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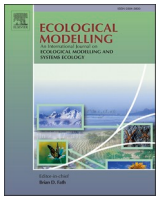

Monitoring with multiple goals: Bayesian methods for changing objectives

Jessie D. Golding [a,b,c,*], Kevin S. McKelvey [b], Michael K. Schwartz [b], Joshua J. Millspaugh [c,d], Jamie S. Sanderlin [e], Scott D. Jackson [f]

[a] University of Arizona, School of Natural Resources and the Environment, 1064 E Lowell St, Tucson, AZ 85721, United States
[b] US. Forest Service, National Genomics Center for Wildlife and Fish Conservation, Rocky Mountain Research Station, 800 E. Beckwith Ave., Missoula, MT 59801, United States
[c] University of Montana, 32 Campus Drive, Missoula, MT 59812, United States
[d] Department of Environmental Biology, State University of New York College of Environmental Science and Forestry, Syracuse, NY 13210, United States
[e] US. Forest Service, Rocky Mountain Research Station, 2500 South Pine Knoll Drive, Flagstaff, AZ 86001, United States
[f] US. Forest Service, Northern Region, 26 Fort Missoula Rd, Missoula, MT 59804, United States

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ABSTRACT

Long-term monitoring is essential for wildlife conservation. Most wildlife population attributes require long-term monitoring to evaluate. Over the time for attributes to resolve through monitoring, however, information needs change. Existing frameworks to accommodate information need changes, such as adaptive monitoring and management, are built for large-scale, programmatic changes. Often, smaller, rapid changes are necessary. Fortunately, information needs can change predictably in wildlife monitoring, even when little is known about populations. Predictable changes include the desire to answer: 1) is the species present?; 2) are multiple individuals present?; 3) is breeding occurring?. We suggest long-term monitoring can accommodate these changes. We propose Goal Efficient Monitoring (GEM), an approach that uses a Bayesian integrated population model (BIPM) to accommodate changing information needs through: a BIPM that links population state changes (e.g., present, multiple individuals present) to population dynamics (e.g., abundance, demographic rates); and sampling rules to allocate effort observation effort based on current knowledge. To test the efficacy of a GEM approach, we ask two research questions: 1) can implementing a GEM approach provide robust population estimates?; and 2) do GEM sampling rules in multiple long-term monitoring settings (i.e., population sizes) accommodate changing questions while providing continual, reliable population inference? To answer these questions, we built a BIPM and conducted a simulation study for a rare species in the US, Canada lynx (*Lynx canadensis*). We simulated lynx populations under five different starting conditions and simulated a GEM approach (10 years of simulated observations with GEM sampling rules), then used our BIPM model to produce estimates and predictions. In 93 % of simulations, 95 % credible intervals for BIMP estimates contained the true value for all biological (abundance of all sexes and age classes, birth events, survival, state transition probabilities) and observation variables (detection probabilities). We demonstrate how a GEM approach can provide reliable long-term inference while being responsive to shifting information needs.

1. Introduction

Long-term monitoring of wildlife populations is essential for understanding and effectively conserving wildlife populations (Holling and Walters, 1978; Yoccoz 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 Johnston, 2017). Monitoring can inform activities ranging from local wildlife management (Cook et al., 2010, 2012) to achieving large global conservation targets, such as those recommended by the Convention on Biological Diversity (Laikre et al., 2010; Buckland and Johnston, 2017). In a setting of limited funding and given the significant logistic and financial investment required for most wildlife monitoring (Field et al., 2004; Reynolds et al., 2016), it is important that monitoring is as useful (Runge et al., 2011) and cost effective relative to information gained (McDonald-Madden et al., 2010) as possible.

Long-term wildlife monitoring has been criticized as being difficult to achieve and unable to answer questions that it was originally designed to address (Legg and Nagy, 2006). It has also been disparaged

* Corresponding author.
E-mail address: jessiegolding@arizona.edu (J.D. Golding).

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for having ill-defined information goals (Nichols and Williams, 2006), as well as lack of focus when there are too many information goals (Lindenmayer and Likens, 2009). In this manuscript we review a common information challenge that we believe is persistently present in many wildlife monitoring settings and likely to become increasingly challenging in the face of landscape and ecological change: monitoring when new information arises as learning occurs. We then discuss where gaps in proposed solutions for this problem remain in wildlife monitoring. Finally, we propose and demonstrate a new monitoring framework to overcome some of the challenges in addressing changing questions that are not addressed in existing long-term monitoring approaches.

1.1. Monitoring when learning leads to new questions

Long-term monitoring frequently leads to new questions that require additional monitoring as monitoring reveals previously unknown information. In times of rapid environmental change, it is likely that this pattern in monitoring will continue to increase (e.g., Conroy et al., 2011; Descamps et al., 2017). Post hoc approaches to changing questions in monitoring can result in inefficient monitoring programs that lack the ability to provide inference about the change that is being monitored (Legg and Nagy, 2006). Monitoring frameworks that incorporate change, such as adaptive monitoring or adaptive management, provide more consistent ways to accommodate new questions as they arise in monitoring programs. Adaptive monitoring is a framework that provides steps and guidance on how to incorporate new questions in monitoring (Lindenmeyer and Likens, 2009) and adaptive management is a management and monitoring framework to implement management activities and use hypothesis testing to generate knowledge about an ecological system (Holling and Walters, 1978). Adaptive monitoring and adaptive management both emphasize programmatic changes to accommodate new questions as they arise in monitoring programs, but approach the topic differently; changes in monitoring in adaptive monitoring are associated with learning from monitoring after programmatic information reviews, whereas changes in monitoring in adaptive management are associated with achieving a specific knowledge goal linked to management. However, both frameworks outline changes in monitoring as something that happens after data collection, analysis, and program review (Lindenmayer et al., 2011; Murphy and Weiland, 2014). Each approach is discussed briefly below.

1.1.1. Monitoring wildlife when questions change using adaptive frameworks

Adaptive monitoring is designed to accommodate new questions as they arise from monitoring through tractable processes. Adaptive monitoring accommodates new questions using an iterative cycle of question setting, design, data collection, and analysis (Lindenmeyer and Likens, 2009). For example, in Booderee National Park in Australia, an existing monitoring program showed an invasion of bitou bush (*Chrysanthemoides monilifera*). After a thorough review of monitoring information, the following steps were taken. To determine if adopting new monitoring to understand the impacts of bitou bush was feasible, a thorough analysis of feasibility was conducted, followed by an additional statistical analysis to calibrate new data collection, followed by a workshop integrating questions and statistical models, and concluding with implementation of additional monitoring (Lindenmayer et al., 2011). Thus, in adaptive monitoring, the adoption of new questions associated with learning happens after data has been analyzed and multiple levels of programmatic review occur.

In adaptive management, new questions that arise as a result of learning in long-term monitoring represent learning about the ecological processes within a system (Holling and Walters, 1978). Like adaptive monitoring, new questions occur after programmatic review (Murphy and Weiland, 2014; e.g., Figs. 1 and 2 in Murphy and Weiland, 2014). For example, adaptive harvest management and associated monitoring for mallard ducks (*Anas platyrhynchos*) has been used to examine model weights for models that explain population dynamics and set harvest limits in North America. After twenty years of harvest data collection and regulations set by that data, the monitoring program generated solid evidence from the models that were tested to suggest that new questions related to more mechanistic models and potentially different monitoring should occur (Johnson et al., 2015). Similar to adaptive monitoring, monitoring to accommodate new questions usually occurs at the end of multiple management, monitoring and analysis cycles. However, there is confusion on adaptive management in practice among researchers, policy makers, and resource managers (Westgate et al., 2013).

1.1.2. Existing approaches and challenges in wildlife monitoring when questions change

While adaptive monitoring and management can provide effective guidance to accommodate learning and new monitoring on a programmatic level, they may not work in some wildlife monitoring settings for several reasons. Learning and changing monitoring questions in many wildlife monitoring settings may occur on more rapid and iterative timescales than the cycles that adaptive monitoring and management frameworks are designed to accommodate. Frequently, learning may occur long before data are analyzed or monitoring programs are reviewed in any official capacity, both of which can be slow due to time and resource limitations (Gibbs et al., 1999; McDonald-Madden et al., 2010). For example, consider a rare species that is generally absent through much of an area of interest: the California spotted owl (*Strix occidentalis*) in the central Sierra Nevada of the USA, a rugged forested mountainous area. For this species, the first monitoring question is typically: are there any present (Mackenzie et al., 2009)? Because the organism exhibits high rates of local colonization and extinction, it is critical that a monitoring effort answer the question of presence as efficiently as possible. However, once the organism is found the question of presence is immediately of less interest than questions of the potential for reproduction (i.e., presence of a breeding pair) and a monitoring design that exclusively asks a presence question will be almost instantly irrelevant. Knowledge of the species' presence leads to a logical next question conditioned on its established presence: is there a breeding pair present? Knowledge of breeding suggests the presence of a population, which will lead to a subsequent question: how many individuals are present? Although there are additional questions that may arise on different time scales, the initial gathering of information about wildlife populations usually proceeds through predictably changing questions that change with learning: 1) is the species present? 2) is there a breeding pair present? 3) Is breeding occurring? (Mackenzie et al., 2009). In different contexts, these same questions may appear in monitoring of invasive species (Guillera-Arroita et al., 2014), reintroductions (Nichols and Armstrong, 2012), or populations introduced for biological control (Fauvergue et al., 2012). For example, in a population of reintroduced fishers (*Pekania pennanti*) that started with 24 females and 16 males in northern California, managers and scientists monitored the population for 8 years after the reintroduction with multiple questions about the population, including if population growth and reproduction were occurring, as well as rates of survival (Green et al., 2022). Other authors have noted the need in wildlife monitoring to use different data sources to ask different questions to understand different aspects of population changes (e.g., Katzner et al., 2007; Descamps et al., 2017; Marcot et al., 2021).

As these examples illustrate, in many cases, questions around learning about populations can be somewhat predictable. Adaptive monitoring and management do not explicitly account for elements of predictable changes in questions about populations, nor is that their intended purpose; these frameworks aim to offer broad guidelines for learning and decision making (in the case of adaptive management) through monitoring. Other strategies to flexibly understand wildlife populations in monitoring use integration of multiple data sources (also

referred to as integrated modeling, data assimilation, data fusion, integrated analysis, inverse modeling, or ensemble estimation) to understand more about populations (Zipkin et al., 2021). For example, one data integration model type using spatial information of wildlife populations focuses on species' distribution models (SDMs), combining structured data from monitoring programs with unstructured data (e.g., Pacifici et al., 2017; Miller et al., 2019). Data integration SDM methods harness the strengths of different data structures while balancing data weaknesses to understand where and why species occur across their ranges, although these methods are not without challenges (Zipkin et al., 2021). In these and other data integration examples, data integration for learning as a result of new questions from monitoring occurs post hoc: data have already been collected in these cases. However, some data integration analyses may be difficult to interpret for those without modeling expertise, which may present barriers to widespread use (Dobson et al., 2020). Therefore, data integration approaches are useful in many settings, particularly existing programs with multiple data sources and modeling expertise, but do not address issues of how to construct monitoring programs with predictable changes in questions built in at the onset.

1.2. A response to existing challenges – goal efficient monitoring

Inspired by the challenges of monitoring wildlife populations are not fully addressed in current literature, we suggest that a monitoring approach should accomplish the following goals:

1) Answer pre-identified predictable knowledge questions that may arise with learning;
2) Provide flexibility in switching monitoring parameters of interest in rapid, but tractable, ways that do not require full programmatic review or change;
3) Provide continuous monitoring data streams that are flexible to changes in populations.

To operationalize a system that achieves these goals, we developed a monitoring framework that we call goal efficient monitoring (GEM). We call the approach GEM because it is designed to rapidly (i.e., within short time periods in a single monitoring program) achieve population information goals of the monitoring program without requiring major changes in monitoring implementation structure by connecting population dynamics to a flexible observation processes and biological states with associated transition probabilities. In this manuscript, we build and test a GEM approach by developing a series of monitoring questions, identifying appropriate population parameters to answer these questions, developing a modeling framework that links the monitoring questions and population parameters, simulating data, and testing using the simulated data to test the GEM approach in multiple monitoring scenarios.

The idea that long-term wildlife monitoring can be accomplished as a single effort that includes changing questions collected as a continuous stream over time with multiple data types is central to the concept of GEM. We suggest that another data integration model type, a Bayesian integrated population model (BIPM) (Schaub and Abadi, 2011), provides a framework that can accommodate changing data needs and questions. Importantly, BIPMs can be updated in a structured and predictable manner, but also provide flexibility for additional learning about populations due to the latent parameters tracked with the population model. BIPMs 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; Zipkin and Saunders, 2018). As a result, BIPMs are frequently being used for wildlife monitoring (e.g., Tempel et al., 2014, Ahrestani et al., 2017). To date most BIPMs, even when used for monitoring, focus on improving population parameter estimates through data integration, rather than their ability to provide a monitoring framework and mechanistic model that allows for flexibility in questions and data collection.

A GEM approach accomplishes the three monitoring goals outlined above through processes of building and implementation: building a BIPM that includes population states of interest linked to a population model (building) and iteratively implementing an observation process based on sampling rules defined using the population states (implementation) (Fig. 1). Much of the work to allow for flexibility in a GEM approach occurs in the building phase. To identify predictable knowledge questions of interest for a population (goal #1), a GEM approach first involves identifying the population of interest, followed by identifying population states of biological and management interest (e.g., presence, breeding) (Fig. 1 steps 1 and 2). These population states represent the foundation of the predictable knowledge questions. To ensure that these population states are biologically meaningful (i.e., can be appropriately linked to underlying population processes), the next step is to build the biological model of the population and write out equations of the state changes (transitions) that can occur using the variables in the biological model (Fig. 1 steps 3 and 4). Next, define sampling rules based on the knowledge questions that might occur when observing the population states (Fig. 1 step 5). Next, construct a BIPM to ensure that there is flexibility in the ability to switch monitoring parameters of interest as knowledge or populations change (goal #2) and provide a monitoring program that provides continuous data streams as population sizes fluctuate (goal # 3). A BIPM built for GEM provides estimates for all variables and population states included in the model, even those with no direct data (latent variables), and links the observation process with sampling rules outlined to the biological model (Fig. 1 step 6), which will inform the state transition predictions.

Implementation of a GEM approach starts with assessing the existing population state knowledge (Fig. 1 step 7). Once that is complete, the GEM sampling rules and observation processes dictate what type of data will be collected based on what is known. Data collected in the field can then be used to produce estimates of all population variables in the BIPM, as well as population state predictions (goals #2 and #3) for the next time period (Fig. 1 steps 8–11). Because we adapt language from both modeling and monitoring literature, as well as conservation practice, we have assembled a glossary of terms that we use throughout this manuscript to describe the GEM approach (Appendix A).

We conceptualized the GEM approach in response to addressing monitoring goals that were based on real-world monitoring challenges that we have observed. However, it is important to understand the efficacy of the GEM approach as both a concept and through implementation, ideally through a variety of investigations, including scenario exploration and real-world application. We were interested in the efficacy of the GEM approach in multiple population and monitoring information settings (e.g., a protected population is monitored as it recovers, little is known about a species in a location). Therefore, our goal was to answer two research questions to understand the efficacy of the GEM approach: 1) can implementing a GEM approach provide robust population estimates?; and 2) do GEM sampling rules in multiple long-term monitoring settings (i.e., population sizes) accommodate changing questions while providing continual, reliable population inference? Because of the broad nature of these questions, we chose to conduct a simulation study to answer these questions, as real-world data collection for all conditions was unrealistic.

We selected the Canada lynx (*Lynx canadensis*) in the northern Rocky Mountains of the USA as an example species to use for our simulation study because it represents multiple population monitoring challenges. Canada lynx have been listed as threatened under the ESA since 2000 (USFWS, 2000) in the USA and in much of its range within the USA the species occurs in small populations that fluctuate over time (McKelvey, 1999), so questions about the species frequently change. Canada lynx are also useful model organisms for a GEM approach because there are specific regulations related to the presence of different population states on the landscape. For example, if a National Forest is designated as

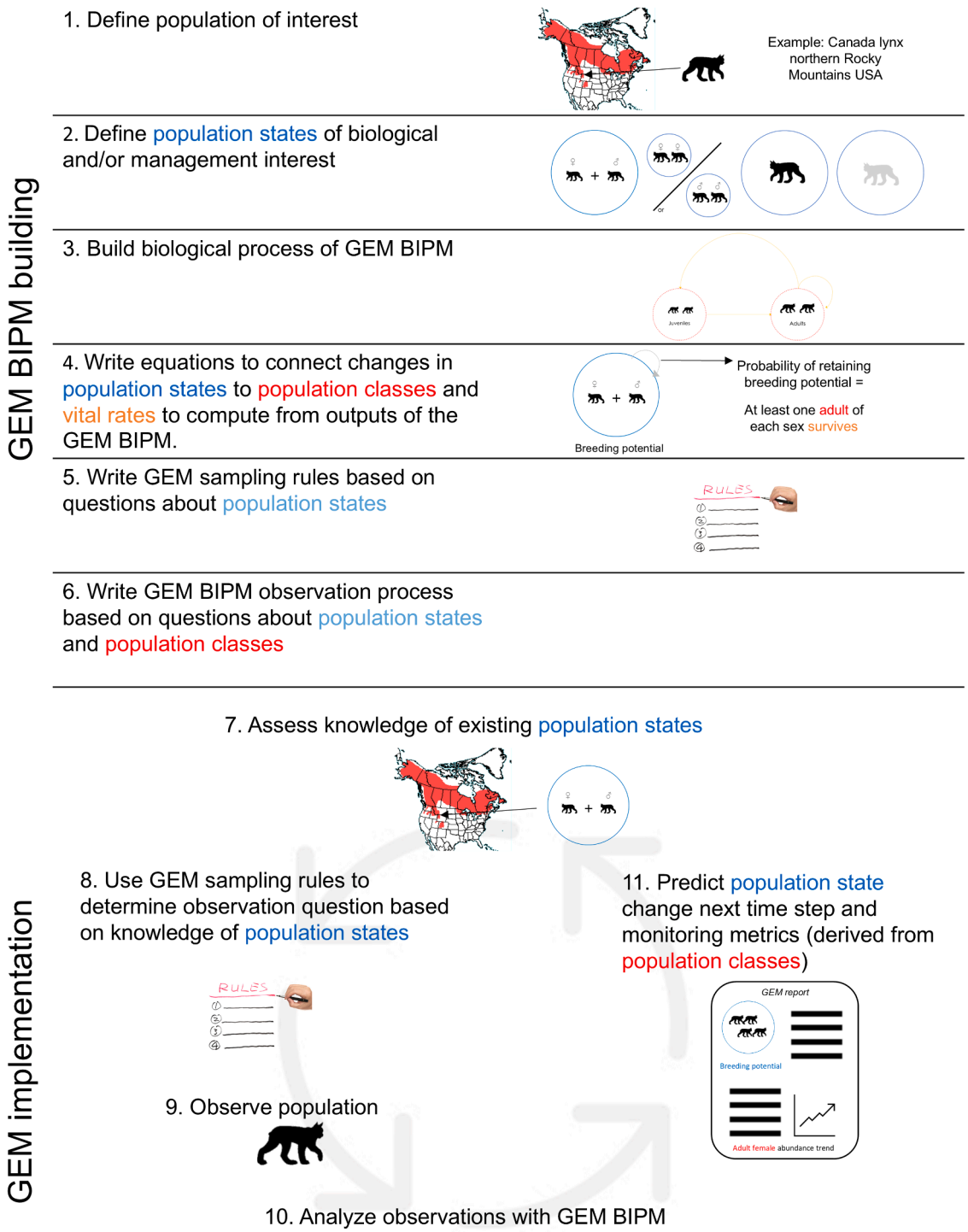

Fig. 1. An overview of the Goal Efficient Monitoring (GEM) approach using an example with Canada lynx (*Lynx canadensis*) in the northern Rocky Mountains of the USA. The linear steps for the Bayesian Integrated Population Model (BIPM) building are described in steps 1 through 6. The iterative steps for the on-the-ground implementation of a GEM approach are described in steps 7 through 11, which are meant to be repeated over time. Blue is used to represent GEM population states (breeding potential, isolated individuals, single isolated individual, and not present), red is used to represent the biological population classes, and orange is used to represent the vital rates of the biological population.

unoccupied by Canada lynx the detection of a population state (such as a female with kittens) alters which land management regulations are applied (USFS, 2007). In addition, surveys for Canada lynx typically employ a variety of non-invasive methods that provide information at multiple resolutions that may be relevant for different population sizes; they include winter track surveys 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 snow tracks (Franklin et al., 2019). Although we do not cover all scenarios in which a GEM may be applied for Canada lynx, our goal was to test and demonstrate the utility of a GEM approach through scenarios that represent different wildlife monitoring challenges.

2. Methods

To answer our two research questions, we conducted a series of steps to build, implement, and evaluate a GEM approach for Canada lynx. Our building steps included building a BIPM and creating GEM sampling rules for Canada lynx. Our implementation steps included simulating Canada lynx populations with the biological process describe in the BIPM over 10 years, simulating observations of those simulated Canada lynx populations with GEM sampling rules, and creating predictions and estimates with the BIPM using the simulated observations as our model data. Finally, our evaluation steps included assessing BIPM estimates and predictions in comparison to known (i.e., simulated) values of the Canada lynx populations (Fig. 2). Each step of this process is described in more detail below.

2.1. Building a GEM approach for Canada lynx

To build a BIPM for a GEM approach to monitor Canada lynx, we created an extension of a BIPM to include a multistate model with the four population states of interest based on previous monitoring priorities described in Golding et al. (2018) as follows;

- breeding potential;
- isolated individuals of single sex;
- isolated individual;
- and not present (Fig. 3).

To build the population model within the BIPM, we used a formulation that included 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. We then created sampling rules to observe each GEM population state based on what was known

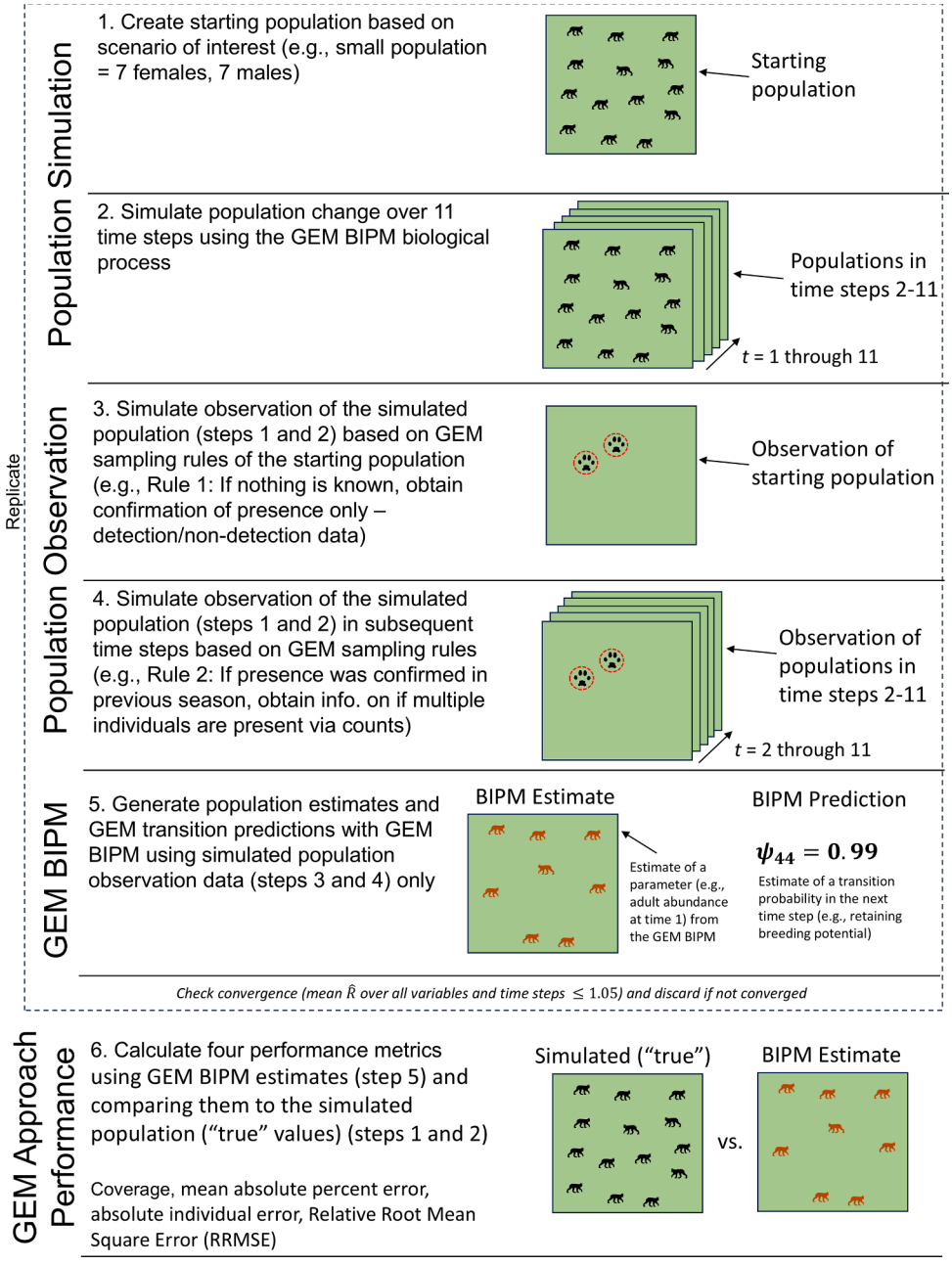

Fig. 2. The process for building and testing a Goal Efficient Monitoring (GEM) approach through simulation undertaken in this analysis.

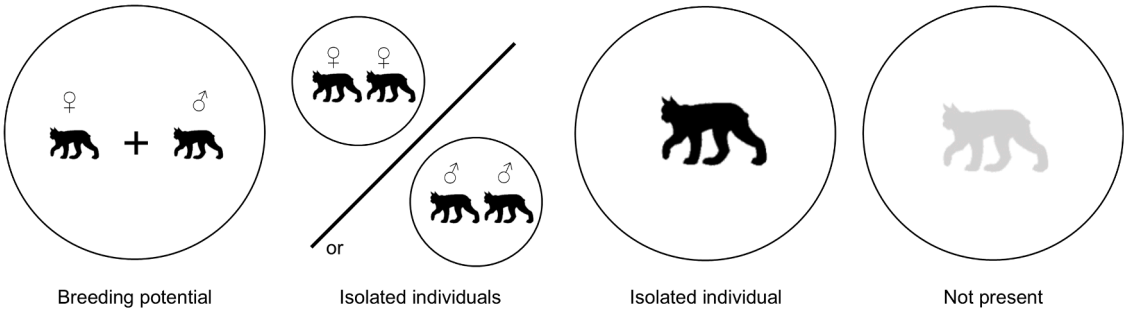

Fig. 3. Symbols for four Goal Efficient Monitoring (GEM) states of interest for Canada lynx (*Lynx canadensis*) (from left to right): breeding potential (one or more females and one or more males) (State 4), isolated individuals (either two or more females or two or more males) (State 3), single isolated individual (State 2), and not present (State 1). GEM states are represented as solid circles.

from the previous time step. Finally, we built the observation process of the BIPM to connect the sampling rules to the population classes. In addition, we defined the likelihood of a change in GEM population state given data and model parameters, represented as transition probabilities for the next time step using the abundance of adult females and males, as well as survival.

We used the Bayesian model terms "biological process" to refer to the portion of the GEM BIPM that describes the dynamics of the population of interest (i.e., states, abundance, and transitions between states over time driven by population dynamics) and "observation process" to refer to portion of the GEM BIPM that describes the process of conducting observations of the population (i.e., surveys to detect individuals, sexes, or states). In addition, we distinguished between BIPM parameters as *estimated*, referring to demographic parameters directly estimated by the BIPM, or *derived,* referring to parameters calculated from *estimated* parameters (e.g., population states), and *predicted*, referring to parameters predicted into future time (e.g., population state transitions). Below we describe our BIPM model.

2.1.1. BIPM biological process

Because both female and male abundance are important for the probability of reproduction in a small population, we modeled each separately. We modeled female, $N_{f,t}$, and male, $N_{m,t}$, abundance for each population at initial time t as Poisson random variables with an average group size, λ (Eqs. 1 and 2). Total individuals, N_t , were a *derived* parameter that was the sum of $N_{f,t}$ and $N_{m,t}$ Eq. (3). We calculated a *derived* population occupancy term for time t, $z1_t$, and assigned occupancy if $N_t > 0$, or unoccupied if $N_t = 0$ Eq. (4). Additionally, we calculated the *derived* GEM state (4=breeding potential, 3=isolated individuals, 2=isolated individual, and 1=not present) for time t, $z2_t$, from the composition of females and males Eq. (5):

$$N_{f,t}|\lambda \sim Poisson\ (\lambda) \tag{1}$$

$$N_{m,t}|\lambda \sim Poisson\ (\lambda) \tag{2}$$

$$N_t = N_{f,t} + N_{m,t} \tag{3}$$

$$z1_t|N_t = \begin{cases} 1 & N_t > 0 \\ 0 & N_t = 0 \end{cases} \tag{4}$$

$$z2_t|N_{f,t}, N_{m,t} = \begin{cases} 4 & N_{f,t} \geq 1 \text{ and } N_{m,t} \geq 1 \\ 3 & (N_{f,t} \geq 2 \text{ and } N_{m,t} = 0) \text{ or } (N_{f,t} = 0 \text{ and } N_{m,t} \geq 2) \\ 2 & (N_{f,t} = 1 \text{ and } N_{m,t} = 0) \text{ or } (N_{f,t} = 0 \text{ and } N_{m,t} = 1) \\ 1 & N_{f,t} = 0 \text{ and } N_{m,t} = 0 \end{cases} \tag{5}$$

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 state, $z2_t$, was breeding potential ($z2_t$=4), and the probability of litter production, $p.litter$, which we assumed was constant over time and populations (Eq. 6); 2) birth events, B_t, occurring, which were modeled as a Binomial random variable with the probability of success l_t with $N_{f,t}$ trials (Eq. 7); 3) and new individuals born, W_t, which was a function of the product of birth events, B_t, and a litter size, *litter size* (Eq. 8), 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 modeled as a binomial random variable with the probability of success set by a sex ratio, sr, out of the W_t trials. The number of males $W_{m,t}$ was then *derived* from the difference between the total W_t and number of females $W_{f,t}$ added to the population in time $t = 1$ (Eqs. 8a and 8b):

$$l_t|z2_t = \begin{cases} p.litter & z2_t = 4 \\ 0 & (z2_t = 3) \text{ or } (z2_t = 2) \text{ or } (z2_t = 1) \end{cases} \tag{6}$$

$$B_t|N_{f,t},\ l_t \sim Binomial\ (N_{f,t},\ l_t) \tag{7}$$

$$W_t = litter\ size * B_t \tag{8}$$

a. $W_{f,t}|W_t, sr \sim Binomial(W_t, sr)$
b. $W_{m,t} = W_t - W_{f,t}$

For time $t = 2$ (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 $S_{m,t+1}$,(Eqs. 9 and 10) plus newly added individuals from births, $W_{f,t}$ and $W_{m,t}$, surviving to $t + 1$ (Eqs. 11 and 12), all of which were modeled as binomial random variables with a probability of success s, survival, which we assumed was constant over time and age classes, and number of trials based on total individuals in that class (Fig. 4). Total surviving individuals for each sex were *derived* as sums of the number of individuals that survive in both classes (Eqs. 13 and 14):

$$S_{f,t+1}|N_{f,t},\ s \sim Binomial(N_{f,t},\ s) \tag{9}$$

$$S_{mt+1}|N_{m,t},\ s \sim Binomial(N_{m,t},\ s) \tag{10}$$

$$W_{ft+1}|W_{f,t},\ s \sim Binomial(W_{f,t},\ s) \tag{11}$$

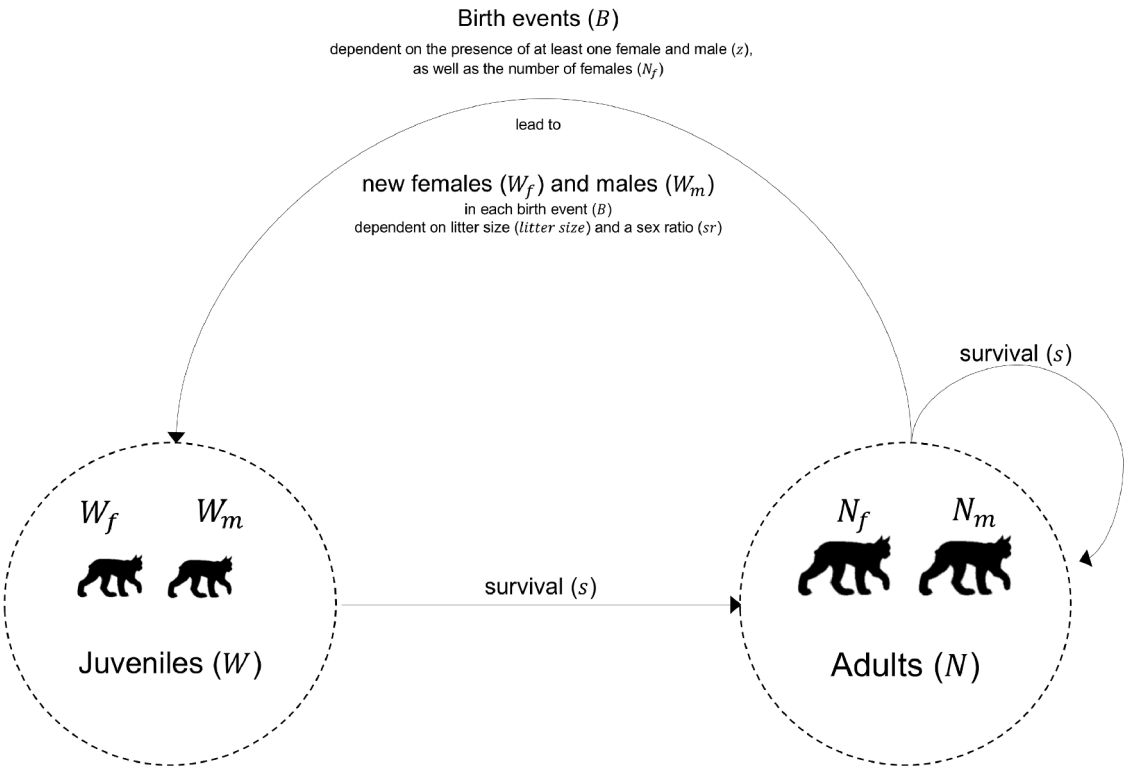

Fig. 4. The Canada lynx (*Lynx canadensis*) population model in the Bayesian Integrated Population Model (BIPM). Population classes are represented as dashed circles. The arrows represent transitions to the next time step for the population class as follows: adult females (N_f) and males (N_m) (shown as the adult class, N) stay adults (arrow from adult class back to adult class) based on a survival probability (s) and the total adults (N) present. Adults produce offspring through birth events (B) (arrow from adult class, N, to juvenile class, W), which is dependent on the presence of at least one female and at least one male ($z2$) and the number of females (N_f). Birth events lead to new individuals (W) from each birth event which are divided into female (W_f) and male (W_m) new juveniles based on a *litter size* and a sex ratio (sr). The new juveniles (W) become adults (N) in the next time step (arrow from juvenile class to adult class) based on a survival (s) probability.

$$W_{mt+1}|W_{m,t},\ s \sim Binomial(W_{m,t},\ s) \tag{12}$$

$$N_{ft+1} = S_{f,t+1} + W_{f,t+1} \tag{13}$$

$$N_{mt+1} = S_{m,t+1} + W_{m,t+1} \tag{14}$$

We linked the transition probabilities of the GEM states, $z2_t$, to the population dynamics of each time t by deriving them from the abundance values at each time step. Thus, the probability of a population transitioning between the end of a time step and the next time step was an *estimated* probability vector $\mathbf{\Psi_t}$. 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 and the reintroduction of the other sex) (Fig. 5). These dynamics, although not reflective of all population conditions, are reflected in Canada lynx populations in the US Northern Rocky Mountain Region, where individuals or small family groups persist with no immigration or emigration until they are no longer detected and presumably die (USFWS, 2017). Thus, the vector $\mathbf{\Psi_t}$ for transitioning to the GEM states in the next time step was modeled as a four-by-four matrix, with probabilities representing the probability of transitioning from the GEM state in the current time step (represented by row and the first number of the subscript) to the other GEM states in the next time step (represented by column and the second number of the subscript) step as follows:

$$\mathbf{\Psi_t} = \begin{bmatrix} 1 & 0 & 0 & 0 \\ \psi_{21} & 1-\psi_{21} & 0 & 0 \\ \psi_{31} & \psi_{32} & 1-\psi_{32}-\psi_{,31} & 0 \\ \psi_{41} & \psi_{42} & \psi_{43} & 1-\psi_{43}-\psi_{42}-\psi_{41} \end{bmatrix}$$

The transition probabilities in the matrix above are dependent on 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, $N_{f,t}$, males, $N_{m,t}$, and survival, 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 population classes, we provide the full description of transition probabilities and the binomial formulations for each possible transition below. If a population was in breeding potential (GEM state 4) it could: transition at time $t+1$ to not present (GEM state 1) based on the probability that all individuals die Eq. (15); transition to an isolated individual (GEM state 2) based on the probability that all individuals but one die Eq. (16); 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 Eq. (17); or stay in breeding potential (GEM state 4), which is the probability of the previously described probabilities not occurring Eq. (18) (Fig. 5a).

$$P(z2_{t+1}=1) = \binom{N_t}{N_t}(1-s)^{N_t} * (s)^{N_t-N_t} \tag{15}$$

$$P(z2_{t+1}=2) = \binom{N_t}{1}(1-s)^{N_t-1} * (s)^{1} \tag{16}$$

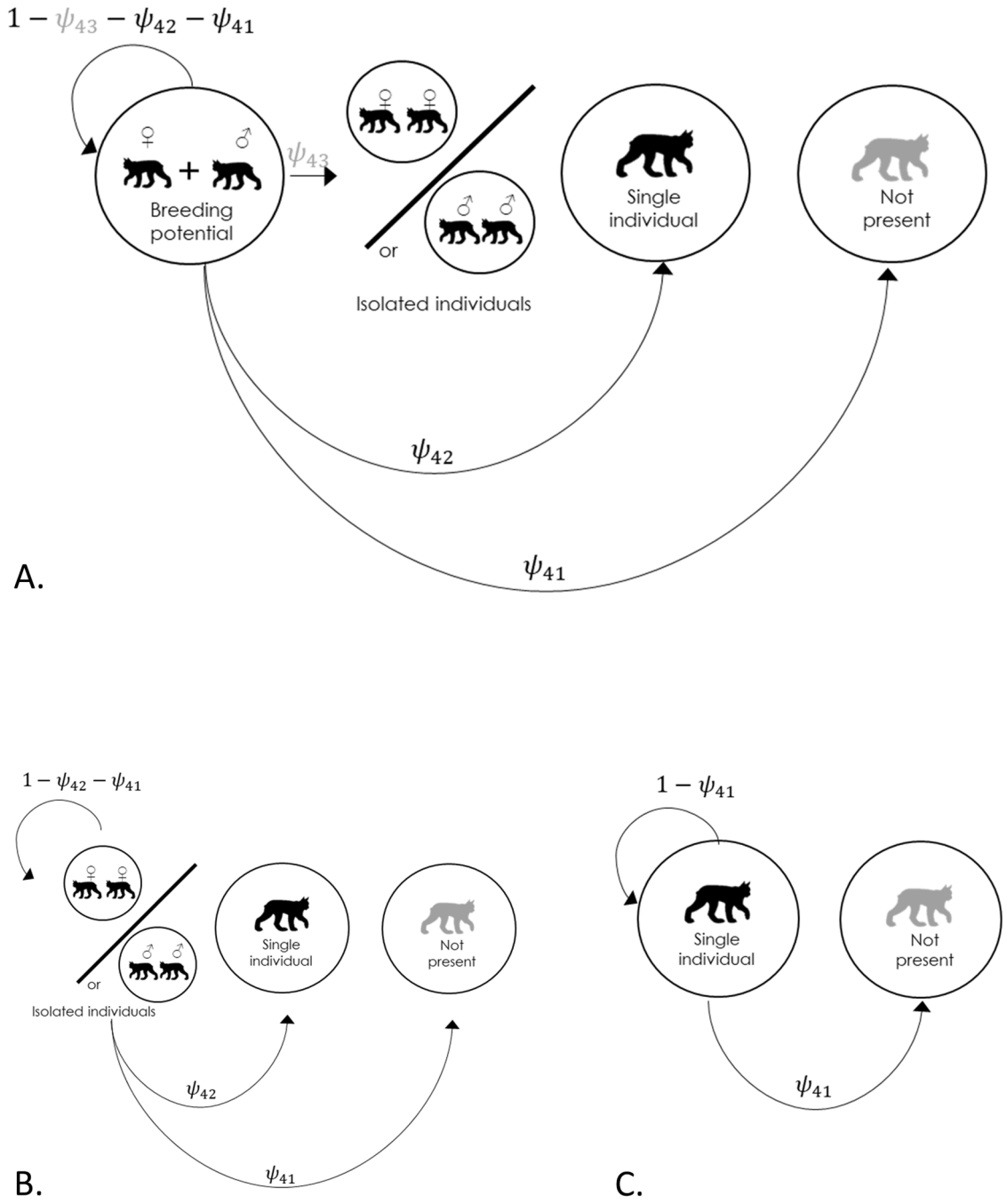

Fig. 5. An example of four Goal Efficient Monitoring (GEM) states of interest for Canada lynx (Lynx canadensis), breeding potential (one or more females and one or more males), isolated individuals (either two or more females or two or more males), single isolated individual, and not present, and their transition probabilities (ψ) within a closed population (i.e., only births and deaths lead to population change). Transitions are shown from the state in which they start: A = transitions from breeding potential (GEM state 4), B = transitions from isolated individuals (GEM state 3), C = transitions from isolated individual (GEM state 2). Note that transition probabilities, ψ, subscripts represent the starting GEM state (first number) and the ending GEM state (second number). Note that because there are multiple ways a population can exist with breeding potential (GEM state 4), in some cases the population can only transition to GEM state 2 or GEM state 1 or stay in GEM state 4. This means that the transition probability from breeding potential (one or more females and one or more males) can be 0, so it is shown in light gray.

$$P(z2_{t+1}=3)=\left(1-\left(\binom{N_{f,t}}{1}(1-s)^{N_{f,t}-1}*(s)^{1}\right)*\binom{N_{m,t}}{N_{m,t}}(1-s)^{N_{m,t}}*(s)^{N_{m,t}-N_{m,t}}\right)+\left(1-\left(\binom{N_{m,t}}{1}(1-s)^{N_{m,t}-1}*(s)^{1}\right)*\binom{N_{f,t}}{N_{f,t}}(1-s)^{N_{f,t}}*(s)^{N_{f,t}-N_{f,t}}\right) \quad (17)$$

There are multiple ways a population could exist with breeding potential (GEM state 4). In the case where breeding potential was achieved by only a single male and single female, the population (pair) could only transition to GEM state 2 or GEM state 1 or stay in GEM state 4. If this was the case, Eq. (17) could still accommodate this and would be calculated as 0.

If a population contained isolated individuals (GEM state 3) it could transition to locally extinct (GEM state 1) based on the probability that all individuals die Eq. (15), transition to isolated individual (GEM state 2) based on the probability that all but one die Eq. (16), or remain as isolated individuals (GEM state 3) Eq. (19) (Fig. 5b).

$$P(z2_{t+1}=4)=1-\left(\left(\left(1-\left(\binom{N_{f,t}}{1}(1-s)^{N_{f,t}-1}*(s)^{1}\right)*\binom{N_{m,t}}{N_{m,t}}(1-s)^{N_{m,t}}*(s)^{N_{m,t}-N_{m,t}}\right)+\left(1-\left(\binom{N_{m,t}}{1}(1-s)^{N_{m,t}-1}*(s)^{1}\right)*\binom{N_{f,t}}{N_{f,t}}(1-s)^{N_{f,t}}*(s)^{N_{f,t}-N_{f,t}}\right)\right)+\left(\binom{N_{t}}{1}(1-s)^{N_{t}-1}*(s)^{1}\right)+\left(\binom{N_{t}}{N_{t}}(1-s)^{N_{t}}*(s)^{N_{t}-N_{t}}\right)\right) \quad (18)$$

$$P(z2_{t+1}=3)=1-\left(\left(\binom{N_{t}}{1}(1-s)^{N_{t}-1}*(s)^{1}\right)+\left(\binom{N_{t}}{N_{t}}(1-s)^{N_{t}}*(s)^{N_{t}-N_{t}}\right)\right) \quad (19)$$

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 individual died Eq. (16), or remained as an isolated individual Eq. (20) (Fig. 5c).

$$P(z2_{t+1}=2)=1-\left(\binom{N_{t}}{N_{t}}(1-s)^{N_{t}}*(s)^{N_{t}-N_{t}}\right) \quad (20)$$

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

2.1.2. BIPM observation process

To accommodate changing questions related to knowledge, the observation process of a GEM approach should 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 counts of individuals from the population, and observing the distribution of females and males within the counts of individuals from the population. We considered the observation of the presence of the species 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 $z1_t$ with a probability of detection that depended on a constant individual detection probability, p, and the total number of individuals present per the Royle and Nichols (2003) formulation: $1-(1-p)^{N_t}$ (Eq. 21). We modeled the observation of counts of individuals, $y_{c,j,t}$, as a binomial random variable with individual detection probability, p, out of the total that were present, N_t (Eq. 22). 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., 2019) 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 of backtracking effort (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 (Eq. 23). 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, $y_{g,j,t}$ (Eq. 23a). 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 (Eq. 23b):

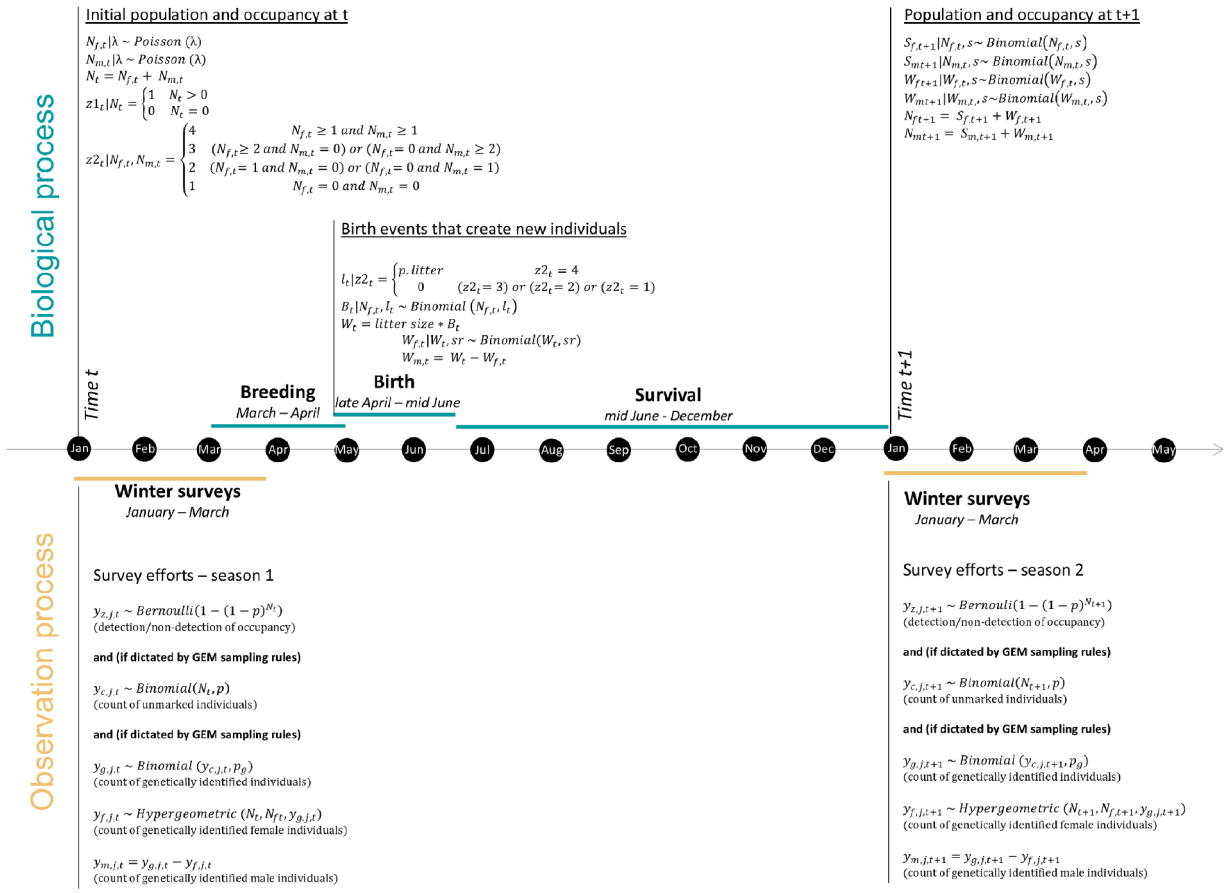

Fig. 6. The Bayesian integrated population model (BIPM) for a hypothetical population of Canada lynx (*Lynx canadensis*) over two time steps. The time scale included shows a full calendar year plus four months (months represented as dots), including notations of t and $t + 1$ relative to the model. The biological process and equations are represented above the timeline and observation process and equations are below. Note that all possible parts of a GEM observation approach are shown in the observation process.

$$y_{z,j,t} \sim Bernoulli\left(1 - (1 - p)^{N_t}\right) \quad (21)$$

$$y_{c,j,t} \sim Binomial\ (N_t,\ p) \quad (22)$$

$$y_{g,j,t} \sim Binomial\left(y_{c,j,t},\ p_g\right) \quad (23)$$

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 was 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 calculated a *derived* population occupancy state in a population at time *t*, $z2_t$, 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) occur. We also assumed a pre-breeding survey, so only adults were observed. Fig. 6 shows an overview of the BIPM structure, which includes both the biological and observation processes, and the relationship of the processes in time.

Finally, we created the GEM sampling rules to apply between sampling seasons as follows:

a) Rule 1: If nothing is known, obtain confirmation of presence only.
b) Rule 2: If presence has been confirmed in the previous season, obtain information on whether multiple individuals are present via counts.
c) Rule 3: If counts are >2 across a single visit in the previous 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) 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) 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 shows an example of these GEM sampling 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 GEM sampling rules to apply will change based on what is known and changes in the population.

2.2. Implementing a GEM approach for Canada lynx using simulation

We conducted a series of multipart simulations which we call replicates in this manuscript. Each replicate contained three parts: 1) a simulated Canada lynx population for 11 time steps; 2) simulated observation data of the simulated Canada lynx population using GEM sampling rules for 11 time steps; and 3) posterior distribution estimates and predictions from the BIPM run with the simulated observation data.

Table 1
Example 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 species. 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	Current knowledge about population	GEM monitoring question	GEM sampling rule	Data to collect this season (based on GEM sampling rule)	Field method (based on GEM sampling rule)	Example season outcome
1	None	Is the species present?	Rule 1: If nothing is known, obtain confirmation of presence only	*Direct observation:* Detection/non-detection	Snow tracking	Presence of species confirmed
2	Presence of species	Are multiple individuals present?	Rule 2: If presence has been confirmed in the previous season, obtain information on whether multiple individuals are present via counts	*Direct observation:* Count *Derived from direct observation:* Detection/non-detection	Snow tracking	Count >2 on a single visit
3	Multiple individuals	Are females and males present?	Rule 3: 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 *Direct observation:* Count of genetic samples and females and males within those samples *Derived from direct observation:* Detection/non-detection, GEM population state (GEM state 4)	Snow tracking plus backtracking to genetic material	Females and males confirmed
4	Females and males	Are females and males present?	Rule 5: If multiple individuals and both sexes were confirmed through counts and sex id last season, obtain information on whether females and males are present via collection of sex identifying information (e.g., genetic material) during counts	Count *Direct observation:* Count of genetic samples and females and males within those samples *Derived from direct observation:* Detection/non-detection, GEM population state (GEM state 4)	Snow tracking plus backtracking to genetic material	Females and males confirmed

Table 2
The demographic and observation parameters used in the simulation study to assess the Goal Efficient Monitoring (GEM) approach. For each parameter, the name, model term, part of the Bayesian Integrated Population Model (BIPM) it was used in, the value of the parameter (which was kept constant in all simulations), and the source of the value is listed.

Variable name	Model term	GEM BIPM process the variable used for	Value	Source
Survival	s	Biological process	0.70	Mowat et al., 2000
Probability of litter	$p.litter$	Biological process	0.50	Kosterman et al., 2018
Number of kittens per litter	*litter size*	Biological process	2	Mowat et al., 2000
Sex ratio	*sr*	Biological process	0.50	Burstahler et al., 2016
Detection probability of lynx	p	Observation process	0.63	Squires et al., 2012
Detection probability of genetic sign (for 1 km search)	$p_{genetic}$	Observation process	0.50	McKelvey et al., 2006
Repeat visits	3	Observation process	3	N/A

In the following section we describe the process for each part of a replicate.

2.2.1. Simulating Canada lynx populations

To create the simulated populations in each replicate we simulated the biological process described above (Eqs. 1–20) with the values described in Table 2. Starting conditions for each replicate were as follows. To answer our first research question if implementing a GEM approach provide robust population estimates, our goal was to apply a GEM approach to a small, isolated population of Canada lynx. Thus, we generated 100 replicates with each population started in breeding potential at time $t = 1$ (GEM state 4, $z2_t = 4$) and abundance of females, $N_{f,t}$, and males, $N_{m,t}$, was drawn from a Poisson distribution with a mean of 7 ($\lambda = 7$). This resulted in a total of 14 starting individuals, which represents a plausible population of a Canada lynx based on survey data from monitoring of a Canada lynx population in Montana (Golding et al., 2022). Throughout the remainder of the manuscript, we refer to this starting condition as "main simulation." The probability of having a 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 Canada 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 Eqs. 6–8 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 Canada lynx survival when snowshoe hare densities are high (Mowat et al., 2000).

To answer our second research question if a GEM approach in multiple long-term monitoring settings (i.e., population sizes) can accommodate changing questions while providing continual, reliable population inference, our goal was to apply a GEM approach to four different sized Canada lynx populations, as Canada lynx are a species that exists in a variety of densities across its global range from Canada through the northern United States. Thus, we generated an additional 100 replicates for each starting condition (400 replicates total). We refer to these starting conditions with scenario names. The four population starting conditions were a single isolated individual (e.g., a new disperser – Scenario A), multiple isolated individuals of a single sex (e.g., new dispersers who interact – Scenario B), a new small population (e.g.,

a female and a male starting a new population – Scenario C), and an established, small population (e.g., a small number of females and males breeding – Scenario D). Other than starting conditions (single individual, three individuals of one sex, one female and one male, and four females and four males, respectively), all other demographic processes were modeled as described in the paragraph above.

2.2.2. Simulating observations using GEM sampling rules

To create the observation data of the population in each replicate ($y_{z,j,t}$, $y_{c,j,t}$, $y_{g,j,t}$), we simulated the observation process (Eqs. 21 - 23) of following the GEM sampling rules. We assumed that the first time step of observation in every replicate for both research questions started with no knowledge of the population. Thus, the first observation season always only involved sampling for presence (Eq. 21), which was simulated with 3 repeat visits within the season to generate detection/non-detection data. To simplify the simulations and compare across replicates, we set detection probability of an individual, p, as 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 Canada lynx in an area with known females and males (Squires et al., 2012). For time steps 2 through 11, we followed the GEM sampling rules and changed the simulated 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, we simulated a count with 3 repeat visits to detect multiple individuals (Eq. 22). 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, which was obtained with a count with 3 repeat visits with collection of genetic material. We set detection probability of genetic material, p_g, at 0.50, which was based on the probability of detection of Canada lynx genetic sign with 1 km of snow tracking effort (McKelvey et al., 2006) (Eq. 23). The order of the sampling steps each year was only set according to GEM 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) were adjusted based on what was known from the previous time step (i.e., survey season). For all detection, count, and genetic observations we assumed that there were no false positives (i.e., individuals that were double counted or misidentified).

2.2.3. Generating predictions and estimates for Canada lynx using the GEM BIPM

Finally, we used the observation data generated by the process described in Section 2.2.2 ($y_{z,j,t}$, $y_{c,j,t}$, $y_{g,j,t}$), as data in to run our BIPM. To run the BIPM, we used the following process. We used 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 $p_{genetic}$) we used uniform distributions constrained between 0 and 1. For each replicate 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 Core Team, 2020) and JAGS version 4.3.0 (Plummer, 2003). Code to generate simulated data, observation, and execute the BIPM is available at https://github.com/jgoldfinch/GEM.

The BIPM produced posterior distributions of *estimated, derived*, and *predicted* parameters related to the population for each replicate. Specifically, we used the BIPM to generate *estimated* ($N_{f,t+1...}$, $N_{m,t+1...}$, $B_{t+1...}$, $W_{f,t+1...}$, $W_{t+1...}$, $S_{f,t+1...}$, $S_{m,\ t+1...}$) and *derived* ($N_{t+1...}$, $z1_{t+1...}$, $W_{m,t+1...}$) demographic and population parameters, *derived* GEM population states ($z2_{t+1...}$), and *predicted* GEM state transition probabilities ($\mathbf{\Psi}_{t+1}$) in each replicate, across all 11 time steps in the replicate.

2.3. Evaluating a GEM approach for Canada lynx

Our first step in evaluating the GEM approach was to assess BIPM convergence for each replicate. To assess BIPM convergence, we visually examined the trace plots (King et al., 2010) and used the $\widehat{R}$ 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 $\widehat{R}$ across all BIPM variable predictions was at or below 1.05 we assumed the model had converged for that replicate. If the average $\widehat{R}$ was higher than 1.05, we discarded the replicate. This process was repeated until we had 100 total replicates that converged for each starting population scenario. Overall, our simulations resulted 500 total replicates; 100 for research question one with a small starting population (main simulation) and 100 for each of the four starting scenarios for research question two (scenarios A-D).

Next, to assess GEM performance in each replicate, we assessed the ability of the BIPM to recover the true parameter values. To accomplish this, we compared BIPM *estimated, derived*, and *predicted* parameters (described in Section 2.2.3), to the known values for the population for that replicate (described in Section 2.2.1). For each replicate, all true parameters were known based on the simulated population and all predicted parameters were derived from the BIPM posterior predictions, which were estimated using the simulated observation data (generated through the BIPM observation process with GEM sampling rules).

We used four metrics to assess the ability of the BIPM to recover the true parameter values: coverage, mean absolute percent error, mean absolute individual error, and relative root mean square error (RRMSE). For all four metrics we calculated the metric first at each of the 11 time steps within a replicate and then took the average of the values across 100 replicates (1100 values total) for each starting population condition. We measured coverage, which is the percentage of simulations in a replicate that the 95 % Bayesian credible interval (CRI) contained the true value of the simulated population. First, we calculated a single coverage value (as a 0 if the CRI did not contain the true value or 1 if the CRI did contain the true value) for each time step (11) in a replicate. Next, we calculated the sum of all replicate time steps across the 100 replicates for each starting population condition (1100 total entries – 11

Table 3
The Goal Efficient Monitoring (GEM) Bayesian Integrated Population Model (BIPM) variables used to assess each research question about applying the GEM approach.

Research question	Population starting condition	Scenario name	Simulation replicates	Variable(s) assessed to answer GEM research question
1. Can a GEM approach provide robust population predictions?	~14 individuals	Main simulation	100	N_{ft} , N_{mt} , N_t, B_t, W_{ft}, W_{mt}, s, $z2_t$, ψ_{41}, ψ_{42}, ψ_{43}, ψ_{44}, p, $p_{genetic}$
2. Can implementing a GEM approach in multiple long-term monitoring settings allow for changing questions while still providing continual, reliable population inference?	Single individual (sex selected randomly)	Isolated individual (Scenario A)	100	ψ_{22}
	Three individuals (sex selected randomly)	Isolated individuals of a single sex (Scenario B)	100	ψ_{33}
	2 individuals (1 female, 1 male)	New, small population (Scenario C)	100	ψ_{44}
	8 individuals (4 females, 4 males)	Small, established population (Scenario D)	100	N_{ft}

Table 4
A) The parameters of the Bayesian Integrated Population Model (BIPM) and performance metrics across 100 replicates, each with 3 MCMC chains, 400,000 iterations, 10,000 burn-in period and thinning at a rate of 10 to reduce the size of data stored for each replicate simulation, with the full observation scenario (counts of males and females with 3 visits and one independent observation of GEM state every time step). RRMSE = relative root mean square error. B) Four different parameters (three predictions – transition probabilities - and one estimate – female adult abundance) relevant to different population sizes and their performance metrics.

Parameter	Description	Mean absolute percent error	Coverage	RRMSE	Mean absolute individual error
Question 1: Can a GEM approach provide robust population predictions?					
Biological process					
$\boldsymbol{N_{ft}}$	Female abundance in time t	66.0 %	91.0 %	0.0177	6.61
$\boldsymbol{N_{mt}}$	Male abundance in time t	74.5 %	87.9 %	0.0203	7.25
$\boldsymbol{N_t}$	Total at time t	54.4 %	98.5 %	0.0166	18.4
$\boldsymbol{B_t}$	Number of birth events in the population at time t	71.0 %	99.9 %	0.0175	3.31*
$\boldsymbol{W_{ft}}$	New females added from birth events at time t	88.0 %	99.7 %	0.0195	3.68
$\boldsymbol{W_{mt}}$	New males added from birth events at time t	91.2 %	99.7 %	0.0196	3.71
$\boldsymbol{s}$	survival	8.10 %	100 %	0.00767	–
$\boldsymbol{z2_t}$	State of population in time t	–	100 %	–	–
$\boldsymbol{\psi}_{41}$	Probability of transitioning from state 4 at time t to 1 at time $t+1$	5.82×10^{25} %	96.2 %	0.0612	–
$\boldsymbol{\psi}_{42}$	Probability of transitioning from state 4 at time t to 2 at time $t+1$	2.33×10^{25} %	95.9 %	0.0406	–
$\boldsymbol{\psi}_{43}$	Probability of transitioning from state 4 at time t to 3 at time $t+1$	7.55×10^{10} %	91.2 %	0.0290	–
$\boldsymbol{\psi}_{44}$	Probability of not transitioning from state 4 at time t to time $t+1$	0.200 %	91.8 %	5.24×10^{-5}	–
Observation process					
$\boldsymbol{p}$	Probability of detection of an individual	16.9 %	96.0 %	0.0191	–
$\boldsymbol{p_{genetic}}$	Probability of detection of genetic sign	4.96 %	96.0 %	0.00498	–

Parameter (population size it is most relevant to)	Description	Mean absolute percent error	Coverage	RRMSE	Mean absolute individual error
Question 2: Can implementing a GEM approach in multiple long-term monitoring settings allow for changing questions while still providing continual, reliable population inference?					
$\boldsymbol{\psi}_{22}$ (for isolated individual)	Probability of a single individual persisting from time t to $t+1$	27.80 %	44.0 %	0.00850	–
$\boldsymbol{\psi}_{33}$ (for isolated individuals of a single sex)	Probability a group of isolated individuals of a single persisting from time t to $t+1$	25.2 %	100 %	0.0197	–
$\boldsymbol{\psi}_{44}$ (for a new, small population)	Probability a population to retain breeding potential from time t to $t+1$	4.46 %	94.2 %	0.00115	–
$\boldsymbol{N_{ft}}$ (for a small, established population)	Abundance of females	65.5 %	93.6 %	0.0157	2.91

* birth events.

time steps for 100 replicates). We then divided this sum by the total number of entries (1100) and multiplied by 100 to get the percent of simulations for that population starting condition where the CRI covered truth. Next, we calculated mean absolute percent error of BIPM estimates, which is the absolute value of the difference between the true simulated population parameter value and estimated BIPM value, divided by the true simulated population parameter value, multiplied by 100. In addition, we added a measure of mean absolute individual error to assist in interpretation of the mean absolute percent error metric in small populations. We believe that mean absolute percent error is difficult to interpret with very small populations because each individual makes can make up a large percentage of the population (i.e., one individual makes up 25 % of a population of 4). Thus, mean absolute individual error is the absolute value of the total individuals that the abundance estimates deviated by. To determine the accuracy of the BIPM estimates, we calculated RRMSE for each parameter using the following Eq. 24:

$$RRMSE = \frac{\sqrt{\left(\frac{1}{r}\right)\sum_{i=1}^{r}(\widehat{\theta}_k - \theta_k)^2}}{\overline{\theta}} \quad (24)$$

where r was the number of replicates, $\widehat{\theta}_k$ is the predicted parameter value and θ_k is the true value at replicate k and $\overline{\theta}$ is the mean true value of the parameter over all replicates. We used RRMSE so that accuracy was comparable across all parameters and replicates.

We used these four metrics to examine different parameters that we felt best addressed our research question. For our first research question, if a GEM approach could provide robust population predictions, we were interested in all biological parameters (adult female, $N_{f,t+1\ldots}$, and male, $N_{m,t+1\ldots}$, abundance, birth events, $B_{t+1\ldots}$, new females, $W_{f,t+1\ldots}$, new males, $W_{m,t+1\ldots}$, total individuals, $N_{t+1\ldots}$, survival, s, and GEM state transition probabilities, Ψ_t), and the observation parameters of individual detection probability (p) and detection probability of genetic sign ($p_{genetic}$), as these are typically unknown. For our second research examining the ability of a GEM approach to make reliable population state predictions across a variety of population settings, we focused on metrics related to management scenarios for each starting population condition. For an isolated individual and isolated individuals of a single sex, we focused on assessing the ability of a GEM monitoring approach to predict the likelihood that a single individual would persist (ψ_{22}) or a group of isolated individuals of a single sex would persist (ψ_{33}), which might be of interest for a land manger if the individuals were a protected species. For the new small population, we focused on assessing if a GEM approach could reliably predict the probability of retaining breeding potential (ψ_{44}) which may be of interest to managers when a small population represents a natural or human-assisted introduction into a new area. Finally, for the small, established population we focused on assessing the ability of a GEM approach to reliably estimate adult female abundance ($N_{f,t}$) over the 11 time steps, as that is often the population variable of interest for many established wildlife populations, as it generally indicates the ability of a population to persist (Table 3).

3. Results

BIPM convergence was achieved for all parameters during the simulations that were kept. Visual inspection of MCMC chain plots all showed visual signs of adequate mixing. In addition, the $\widehat{R}$ statistics for each parameter for all simulations that were kept were all ~ 1. All results presented in this section are summarized over 100 replicates for each starting population condition, including all time steps within each 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 summarized below are described fully in Table 4.

3.1. Simulated Canada lynx populations and observations

For our first research question, each population in each of the 100 replicates with a starting condition of ~14 individuals (main simulation) persisted for the entire 11 years in breeding potential (GEM state 4). As a result, the breeding potential was retained each time step and no state transitions occurred. The mean population size over all time steps and all replicates was 18, with a range from a minimum of 6 individuals to a maximum of 126 individuals. For our second research question, the simulated populations varied as follows. The 100 replicates that started as an isolated individual (Scenario A), the mean population size was 1 and transitions to extinction occurred in only 2 % of simulations (125/1100). For the 100 replicates that started as isolated individuals of a single sex (Scenario B), the mean population size was 1 and transitions to a single isolated individual and to extinction occurred in 81 % (887/1110) and 3 % (36/1100) of simulations, respectively. In contrast, both the new, small population replicates (Scenario C) and the small established population replicates (Scenario D) persisted for most simulations, with 94 % (1034/1100) and 98 % (1074/1100) persisting with breeding potential, respectively. For additional details on the simulated populations see Appendix B, Table B1.

Our simulated observation data with GEM sampling rules resulted in primarily count and genetic data for our 100 replicates with ~ 14 starting individuals (main simulation), with 72.7 % (900/1100) time steps where the observation question was "Are females and males present?" with count and genetic data collected. The remainder of the time steps were mostly count data, where the observation question was "Are multiple individuals present?" (18.2 %; 200/1100), and a small proportion (9.1 %; 100/1100) were detection/non detection data where the question was "Is the species present?". For additional details on the simulated observations, including observations for research question two, see Appendix B, Table B2. For an example of the observation data (and resulting BIPM abundance predictions) generated for a single population replicate, see Appendix C.

3.2. GEM approach for Canada lynx performance

For the remainder of the section below we focus on coverage and RRMSE, as their patterns are reflective of the patterns in the other error metrics (mean absolute percent error and mean absolute individual error). Overall, the BIPM estimated biological process variables well. Results of the main simulation indicated that a GEM approach provided robust population estimates (research question 1). Coverage for all variables examined (Table 3) was over 90 %, with the single exception of adult male abundance, N_m, which was 87.9 %. Of all the biological process variables, the probability of retaining breeding potential, ψ_{44}, was predicted with the lowest error (lowest RRMSE; highest accuracy) at 5.24×10^{-5}, followed by survival, *s*, at 0.00767 and total abundance, N_t, at 0.0166. The transitions that did not occur in the simulations, the transition from breeding potential to single sex population, ψ_{43}, the transition between a single sex population and a single individual, ψ_{42}, and the transition from breeding potential to not present, ψ_{41}, were the variables predicted with the lowest accuracy (highest RRMSE) at 0.0290, 0.0406, and 0.0612, respectively.

The BIPM when implementing a GEM sampling rules also produced robust estimates of the observation process variables well. For the main simulation, coverage for both individual, *p*, and genetic sign, $p_{genetic}$, detection probabilities was high at 96.0 %. Individual detection probability, *p*, was estimated with lower accuracy than genetic sign detection probability, $p_{genetic}$, with RRMSE values of 0.0191 and 4.98×10^{-3}, respectively. This is likely due to the smaller sample size from which genetic sign detection probability, $p_{genetic}$, was estimated.

The BIPM population predictions were robust for all starting population scenarios with multiple individuals (Scenarios B-D), although were less robust for a single individual (Scenario A). For the 100 replicates that started as multiple individuals of a single sex (Scenario B), the probability that a population persisted as multiple individuals of a single sex, ψ_{33}, was well predicted by the BIPM with coverage of 100 % and RRMSE of 0.0197. For the 100 replicates that started as a new small population (Scenario C), the probability that a population retained breeding potential, ψ_{44}, was well predicted by the BIPM with coverage of 94.2 % and a low RRMSE at 0.00115. For the 100 replicates that started as an established small population (Scenario D), female adult abundance, N_f, was predicted well by the BIPM: coverage was 93.7 % and RRMSE was 0.0157. For the 100 replicates that started as a single individual (Scenario A), the probability that the single individual persisted, ψ_{22}, was the most poorly predicted biological variable tested for coverage, with a value of 44 %. However, the prediction still had a relatively low RRMSE of 0.00850. Additional results from applying a GEM approach in these multiple population setting simulations are available in Appendix D.

4. Discussion

We demonstrate GEM as a monitoring approach that allowed us to provide robust population predictions in a variety settings. We were able to show that a GEM approach could accomplish the monitoring goals we defined of answering pre-identified questions (goal #1), providing flexibility in switching monitoring (goal #2), and providing a continuous monitoring data stream flexible to population changes (goal #3). In almost every condition we tested, the BIPM consistently predicted the biological variables of interest accurately while accommodating flexibility in monitoring parameters. A GEM approach provides a way one can outline the dynamics of change initially for a population of interest (goal #1), adjust sampling in a predictable way with sampling rules based on what is currently known about the population, and examine at various points additional monitoring variables that are of interest (goal #2). Building flexibility like this into monitoring contrasts with current approaches to changes in monitoring programs, which currently are mostly accomplished through large, programmatic changes (e.g., Dai et al., 2025). In addition, by providing a quantitative link between observation and the population through GEM 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. Finally, the sampling rules allow for a series of changing questions that are common for rare wildlife and small populations (Golding et al., 2018), but they are flexible enough to still work when a population is larger, as shown with the small established population example (goal # 3).

4.1. Answering pre-identified, predictable questions that may arise with learning (monitoring program goal #1)

By constructing a GEM process that linked population states, population parameters, and observation rules, we were able to show how a monitoring system could answer pre-identified predictable knowledge questions that we identified for this system (goal # 1). Our results from answering our first research question (Can a GEM approach provide robust population predictions?), showed support for being able to identify and answer pre-defined knowledge questions. For example, in our simulations, we had the following breakdown of questions answered during each time steps: 9.1 % "Is the species present?" (i.e., detection data collected); 18.2 % "Are multiple individuals present?" (i.e., count data collected); and 72.7 % "Are females and males present?" (i.e., count and genetic data collected). Thus, with simulated populations changing and a set of sampling rules that resulted in simulated data collection, we

were able to answer different monitoring questions and provide reliable population information. For example, coverage of the GEM state predictions was 100 % and total abundance, N_t, was one of the variables predicted with the highest accuracy (i.e., lowest RRMSE at 0.0166).

An ongoing large problem of long-term monitoring is uncertainty on what to monitor (e.g., Nichols and Williams, 2006; Lindenmayer and Likens, 2009; McDonald-Madden et al., 2010) and some authors have suggested monitoring designed with system models can help guide what to monitor (Lindenmayer and Likens, 2009). We believe that using a system model (Canada lynx population model) can also help facilitate monitoring flexibility. By defining question using the Canada lynx population as our biological system model, we were able to build in flexibility in monitoring questions that related to the population. Although we show this using a single example species, we think this concept will work well for additional species. For example, the California spotted owl is a rare species in the California Sierra Nevada that has been previously characterized using multistate models with population states similar to the GEM states described in this manuscript (Mackenzie et al. 2009). A GEM approach to monitoring spotted owl could allow for different monitoring resource allocation based on what is known, while providing inference to connect those states to a BIPM so mechanisms of local change could be better linked to population changes.

4.2. Flexibility in switching monitoring parameters of interest in rapid, but tractable, ways that do not require full programmatic review or change (monitoring program goal #2)

By constructing a GEM process that relied on an underlying BIPM with pre-identified questions and connected sampling rules, with results from simulations to answer our first research question (Can a GEM approach provide robust population predictions?) we were able to show that a GEM system could be constructed to allow for prioritization of different monitoring parameters and sampling methods is a rapid (i.e., between sampling seasons) and tractable way (goal #2). The GEM sampling rules made the changes in sampling tractable and, combined with the BIPM structure, allowed us to predict both "unobserved" (latent) and "observed" population variables (although precision tends to be lower with latent variables not directly observed, as in Sanderlin et al., 2019). For example, we showed that we could predict "observed" and "unobserved" variables our results showed that abundance (N_t, N_{ft}, N_{mt}) and GEM state occupancy values ($z2_t$) that were directly "observed" in the simulation through detection of adults were predicted with similar credible interval coverage ($N_t = 98.5\%$; $N_{ft} = 91.0\%$; $N_{mt} = 87.9\%$; $z2_t = 100\%$) as those that were not directly "observed", such as birth events per season ($B_t = 99.9\%$) and new individuals ($W_{ft} = 99.7\%$; $W_{ft} = 99.7\%$). This means that data that are difficult to obtain (i.e., survival), do not have to be directly observed to be estimated with quantifiable uncertainty, which can be useful in populations where stochastic dynamics make population predictions difficult. Having unobserved variables as part of the long-term data stream also means that future monitoring can shift to focus on a previously unobserved parameter while maintaining a consistent data stream for that parameter from the start of monitoring. More potential mechanistic understandings are available with this full knowledge (and thus ability to evaluate conservation and management actions on demographic parameters critical for population persistence) than with monitoring confined to a single, repeated question.

The flexibility afforded by the observation process of a BIPM may allow for a GEM approach in many systems. The ability to change data collection methods may be useful in many settings, including for common species when range expansions or contractions occur and there is interest in population dynamics at range edges (Miller et al., 2019). The nested nature of some population observation questions can also lead to operational efficiencies using multiple data sources. For instance, in the initial state of asking if the species is present, methods can be designed to detect unmarked individuals using non-invasive methods such as camera sets (Steenweg et al., 2017), snow-print based DNA samples (Franklin et al., 2019), and automated recording units (Rhinehart et al., 2020). Once an organism has been detected, sampling can be adjusted to more demanding methods: examples include more rigorous camera-based detections that allow the application of space to detection models (Moeller et al., 2018), 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, or collaring of an individual animal. Because the implementation of more intensive sample collection methods are only undertaken once there is knowledge that the area is occupied (using sampling rules), they are only applied in areas where they are adding 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, as well as some adaptive sampling approaches within sampling seasons (e.g., Pacifici et al., 2012). The GEM BIPM with state transitions, however, formalizes the application of maximizing information gain into a coherent long-term monitoring program.

4.3. Provide continuous data streams flexible to changes in populations (monitoring program goal #3)

A GEM state structure and transition probabilities are designed to allow for tracking population conditions through various phases of 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 or increase to establishment. Results from our simulations to answer our second research question (Can implementing a GEM approach in multiple long-term monitoring settings allow for changing questions while still providing continual, reliable population inference?) show that a GEM approach can effectively track dynamics in many population settings. For example, across three population starting conditions with multiple individuals, a GEM approach resulted in estimates of variables that might be most relevant to each state with high coverage: for an established, small population (8 individuals, 4 females and 4 males), number of adult females ($N_{ft} = 93.6\%$); for a new small population of a female and a male, probability to retain breeding potential at the next time step ($\psi_{44} = 94.2\%$); and for multiple isolated individuals of a single sex, the probability of at least two individuals persisting to the next time step ($\psi_{33} = 100$ %). This performance across different conditions is because each of the GEM states and transition probabilities are derived from the BIPM linking changes in population dynamics to the same population parameters, regardless of population size. However, the coverage for the prediction for a single individual persisting was comparatively poor ($\psi_{22} = 44.0\%$), because it is based on survival, which is known to be poorly estimated with detection/non-detection data, especially without additional data sources for survival (Sanderlin et al., 2019).

The GEM state structure provides the ability to produce meaningful information for the immediate future using information that is part of, rather than detracting efforts from, the long-term data stream. A key feature for any long-term monitoring system to remain relevant through societal or environmental changes is to provide information relevant on multiple time scales. The flexibility to track transition probabilities and population metrics at different conditions makes a GEM monitoring approach well suited to use in monitoring for adaptive management (McFadden et al., 2011), as it provides the ability to change monitoring questions based on what is known and the biological conditions present. 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. In the same system, if the desired type of information changes after a population recovers to adult abundance rather than breeding probability, or even to other metrics that are outlined in the population model portion of the BIPM and linked to the multistate structure, this shift can be accommodated seamlessly. In addition, not only has abundance been tracked, but because of the BIPM structure additional observation data can be collected and integrated with the existing data stream (an example is shown in Appendix E).

4.4. Limitations

There are limitations to consider for the execution of a GEM approach as presented. One practical limitation for developing a GEM BIPM for small populations is the difficulty of building and testing the BIPM and setting initial values: the Bayesian GEM structure at low population values is sensitive to initial values and at very low abundance numbers (which may be realistic) may be difficult to initiate due to the stochastic nature of such populations. In addition, as with many multistate and BIPM 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). Finally, the limitations of the BIPM and sampling rules for a given species may not be apparent until simulations are run or data is collected. For example, our sampling rules and BIPM provided robust estimates for the variables of interest for all population conditions we tested except for a population that started as a single isolated individual. A manager might be interested in the ability of this individual to persist, but with our example GEM state structure this probability is entirely dependent on survival, which is known to be poorly estimated with detection/non-detection data (Sanderlin et al., 2019). However, we note that additional data streams targeting survival can still be accommodated in a BIPM, so this issue can be overcome with either additional data collection methods added to the monitoring effort or an adjustment of the sampling rules to collect more appropriate data when only a single individual is present.

We present an example of a GEM approach to show its utility and suggest that many possible extensions or iterations can be built based on the principles provided here. We recommend that further iterations include different species, different or additional biological parameters, such as emigration and immigration, to reflect the population of interest, as well as additional observation processes. In addition, a GEM approach may be useful for a recovering species that becomes locally abundant species such as the black-tailed prairie dog (*Cynomys ludovicianus*) (Ceballos et al., 2010) or western snowy plover (*Charadrius nivosus*) (Marcot et al. 2021), both of which experienced unexpected population changes due to factors ranging from disease (black-tailed prairie dogs) to recovery from endangered status (western snowy plover; USFWS, 1993), which have complicated monitoring efforts (e.g., Marcot et al., 2021). A GEM approach for these settings could incorporate the potential for populations to change from present in small numbers to fully recovered with a large population and allow for a continuous data stream about the populations that maximizes information gain and minimizes sampling costs (i.e., Sanderlin et al., 2014). Finally, we suggest that additional simulation or real-world data collection efforts be conducted to explore the effort (i.e., cost) and knowledge gained in a GEM approach compared with more traditional wildlife monitoring metrics such as abundance or occupancy monitoring.

5. Conclusion

Additional simulation and empirical research with real world data (i.e., survival probabilities varying over time, varying litter size for Canada lynx) should be conducted to further develop GEM approaches. For the purposes of providing a GEM proof of concept, we made simplifying assumptions about the population dynamics of Canada lynx, including demographic rates that were constant (litter probability, survival) and lack of movement, so additional work that explores how variability in these parameters might affect a GEM approach would be valuable. In addition, further research into GEM transition probabilities and quantifying uncertainty around those probabilities to guide field work and decision making would be useful. We further suggest future research into integrating different data and sampling approaches into a GEM approach, including incorporating existing data or monitoring programs (Barker et al., 2015) and optimal sample design frameworks (i.e., Sanderlin et al., 2014). To illustrate a GEM approach, 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 a GEM approach. 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 (*Gulo gulo*) across 3 disjunct mountain ranges to ~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 a GEM approach 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 a GEM approach is an important step forward in monitoring wildlife populations under changing conditions. Although we present an example with a rare species, where information gains are often rapid and questions change frequently, we think this approach can be broadly useful in wildlife monitoring. As we face unprecedented and unpredictable change in the climate and environment, there little doubt that many of our 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 shift monitoring from a frequently static, iterative process, to a flexible, dynamic, approach that can be rapidly adapted for 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 such an approach, including the ability to have a continuous data stream as questions change or species change from rare to common or common to rare. These modeling structures can also be extended to incorporate information about the demographic processes that lead to species' range expansions or contractions by adding data integration SDM approaches (Miller et al., 2019) to the modeling structure. But more importantly, we see the need for a shift in thinking about how wildlife monitoring can respond to changing information needs. Ultimately, we believe that we must build monitoring systems capable of evolving; otherwise monitoring programs, and the information that they provide that once seemed relevant, will go extinct.

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CRediT authorship contribution statement

Jessie D. Golding: Writing – review & editing, Writing – original draft, Visualization, Supervision, Software, Methodology, Investigation, Formal analysis, Conceptualization. **Kevin S. McKelvey:** Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Michael K. Schwartz:** Writing – review & editing, Writing – original draft, Conceptualization. **Joshua J. Millspaugh:** Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Jamie S. Sanderlin:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Scott D. Jackson:** Writing – review & editing, Writing – original draft, Conceptualization.

Declaration of competing interest

The authors declare no conflict of interest.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2025.111196.

Data availability

Simulation data files will be made available and linked through the Github repository: https://github.com/jgoldfinch/GEM.

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