or change in monitoring, could not only be useful to understand future conditions, it could help to identify if and how there were appropriate mechanisms for them to change within the system to occur. Different scenarios related to protection (which can be broadly defined to also include management) could be adjusted according to different risk tolerances, protection levels, monitoring funding, or other factors. More user-centered prototyping could be carried out for the steps and arrows, including story boards, experience prototyping, scenario description swim lanes to describe how a team might interact with information at certain steps. Because the purpose would be to keep breeding potential of lynx in the landscape of interest, this could be determined through the system-wide simulation, separate from the usability of each step. However, the simulation could be modified to see what decreasing usability in each step would do to the entire system to achieve the goal of maintaining breeding potential. Because there is biological processes occurring in this process, it is possible that the system would change regardless. But with a biological processes built into the simulation, the sensitivity of that metric to the entire system could be test.

Importantly, this Design process linking the biology and conservation of the species, tested with simulation and user-centered prototyping, could be transparently described and documented. Finally, a full plan for the system with the design processes well documented, could be presented and implemented.

## WHAT MIGHT A FIELD OF CONSERVATION DESIGN LOOK LIKE?

We have presented a broad overview of just a few ways in which we envision a Designer using Design thinking could add value to and innovate with and expand conservation practice.

However, we envision a broader potential future of this idea as a field of "Conservation Design"
where the fields of Design, conservation practice, and conservation biology can all grow together. We see tremendous need not only for the innovation and efficiency brought by Design, but for the role that a conservation Designer could play. In conservation practice many have recognized the need for a boundary spanning positions (e.g., Cook et al. 2013; Enquist et al. 2017). There have been multiple proposals for who the boundary spanner should be and their role. Some have proposed that scientists function in this role (Ruckelshaus et al. 2020), but others have noted that the role truly remains undefined and there is a lack of ownership of conducting the overall process of conservation practice (Carr et al. 2017). This lack of defined roles potentially leaves the crucial connecting steps (i.e., the arrows in all the cycles) and the functioning of the entire system as a whole almost always undesigned (there has been no one single role to design it). Having a conservation Designer in the role of a boundary spanner but who actively Designs conservation practice action could solve these issues. A Designer in the role of Designing conservation practice system would ensure not only that all arrows and steps work together, but that each process is built for specific users; a Designer is invested in the functioning of the solution rather than the work underpinning the solution (i.e., conservation biologist), and is a professional trained to recognize, understand, and design with knowledge from users and stakeholders of a product. Professional Designers are expert planners to achieve ideas. In addition, there is growing recognition that Designers can play more collaborative roles that facilitate collaborative Designing (Sanders \& Stappers 2008).

As a discipline, we would envision research in conservation Design that innovates with the research in Design and conservation biology and practice. We have highlighted a few places where we see possibilities, including new approaches to ideating for conservation, designing conservation practice framework operation, and entirely new ways to design conservation
practice. We envision students of Conservation Design trained in both Design and conservation biology, and practitioners with the ability to work as a Designer or biologist. Together, these disciplines could innovate test long-term conservation solutions, envisioned with the rigor of science and creativity of Design.

## THE FUTURE

We hope this is the start of new discussions and collaborations between Designers of all disciplines, conservation biologists, conservation practitioners, and stakeholders who are involved in conservation. We invite potential collaborators to get in touch because we feel we must approach the use of Design thinking in conservation as both Designers and scientists: like Designers, we must actively Design and build, not just theorize about Design, and like scientists, we must document if and how it is successful. We are confident that with optimism and creativity, we can reimagine the future of conservation.

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| Approach | Visual | Does the approach include on the ground action? | Targeted user or user group | Benefits of a Designer in the approach | Areas of innovation with Design |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Salafsky et al. 2019 |  |  |  |  |  |
| Systematic conservation planning |  |  |  |  |  |
| A framework for structured, systematic conservation planning to ensure that protected areas remain representative and provide for the persistence of biodiversity targets |  | Yes, broadscale on the ground action | Governments or land managers | Build connections and information delivery systems for monitoring feedback that can be easily updated and accessed by the team responsible for management | Develop novel brainstorming processes to set goals (step 2 ) and filtering criteria that is evidence, resource, and theoretically based |

Margules and
Pressey 2000



| Approach |
| :--- | :--- | :--- |


| Approach |
| :--- | :--- | :--- | :--- |

Table 3-1) An example of how Design may compliment and innovate with some of the most widely used existing conservation practice frameworks and processes.


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[^1]:    1 Plan to submit to Ecological Applications as Golding JD, KS McKelvey, MK Schwartz, JJ Millspaugh, JS Sanderlin, and SD Jackson. Goal efficient monitoring: an approach to monitoring as information changes.

[^2]:    ${ }^{2}$ Planned: submit to Conservation Biology

[^3]:    ${ }^{3}$ Plan to submit to Biological Conservation as Golding JD, MK Schwartz, and S Ishizaki. Conservation design.

