USER GUIDE

Endangered Butterflies as a Model System for Managing Source-Sink Dynamics on Department of Defense Lands

A Managers Guide to Spatially Explicit Individual-Based Models: Exploring the Benefits and Drawbacks for Wildlife Habitat Management

SERDP Project RC-2119

SEPTEMBER 2017

Elizabeth Crone
Tufts University

Christine Damiani
Institute for Wildlife Studies

Gina K. Himes Boor
Montana State University

Page Intentionally Left Blank

Page Intentionally Left Blank

REPORT DOCUMENTATION PAGE

Form Approved
OMB No. 0704-0188

1. REPORT DATE *(DD-MM-YYYY)*	2. REPORT TYPE	3. DATES COVERED *(From - To)*
09/15/2017	SERDP User Guide	7/31/2014 - 1/30/2018

4. TITLE AND SUBTITLE
Endangered Butterflies as a Model System for Managing Source-Sink Dynamics on Department of Defense Lands

A Managers Guide to Spatially Explicit Individual-Based Models: Exploring the Benefits and Drawbacks for Wildlife Habitat Management

5a. CONTRACT NUMBER
Contract: 14-C-0044

5b. GRANT NUMBER

5c. PROGRAM ELEMENT NUMBER

6. AUTHOR(S)
Elizabeth Crone, Tufts University
Christine Damiani, Institute for Wildlife Studies
Gina K. Himes Boor, Montana State University

5d. PROJECT NUMBER
RC-2119

5e. TASK NUMBER

5f. WORK UNIT NUMBER

7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES)
Tufts University
163 Packard Ave
Barnum 016
Medford, MA 02155

8. PERFORMING ORGANIZATION REPORT NUMBER
RC-2119

9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES)
Strategic Environmental Research and Development Program
4800 Mark Center Drive, Suite 17D03
Alexandria, VA 22350-3605

10. SPONSOR/MONITOR'S ACRONYM(S)
SERDP

11. SPONSOR/MONITOR'S REPORT NUMBER(S)
RC-2119

12. DISTRIBUTION/AVAILABILITY STATEMENT
Distribution A; unlimited public release

13. SUPPLEMENTARY NOTES

14. ABSTRACT
Spatially explicit individual-based models (SEIBMs) are potentially powerful tools for guiding habitat management decisions in fragmented landscapes. However, most managers are unaware of their potential, or wary of their practical applicability. In this paper, we address these concerns, using examples from working SEIBMs used to inform habitat management. Although simpler decision-making methods exist, they may not always be the best available science for guiding management of species whose viability is influenced by behavior and/or spatial structure. Limitations in data availability and modeling experience can be overcome with pattern-oriented modeling approaches and collaborations with modelers.

15. SUBJECT TERMS
spatially explicit individual-based models, habitat management, habitat models, resource selection functions, demographic matrix models, pattern-oriented modeling

16. SECURITY CLASSIFICATION OF: a. REPORT	b. ABSTRACT	c. THIS PAGE	17. LIMITATION OF ABSTRACT	18. NUMBER OF PAGES	19a. NAME OF RESPONSIBLE PERSON
					Elizabeth Crone
					19b. TELEPHONE NUMBER *(Include area code)*
UNCLASS	UNCLASS	UNCLASS	UNCLASS	65	406-531-3498

Page Intentionally Left Blank

Abstract

Spatially explicit individual-based models (SEIBMs) are potentially powerful tools for guiding habitat management decisions in fragmented landscapes. However, most managers are unaware of their potential, or wary of their practical applicability. An informal survey of 27 Department of Defense natural resource managers revealed that although only 22% had previous experience with SEIBMs, 89% were open to the idea of using them. The managers cited insufficient data, lack of modeling experience, distrust in reliability of predictions, and availability of simpler decision-making methods as reasons they might not use an SEIBM. In this paper, we address these concerns, using examples from working SEIBMs used to inform habitat management. Although simpler decision-making methods exist, they may not always be the best available science for guiding management of species whose viability is influenced by behavior and/or spatial structure. Limitations in data availability and modeling experience can be overcome with pattern-oriented modeling approaches and collaborations with modelers. However, the cost of data collection and model development may limit military use of SEIBMs to situations where maintaining viability of the species is vital to the military mission and thus justifies the expense. Although sensitivity to parameter uncertainty limits the ability of SEIBMs to make absolute numerical predictions, they have proven robust enough for comparative predictions. Furthermore, the dynamic process of building, testing, and updating models improves understanding of complex systems with each iteration. When treated as components of long term adaptive management programs rather than as short term predictive tools, SEIBMs have yielded meaningful insights that have enhanced the ability of managers to make science-based decisions when managing habitat for wildlife.

Keywords: spatially explicit individual-based models, habitat management, habitat models, resource selection functions, demographic matrix models, pattern-oriented modeling

TABLE OF CONTENTS

1. Introduction……………………………………………………………………………………………………5

2. SEIBM construction and data requirements……………………………………………………………6

2.1 Data requirements……………………………………………………………………………………6

2.1.1 Habitat data……………………………………………………………………………………7

2.1.2 Demographic data……………………………………………………………………………8

2.1.3 Movement data………………………………………………………………………………9

2.2 Simulations……………………………………………………………………………………………10

2.3 Case Study……………………………………………………………………………………………12

3. Applicability of SEIBMs for DoD natural resource managers…………………………………………15

3.1 Survey of natural resource managers………………………………………………………………15

3.1.1 Methods…………………………………………………………………………………………15

3.1.2 Results and discussion………………………………………………………………………15

3.2 Literature review………………………………………………………………………………………18

3.2.1 Advantages of SEIBMs over other models………………………………………………18

3.2.1a Advantages over habitat-based models…………………………………………20

3.2.1b Advantages over non-spatial demographic models……………………………21

3.2.2 Limitations of SEIBMs……………………………………………………………………… 23

3.2.2a Data limitations………………………………………………………………………23

3.2.2b Model complexity and cost…………………………………………………………27

3.2.2c Reliability of SEIBMs…………………………………………………………………28

4. Conclusion……………………………………………………………………………………………………32

5. Literature Cited……………………………………………………………………………………………34

6. Tables………42

Table 1. List of the 26 installations that participated in the survey, and the species for which managers provided information on monitoring data…………………………………42

Table 2. A comparison of habitat-based models, demographic models, and spatially

explicit individual-based models for predicting effects of habitat management on wildlife……43

Table 3. A list of SEIBMs applied to wildlife habitat management that document the number of parameters used in the model……44

Table 4. The subset of 9 wildlife habitat management SEIBMs whose data sets were reviewed……44

Table 5. Availability of habitat and population size data for the species of interest for 9 SEIBMs developed to guide habitat management……45

Table 6. Survival data available for the species of interest for 9 SEIBMs developed to guide habitat management……46

Table 7. Fecundity data available for the species of interest for 9 SEIBMs developed to guide habitat management……47

Table 8. Movement data available for the species of interest for 9 SEIBMs used for habitat management……48

Table 9. Monitoring data collected at Department of Defense installations that manage or restore habitat for wildlife……49

Table 10. Tests of reliability reported for published habitat restoration SEIBMs……50

7. Figures……51

Figure 1. Types of habitat management conducted by the 27 managers surveyed, and the types of management questions they need to address……51

Figure 2. Types and amounts of monitoring data collected on DoD-managed species……52

Figure 3. DoD managers' experience and perception of SEIBMs……53

Figure 4. Factors that would prevent managers from considering using SEIBMs……54

Appendix A. Questionnaire sent to DoD managers ……55

Appendix B. Written comments provided by managers in response to questions 4-6 in the "SEIBM perception and experience" section of the questionnaire……58

1. Introduction

Habitat loss and degradation are among the greatest threats to wildlife (Wilcove et al. 1998, Brooks et al. 2002, Schipper et al. 2008). Populations in fragmented landscapes must contend with smaller patches of suitable habitat and reduced connectivity to other patches, making them vulnerable to stochasticity (Shaffer 1981), invasion by undesirable species (Lurz et al. 2003), and increased mortality risk to individuals that leave the patch (Lamberson et al. 1992). Even intact habitats may be degraded by loss of natural disturbance regimes, making them less valuable to wildlife. Approaches to counter habitat loss and degradation include protection of existing habitat, restoration of degraded habitat, and creation of new patches or dispersal corridors. Disturbance regimes may also be managed to maintain or restore disturbance-dependent habitats.

Implementing these strategies requires managers to assess: how much habitat is needed to sustain a viable population, which patches have the most potential conservation value, and what frequency of disturbance restores habitat while minimizing mortality? There is often no clear answer to these questions, leaving managers with difficult choices among multiple alternative actions. To justify cost and feasibility of decisions, managers need science-based methods that predict management outcomes and allow them to weigh alternative strategies.

A challenge to predicting species response to habitat management is that decisions often can't be guided directly by empirical studies (Heppell et al. 1994, Cooper et al. 2002). Landscape-level manipulations on rare species can be ethically questionable, logistically unfeasible, and unable to be replicated sufficiently to assert that results were not observed by chance. Population models that forecast viability (*i.e.*, population viability analyses, or PVAs) have been useful for guiding wildlife management in situations where empirical studies are not feasible (Morris and Doak 2002). However, in fragmented landscapes, aspects of viability (*e.g*. connectivity) are driven not only by population dynamics, but spatial arrangement of habitat (Andren 1994, Turner et al. 1995) and dispersal behavior (Baguette et al. 2013).

Spatially explicit individual-based models (SEIBMs) simulate the behavior of individuals on a virtual landscape as a way to understand population-level patterns (Grimm and Railsback 2013). They are spatially explicit because simulated individuals move through a two-dimensional space representing a real or simplified landscape. They are individual-based, because simulated individuals interact with one another and the landscape, reproduce, and die according to rules derived from data or hypotheses on individual vital rates (*e.g.,* survival probability) and behavior (*e.g.,* frequency of dispersal). The collective behavior of these individuals is recorded over time to produce population-level metrics such as population trajectories, spatial distribution, and extinction probability. SEIBMs are similar to other simulation models used in ecology, such as PVAs, in that they generally use parameters estimated from empirical data to predict future outcomes. SEIBMs differ from PVAs in that their simulations focus on individual-level dynamics rather than population-level dynamics.

SEIBMs are theoretically well suited for addressing questions related to habitat restoration and management (Dunning et al. 1995). They can simultaneously incorporate spatial, behavioral, and demographic drivers of viability in fragmented landscapes. They can describe habitat arrangement in a realistic manner, and can therefore address questions specific to real landscapes. They can update habitat characteristics over time, and are therefore capable of capturing a landscape's temporal dynamics associated with habitat management, natural succession, and human and wildlife impacts. Therefore, a well parameterized SEIBM acts like a virtual laboratory in which one can conduct multiple landscape-level experiments that would otherwise be unfeasible. Unlike habitat restoration experiments, simulations can be replicated, allowing conclusions to be statistically defensible.

However, SEIBMs are complex models with potentially heavy data requirements and it is no trivial undertaking to construct one. Furthermore, despite 20 years of development and use, it has largely been unreported whether these models have been successful in guiding managers towards effective management strategies. The objective of this paper is to evaluate the benefits and impediments of SEIBMS to natural resource managers who conduct habitat restoration and management. To this end, we conducted an informal survey of managers to find out what monitoring data they collect and what factors would limit them from using SEIBMs. Guided by managers' questions and concerns, we use case studies to describe advantages SEIBMs may have over simpler approaches, discuss the limitations posed by their data requirements, and evaluate their value as decision-making tools.

2. SEIBM construction and data requirements

2.1 Data requirements

SEIBMs are composed of a virtual landscape on which virtual individuals interact with the landscape and each other over time, progressing through their life cycles, and potentially reproducing to create the next generation of individuals. The output of an SEIBM is the collective behavior of all individuals, measured as population- or community-level outcomes. Information necessary to build an SEIBM varies considerably depending on the question to be addressed and the data available to parameterize the model, but at their most basic, SEIBMs require a map of the landscape, knowledge about individual behaviors and vital rates, and information about how those behaviors and vital rates are affected by the landscape. In this section, we discuss each of these components in more detail and describe how they are brought together to create an SEIBM, with the caveat that there are few absolutes when it comes to construction methods and data requirements for SEIBMs. The aim of this brief introduction to SEIBMs is not meant to be comprehensive, but rather to introduce the concepts sufficiently so that managers can decide whether an SEIBM might be feasible and useful for the questions they are interested in addressing.

2.1.1 Habitat data

The first component necessary for building an SEIBM is a map – a virtual representation of the landscape relevant to the management question. The map is often a simplified delineation of habitats or cover-types through which the species under consideration moves in the real world, and is most often tied to a real geographic location. For example, if the focal species is a bird known to nest in riparian forests and to forage or preferentially travel through other forest types, the SEIBM map could be composed of three habitat types: riparian forest, upland forest, and open areas (which would include all non-forested areas). Such a map could be constructed from aerial photographs or satellite imagery (*e.g*., Landsat or NLCD from USGS) in which riparian forests can be distinguished from other forest types and open areas can be distinguished from forests. When habitat types are delineated by hand from aerial photos, it is most usually done using GIS, and the map that results is most often made up of a grid of cells or pixels, each of which is associated with a location as well as a descriptor or label (*e.g.*, riparian forest). With the availability of remotely sensed images and the relative ease of map digitizing, GIS layers of information for maps are generally one of the easiest types of data to obtain.

Each cell on a map can also be associated with additional environmental descriptors. For example, a cell might have a habitat suitability level or a measure of available resources such as forage biomass, number of nest sites available, or number of host plants. Such data could be derived from vegetation and habitat surveys that quantify the level of available resources in different habitats, from telemetry studies that provide information on how frequently individuals use different habitats (*e.g.*, open meadows are used preferentially for foraging, but riparian corridors are used secondarily, and upland forests not at all), or from expert knowledge on how important various habitats are for the focal species. The environmental descriptors or habitat types can be static or can change over time. Changes can occur independent of the focal species (*e.g*., through successional phases), in response to interactions with focal species (*e.g*., consumption of resources or occupation of nest sites), or in association with landscape neighbors (*e.g*., spread of an invasive species). Some SEIBM maps partition the landscape into only two habitat types (*e.g.*, suitable/unsuitable, Rushton et al. 1997, Letcher et al. 1998);

others contain myriad habitat types or landscape features (*e.g*., Carroll et al. 2006, Watkins et al. 2015). The level of habitat detail will be dictated by the number of landscape features affecting the focal species' behavior or demography in a way that is relevant to the modeling goal. If an individual or population does not respond in some unique way to a habitat type or feature, then including it in the map is unnecessary from a modeling perspective.

2.1.2 Demographic data

The second component of SEIBMs is a set of "rules" that govern an individual's survival and reproduction. These rules can take the form of per-time-step probabilities of surviving/reproducing (*e.g*., Fahrig 2001), mortality as a function of age (*e.g.*, Conner et al. 2008), or assigned characteristics at birth (pre-determined lifespan, *e.g.*, McIntire et al. 2007). Multiple types of data that are commonly collected on the species of interest can be used to parameterize these aspects of a model, including annual survival and reproduction rates, average life-span, age-at-first reproduction, age of senescence, litter size, or lifetime reproductive capacity. Such data are generally obtained from mark-recapture studies, radio and satellite telemetry, studies that track a sample of individuals through time, or age-specific censuses over time. In models for which differences occur between categories of individuals, or ages or life stages are critical to the modeling goal, data on group-specific vital rates (*e.g.*, age-specific reproductive rates) or behaviors (*e.g.,* gender-specific dispersal rates) will be necessary. In addition, individual variation can be incorporated into the model if the variability around a mean demographic rate is known (*e.g.*, Brown and Crone 2016a). For some SEIBMs, demographic rates are emergent outputs of the model rather than input parameters. For example, survival and reproduction can be based on body condition, which is in turn based on foraging decisions and success (*e.g.*, the amount of forage available and energy consumed, Kostova et al. 2004). In these cases, data on consumption rates or foraging success rates in association with body condition or reproductive success can be used to parameterize the model. Such data are generally obtained from observations of individuals (potentially in combination with allometric measurements) and/or mark-recapture studies.

Some SEIBMs tie population dynamics to the landscape by using habitat-specific vital rates. For some species this may simply require knowledge about preferred mating or birthing habitat. For example, if reproductive sites (*e.g.*, dens, nests, host plants) only occur within one habitat type, the model can restrict reproduction to that habitat type. For other species, individuals that occupy different locations or habitats may have different vital rates, thus requiring location-specific estimates. For example, individual red-cockaded woodpeckers at Fort Bragg might be subject to one survival rate, while woodpeckers at Eglin Air Force Base would be subject to Eglin-specific survival rates. Alternatively, an average set of survival and reproductive rates may be weighted by a habitat suitability score calculated for the occupied cell (Carroll et al. 2006, USFWS 2011). For instance, Carroll et al. (2006) calculated a wolf survival metric for each cell on their map, based on habitat characteristics (*e.g.*, road density, human population density) for the cell that are correlated with wolf survival. Average wolf survival rates were multiplied by the survival metric of the occupied cell, so that wolves occupying cells with higher survival metrics had higher survival rates. Such an approach would be appropriate if habitat relationships were known, but site-specific or habitat-specific vital rates were not known.

2.1.3 Movement data

The third component of SEIBMs is a set of rules governing individual movement behavior (*e.g*., movement initiation, direction, and distance). We will call these rules the movement submodel. Data to parameterize this component of an SEIBM are likely the least familiar to managers, but are what distinguish individual-based models from other simulation modeling and what give SEIBMs the potential to be highly beneficial tools in guiding management actions related to habitat management. The complexity of the movement submodel, and thus the level of data requirements, will depend on the question to be addressed, and the life history and spatial dynamics of the species. In general, the movement submodel dictates how individuals move through their environment, whether that movement is related to obtaining food, looking for mates, finding suitable habitat, or dispersing. To a certain extent, the movement submodel (or the questions to be addressed with the model) can be adjusted to fit the available data.

In some cases, very little data are required to build a movement submodel. For example, because Lurz et al. (2003) only had empirical data on maximum dispersal distance, their dispersal submodel simply assumed individuals dispersed when patch carrying capacity was exceeded, and dispersal was successful if another patch was available within maximum dispersal distance; otherwise, the individual died. Using this relatively simple movement submodel, they were able to use their SEIBM to assess the impacts of various forest management practices on a red squirrel conservation area. Similarly, Letcher et al. (1998) built a movement submodel based solely on the knowledge that dispersing individuals tend to move in straight lines; they used their model to determine the population sensitivity to spatial distribution of territories. In these examples, expert knowledge or very basic empirical data were used to create a movement submodel that allowed managers to better assess the needs of the focal species and the impacts of management actions.

In contrast, when data are available, detailed movement submodels can be developed that link movement behavior to landscape structure by including habitat-specific movement behaviors, incorporating habitat-boundary crossing behaviors (*e.g.*, Schultz and Crone 2001), or both. For example, Hudgens et al. (2012) modeled butterfly movement by assigning butterflies different movement characteristics in each different habitat they encountered, such that the likelihood of resting, for example, was higher in areas containing their host plant, and their per-move step distance was longer in non-host habitats. The full model included habitat-specific move/resting probabilities, rest times, move distances, turning angles, and boundary crossing probabilities. The data used to parameterize the model were obtained by following individual butterflies and recording their movement behavior in different habitats, but could also be obtained from fine scale telemetry data. While the level of data required for such habitat-specific movement can be quite high, models that incorporate these details can have advantages over simpler models. Hudgens et al. (2012) found that an SEIBM that included habitat-specific movement and boundary behaviors was better able to identify potential dispersal barriers for an endangered butterfly species in a restored landscape than a simple model with dispersal based on inter-patch distance only (*i.e.*, a butterfly was more likely to move to another host patch if it was closer than if it was farther away). Further, they argued that this increased predictive accuracy came at only a slightly higher financial cost for data collection and model development.

In addition to the types of data mentioned above, information that can be used to parameterize movement submodels include dispersal information such as speed or mean dispersal distance, home range size, habitat preferences, proportion of population that migrates or disperses, patch occupancy estimates, and almost any data pertaining to spatial use patterns. These kinds of information can be obtained from mark-recapture studies, telemetry data, and in some cases, presence/absence surveys in multiple habitats or locations of interest. For example, when movement behavior data are relatively minimal but habitat preferences are known, a biased random walk approach can be used where the bias is toward preferred habitats (*e.g.*, Richards et al. 2004, McIntire et al. 2007). Other details that can be considered when developing the movement submodel include whether demographic parameters change as a result of dispersal (*i.e.*, survival rates are lower for dispersing individuals than stationary ones), or if movement behaviors differ between classes of individuals (*e.g.*, sexes, age-classes, or categories, Letcher et al. 1998, Conner et al. 2008).

2.2 Simulations

To understand how SEIBMs work, it is useful to understand what happens in an SEIBM simulation. Once the data for the three primary components (map, demography, and movement submodel) are assembled and coded into a model, simulations are run. To begin a simulation, individuals are placed on the virtual landscape and each are assigned a set of characteristics (*e.g.*, age, sex, reproductive status, energy level) depending on the purpose of the model. For example, if the purpose of the model is to assess the effectiveness of culling a portion of an invasive population and culling males and females is expected to have different effects, the number of individuals placed on the landscape would be the current estimated population size and the male to female ratio would be based on empirical data if possible. If the ratio is unknown, a 50:50 ratio might be used, then tested to see if the model output is sensitive to this model assumption. Characteristics that are not fixed (*e.g.*, reproductive status) may be updated with the individuals' age or time of day as the simulation proceeds. Within a defined time step (*e.g.*, year, season, day), each individual goes through a sequence of events. The outcome of each event is probabilistically determined by the individual's assigned characteristics, behavioral rules, and the context of the individual's location. If the time step is a year, the sequence might be to evaluate survival (*i.e*., does the individual die or survive, based on empirical survival rates), update age (*i.e*., if the individual has survived, its age is incremented by one), disperse/establish territory (*e.g*., does the individual stay in its current location or does it leave the colony based on empirical rates of emigration), and reproduce (*i.e*., does the individual successfully produce offspring or not based on empirical reproductive rates, *e.g*., Schumaker et al. 2014). If the time step is a day, the sequence might be to rest/move (*i.e*., does the individual stay in the same place or move to a new location, and if it moves where to, based on empirical movement distances), forage (*e.g*., if the individual is in a location where it can eat, it will consume a fixed amount of forage based on known foraging rates, otherwise it does not eat), attempt to mate (*e.g*., if an individual of the opposite sex is within a certain distance of the individual, they will mate, based on expert opinion), and evaluate survival as a function of age (*e.g*., if the individual's age exceeds the average lifespan, then the individual will die) or meeting minimum energy reserves (e.g., if the individual has managed to acquire sufficient forage, it will survive, if not, it will die, based on known minimum food requirements, *e.g*., Watkins et al. 2015). The simulation continues this process, iterating over all individuals at each time step, then moving on to the next time step and repeating the process, until a fixed time-period is reached (*e.g*., 20 years) or until the population reaches some designated threshold (*e.g*., goes extinct). Other processes may be simulated at time scales longer than the time-step (*e.g*., seasons, years). For example, reproduction (*e.g*., give birth to offspring) might only occur in the spring, or movement/foraging behavior might be different in winter than in summer, or movement is only simulated during the summer.

At the end of each time step or season, or the end of the simulation, individuals are "censused" and different types of outputs may be calculated. For example, population size and growth rate can be estimated from counts of individuals on the landscape over time, either at the whole landscape level or within individual habitats or populations. Because multiple replicate simulations may be run, predicted population trajectories can be used to estimate probabilities of extinction risk. Spatial distribution or habitat use may be quantified by the proportion of individuals using different patches or habitat types. Dispersal and connectivity can be measured by counting the number of individuals that leave a patch/population/habitat type or move between patches or other landscape features. The metrics output by the model, will of course, depend on the purpose of the model. If different management scenarios are to be assessed, then the model is run again applying the other scenarios. For example, if the impact of a clear-cut is under assessment, the model can be run using the current landscape, then again using a landscape in which the proposed clear-cut area is changed from, say a closed canopy forest to an open area. For all model outputs, it is possible for SEIBMs to make absolute predictions, however, if the aim of the modeling exercise is to compare outcomes of different management strategies, there is more leeway in the accuracy of information used to parameterize the model. In these cases, since relative ranking is more important than absolute outcome, one can parameterize SEIBMs with educated guesses (*e.g*., we assume that all female butterflies are mated and therefore can oviposit eggs) or uncertain data (*e.g*., using published vital rates from a surrogate species or from a different population), as long as the data are consistently applied to all alternatives and appropriate validation procedures are followed. When expert knowledge or uncertain data are used, sensitivity analyses can also be conducted to determine how dependent model output is on these uncertain inputs and modeling decisions. Because of their sensitivity to parameter uncertainty, SEIBMs are stronger at predicting relative outcomes.

2.3 Case Study

Here we present a case study designed to provide a more detailed example of how an SEIBM is constructed based on available data. As our example, we use a model we developed for an endangered butterfly found in Washington and Oregon, including on Joint Base Lewis-McChord (Himes Boor et al. *In review*). To facilitate recovery of the species, restoration efforts have been underway to restore native prairie habitat, specifically focusing on two of the butterfly's host plants on which adults oviposit eggs and larvae rely for their primary food source. The management questions to be addressed by the SEIBM are whether it is best to restore host plant patches in one contiguous patch or multiple smaller patches, and how multiple patches should be arranged. Below we outline the process we used to develop one of the two models we used to address the question of optimal restoration strategy – only providing enough detail to illustrate the SEIBM development process. For more detailed information about data collection and the models, we refer readers to the published papers that include more of these details (Brown and Crone 2016a, b, Himes Boor et al. *In review*).

Our SEIBM landscape described two sites at which restoration was actively underway or planned for the future. We obtained a GIS layer of property boundaries from the Center for Natural Lands Management, an NGO, and used a high resolution aerial photo of the area obtained from the USGS (https://earthexplorer.usgs.gov/). Using ArcGIS we combined these sources and digitized forest, prairie, field, and exurban habitat. We used expert knowledge (from field work in the area) to distinguish fields and exurban areas that did not contain butterfly resources, from restored prairies that contained nectar plants and a low density of host plants. Onto this base map we added potential restored patches of concentrated host plants, creating a series of landscapes with different restoration configurations.

We made decisions about how to structure the model based on our questions and the available data. Few data are available on Taylor's checkerspot demography and movement, so most of the data used to parameterize our SEIBM came from a surrogate species, the Baltimore checkerspot. The choice of surrogate species was based on similarities between their life cycles, general movement characteristics, and general population dynamics (*e.g.*, they both appear to go through "boom-bust" phases). From one population of Baltimore checkerspot, we obtained estimates of daily adult survival rates, lifetime fecundity, nest size, egg survival, larval overwinter survival, and maximum lifespan (Brown and Crone 2016a, b). For butterfly movement, we used data obtained by following individual Baltimore checkerspots and recording the time spent resting and moving, step distances, turn angles, and likelihood of crossing forest boundaries (Brown et al. 2017). These movement behaviors were recorded every 15 seconds, so we used this as the time-step in our SEIBM and converted daily survival probabilities into survival per 15-second interval.

Our model only simulated female butterflies, assuming they all had mated and were gravid. We simulated adult female behavior over 15-second intervals, for 4 flight hours per day (based on observations of Baltimore checkerspots). At each time step, a female could move or rest (based on the empirical probability of resting, 0.385). If she rested, the model drew a time from a Poisson probability distribution (based on empirical data) to determine how long she rested. If she moved, the new location was determined by a turn angle drawn from a wrapped Cauchy distribution, and a step-length drawn from a Gamma distribution. The precise distance and turn-angle distributions depended on the habitat currently occupied by the butterfly. If, for example, the butterfly was in a host patch, the mean and variance of the step length distribution were much smaller than if it was in nectar meadow habitat because butterfly flight paths tend to be more sinuous, with more frequent stops and higher tendency to turn in preferred habitat. If the female was in a host patch after moving or resting, she could oviposit eggs, with the probability of oviposition determined from lifetime fecundity data. Oviposition was not allowed in any other habitat type. If the female oviposited, the number of eggs was drawn from a Poisson distribution. Individuals also had a chance of dying at each time step, based on empirically estimated daily survival probabilities scaled to the 15-second time-step, but maximum possible lifespans were limited to four weeks based on observations of Baltimore checkerspots.

Once all adult butterflies had died in a given year, half of all oviposited eggs were removed to account for our female-only model (we assumed a 50:50 male-female ratio). A combined egg and larval survival probability was applied to the eggs, which dictated how many of the eggs and subsequent pre-diapause larvae survived to become adults the following year. Using this model structure and the empirical data from Baltimore checkerspots, our simulated populations would continue to grow indefinitely given our base landscape map containing 1.44 ha of host patch habitat, about twice the size of the estimated critical minimum patch size. However, we would not expect butterfly populations to grow indefinitely, so we limited population growth based on limited information on Taylor's checkerspot population dynamics and several modeling assumptions. We only had good population estimates over time (9 yrs) at a single Taylor's checkerspot site. This population, along with anecdotal information from other Taylor's populations and other checkerspots, suggest that they experience boom-bust dynamics, in which populations grow rapidly, then crash after reaching high densities. We did not know the mechanism behind such dynamics, but wanted to emulate them in our SEIBM, so in the model described here, we assumed that the population was limited by some type of density dependence and that the crashes were caused by inter-annual environmental variation. We set a mean carrying capacity within the host patch based primarily on expert opinion (and other modeling factors; see Himes Boor et al. *In review*) and varied it annually by imposing environmental stochasticity. The environmental stochasticity had a mean of zero and a standard deviation set through model experimentation to yield a population size coefficient of variation (CV) in simulated populations that matched the CV of the single Taylor's checkerspot population for which we had population size data. Under this model structure, if the number of surviving larvae exceeded the carrying capacity plus environmental stochasticity for that year, then the surviving larvae would be reduced to the carrying capacity. All remaining larvae, whether reduced to carrying capacity or not, turned into adult butterflies, and the next simulation year began.

We ran each simulation for 30 years or until the population went extinct, whichever came first. We compared 21 restoration scenarios, keeping the total restored area the same, but altering the number of patches and the distance between patches. We ran 100 simulations for each restoration scenario map. During each simulation, we recorded the annual adult population over all years of the simulation, and from those model outputs from all 100 simulations, we calculated 1) mean population size, 2) the population size coefficient of variation (CV), and 3) the extinction risk, calculated as the proportion of the 100 simulations in which the population went extinct. We compared these three metrics among all 21 restoration scenarios to determine the best restoration strategy as indicated by the lowest extinction risk and population size CV, and the highest mean population size.

3. Applicability of SEIBMs for DOD natural resource managers

3.1 Survey of natural resource managers

3.1.1 Methods

To assess the practical applicability of SEIBMs for guiding habitat management, we conducted an informal survey of Department of Defense (DoD) natural resource managers to gain a better understanding of their management needs, their perceptions of SEIBMs, and their capability for building SEIBMs using current monitoring data. We invited 115 natural resource managers at 90 DoD installations to participate in a survey on the utility of SEIBMs for managing habitat for wildlife. Those who accepted the invitation were asked to read a short paragraph about SEIBMs and complete a three part, multiple-choice questionnaire (Appendix A). In the first part, managers were asked what types of habitat management were conducted on their installations and whether the questions commonly addressed by SEIBMs would be important for managing their species. In the second part, managers were asked to provide information on the types of monitoring data collected for at least one species whose habitat is being restored or managed on the installation. They were asked whether they collect the types of data required to build an SEIBM, namely habitat, survival, fecundity, movement, and population size data. In the third part, managers were asked about whether they felt SEIBMs would enhance their ability to manage species on their installation, and what factors would limit them from using SEIBMs. In addition to the multiple-choice questions, managers were given the opportunity to provide written comments (see Appendices A and B).

3.1.2. Results and discussion

We identified 27 managers at 26 installations (Table 1) who were responsible for restoring and managing habitat for threatened, endangered, or rare species (TERS) and willing to participate in the survey. Most habitat management conducted on participating installations involved restoring existing degraded habitat using prescribed burns, herbicides, and mechanical treatments (Figure 1a). Fewer installations attempted to create new habitat or acquire land to preserve habitat. Only a few attempted to create dispersal corridors. About a third of the installations reintroduced animals into habitat that had been created or restored.

When asked about management questions that need to be addressed, most managers indicated a need to know which habitat patches should be restored or managed to have the greatest impact on viability, and whether restoring all available habitat will improve viability (Figure 1b). Over half the managers also wanted to know where to locate new areas of habitat to ensure connectivity, whether restoration or creation of habitat would mitigate for the loss of suitable habitat, and whether viability is affected by the timing and frequency of disturbances used to manage habitat. Although only 7% of managers create corridors on their installations, 44% wanted to know if adding corridors would improve population viability. About a third of the managers wanted to know where animals should be reintroduced. Only 37% of managers indicated they were in a position where they needed to choose between alternative restoration strategies to meet management objectives. In addition, three managers who are trying to deter wildlife from entering airfields or firing ranges, asked if SEIBMs could predict whether restoring or creating habitat would draw animals away from areas of military use. One manager also wanted to know whether animals would use new habitat after it had been created.

Managers provided information on 25 monitoring data sets for animal wildlife species whose habitats were being restored or managed on 23 installations (Fort Bragg and Vandenberg AFB each provided information for two species, Table 1). Of these data sets, 12 were birds, six were insects, five were reptiles, and two were mammals. Nearly all installations (96%) collected data on population size, and 88% had habitat data in a GIS database (Figure 2a). Over half also collected demographic and movement data, and 48% had behavioral information on individual movement paths. Of the 12 bird data sets, seven were red-cockaded woodpecker (*Picoides borealis*), a species whose recovery efforts have been guided by SEIBMs since the late 1990s (USFWS 2003). Therefore, installations managing red-cockaded woodpeckers likely already collect the types of data necessary to parameterize an SEIBM. Likewise, since our research group is building SEIBMs for Fender's blue butterfly (*Icaricia icarioides fenderi*) and St. Francis' satyr (*Neonympha mitchellii francisci*), data sets for these species are also adequate for building SEIBMs. If we omit the red-cockaded woodpecker, Fender's blue butterfly, and St. Francis' satyr data sets to better reflect the typical amount of data a DoD manager is likely to possess, a slightly smaller proportion of the remaining 16 data sets on 15 installations possess the types of data to parameterize an SEIBM (Figure 2a), and the amount of population size data shifts downward, with the percentage of data sets with greater than 10 years of data decreasing from 52% to 25% (Figure 2b). However, most installations (81%) still had GIS databases of environmental variables that could be used to construct habitat maps (Figure 2a), and most data sets (69%) had more than 5 years of population size data. Approximately half of the installations collected multiple years of data on survival and reproductive success, and 44%

possessed radio telemetry or satellite tag data that could be used to estimate movement parameters.

Only six (22%) of the 27 managers surveyed had previous experience with SEIBMs and only one (Eglin AFB) was currently using an SEIBM to manage species on the installation (Figure 3). Nevertheless, 89% were open to the idea of using an SEIBM, with 33% responding that they definitely thought using an SEIBM would enhance their ability to manage habitat and 56% undecided. (Figure 3). The main factors that managers felt would prevent them from using SEIBMs (Figure 4) were lack of modeling experience (74%), lack of data (52%), and lack of resources to collect necessary data (52%). 30% of managers had doubts about the reliability of predictions, and 26% felt that the simpler decision-making methods they currently use were adequate. In these cases, methods were generally habitat-based and decisions depended more on practicality or needs of the military that were not related to viability of the species being managed. Only 7% of managers felt the types of questions that SEIBMs address were not relevant to management on DoD installations. A table of managers' written comments is provided in Appendix B.

After reviewing the questionnaires, we believe SEIBMs have potential for general application on military installations. Most questions typically addressed by SEIBMs are the same questions that the surveyed DoD managers take into consideration when making habitat management decisions; in particular, what is the impact of restoring habitat on population viability, and which patches have the greatest impact on viability? In addition, SEIBMs are capable of addressing two other questions brought up by military managers: whether animals will actually use habitat that has been newly created, and whether habitat can be created or restored in such a way to draw animals away from an area of military use. In fact, SEIBMs have previously been applied to similar questions. Kanagaraj et al. (2013) used an SEIBM to predict whether tigers will find and use corridors connecting habitat patches in India and Nepal, based on landscape context and individual movement behavior. In Japan, an SEIBM has been used to design a strategy of establishing "alternate feeding areas" to alleviate damage to wheat crops by white-fronted geese (Amano et al. 2007). Therefore, the types of questions that SEIBMs address have applicability to management of TERS habitat on military installations.

In general, the DoD managers surveyed were open to using SEIBMs, but their main concerns were that that simpler methods like habitat-based models are sufficient for their needs, that SEIBM data requirements are too high, that managers lack appropriate modeling experience, and that SEIBM predictions can't be trusted. Based on their answers, we conducted a literature review to address these concerns, using examples from working SEIBMs that are used to inform habitat management.

3.2 Literature review

3.2.1 Advantages of SEIBMs over other models

Simpler analytical models have been used to identify and rank habitat (Carroll et al. 2001, Johnson et al. 2004, Chetkiewicz and Boyce 2009), estimate minimum viable patch size (Rushton et al. 1999, Crone and Schultz 2003), and quantify connectivity (Schultz 1998, Flather and Bevers 2002). However, when populations respond to environmental change through individual behavior and vital rates, when species have complex life histories, when landscapes are fragmented or heterogeneous, or when specific questions need to be addressed for real landscapes, SEIBMs have advantages over their analytical counterparts for guiding decisions on habitat management.

When populations respond to environmental change through changes in individual behavior and vital rates, variation in individual response can influence population-level patterns of distribution and persistence (Revilla and Wiegand 2008, Baguette et al. 2013, Brown and Crone 2016a, Kautz et al. 2016). Therefore, analytical models that treat all individuals the same may be limited in their ability to predict population responses to habitat alteration. In contrast, SEIBMs can explicitly represent individual variation in vital rates (Wiegand et al. 2004, McRae et al. 2008), foraging behavior (DeAngelis et al. 1998, Bennett et al. 2009, Watkins et al. 2015) territory establishment (Elderd and Nott 2008, Heinrichs et al. 2010, Marucco and McIntire 2010) and movement (Revilla et al. 2004, Graf et al. 2007, Kanagaraj et al. 2013), and translate these individual-level mechanisms into population-level indices like connectivity, distribution, patch occupancy, and persistence (Revilla et al. 2004, McIntire et al. 2007, Nabe-Nielsen et al. 2010).

For species with complex dynamics, individual-based models have the flexibility to incorporate unique biological details like cooperative breeding (Letcher et al. 1998, Cooper et al. 2002), pack social structure (Pitt et al. 2003, Conner et al. 2008, Marucco and McIntire 2010), context-dependent dispersal (Stephens et al. 2002, Pietrek et al. In review), communal hibernation (Stephens et al. 2002), or group attack behavior (Kautz et al. 2016) that may be critical for predicting species response to environmental change or habitat management. When dynamics are driven by individual-level mechanisms, population-level patterns that emerge from the collective fates of simulated individuals have more closely represented population dynamics than predictions from analytical models (Carroll et al. 2003, Graf et al. 2007, Zeigler and Walters 2014). Furthermore, individual-based models can more easily incorporate behavior, which is critical for modeling species whose population dynamics are influenced by social structure (Zeigler and Walters 2014). For instance, for socially-structured species like red cockaded woodpeckers and wolves, subordinate individuals do not reproduce until the dominant individuals are dead or until the subordinates can establish their own territory. SEIBMs can model this behavior by setting fecundity of subordinate individuals to zero until the death of the dominant individual or until the subordinate finds a territory. For instance, in Letcher et al.'s (1998) red-cockaded woodpecker SEIBM, 19% of simulated male fledglings dispersed in their first year to become floaters and the rest remained in their natal territory to help raise their siblings. Both helpers and floaters had fecundities of zero. When a vacant territory became available, all floaters and helpers within a 3 km radius competed for the territory, and the winner was determined by a set of rules that arose from knowledge of the species' natural history. For instance, the closest male won and if there was a tie, helpers won over floaters. If both competitors were the same type, the oldest male won. Upon winning a territory, the helper or floater acquired the potential to become a breeder with a non-zero fecundity. It has been argued that because dynamics predicted by behavior-based models are the product of behavioral decisions that optimize fitness, rather than pre-determined demographic and dispersal rates, such models are more realistic than analytical models for describing how animals react to environmental change (Stephens et al. 2002, Goss-Custard et al. 2006).

Another advantage of SEIBMs is they explicitly describe the spatial arrangement of habitat in heterogeneous landscapes. This is an advantage over traditional population models that assume homogeneous environments, because viability in fragmented populations depends not only on demography, but on the ability of individuals to disperse between habitat patches (Turner et al. 1995, Nabe-Nielsen et al. 2010). Thus, SEIBMs are more appropriate for situations where changes in the amount and configuration of habitat have a greater impact on viability than stochastic changes in demographic rates, as Elderd and Nott (2008) found for the Cape Sable seaside sparrow. Because SEIBMs describe shape, size, and arrangement of habitat patches, they have been able to address habitat management questions that analytical models can't (Dunning et al. 1995, Letcher et al. 1998, Rushton et al. 1999, McIntire et al. 2007). Connectivity (Revilla et al. 2004, Carroll and Miquelle 2006, Revilla and Wiegand 2008, USFWS 2011, Kanagaraj et al. 2013, Watkins et al. 2015), allee effects (Lande 1987, Stephens et al. 2002), and source-sink dynamics (Pulliam et al. 1992, Heinrichs et al. 2010, Schumaker et al. 2014) are all properties that emerge from the synergy of demography, behavior, and landscape structure, so these questions are best answered with models that can simultaneously evaluate all three factors.

Finally, because of their ability to incorporate specific biological and landscape details, SEIBMs are well equipped to address specific questions in real landscapes (Rushton et al. 1999, Richards et al. 2004, Kanagaraj et al. 2013, Schumaker et al. 2014) and model realistic patterns of habitat degradation (Elderd and Nott 2008). For example, although simple analytical models indicated that most habitat patches available for restoration were too small or too isolated to support subpopulations of Fender's Blue Butterfly on their own, only an SEIBM was able to evaluate the conservation value of specific patches in the context of the actual landscape, and determine whether restoring the whole network of small and isolated patches could result in a connected and viable population (McIntire et al. 2007).

3.2.1a Advantages over habitat-based models

Below, we detail the advantages of SEIBMs over two specific types of models commonly used to guide habitat management decisions: habitat-based models and demographic matrix models (Table 2). Known by many names (*e.g.*, resource selection function, habitat suitability index, associative model, ecological niche model) habitat-based models are typically general linear models that use the relationship between habitat variables and species occurrence to predict species redistribution following habitat restoration. When linked to GIS data, they can explicitly describe the amount and spatial arrangement of suitable habitat on real landscapes. To extrapolate habitat suitability to predictions of species distribution, habitat-based approaches assume that habitat quality is a good surrogate for abundance or viability, which is not necessarily true. Simple relationships between habitat variables and species occurrence may work well to predict distributions of specialists that are closely associated to key environmental features (Meyer et al. 1998, Shirk et al. 2014). However, they are less reliable in situations where species are not strongly associated with key habitat features (Mitchell 1998, Tirpak et al. 2009, Rittenhouse et al. 2010), where the presence of a mobile species may indicate migrants rather than a viable population (Rushton et al. 1999, Marucco and McIntire 2010), or where individuals occur in sink habitats (Aldridge and Boyce 2007, Heinrichs et al. 2010).

Even if habitat-based models perfectly predict distribution of suitable habitat, they tend to overestimate the species' potential distribution, because they don't account for factors limiting individuals' ability to utilize all available habitat (Turner et al. 1995, Carroll et al. 2003, Johnson et al. 2004). By incorporating dispersal, demography, and behavior, SEIBMs increase the precision of predictions, because they narrow down where animals may potentially occur to where they are likely to persist given life history and dispersal abilities. For example, because habitat-based models do not include demography, they have been limited in assessing whether locations that appear to be suitable habitat actually support viable populations. 39% of the landscape predicted by a resource selection function to be suitable habitat for Ord's kangaroo rat was determined by an SEIBM to be sink habitat (Heinrichs et al. 2010). Because habitat-based models do not include behavior, they have failed to account for the effects of territoriality and social structure in limiting population size. An SEIBM predicted more realistic wolf densities in protected areas than a resource selection function, because the habitat-based model did not account for pack territoriality placing limits on density in high quality habitats (Carroll et al. 2003). Because habitat-based models do not include dispersal, they have difficulty assessing whether all potential habitat is accessible for colonization. SEIBMs have been able to narrow down distributions of habitat that individuals can actually access (Carroll et al. 2003, McRae et al. 2008). When Rushton et al. (1999) used a resource selection function to estimate minimum viable patch size for red squirrels, it was unable to distinguish conservation value among woodlands larger than 10 ha. An SEIBM likewise predicted that populations persisted in a range of woodland from 9-403 ha. However, given the set of demographic and dispersal parameters that best fit the population data, the SEIBM was able to narrow down the most likely minimum patch size to support a viable population to 46.2 – 56 ha.

Habitat-based models are typically derived from short term data and represent static relationships between animals and their environment. They are therefore limited in their ability to predict how those relationships change following habitat restoration (Pereira and Itami 1991, Rushton et al. 1997, Chetkiewicz and Boyce 2009). Because they are simulations, SEIBMs have the flexibility to use updated GIS data or landscape simulator submodels to advance the age of habitat in each cell (Liu 1993, McKelvey et al. 1993, Carroll et al. 2003, McRae et al. 2008), thus allowing the distribution of suitable and unsuitable habitat to change over time. For instance, the McRae et al. (2008) SEIBM integrated a forest dynamics simulator that projected a time series of forest composition maps. Their model was capable of simulating both the conversion of coniferous stands to early seral stages by forest harvest and conversion to older seral stages by succession, allowing them to explore future effects of climate change and forest management on distributions of songbirds. Thus, although SEIBMs require behavioral and demographic parameters that habitat-based models don't, their assumptions and predictions are more realistic.

3.2.1b Advantages over non-spatial demographic models

For conservation planning, demographic models usually take the form of an age- or stage-based projection matrix (Morris and Doak 2002). Models that only require demographic data are good at predicting relative population densities or growth rates at equilibrium (Stephens et al. 2002), or gaining insights about which life stages or vital rates contribute most to population growth (McKelvey et al. 1993, Heppell et al. 1994, Richards 2003). However, demographic models have been limited in their ability to accurately predict population dynamics when movement behavior is an integral component. Demographic matrices do not specify the spatial arrangement of habitat, and may overestimate population growth because they do not account for difficulties in finding suitable habitat or mates in fragmented landscapes (Lande 1987, Heppell et al. 1994, Stephens et al. 2002, Richards et al. 2004). SEIBMs, which incorporate spatial structure, have been found to be more appropriate for describing these dynamics (McKelvey et al. 1993, Letcher et al. 1998, Richards et al. 2004).

Dispersal has been incorporated into some stage-based matrices by using transition probabilities to describe movement of individuals between territories or habitat patches (McKelvey et al. 1993, Heppell et al. 1994, Stephens et al. 2002). However, transition probabilities have not produced realistic patterns of dispersal when the outcome depends on behavior and habitat arrangement. When movement is determined solely by probability, modeled individuals tend to disperse randomly to vacant territories regardless of location, instead of the more realistic pattern of dispersing to sites closer to the natal territory (McKelvey et al. 1993, Stephens et al. 2002, USFWS 2003, although see Hunter and Caswell 2005). This in turn causes the model to misrepresent predicted levels of reproductive success and dispersal mortality. Stephens et al. (2002) further found that in a system of communal hibernation where larger marmot groups retain more heat and therefore experience lower winter mortalities, the use of transition probabilities caused simulated individuals to make dispersal decisions that didn't make sense from a fitness perspective (*i.e.,* dispersing when vacant territories were sparse and remaining at the natal territory would increase survival for the individual and its siblings). In contrast, an SEIBM in which the decision to disperse was based on behaviors maximizing fitness outperformed demographic models in accurately predicting not only equilibrium densities, but also variation in population size, dispersal rates, winter mortality, and distributions of group sizes on the landscape.

SEIBMs also outperform demographic models in their ability to predict dynamics of socially structured populations. Because demographic matrices assume a fixed proportion of the population will breed, they can't capture how social populations in which subordinates quickly fill breeding vacancies can maintain a stable number of breeders, even when the population declines. Thus, they may overestimate extinction risk for small populations. Models that ignore social structure and assume all adults reproduce may also overestimate population growth of social species for which dominant breeders suppress fecundity of subordinates. For example, red-cockaded woodpeckers are "cooperative breeders" whose breeding groups include subordinate "helpers" that remain on the natal territory to help raise siblings and only breed if they can inherit the natal territory or disperse to an available adjacent territory (Walters et al. 1988). Social structure imposes reproductive constraints on helpers that can't acquire their own territories, especially in fragmented landscapes where subordinates are unable to disperse to vacant territories (Zeigler and Walters 2014). Stage-based matrices can incorporate social structure to some extent by modeling breeders and subordinates as separate classes with different fecundities (Heppell et al. 1994). These models have been shown to make reasonable predictions of population growth. However, for socially structured populations in fragmented habitats, an SEIBM that can incorporate both social and spatial structure is a better predictor of population size than simpler demographic or individual-based models. In the case of the red cockaded woodpecker, an SEIBM was determined to be more useful than a demographic matrix, because it could explicitly model distance to vacant territories and incorporate the social structure and movement behavior critical to describing dynamics of this species (Zeigler and Walters 2014). SEIBMs yielded the results that red-cockaded woodpeckers were surprisingly resilient to demographic (Letcher et al. 1998) and environmental (Walters et al. 2002) stochasticity due to the dynamic of cooperative breeding, but only if territories are aggregated enough so that a breeder that dies can be replaced quickly by a helper in the same or nearby territory. These insights led to Recovery Plan guidelines (USFWS 2003) that new habitat (recruitment clusters) should be placed within 3.2 km of existing clusters to increase population size. Largely as a result of these general management guidelines, red-cockaded woodpecker populations have met or exceeded recovery milestones (Ten Brink 2012, Helmuth 2014, Lammertink 2014).

3.2.2 Limitations of SEIBMs

3.2.2a Data limitations

Although an SEIBM's ability to describe complex dynamics is one of its greatest benefits, this complexity comes at the cost of a significant number of parameters. To assess how SEIBMs are parameterized and used in practice, we reviewed a set of SEIBMs used to guide habitat restoration or management for wildlife. This set of studies was compiled by searching Google Scholar for papers published between 2000-2015, using the terms "spatially explicit individual based model" and "spatially explicit population model". In addition, we included 3 SEIBMs known to us. Of approximately 26 SEIBMs we reviewed that were used to guide wildlife habitat management, the five that documented their parameter sets contained an average of 30 parameters (Table 3). Because of the large numbers of parameters, SEIBMs are vulnerable to error propagation (Conroy et al. 1995). For example, Liu et al. (1995) cautioned that their SEIBM's prediction, that the U.S. Forest Service could meet its goal of 115 Bachman's sparrow breeding pairs under current management, might be overly optimistic if juvenile survivorship was overestimated by just 10%. Also, Richards et al. (2004) found SEIBM predictions of crocodile population size, nest number, and young of year survival to be highly sensitive to variation in parameter estimates, suggesting that at least for this species, these parameters should be estimated within 1% accuracy.

Since fluctuations in population size can result in chance extinctions, models that don't account for stochasticity may underestimate extinction risk, especially for small populations (Morris and Doak 2002). Thus, managers wishing to build SEIBMs not only have to collect enough data to estimate parameters accurately and distinguish habitat-specific differences, but also collect data over a number of years to quantify their temporal variability. Multiple years of data are also desirable to validate models. Because extensive amounts of demographic and behavioral data can be difficult to obtain, it has been questioned whether it is feasible for managers to collect the data necessary to parameterize SEIBMs (Wennergren et al. 1995, Beissinger and Westphal 1998). Indeed, 52% of the DoD managers said lack of data would prevent them from building an SEIBM.

It should be noted that the absence of some of the empirical data needed to build an SEIBM does not necessarily preclude development of the model. For species that have been well studied, demographic data can sometimes be obtained from published studies (McKelvey et al. 1993, Stephens et al. 2002, Carroll et al. 2003, McRae et al. 2008). For example, Carroll et al. (2003) used survival and fecundity data from wolf packs in Alaska (Ballard et al. 1987), Minnesota (Fuller 1989), and Montana and British Columbia (Pletscher et al. 1997) to parameterize an SEIBM to predict wolf distribution and viability in Colorado. For species that are less well-studied, data from species or subspecies whose life histories or phylogenies are similar enough to the target species to be considered "surrogates" have been used (Cooper et al. 2002, Buenau and Gerber 2004, Hudgens et al. 2012). For example, Cooper et al. (2002) collected brown treecreeper field data for most of the demographic parameters needed for an SEIBM, but were missing data on dispersal speed and mortality. For these parameters, they used data from the red-cockaded woodpecker, which was deemed a reasonable surrogate because both bird species are cooperative breeders, cavity nesters, and insectivores.

Because SEIBM predictions can be sensitive to variability in parameter estimates, researchers must be cautious when substituting data from surrogate species or even a different population of conspecifics (Carroll et al. 2003, Schiegg et al. 2005, Rushton et al. 2006). For example, Rushton et al. (2006) demonstrated that an SEIBM overpredicted abundance of the endangered Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) when surrogate data from the non-endangered core population of red squirrels (*T. hudsonicus*) were used. A frequently used solution is to use the information available from field data, literature, and/or surrogates to estimate reasonable starting ranges of values for each unknown parameter. Within each range, parameter values are adjusted or "tuned" and model simulations are run, predicting the population growth trends that result from different combinations of parameter values (Carroll et al. 2003, Richards et al. 2004, Kramer-Schadt et al. 2005). Likelihood analysis is used to determine the set of estimated parameter values that are most likely to predict 5-10 years of observed population growth. This type of approach is referred to as "pattern-oriented modeling", and may even be used to estimate a best fit parameter set when data are completely lacking for multiple parameters (Stephens et al. 2002, Kramer-Schadt et al. 2007).

To give an idea of the amount of data used to build working SEIBMs, we summarized data collected for nine of the wildlife habitat management SEIBMs we reviewed (Table 4). The criteria for selection of this subset were that the SEIBMs were applied to decision-making for an actual habitat restoration project, and that they provide documentation or references for data used to parameterize the model.

Of the nine SEIBMs reviewed, all had enough data on variables such as vegetation, stand age, canopy cover, topography, soils, or hydrology to produce GIS maps of the study area that explicitly describe spatial distribution of habitat (Table 5). Seven indicated that population count data were available either to validate models or estimate unknown parameters with pattern-oriented modeling, and five of these data sets contained at least 10 years of data (Table 5). Six SEIBMs were parameterized with empirical survival data from the species of interest, mostly obtained from capture-recapture studies or monitoring of marked or radio-tagged individuals (Table 6). All of these survival data sets were age- or stage-specific, and two were habitat-specific. The amount of survival data varied widely, with sample sizes ranging from 16 to over 5000 individuals, and number of years of data ranging from 1 to 24 years. Of the three remaining SEIBMs, two (Bachman's sparrow, St. Francis' satyr) estimated survival using pattern-oriented modeling or surrogate data (see Table 6). For the third SEIBM (wood stork), mortality was imposed not by a predetermined rate but by whether an individual's energy reserves fell below a minimum threshold. Thus, this model did not require survival data *per se*. All SEIBMs were parameterized with empirical fecundity data from the target species, mostly gathered by observing nests or monitoring reproductive activities of marked individuals (Table 7). Only two fecundity data sets were age- or stage-specific and only two were habitat-specific. Studies ranged from 1 to 24 years, and sample sizes ranged from 24 nests to over 16,000 individuals.

Seven of the nine SEIBMs based their movement submodel on at least some field-collected data (Table 8). Four movement data sets (Cape Sable seaside sparrow, gray wolf, northern spotted owl, red-cockaded woodpecker) were obtained by tracking radio-marked individuals or recording locations of marked individuals. These types of studies ranged from less than one year with 31 individuals to 11 years and over 1000 individuals, and provided information on dispersal distances and probability of dispersal. Only one of these four studies (northern spotted owl) collected data on dispersal direction. Movement data for the two butterfly SEIBMs were collected by recording movement paths of individuals released in different habitats. These single-year studies had sample sizes of 42-606 individuals, and yielded fine scale data on habitat-specific move lengths and turn angles. For the St. Francis' satyr model, probabilities of crossing habitat boundaries were parameterized with habitat-specific data from the St. Francis' satyr and a surrogate species, the Appalachian brown butterfly. Resting times and habitat-specific move lengths and turn angles were estimated solely from individual flight paths of the surrogate species. Only two SEIBMs included field-collected estimates of dispersal mortality.

To explore whether managers possess sufficient data to build SEIBMs, we compared the data in Tables 4-7 against monitoring data collected for 16 species whose habitats are being restored or managed on 15 Department of Defense installations (Table 9). Data sets for red-cockaded woodpecker, St. Francis' satyr, and Fender's blue butterfly were omitted, because SEIBMs for these species were among the nine case studies listed in Table 4, and therefore the available data might be atypical of what the average manager would possess. Of the 16 remaining monitoring data sets, 81% had GIS databases of environmental variables that could be used to construct habitat maps. Most data sets (69%) had more than five years of population size data, and 25% had more than 10 years. Seven installations (44%) had conducted multi-year studies of survival on marked individuals, with three of those estimating habitat-specific survival. Nine data sets (59%) contained multiple years of information on reproductive success, with three containing habitat-specific data. Seven installations (44%) possessed radio telemetry or satellite tagging data that could be used to estimate some movement parameters.

Besides the installations that manage for red-cockaded woodpecker, St. Francis' satyr, and Fender's blue butterfly, four installations (Camp Shelby, U.S. Air Force Academy, Camp Grayling, and Fort Riley) currently seem to have sufficient data to consider building SEIBMs for the gopher tortoise, Preble's meadow jumping mouse, massasauga, and greater prairie chicken. However, other installations, although their data sets are incomplete, likely also have sufficient data. Most of the installations had sufficient habitat data to build maps. Although half the data sets lacked data to empirically estimate survival and fecundity, most had enough population size data to estimate these parameters using pattern-oriented modeling. The greatest data limitation would be the paucity of information on movement behavior. Although most of the working SEIBMs were parameterized with some empirical movement data, less than half the managers surveyed collected this type of data, probably due to differences in monitoring goals. Some analyses have suggested that uncertainty in dispersal parameters, especially dispersal mortality, may translate to large errors in SEIBM predictions (Wennergren et al. 1995, Ruckelshaus et al. 1997; but see Mooij and DeAngelis 1999, South 1999). Thus, managers wishing to build SEIBMs might focus more resources towards obtaining accurate estimates of dispersal capability and mortality.

3.2.2b Model complexity and cost

A second concern of managers was the complexity of coding the simulations. Building an SEIBM requires many decisions on factors such as spatial scale and resolution, species-habitat relationships, and behavioral rules. Due to the large number of decisions and processes involved, it can be easy to make mistakes in formulating the model (Macdonald and Rushton 2003). These structural errors can result in erroneous predictions, even when all parameters are estimated correctly (Conroy et al. 1995). 74% of managers surveyed said lack of modeling experience would prevent them from using an SEIBM.

However, limited modeling experience can be overcome by reaching out to researchers who specialize in ecological modeling. Such researchers have the ability to develop, code, and update SEIBMs, and are often interested in applying their skills to real life problems. Some researchers are consultants who contract their services (*e.g.*, www.langrailsback.com, https://www.fws.gov/rcwrecovery/rcw_model.html). Others are academics who may have access to funding and graduate students who are looking for applied projects on which to develop their skills. The most successful collaborations require close coordination between manager and modeler, so the modeler has the appropriate biological information and understanding of the system, and the manager understands interpretation of model outputs.

It is difficult to present a general cost estimate for data collection and model development for SEIBMs, because expense varies widely depending on complexity of the question to be addressed (and therefore the complexity of the model), level of expertise of the contractors, level of difficulty in collecting the necessary data for the species of interest, and amount of data already available from other sources. Cost will also depend on how sensitive the model predictions are to accurate parameter estimates, which in turn depends on the life history of the species of interest. With this caveat, we present some examples to give an idea of how much it can cost to develop an SEIBM.

The Fender's Blue Butterfly (FBB) SEIBM that is being developed by our research group addresses different habitat restoration questions for two different populations: the ideal frequency of controlled burns at Baskett Slough National Wildlife Refuge, and the source-sink dynamics resulting from creating new habitat adjacent to the FBB population at The Nature Conservancy's Willow Creek Reserve. Demographic, movement, and population count data for the Willow Creek population are available from prior surveys or ongoing monitoring. However, for Baskett Slough, these data need to be collected at multiple sites that reflect different burn frequencies. The estimated cost for five years of data collection and development of this SEIBM is approximately $920,000.

Our group is also developing an SEIBM to analyze how methods of wetland habitat restoration (hardwood removal vs inundation) and placement of restoration sites (close or far from extant colonies) influence population growth of the Saint Francis' satyr butterfly (SFS) on the Fort Bragg Army Base. Adult survival, population size, and movement data were collected at each restoration site, and cage experiments were conducted to estimate juvenile survival. The approximate cost for five years of data collection and development of this SEIBM is $532,000.

Both of these SEIBMs were developed with teams of academic experts that included university professors, postdoctoral researchers, and graduate students. It is possible that military installations could achieve data collection and model development at lower cost if their research needs could be framed in terms of a graduate student's dissertation project. It is also less expensive to build an SEIBM if much of the data can be collected through the installation's ongoing monitoring for the species of interest, and the installation only needs to pay for model development. For instance, the developers of the red-cockaded woodpecker SEIBM charge $6,500-$13,000 to use their model to analyze existing demographic and dispersal data to predict population trajectories, probability of territory abandonment, and probability of recruitment cluster occupation (https://www.fws.gov/rcwrecovery/rcw_model.html).

3.2.2c Reliability of SEIBM predictions

30% of the managers surveyed indicated that their reluctance to use SEIBMs stemmed from distrust in reliability of model predictions. Potential sources of error in SEIBMs are input error and structural error. SEIBMs include many parameters that are likely to be estimated with little or no data. For example, managers may not have access to data collected outside their installation. And as has been previously discussed, there may be problems with using data from surrogate species or other populations. Because of the large number parameters in an SEIBM, errors in parameter estimation may be compounded into significant errors in prediction (Ruckelshaus et al. 1997).

On the other hand, despite their complexity, SEIBMs are simplified versions of ecological systems that are even more complex. Therefore, even if parameters are estimated accurately, predictions can still be unreliable if the assumptions that go into structuring the model are incorrect, or if a critical dynamic is missing. For example, Rushton et al. (1999) under-predicted red squirrel distribution because their SEIBM didn't include the dynamic that squirrels can exist in woodlands too small to support viable populations by incorporating multiple patches into their home ranges, as long as patches are within dispersal distance.

Information on the reliability of SEIBM predictions has been largely unreported in the literature, because it is difficult to evaluate their success. First, predicted outcomes may take decades to be realized. For example, the Comprehensive Everglades Restoration Plan, whose development was informed by SEIBM results (DeAngelis et al. 1998) is expected to take over 30 years to complete. Furthermore, it is difficult to conclude statistically whether predictions from a stochastic model are "true" (Conroy et al. 1995, Rushton et al. 1997, Beissinger and Westphal 1998, McCarthy et al. 2001). However, "validation", the process of comparing primary model predictions (*e.g.,* population growth, population size) to data independent of those used to construct the model, can help assure that the SEIBM recreates dynamics well enough to make credible conservation decisions. Testing the validity of secondary predictions such as transition probabilities, population structure, or dispersal behavior further verifies that model assumptions are correct. Another test of the model's reliability that should especially be undertaken when using data that are not site- and species- specific, is to perform "sensitivity analyses" that test whether changing the value of parameter estimates by 10-25% drastically changes model predictions (Liu 1993, Cooper et al. 2002). Predictions that are robust to uncertainty in parameter estimates can lend more confidence to models that are parameterized with less than ideal data sets.

Of the eight published habitat restoration SEIBMs we reviewed, six reported that they validated primary predictions using between 4-23 years of population count data. One reported that they validated secondary predictions, and five reported that they performed sensitivity analysis (Table 10). The spotted owl SEIBM (USFWS 2011, Schumaker et al. 2014) was calibrated with population size and dispersal distance data, but we found no documentation that it was validated with independent data.

Critics have suggested that SEIBMs cannot predict population size with any degree of accuracy, because they cannot fully capture the complexity of systems that are poorly understood, and their results are sensitive to parameter uncertainty (Dunning et al. 1995, Liu et al. 1995, Beissinger and Westphal 1998, Conroy 2000). In some cases, it is true that validated SEIBMs failed to accurately predict population size (Stephens et al. 2002, Schiegg et al. 2005), and distribution (Rushton et al. 1997). On the other hand, SEIBMs have also proved capable of accurately recreating patterns of distribution (Liu 1993, Rushton et al. 1997, Carroll et al. 2003) and population trends (McIntire et al. 2007, Elderd and Nott 2008), in some cases predicting population size (Schiegg et al. 2005, Zeigler and Walters 2014) or density (Stephens et al. 2002) within 5% of observed values.

Fewer studies have validated secondary predictions that emerge from the SEIBM's foundation of rules and assumptions. However, SEIBMs have been shown to accurately predict a number of secondary outputs, including dispersal behavior, winter mortality, age distribution of breeders, group size distribution, and rates of turnover for dominant individuals (Stephens et al. 2002, Schiegg et al. 2005). Because these secondary outputs are products of multiple parameters and processes, their accurate prediction verify that the model's underlying structure and levels of stochasticity are realistic (Beissinger and Westphal 1998). Such validation provides added assurance that even when SEIBMs are imperfect at forecasting specific outcomes, their predictions are robust enough to be used for ranking relative outcomes of alternative management plans (Richards et al. 2004, Schiegg et al. 2005, Carroll et al. 2006, USFWS 2011, White et al. 2016).

In some cases (Macdonald and Rushton 2003, Carroll et al. 2006), sensitivity analyses have demonstrated that SEIBMs are robust enough to make credible conservation decisions despite parameter uncertainty. However, other sensitivity analyses (Liu et al. 1995, Richards et al. 2004, Rushton et al. 2006, Bennett et al. 2009) have shown that SEIBM predictions are highly sensitive to the values input for one or more parameters. Although these latter results seem to be failures, they are useful for identifying field work that should be undertaken to estimate more sensitive parameters with greater accuracy. Likewise, validation failure can help improve model performance by identifying the SEIBM's structural errors (Schiegg et al. 2005). Thus, the SEIBM's value lies not only in its ability to assess relative effectiveness of alternate management options, but in the process of organizing known information to build the model, testing it to identify which assumptions are correct or incorrect, conducting further research to fill knowledge gaps, refining the model with new information, and testing again. When treated as components of long term adaptive management programs rather than short term predictive tools, SEIBMs have improved understanding of complex systems and been instrumental in guiding decision-making.

An example of an SEIBM that has been used iteratively in a long-term process to develop a conservation plan is the model developed for red squirrels in the UK. Rushton et al. (1997) built an SEIBM to test the hypothesis that decline of the native red squirrel in Norfolk could be attributed to competition with the American gray squirrel. Starting with values from the literature, they used pattern-oriented modeling to estimate demographic and movement parameters that best predicted historical population trends. The SEIBM was reasonably capable of replicating historical change in squirrel distributions, but some mismatches indicated areas where the model could be improved. For instance, the authors suggested that saturation dispersal would be more realistic if patch carrying capacity were based on food availability rather than the number of core ranges that would fit within the patch. Also, carrying capacity, survival, and fecundity should be linked to temporal variability in food availability. Data available at the time did not allow them to distinguish between conifer species that differ in quality as food sources, so their model assumed all conifer woodland was of equal quality, and applied average vital rates from the literature to all patches.

Lurz et al. (2003) expanded the SEIBM to include a dynamic seed crop submodel that predicted annual seed crop quality for each forest sub-compartment based on tree age and composition, and linked vital rates to seed crop quality. This SEIBM predicted that current timber operations on Kidland Forest would result in significant loss of cone-bearing trees before restocked trees could mature, leading to possible extirpation of the red squirrel population. These results led the Forestry Commission to retain 180 ha of forest, after the SEIBM verified this plan would likely allow red squirrels to persist through the next forest rotation. Although it is too soon to conclusively state whether the revised management was successful, Parrott et al. (2009) reported that monitoring data from Kidland Forest detected no adverse effects of harvest operations on red squirrel population size.

White et al. (2016) further revised the SEIBM to inform future management of Kidland and Uswayford forests. They refined the method for calculating carrying capacity for each forest compartment, basing it on area, forest composition, and published estimates of squirrel abundance for each tree species in good and bad years. Thus, the model could simulate change in carrying capacity over time as trees were harvested and restocked. Population predictions from this SEIBM were well supported by monitoring data from Kidland Forest. The model predicted that under the Forestry Commission's proposed future harvest and restocking schedule (scenario A), carrying capacity in both forests would be poor in 10 years and squirrel populations would decline. The Kidland population would recover as trees matured, but the Uswayford population had a 65-85% chance of extirpation. The model further predicted that extinction risk could be reduced by adjusting the harvest schedule so carrying capacity wasn't simultaneously low in both forests, and improving connectivity between forests. These results led the Forestry Commission to develop three new plans: scenario B, which delayed the Uswayford harvest so it didn't occur at the same time as the Kidland harvest; scenario C, which delayed the Uswayford harvest, reduced harvest in Kidland, and restocked with a mix of trees that support higher squirrel densities; and scenario D, which was the same as C but restocked with Sitka spruce – a less costly species that supports fewer squirrels. White et al. (2016) compared squirrel viability under these three options, with and without a corridor linking the forests, and concluded that scenarios C and D provided the most viable habitat for squirrels, with a corridor improving viability under all scenarios. Scenario C supported the highest total abundance of squirrels. However, the more economical scenario D, while supporting a slightly lower total abundance than C, had the lowest extinction risk for Uswayford. This case study serves both as an example of the iterative process over which a SEIBM is developed and improved, and how SEIBMs can inform management decisions by providing repeatable, science-based predictions on the relative outcomes of alternate strategies.

4. Conclusion

The predictive abilities of SEIBMs are not perfect. A few have proved capable of making extremely accurate predictions but for the most part, the systems modeled have either been too complex for SEIBMs to fully capture their dynamics, or too variable for predictions to be robust. Yet, even if SEIBMs cannot predict the exact outcomes of management (*i.e*., will the population reach a certain size if plan A is implemented), they can improve understanding of what *could* happen if model assumptions were true, and compare relative outcomes among management options (*i.e.*, is the population more likely to reach a certain size if plan A is implemented vs. no restoration). SEIBMs are uniquely suited for describing complex life histories in which dynamics may be driven by individual variation or context-dependent behavior, and persistence depends on a synergy between demography, behavior, dispersal ability, and landscape structure. Under these conditions, SEIBMs have outperformed simpler methods for addressing habitat management questions. Thus, they have been well suited for modeling small populations that are disproportionately affected by variation in individual behavior or demography, social species whose population dynamics are driven by behavior, and fragmented populations whose size is limited by dispersal or carrying capacity rather than vital rates. SEIBMs have proven robust enough for comparative studies, making them a scientifically defensible method for ranking proposed management alternatives when decisions can't be informed empirically. For example, after peer reviewers rejected the 2008 Northern Spotted Owl recovery plan for being based on stakeholder interests rather than science, the U.S. Fish and Wildlife Service (USFWS 2011) incorporated an SEIBM into the revised plan, citing it as the best available science for evaluating the effect of potential threats to owl viability.

Lack of modeling experience or resources for data collection are not insurmountable obstacles to using SEIBMs to guide habitat management, if managers collaborate with researchers specializing in ecological modeling. Still, the cost of data collection and model development may limit military use of SEIBMs to situations where maintaining viability of the species is vital to the military mission and thus justifies the expense. This was the case for the red-cockaded woodpecker, whose status as an endangered species threatened to restrict military training on bases with longleaf pine forests, unless habitat could be managed to increase woodpecker populations to meet USFWS recovery goals.

Despite their heavy data requirements, pattern-oriented modeling allows SEIBMs to be constructed even with incomplete data sets. Early predictions should be interpreted with caution. However, if primary and secondary predictions are validated with independent data, and sensitivity analyses are conducted to ensure that parameter uncertainty does not affect relative predictions, SEIBMs are capable of ranking management plans even with relatively sparse data. Thus, we encourage managers who are interested in using SEIBMs to reach out to a modeler, even if data are sparse and little is known about the system. What information is known about the system can be integrated into a modeling framework, and the process of validation and sensitivity analysis will indicate the most critical knowledge gaps and how accurately data need to be collected. With each iteration of data collection, updating, and validating the model, new insights will be learned and model predictions will become more refined. Answers to complex problems do not come quickly and in many situations, simpler approaches will suffice to address the management question of interest. However, when viewed as part of a long term, ongoing process, SEIBMs have proven they can be reliable and useful tools for increasing understanding of complex population dynamics and enhancing the ability of managers to effectively restore and manage habitat.

5. Literature cited

Aldridge, C. L., and M. S. Boyce. 2007. Linking Occurrence and Fitness to Persistence: Habitat-Based Approach for Endangered Greater Sage-Grouse. Ecological Applications **17**:508-526.

Amano, T., K. Ushiyama, G. O. Fujita, and H. Higuchi. 2007. Predicting grazing damage by white-fronted geese under different regimes of agricultural management and the physiological consequences for the geese. Journal of Applied Ecology **44**:506-515.

Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos:355-366.

Aschehoug, E. T., F. S. Sivakoff, H. L. Cayton, W. F. Morris, and N. M. Haddad. 2015. Habitat restoration affects immature stages of a wetland butterfly through indirect effects on predation. Ecology **96**:1761-1767.

Baguette, M., S. Blanchet, D. Legrand, V. M. Stevens, and C. Turlure. 2013. Individual dispersal, landscape connectivity and ecological networks. Biological Reviews **88**:310-326.

Ballard, W. B., J. S. Whitman, and C. L. Gardner. 1987. Ecology of an exploited wolf population in south-central Alaska. Wildlife Monographs:3-54.

Beissinger, S. R., and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. Journal of Wildlife Management **62**:821-841.

Bennett, V. J., M. Beard, P. A. Zollner, E. Fernandez-Juricic, L. Westphal, and C. L. LeBlanc. 2009. Understanding wildlife responses to human disturbance through simulation modelling: a management tool. Ecological Complexity **6**:113-134.

Brooks, T. M., R. A. Mittermeier, C. G. Mittermeier, G. A. B. Da Fonseca, A. B. Rylands, W. R. Konstant, P. Flick, J. Pilgrim, S. Oldfield, G. Magin, and C. Hilton-Taylor. 2002. Habitat Loss and Extinction in the Hotspots of Biodiversity. Conservation Biology **16**:909-923.

Brown, L. M., and E. E. Crone. 2016a. Individual variation changes dispersal distance and area requirements of a checkerspot butterfly. Ecology **97**:106-115.

Brown, L. M., and E. E. Crone. 2016b. Minimum area requirements for an at-risk butterfly based on movement and demography. Conservation Biology **30**:103-112.

Brown, L. M., R. K. Fuda, N. Schtickzelle, H. Coffman, A. Jost, A. Kazberouk, E. Kemper, E. Sass, and E. E. Crone. 2017. Using animal movement behavior to categorize land cover and predict consequences for connectivity and patch residence times. Landscape Ecology **32**:1657-1670.

Carroll, C., and D. G. Miquelle. 2006. Spatial viability analysis of Amur tiger *Panthera tigris altaica* in the Russian Far East: the role of protected areas and landscape matrix in population persistence. Journal of Applied Ecology **43**:1056-1068.

Carroll, C., R. F. Noss, and P. C. Paquet. 2001. Carnivores as focal species for conservation planning in the Rocky Mountain region. Ecological Applications **11**:961-980.

Carroll, C., M. K. Phillips, C. A. Lopez-Gonzalez, and N. H. Schumaker. 2006. Defining Recovery Goals and Strategies for Endangered Species: The Wolf as a Case Study. BioScience **56**:25-37.

Carroll, C., M. K. Phillips, N. H. Schumaker, and D. W. Smith. 2003. Impacts of Landscape Change on Wolf Restoration Success: Planning a Reintroduction Program Based on Static and Dynamic Spatial Models. Conservation Biology **17**:536-548.

Chetkiewicz, C. L. B., and M. S. Boyce. 2009. Use of resource selection functions to identify conservation corridors. Journal of Applied Ecology **46**:1036-1047.

Conner, M. M., M. R. Ebinger, and F. F. Knowlton. 2008. Evaluating coyote management strategies using a spatially explicit, individual-based, socially structured population model. Ecological Modelling **219**:234-247.

Conroy, M. J. 2000. An adaptive approach to habitat management for migratory birds in the southeastern United States. Pages Pp. 63-69 *in* R. Bonney, D. N. Pashley, R. J. Cooper, and L. Niles, editors. Strategies for Bird Conservation: the Partners in Flight planning process; Proceedings of the 3rd Partners in Flight Workshop; 1995 October 1-5; Cape May, NJ. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT.

Conroy, M. J., Y. Cohen, F. C. James, Y. G. Matsinos, and B. A. Maurer. 1995. Parameter estimation, reliability, and model improvement for spatially explicit models of animal populations. Ecological Applications **5**:17-19.

Cooper, C. B., J. R. Walters, and J. Priddy. 2002. Landscape patterns and dispersal success: simulated population dynamics in the brown treecreeper. Ecological Applications **12**:1576-1587.

Crone, E., and C. Schultz. 2003. Movement behavior and minimum patch size for butterfly population persistence. Pages 561-576 *in* C. Boggs, P. Ehrlich, and W. Watt, editors. Butterflies: ecology and evolution taking flight. University of Chicago Press, Chicago.

Crowder, L.B., J.A. Priddy, and J.R. Walters. 1998. Demographic isolation of red-cockaded woodpecker groups: a model analysis. USFWS Project Final Report. Duke University Marine Laboratory, Beaufort, NC and Virginia Polytechnic Institute and State University, Blackburg, VA.

DeAngelis, D. L., L. J. Gross, M. A. Huston, W. F. Wolff, D. M. Fleming, E. J. Comiskey, and S. M. Sylvester. 1998. Landscape modeling for Everglades ecosystem restoration. Ecosystems **1**:64-75.

Dunning, J. B., D. J. Stewart, B. J. Danielson, B. R. Noon, T. L. Root, R. H. Lamberson, and E. E. Stevens. 1995. Spatially explicit population models: current forms and future uses. Ecological Applications **5**:3-11.

Dunning Jr, J. B., B. J. Danielson, B. D. Watts, L. Liu, and D. G. Krementz. 2000. Studying wildlife at local and landscape scales: Bachman's Sparrows at the Savannah River Site. Studies in Avian Biology **21**:75-80.

Elderd, B., and M. P. Nott. 2008. Hydrology, habitat change and population demography: an individual-based model for the endangered Cape Sable seaside sparrow *Ammodramus maritimus mirabilis*. Journal of Applied Ecology **45**:258-268.

Fahrig, L. 2001. How much habitat is enough? Biological Conservation **100**:65-74.

Flather, C. H., and M. Bevers. 2002. Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. The American Naturalist **159**:40-56.

Fleming, D. M., W. F. Wolff, and D. L. DeAngelis. 1994. Importance of landscape heterogeneity to wood storks in Florida Everglades. Environ Manage **18**:743-757.

Forsman, E. D. 2011. Population Demography of Northern Spotted Owls. University of California Press, Berkeley, CA.

Forsman, E. D., R. G. Anthony, J. A. Reid, P. J. Loschl, S. G. Sovern, M. Taylor, B. L. Biswell, A. Ellingson, E. C. Meslow, and G. S. Miller. 2002. Natal and breeding dispersal of northern spotted owls. Wildlife Monographs:1-35.

Fuller, T. K. 1989. Population Dynamics of Wolves in North-Central Minnesota. Wildlife Monographs:3-41.

Goss-Custard, J. D., N. H. Burton, N. A. Clark, P. N. Ferns, S. McGrorty, C. J. Reading, M. M. Rehfisch, R. A. Stillman, I. Townend, and A. D. West. 2006. Test of a behavior-based individual-based model: response of shorebird mortality to habitat loss. Ecological Applications **16**:2215-2222.

Graf, R. F., S. Kramer-Schadt, N. Fernández, and V. Grimm. 2007. What you see is where you go? Modeling dispersal in mountainous landscapes. Landscape Ecology **22**:853-866.

Grimm, V., and S. F. Railsback. 2013. Individual-based modeling and ecology. Princeton university press.

Heinrichs, J. A., D. J. Bender, D. L. Gummer, and N. H. Schumaker. 2010. Assessing critical habitat: evaluating the relative contribution of habitats to population persistence. Biological Conservation **143**:2229-2237.

Helmuth, L. 2014. Species worth saving: why we should be thankful for the red-cockaded woodpecker. Slate Magazine, http://www.slate.com/articles/health_and_science/science/2014/11/red_cockaded_woodpecker_recovery_success_thankful_for_endangered_species.html.

Heppell, S. S., J. R. Walters, and L. B. Crowder. 1994. Evaluating management alternatives for red-cockaded woodpeckers: a modeling approach. The Journal of Wildlife Management **58**:479-487.

Himes Boor, G. K., C. B. Schultz, E. E. Crone, and W. F. Morris. *In review*. Mechanism matters: the cause of fluctuations in boom-bust populations governs optimal habitat restoration strategy. Ecological Applications.

Hudgens, B. R., W. F. Morris, N. M. Haddad, W. R. Fields, J. W. Wilson, D. Kuefler, and T. Jobe. 2012. How complex do models need to be to predict dispersal of threatened species through matrix habitats? Ecological Applications **22**:1701-1710.

Hunter, C. M., and H. Caswell. 2005. The use of the vec-permutation matrix in spatial matrix population models. Ecological Modelling **188**:15-21.

Johnson, C. J., D. R. Seip, and M. S. Boyce. 2004. A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. Journal of Applied Ecology **41**:238-251.

Kahl, M. P. 1964. Food Ecology of the Wood Stork (Mycteria americana) in Florida. Ecological Monographs **34**:97-117.

Kanagaraj, R., T. Wiegand, S. Kramer-Schadt, and S. P. Goyal. 2013. Using individual-based movement models to assess inter-patch connectivity for large carnivores in fragmented landscapes. Biological Conservation **167**:298-309.

Kautz, M., M. A. Imron, K. Dworschak, and R. Schopf. 2016. Dispersal variability and associated population-level consequences in tree-killing bark beetles. Movement ecology **4**:9.

Kostova, T., T. Carlsen, and J. Kercher. 2004. Individual-based spatially-explicit model of an herbivore and its resource: the effect of habitat reduction and fragmentation. Comptes Rendus Biologies **327**:261-276.

Kramer-Schadt, S., E. Revilla, and T. Wiegand. 2005. Lynx reintroductions in fragmented landscapes of Germany: Projects with a future or misunderstood wildlife conservation? Biological Conservation **125**:169-182.

Kramer-Schadt, S., E. Revilla, T. Wiegand, and V. Grimm. 2007. Patterns for parameters in simulation models. Ecological Modelling **204**:553-556.

Lamberson, R. H., R. McKelvey, B. R. Noon, and C. Voss. 1992. A dynamic analysis of northern spotted owl viability in a fragmented forest landscape. Conservation Biology **6**:505-512.

Lammertink, M. 2014. Trends in threat status and priorities in conservation of the woodpeckers of the world. Acta Ornithologica **49**:207-219.

Lande, R. 1987. Extinction thresholds in demographic models of territorial populations. The American Naturalist **130**:624-635.

Letcher, B. H., J. A. Priddy, J. R. Walters, and L. B. Crowder. 1998. An individual-based, spatially-explicit simulation model of the population dynamics of the endangered red-cockaded woodpecker, *Picoides borealis*. Biological Conservation **86**:1-14.

Liu, J. 1993. ECOLECON: An ECOLogical-ECONomic model for species conservation in complex forest landscapes. Ecological Modelling **70**:63-87.

Liu, J., J. B. Dunning, and H. R. Pulliam. 1995. Potential effects of a forest management plan on Bachman's sparrows (*Aimophila aestivalis*): linking a spatially explicit model with GIS. Conservation Biology **9**:62-75.

Lockwood, J. L., H. F. Katherine, J. L. Curnutt, D. Rosenthal, K. L. Balent, and A. L. Mayer. 1997. Life History of the Endangered Cape Sable Seaside Sparrow. The Wilson Bulletin **109**:720-731.

Lurz, P., N. Geddes, A. Lloyd, M. Shirley, S. Rushton, and B. Burlton. 2003. Planning a red squirrel conservation area: using a spatially explicit population dynamics model to predict the impact of felling and forest design plans. Forestry **76**:95-108.

Macdonald, D. W., and S. Rushton. 2003. Modeling space use and dispersal of mammals in real landscapes: a tool for conservation. Journal of Biogeography **30**:607-620.

Marucco, F., and E. McIntire. 2010. Predicting spatio-temporal recolonization of large carnivore populations and livestock depredation risk: wolves in the Italian Alps. Journal of Applied Ecology **47**:789-798.

McCarthy, M. A., H. P. Possingham, J. R. Day, and A. Tyre. 2001. Testing the accuracy of population viability analysis. Conservation Biology **15**:1030-1038.

McIntire, E. J. B., C. B. Schultz, and E. E. Crone. 2007. Designing a network for butterfly habitat restoration: where individuals, populations and landscapes interact. Journal of Applied Ecology **44**:725-736.

McKelvey, K., B. Noon, and R. Lamberson. 1993. Conservation planning for species occupying fragmented landscapes: the case of the northern spotted owl. Pages 424-450 *in* P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. Biotic Interactions and Global Change. Sinauer Assoc. Inc., Sunderland, MA.

McRae, B. H., N. H. Schumaker, R. B. McKane, R. T. Busing, A. M. Solomon, and C. A. Burdick. 2008. A multi-model framework for simulating wildlife population response to land-use and climate change. Ecological Modelling **219**:77-91.

Meyer, J. S., L. L. Irwin, and M. S. Boyce. 1998. Influence of habitat abundance and fragmentation on northern spotted owls in western Oregon. Wildlife Monographs **139**:3-51.

Mitchell, W. A. 1998. Species Profile: Bachman's Sparrow (*Aimophila aestivalis*) on Military Installations in the Southeastern United States. Technical Report SERDP-98-11, US Army Corps of Engineers Waterways Experiment Station, Vicksburg, MS.

Mooij, W.F. and D.L. DeAngelis. 1999. Error propagation in spatially explicit population models: a reassessment. Conservation Biology 13(4):930-933.

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Sunderland, Mass.

Nabe-Nielsen, J., R. M. Sibly, M. C. Forchhammer, V. E. Forbes, and C. J. Topping. 2010. The effects of landscape modifications on the long-term persistence of animal populations. PLoS One **5**:e8932.

Parrott, D., R. Quy, K. Van Driel, P. Lurz, S. Rushton, J. Gurnell, N. Aebischer, and J. Reynolds. 2009. Review of red squirrel conservation activity in northern England. Natural England Commissioned Report NECR019. Natural England, Sheffield UK. 111 pp.

Pereira, J. M. C., and R. M. Itami. 1991. GIS-based habitat modeling using logistic multiple regression: A study of the Mt. Graham red squirrel. Photogrammetric engineering and remote sensing **57**:1475-1486.

Pietrek, A. G., G. K. Himes Boor, and W. F. Morris. In review. Doomed to failure: Using "culling zones" to manage biological invasions in the face of long distance dispersal. Biodiversity & Conservation.

Pitt, W. C., P. W. Box, and F. F. Knowlton. 2003. An individual-based model of canid populations: modelling territoriality and social structure. Ecological Modelling **166**:109-121.

Pletscher, D. H., R. R. Ream, D. K. Boyd, M. W. Fairchild, and K. E. Kunkel. 1997. Population Dynamics of a Recolonizing Wolf Population. The Journal of Wildlife Management **61**:459-465.

Pulliam, H. R., J. B. Dunning, and J. Liu. 1992. Population dynamics in complex landscapes: a case study. Ecological Applications **2**:165-177.

Revilla, E., and T. Wiegand. 2008. Individual movement behavior, matrix heterogeneity, and the dynamics of spatially structured populations. Proceedings of the National Academy of Sciences **105**:19120-19125.

Revilla, E., T. Wiegand, F. Palomares, P. Ferreras, and M. Delibes. 2004. Effects of matrix heterogeneity on animal dispersal: from individual behavior to metapopulation-level parameters. The American Naturalist **164**:E130-E153.

Richards, P. 2003. Evaluating the relative effects of life history stages in the conservation of the American crocodile (*Crocodylus acutus*) in Florida. Florida Scientist **66**:273-286.

Richards, P. M., W. M. Mooij, and D. L. DeAngelis. 2004. Evaluating the effect of salinity on a simulated American crocodile (*Crocodylus acutus*) population with applications to conservation and Everglades restoration. Ecological Modelling **180**:371-394.

Rittenhouse, C. D., F. R. Thompson III, W. D. Dijak, J. J. Millspaugh, and R. L. Clawson. 2010. Evaluation of habitat suitability models for forest passerines using demographic data. Journal of Wildlife Management **74**:411-422.

Ruckelshaus, M., C. Hartway, and P. Kareiva. 1997. Assessing the data requirements of spatially explicit dispersal models. Conservation Biology **11**:1298-1306.

Rushton, S., P. Lurz, R. Fuller, and P. Garson. 1997. Modelling the distribution of the red and grey squirrel at the landscape scale: a combined GIS and population dynamics approach. Journal of Applied Ecology **34**:1137-1154.

Rushton, S., P. Lurz, A. South, and A. Mitchell-Jones. 1999. Modelling the distribution of red squirrels (*Sciurus vulgaris*) on the Isle of Wight. Animal Conservation **2**:111-120.

Rushton, S., D. Wood, P. Lurz, and J. Koprowski. 2006. Modelling the population dynamics of the Mt. Graham red squirrel: Can we predict its future in a changing environment with multiple threats? Biological Conservation **131**:121-131.

Schiegg, K., J. R. Walters, and J. A. Priddy. 2005. Testing a spatially explicit, individual-based model of red-cockaded woodpecker populaiton dynamics. Ecological Applications **15**:1495-1503.

Schipper, J., J. S. Chanson, F. Chiozza, N. A. Cox, M. Hoffmann, V. Katariya, J. Lamoreux, A. S. L. Rodrigues, S. N. Stuart, H. J. Temple, J. Baillie, L. Boitani, T. E. Lacher, R. A. Mittermeier, A. T. Smith, D. Absolon, J. M. Aguiar, G. Amori, N. Bakkour, R. Baldi, R. J. Berridge, J. Bielby, P. A. Black, J. J. Blanc, T. M. Brooks, J. A. Burton, T. M. Butynski, G. Catullo, R. Chapman, Z. Cokeliss, B. Collen, J. Conroy, J. G. Cooke, G. A. B. da Fonseca, A. E. Derocher, H. T. Dublin, J. W. Duckworth, L. Emmons, R. H. Emslie, M. Festa-Bianchet, M. Foster, S. Foster, D. L. Garshelis, C. Gates, M. Gimenez-Dixon, S. Gonzalez, J. F. Gonzalez-Maya, T. C. Good, G. Hammerson, P. S. Hammond, D. Happold, M. Happold, J. Hare, R. B. Harris, C. E. Hawkins, M. Haywood, L. R. Heaney, S. Hedges, K. M. Helgen, C. Hilton-Taylor, S. A. Hussain, N. Ishii, T. A. Jefferson, R. K. B. Jenkins, C. H. Johnston, M. Keith, J. Kingdon, D. H. Knox, K. M. Kovacs, P. Langhammer, K. Leus, R. Lewison, G. Lichtenstein, L. F. Lowry, Z. Macavoy, G. M. Mace, D. P. Mallon, M. Masi, M. W. McKnight, R. A. Medellín, P. Medici, G. Mills, P. D. Moehlman, S. Molur, A. Mora, K. Nowell, J. F. Oates, W. Olech, W. R. L. Oliver, M. Oprea, B. D. Patterson, W. F. Perrin, B. A. Polidoro, C. Pollock, A. Powel, Y. Protas, P. Racey, J. Ragle, P. Ramani, G. Rathbun, R. R. Reeves, S. B. Reilly, J. E. Reynolds, C. Rondinini, R. G. Rosell-Ambal, M. Rulli, A. B. Rylands, S. Savini, C. J. Schank, W. Sechrest, C. Self-Sullivan, A. Shoemaker, C. Sillero-Zubiri, N. De Silva, D. E. Smith, C. Srinivasulu, P. J. Stephenson, N. van Strien, B. K. Talukdar, B. L. Taylor, R. Timmins, D. G. Tirira, M. F. Tognelli, K. Tsytsulina, L. M. Veiga, J.-C. Vié, E. A. Williamson, S. A. Wyatt, Y. Xie, and B. E. Young. 2008. The Status of the World's Land and Marine Mammals: Diversity, Threat, and Knowledge. Science **322**:225-230.

Schultz, C. B. 1998. Dispersal behavior and its implications for reserve design in a rare Oregon butterfly. Conservation Biology **12**:284-292.

Schultz, C. B., and E. E. Crone. 2001. Edge-mediated dispersal behavior in a prairie butterfly. Ecology **82**:1879-1892.

Schumaker, N. H. 1998. A users guide to the PATCH model. National Health and Environmental Effects Research Laboratory, Office of Research and Development, US Environmental Protection Agency.

Schumaker, N. H., A. Brookes, J. R. Dunk, B. Woodbridge, J. A. Heinrichs, J. J. Lawler, C. Carroll, and D. LaPlante. 2014. Mapping sources, sinks, and connectivity using a simulation model of northern spotted owls. Landscape Ecology **29**:579-592.

Shaffer, M. L. 1981. Minimum Population Sizes for Species Conservation. BioScience **31**:131-134.

Shirk, A. J., M. G. Raphael, and S. A. Cushman. 2014. Spatiotemporal variation in resource selection: insights from the American marten (*Martes americana*). Ecological Applications **24**:1434-1444.

Sivakoff, F. S., W. F. Morris, E. T. Aschehoug, B. R. Hudgens, and N. M. Haddad. 2016. Habitat restoration alters adult butterfly morphology and potential fecundity through effects on host plant quality. Ecosphere **7**:e01522-n/a.

South, A. 1999. Dispersal in Spatially Explicit Population Models. Conservation Biology 13(5):1039-1046.

Stephens, P. A., F. Frey-roos, W. Arnold, and W. J. Sutherland. 2002. Model complexity and population predictions. The alpine marmot as a case study. Journal of Animal Ecology **71**:343-361.

Ten Brink, C. 2012. USMC's Camp Lejeune Red-Cockaded Woodpecker Recovery. LiveBetter magazine, http://livebettermagazine.com/article/usmcs-camp-lejeune-red-cockaded-woodpecker-recovery/.

Tirpak, J. M., D. T. Jones-Farrand, F. R. Thompson III, D. J. Twedt, C. K. Baxter, J. A. Fitzgerald, and W. B. Uihlein III. 2009. Assessing ecoregional-scale habitat suitability index models for priority landbirds. Journal of Wildlife Management **73**:1307-1315.

Turner, M. G., G. J. Arthaud, R. T. Engstrom, S. J. Hejl, J. Liu, S. Loeb, and K. McKelvey. 1995. Usefulness of spatially explicit population models in land management. Ecological Applications **5**:12-16.

USFWS. 2003. Red-cockaded Woodpecker (*Picoides borealis*) Recovery Plan: Second Revision. US Fish and Wildlife Service, Atlanta, GA.

USFWS. 2011. Revised recovery plan for the northern spotted owl (*Strix occidentalis caurina*). U.S. Fish and Wildlife Service. xvi+258 pp, Portland, Oregon, USA.

Walters, J. R., P. Baldassaro, K. M. Convery, R. McGregor, L. B. Crowler, J. A. Priddy, D. C. Kessler, and S. A. Tweddale. 2011. A decision support system for identifying and ranking critical habitat parcels on and in the vicinity of Department of Defense installations (RC-1472). Department of Defense, Washington, D.C., USA.

Walters, J. R., L. B. Crowder, and J. A. Priddy. 2002. Population viability analysis for red-cockaded woodpeckers using an individual-based model. Ecological Applications **12**:249-260.

Walters, J. R., P. D. Doerr, and J. Carter. 1988. The cooperative breeding system of the red-cockaded woodpecker. Ethology **78**:275-305.

Watkins, A., J. Noble, R. Foster, B. Harmsen, and C. Doncaster. 2015. A spatially explicit agent-based model of the interactions between jaguar populations and their habitats. Ecological Modelling **306**:268-277.

Wennergren, U., M. Ruckelshaus, and P. Kareiva. 1995. The promise and limitations of spatial models in conservation biology. Oikos **74**:349-356.

White, A., H. Jones, P. Lurz, and M. Boots. 2016. A modelling assessment of the population dynamics of red squirrels in the Kidland and Uswayford forest, Northumbria, in relation to proposed forest design plans. Forestry Commission commissioned report. June 8, 2016. 30 pp. Downloaded 2/1/17 from www.macs.hw.ac.uk/~awhite/FC_Kidland_FinalReport.pdf.

Wiegand, T., F. Knauer, P. Kaczensky, and J. Naves. 2004. Expansion of brown bears (*Ursus arctos*) into the eastern Alps: a spatially explicit population model. Biodiversity and Conservation **13**:79-114.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying Threats to Imperiled Species in the United States. BioScience **48**:607-615.

Wolff, W. 1994. An individual-oriented model of a wading bird nesting colony. Ecological Modelling **72**:75-114.

Zeigler, S. L., and J. R. Walters. 2014. Population models for social species: lessons learned from models of Red-cockaded Woodpeckers (*Picoides borealis*). Ecological Applications **24**:2144-2154.

Table 1. List of the 26 installations that participated in the survey, and the species for which managers provided information on monitoring data

Installation	State	Branch	Species
Camp Bowie	TX	ARMY	Black-capped vireo
Camp Grayling	MI	ARMY	Massauga
Camp Lejeune	NC	USMC	Red-cockaded woodpecker
Camp McCain	MS	ARMY	Northern long-eared bat
Camp Shelby	MS	ARMY	Gopher tortoise
Camp Swift	TX	ARMY	Comanche harvester ant
Eglin Air Force Base	FL	USAF	Red-cockaded woodpecker
Fort Bragg	NC	ARMY	Saint Francis' Satyr, Red-cockaded woodpecker
Fort Custer	MI	ARMY	Eastern box turtle
Fort Gordon	GA	ARMY	Red-cockaded woodpecker
Fort Jackson	SC	ARMY	Red-cockaded woodpecker
Fort Pickett	VA	ARMY	Michaux's sumac
Fort Polk	LA	ARMY	Red-cockaded woodpecker
Fort Riley	KS	ARMY	Greater prairie chicken
Fort Stewart	GA	ARMY	Red-cockaded woodpecker
Joint Base Lewis-McChord	WA	ARMY	Taylor's checkerspot butterfly
Naval Facilities Engineering Command, Hawaii (Joint Base Pearl Harbor-Hickam)	HI	NAVY	Hawaiian stilt
Kansas Army National Guard	KS	ARMY	
McConnell Air Force Base	KS	USAF	
Naval Air Station Patuxent River	MD	NAVY	Northern diamondback terrapin
Naval Base Guam	GU	NAVY	Green sea turtle
Naval Support Activity Monterey	CA	NAVY	Smith's blue butterfly
Pueblo Chemical Depot	CO	ARMY	Mountain plover
USACE Willamette Valley Project (Fern Ridge Reservoir)	OR	ARMY	Fender's blue butterfly
US Air Force Academy	CO	USAF	Preble's meadow jumping mouse
Vandenberg Air Force Base	CA	USAF	El Segundo blue butterfly, Western snowy plover

Table 2. A comparison of habitat-based models, demographic models, and spatially explicit individual-based models for predicting effects of habitat management on wildlife. This table compares the types of predictions made, data required, modeling capabilities, and situations most appropriate for each model.

		HABITAT-BASED MODELS	DEMOGRAPHIC MODELS	SEIBMS
PREDICTIONS	Distribution of available habitat	X		X
	Species distribution	X		X
	Population viability		X	X
	Influence of life stages or vital rates		X	X
	Connectivity			X
DATA	GIS habitat data	Required		Required
	presence/absence	Optional		Optional
	population size	Optional	Optional	Optional
	demographic rates		Required	Required
	movement/dispersal		Optional	Required
	behavior		Optional	Optional
MODELING CAPABILITIES	Heterogeneous landscapes	Can model spatial structure. Predicts availability of habitat	Difficult to incorporate spatial structure	Can model spatial structure. Predicts availability and occupancy of habitat
	Habitat change	Static species-habitat relationships limit ability to predict response to habitat change	Don't model landscape or habitat	Can simulate dynamic landscapes and resulting population response to habitat change
	Demographic variation	No demographic variation; all individuals the same	Model demographic variation among groups	Model demographic variation among individuals
	Social structure	Don't model social structure	Difficult to model effects of social structure on vital rates	Can model individual variation in vital rates due to behavior and social structure
	Dispersal	Don't model dispersal	Dispersal success determined by probability only	Dispersal success determined by behavior and landscape configuration
	Population Viability	Predictions of habitat suitability don't equate to viability, because models don't include demography or dispersal success	Suitable for predicting viability when most demographic variation is due to stochasticity, and dynamics don't depend on dispersal	Suitable for predicting viability when variation in demographic rates and dispersal success depends on behavior or habitat configuration
GOOD FOR THESE SITUATIONS:		• Fragmented or heterogeneous landscapes • Static landscapes • Habitat specialists • All individuals have similar vital rates	• Homogeneous landscapes • Static landscapes • Population dynamics not strongly influenced by social structure or dispersal	• Fragmented or heterogeneous landscapes • Dynamic landscapes • Population dynamics influenced by social structure or dispersal • Source-sink dynamics present

Table 3. A list of SEIBMs applied to wildlife habitat management that document the number of parameters used in the model

Species	Reference	Number of parameters
American crocodile	Richards et al. (2004)	36
Cape Sable seaside sparrow	Elderd and Nott (2008)	11
Jaguar	Watkins et al. (2015)	17
Red-cockaded woodpecker	Letcher et al. (1998)	47
Yellow-headed blackbird	Bennett et al. (2009)	39

Table 4. The subset of 9 wildlife habitat management SEIBMs whose data sets were reviewed

Species	Model reference(s)	Agency using model	Model application
Bachman's sparrow	Pulliam et al. (1992); Liu et al. (1995)	U.S. Forest Service	Predict how forest management plans targeting red-cockaded woodpecker impacts Bachman's sparrow at Savannah River Site
Cape Sable seaside sparrow	Elderd and Nott (2008); Nott et al. (1998)	U.S. Geological Survey	Predict impacts of altered hydrological regimes resulting from Everglades restoration on viability of Cape Sable seaside sparrow population
Fender's blue butterfly	McIntire et al. (2007); Smokey et al. (In prep)	West Eugene Wetlands Project; U.S. Army Corps of Engineers Willamette Valley Project	Model has been used to assess whether restoration of available habitat patches would likely result in long term persistence of Fender's blue butterfly in Eugene. Model is currently being updated to test alternative prescribed fire strategies for restoring butterfly habitat while minimizing mortality of caterpillars.
Gray wolf	Carroll et al. (2006)	U.S. Fish and Wildlife Service	Prioritize reintroduction, road removal, or habitat protection as recovery strategies for the gray wolf
Northern spotted owl	USFWS(2011); Schumaker et al. (2014)	U.S. Fish and Wildlife Service	Assess connectivity and identify source and sink areas for northern spotted owl, in order to evaluate the efficacy of a network of habitat reserves to support owl recovery.
Red-cockaded woodpecker	Letcher et al. (1998); Walters et al. (2002)	U.S. Fish and Wildlife Service	Inform recovery guidelines for placement of recruitment clusters for red-cockaded woodpecker
Red squirrel	Rushton et al. (1997); Lurz et al. (2003)	U.K. Forestry Commission; Forest Enterprise	Predict whether squirrel will be viable under current forest harvest and restocking plan. Compare viability under current plan with alternative forest management plans.
Saint Francis' satyr	Himes Boor et al. (In prep)	U.S. Army Fort Bragg	Inform size and location of restoration sites needed to maximize butterfly population growth
Wood stork	Wolff (1994)	U.S. Geological Survey	To predict the effects of water management practices in the Everglades on the redistribution and abundance of storks

Table 5. Availability of habitat and population size data for the species of interest for 9 SEIBMs developed to guide habitat management. NR = not reported. Because some data were obtained from multiple studies, number of years of population size data are approximate. This table is only intended to give a general idea of the amount of data used to parameterize SEIBMs.

		Habitat		
Species	**Reference(s)**	**GIS data?**	**Data layers**	**Yrs pop size data**
Bachman's sparrow	Liu et al. (1995); Dunning et al. (2000)	Y	age, type, size, and boundaries of forest stands	4
Cape Sable seaside sparrow	Elderd and Nott (2008)	Y	topography, hydrology, vegetation	5
Fender's blue butterfly	C. Schultz, E. Crone, J. Smokey (pers. Comm.)	Y	vegetation/land cover	23
Gray wolf	Carroll et al. (2003, 2006)	Y	road density, human population, tasseled cap greenness, slope, vegetation	NR
Northern spotted owl	Forsman (2011); USFWS (2011)	Y	owl distribution, nest sites, vegetation, tree basal area, tree density, canopy cover, stand height, stand age, snags, coarse woody debris	17-24
Red-cockaded woodpecker	Schiegg et al. (2005); Zeigler and Walters (2014)	Y	cavity tree clusters, vegetation/land cover	12-13
Red squirrel	Rushton et al. (1997); Lurz et al. (2003)	Y	age, species, and location of forest stands	16
Saint Francis' Satyr	G. Himes Boor (pers. comm.)	Y	vegetation/land cover	4-14
Wood Stork	DeAngelis et al. (1998)	Y	vegetation, surface elevation, soil type, road locations	NR

Table 6. Survival data available for the species of interest for 9 SEIBMs developed to guide habitat management. Available data may either have been collected specifically for the SEIBM or obtained from literature. NR = not reported. Because some data were obtained from multiple studies, years and sample sizes are approximate. This table is only intended to give a general idea of the amount and types of data used to parameterize SEIBMs.

Species	Reference(s)	Survival data avail?	Method	Stage specific	Habitat specific	n	# yrs
Bachman's sparrow	Pulliam et al. (1992); Liu et al. (1995)	N	No data; Pattern-oriented modeling	N/A	N/A	N/A	0
Cape Sable seaside sparrow	Nott et al. (1998); Elderd and Nott (2008);	Y	Survival rates based on literature for Cape Sable seaside sparrow and surrogate species. Data collection methods unknown.	Y	N	16-112 indiv.	1-10
Fender's blue butterfly	C. Schultz, E. Crone, and J. Smokey (pers. comm.)	Y	Estimate larval survival by counting eggs, plants w/ larval damage, and adults in plots and analyzing with general linear mixed model. Estimate avg. adult life span to be 15 days	Y	Y	934 total plots	3
Gray wolf	Ballard et al. (1987); Carroll et al. (2003, 2006); Fuller 1989; Pletscher et al. 1997	Y	Radio telemetry	Y	N	52-151 indiv.	7-14
Northern spotted owl	Forsman (2011); USFWS (2011); Schumaker et al. (2014)	Y	Capture/resight studies of marked individuals	Y	Y	5224 total indiv.	17-24
Red-cockaded woodpecker	Letcher et al. (1998); Schiegg et al. (2005); Zeigler and Walters (2014)	Y	Monitor marked individuals	Y	N	>5000 indiv.	15
Red squirrel	Lurz et al. (2003)	Y	Survival rates based on literature for red squirrel. Data collection methods unknown	Y	N	NR	NR
Saint Francis' Satyr	Aschehoug et al. (2015); Sivakoff et al. (2016); G. Himes Boor, W. Morris, and N. Haddad (pers. comm.)	N	Surrogate data from Appalachian brown butterfly. Habitat-specific larval survival from 1 yr mesocosm study (n=480). Habitat-specific adult survival from 1 yr mark recapture study (n=87)	N/A	N/A	N/A	0
Wood stork	Wolff (1994)	N	Mortality in model is based on energetic threshold and does not require survival data	N/A	N/A	N/A	0

Table 7. Fecundity data available for the species of interest for 9 SEIBMs developed to guide habitat management. Available data may either have been collected specifically for the SEIBM or obtained from literature. NR = not reported. Because some data were obtained from multiple studies, years and sample sizes are approximate. This table is only intended to give a general idea of the amount and types of data used to parameterize SEIBMs.

Species	Reference(s)	Data avail	Method	Stage specific	Habitat specific	n	# yrs
Bachman's sparrow	Haggerty (1988); Pulliam et al. (1992); Liu et al. (1995)	Y	Observe marked nests	N	N	66 nests	3
Cape Sable seaside sparrow	Lockwood et al. (1997); Elderd and Nott (2008);	Y	Observe marked nests	N	N	24 nests	2
Fender's blue butterfly	C. Schultz, E. Crone, and J. Smokey (pers. comm.)	Y	Count eggs in plots. Use general linear mixed models to estimate fecundity based on observed growth rates	N	Y	934 total plots	3
Gray wolf	Ballard et al. (1987); Carroll et al. (2003, 2006); Fuller 1989; Pletscher et al. 1997	Y	Count placental scars and observe packs	N	N	4-16 indiv, 1-28 packs	1-13
Northern spotted owl	Forsman (2011); USFWS (2011); Schumaker et al. (2014)	Y	Monitor marked individuals	Y	Y	11450 indiv.	17-24
Red-cockaded woodpecker	Letcher et al. (1998); Schiegg et al. (2005); Zeigler and Walters (2014)	Y	Monitor marked individuals	Y	N	>5000 indiv.	15
Red squirrel	Rushton et al. (1997); Lurz et al. (2003)	Y	Litter size and % females breeding based on literature for red squirrel. Data collection methods unknown.	N	N	NR	NR
Saint Francis' Satyr	G. Himes Boor (pers. comm.)	Y	Some data from counting eggs from captive butterflies. Also used pattern-oriented modeling	N	N	81 indiv.	1
Wood stork	Kahl (1964); Wolff (1994)	Y	Observation of nesting pairs threshold and does not require survival data	N	N	>16000 nesting pairs	7

Table 8. Movement data available for the species of interest for 9 SEIBMs used for habitat management. NR = not reported. Because some data were obtained from multiple studies, years and sample sizes are approximate. This table is only intended to give a general idea of the amount and types of data used to parameterize SEIBMs.

			Movement							
Species	**Reference(s)**	**Method**	**Habitat specific**	**Probability of dispersal**	**Dispersal distance**	**Dispersal direction**	**Individual movement paths**	**Dispersal mortality**	**n**	**# yrs**
Bachman's sparrow	Liu et al. (1995)	No data; use best estimates	N/A	N	N	N	N	N	N/A	0
Cape Sable seaside sparrow	Elderd and Nott (2008)	Radio telemetry	N	N	Y	N	N	N	31	7 mos.
Fender's Blue Butterfly	Schultz and Crone (2001); Schultz et al. (2012); C. Schultz, E. Crone, and J. Smokey (pers. comm.)	Follow flight paths of individuals released in different habitats	Y	Y	Y	Y	Y	N	98-606 indiv.	1-2 yrs, depending on habitat
Gray wolf	Ballard et al. (1987); Carroll et al. (2006); Fuller 1989	Radio telemetry	N	Y	Y	N	N	Y	81-151 indiv.	7
Northern spotted owl	USFWS (2011); Forsman et al. (2002); Schumaker et al. (2014)	Track radio-marked and banded individuals.	N	Y	Y	Y	Y	Y	324 radio-marked, 1151 banded indiv.	11
Red-cockaded woodpecker	Letcher et al. (1998); Walters et al. (2002);	Record locations of marked individuals	N	Y	Y	N	N	N	>1000 records	15
Red squirrel	Rushton et al. (1997); Lurz et al. (2003)	No data	N/A	N	N	N	N	N	N/A	0
Saint Francis' satyr	G. Himes Boor (pers. comm.)	Probability of moving between habitats measured by following SFS individuals. Also used individual flight paths from surrogate species Appalachian brown butterfly to quantify habitat-specific move lengths and turn angles	Y	Y	N	N	N	N	42 indiv.	1
Wood stork	Kahl (1964); Wolff (1994)	followed individuals in a plane	N	N	Y	N	N	N	NR	NR

Table 9. Monitoring data collected at Department of Defense installations that manage or restore habitat for wildlife

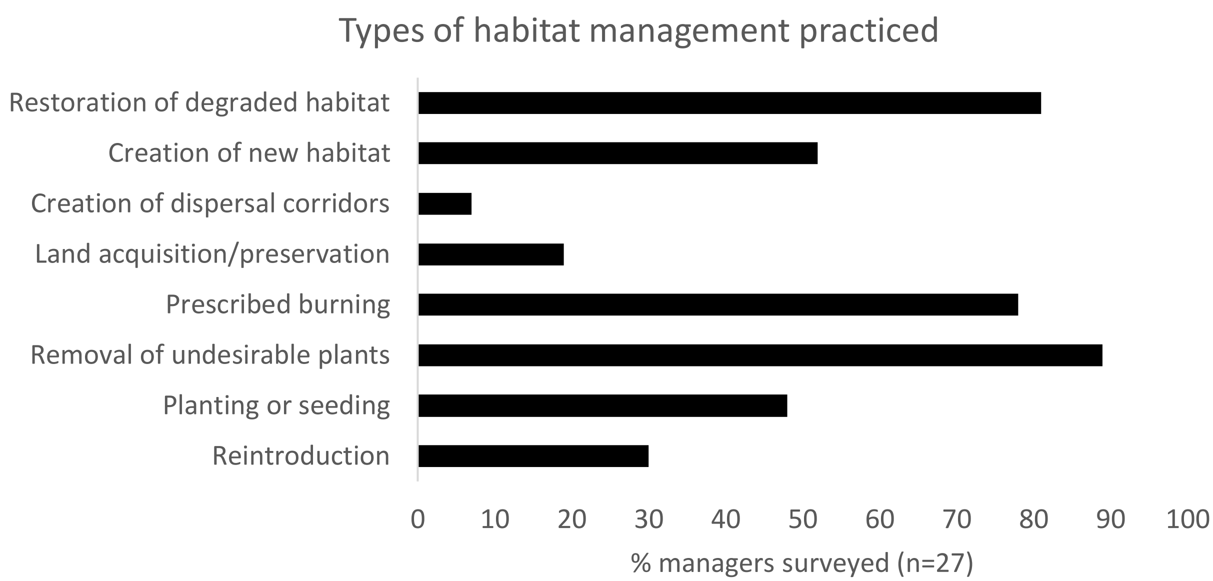
				Survival		Fecundity		Movement				
Installation	**Species**	**GIS habitat maps**	**yrs pop. size data**	**yrs**	**Habitat specific**	**yrs**	**Habitat specific**	**yrs**	**Probability of dispersal**	**Dispersal distance**	**Ind. move paths**	**Habitat specific**
Camp Bowie	Black-capped vireo	x	6-10	0		6-10		0				
Camp Grayling	Massasauga	x	6-10	6-10	x	6-10		6-10	x	x	x	x
Camp McCain	Northern long-eared bat		1	0		0		0				
Camp Shelby	Gopher tortoise	x	>10	6-10	x	6-10	x	6-10	x	x	x	
Camp Swift	Comanche harvester ant	x	6-10	0		0		0				
Fort Custer	Eastern box turtle	x	2-5	2-5		2-5		2-5	x	x	x	
Fort Riley	Greater prairie chicken	x	6-10	2-5		2-5		2-5	x	x	x	x
Joint Base Lewis-McChord	Taylor’s checkerspot butterfly	x	6-10	0		0		0				
Joint Base Pearl Harbor-Hickam	Hawaiian stilt		0	0		0		1			x	
NAS Patuxent River	Northern diamondback terrapin	x	2-5	2-5		2-5		0				
Naval Base Guam	Green sea turtle	x	6-10	0		2-5		1	x		x	
Naval Support Activity Monterey	Smith’s blue butterfly		2-5	0		0		0				
Pueblo Chemical Depot	Mountain plover	x	>10	0		0		0				
USAF Academy	Preble’s meadow jumping mouse	x	>10	>10	x	>10	x	>10	x	x	x	
Vandenberg AFB	El Segundo blue butterfly	x	6-10	0		0		0				
Vandenberg AFB	Western snowy plover	x	>10	6-10		6-10		0				

Table 10. Tests of reliability reported for published habitat restoration SEIBMs

Species	Model reference	Validation/sensitivity analysis reference	Primary prediction	Secondary prediction	Sensitivity analysis
Bachman's sparrow	Pulliam et al. (1992); Liu (1993); Liu et al. (1995); Dunning Jr et al. (2000)	Liu (1993), Liu et al. (1995)	distribution		Yes
Cape Sable seaside sparrow	Elderd and Nott (2008)	Elderd and Nott (2008)	population size		Yes
Fender's blue butterfly	McIntire et al. (2007)	McIntire et al. (2007)	population size		No
Gray wolf	Schumaker (1998); Carroll et al. (2001); Carroll et al. (2003); Carroll et al. (2006)	Carroll et al. (2003); Carroll et al. (2006)	distribution		Yes
Northern spotted owl	USFWS (2011); Schumaker et al. (2014)				No
Red-cockaded woodpecker	Letcher et al. (1998); Walters et al. (2011)	Letcher et al. (1998); Schiegg et al. (2005); Zeigler and Walters (2014)	population size, number of territories gained and lost, social structure, population growth rate	natal dispersal distance, dispersal success, age distribution of first time breeders	Yes
Red squirrel	Rushton et al. (1997); Rushton et al. (1999); Lurz et al. (2003)	Rushton et al. (1997); Rushton et al. (1999)	distribution		Yes
Wood stork	Wolff (1994); Fleming et al. (1994); DeAngelis et al. (1998)				No

Figure 1. (a) Types of habitat management conducted by the 27 managers surveyed, and (b) the types of management questions they need to address

a)



b)

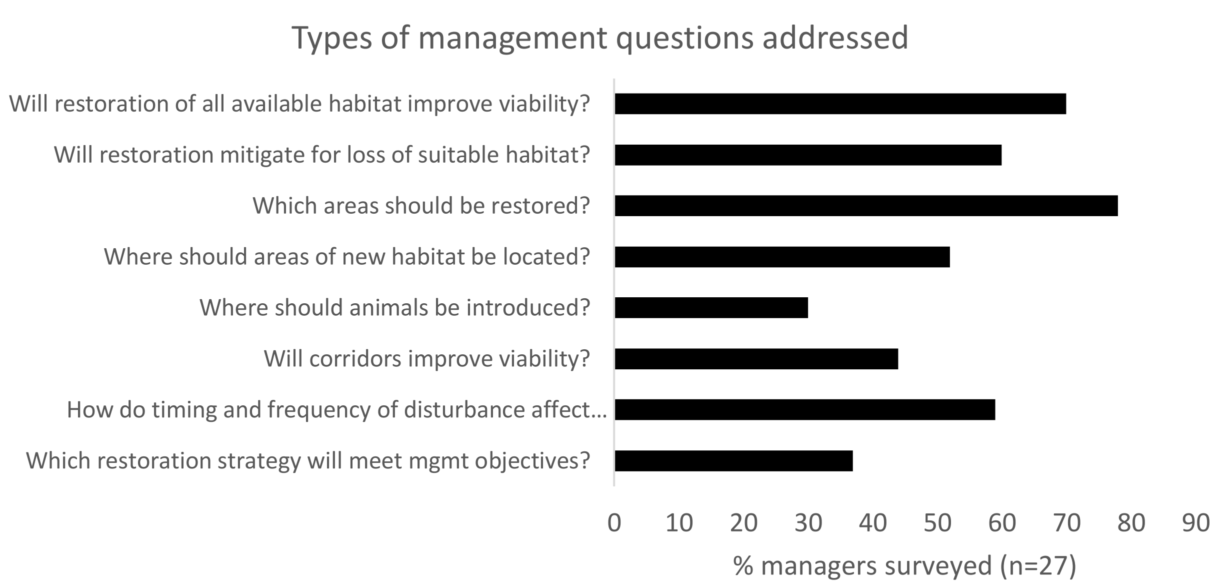
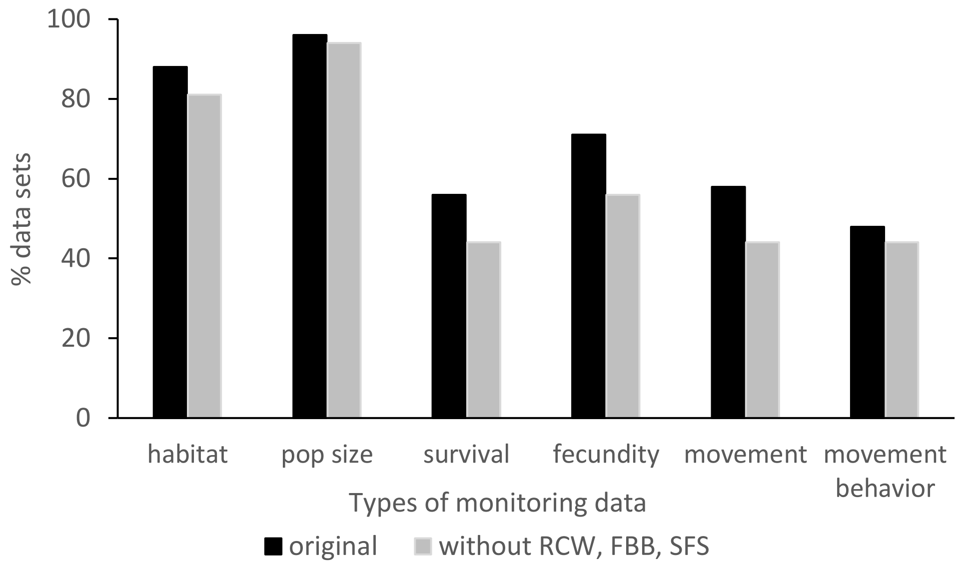


Figure 2. Types and amounts of monitoring data collected on DoD-managed species. Figure (a) shows the % of monitoring data sets that include habitat, population size, survival, fecundity, movement (any type), and individual movement path data. Figure (b) shows the % of data sets for which 0, 1, 2-5, 6-10, and >10 years of population size data are collected. Black bars indicate the original collection of data sets with red-cockaded woodpeckers included (n=25). Red bars indicate the data sets remaining after the red-cockaded woodpecker, Fender's blue butterfly, and St. Francis' Satyr data sets are removed (n=16).

a)



b)

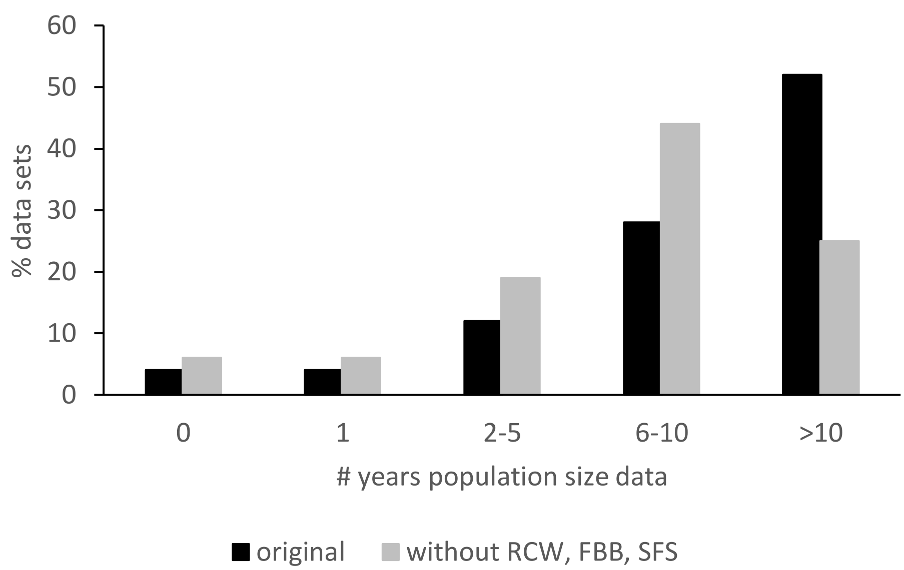


Figure 3. DoD managers' experience and perception of SEIBMs. n=27 manager responses.

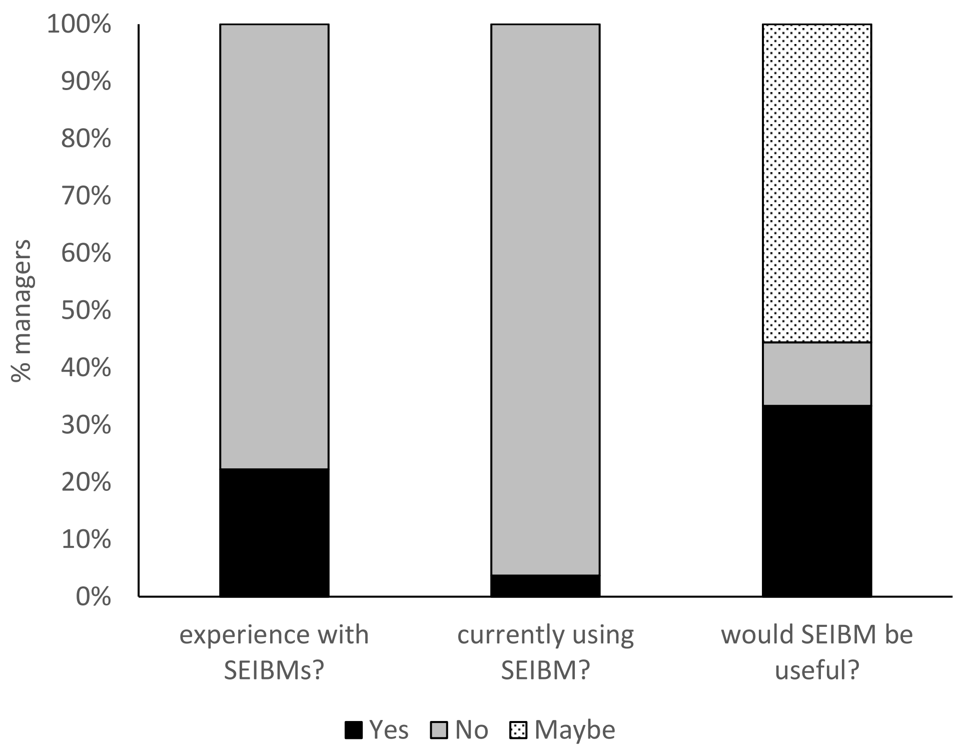
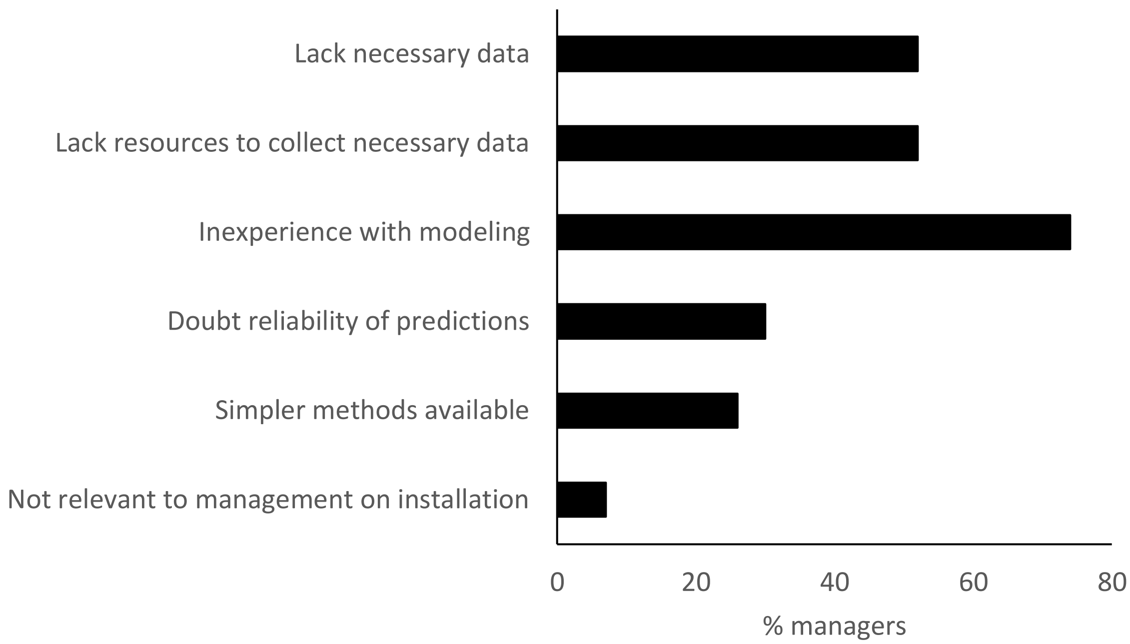


Figure 4. Factors that would prevent managers from considering using SEIBMs. n = 27 manager responses.



Appendix A. The questionnaire used for the informal survey of DoD managers

Name:

Installation:

Mailing Address:

Habitat Management

1) Species whose habitat is being managed:

2) Type of management (check all that apply)

- ☐ Restoration of degraded habitat
- ☐ Creation of new habitat
- ☐ Creation of dispersal corridors
- ☐ Land acquisition/preservation
- ☐ Prescribed burning
- ☐ Removal of undesirable plants (mowing, grazing, logging, herbicides, etc.)
- ☐ Planting or seeding
- ☐ Reintroduction of animals into new or restored habitat
- ☐ Other (describe):

3) Brief description of habitat management (or you can attach a document that describes management if you prefer):

4) Types of management questions that need to be addressed (check all that apply):

- ☐ How will protection (or loss) of a specific habitat patch affect population viability?
- ☐ Will restoring or protecting habitat available achieve goals of species persistence?
- ☐ Will creation/restoration of habitat mitigate for loss of suitable habitat?
- ☐ Which areas should be managed to have the greatest impact on population viability?
- ☐ Where should areas of newly created habitat be located to ensure connectivity?
- ☐ Where should animals be reintroduced?
- ☐ Will adding corridors improve population viability?
- ☐ How does timing and frequency of disturbance affect population viability?
- ☐ Which of two alternative restoration strategies is more likely to meet management objectives?
- ☐ Other (describe):

Available Data (check all that apply)

- ☐ GIS habitat map
- ☐ Annual estimates of population size

Number years of data: ☐ 1 year ☐ 2-5 years ☐ 6-10 years ☐ > 10 years

Demographic data

- ☐ Survival rates or probabilities
  - Number years of data: ☐ 1 year ☐ 2-5 years ☐ 6-10 years ☐ > 10 years
  - Is data habitat-specific? ☐ yes ☐ no
- ☐ Rates of reproductive success
  - Number years of data: ☐ 1 year ☐ 2-5 years ☐ 6-10 years ☐ > 10 years
  - Is data habitat-specific? ☐ yes ☐ no
- ☐ Clutch/litter size
  - Number years of data: ☐ 1 year ☐ 2-5 years ☐ 6-10 years ☐ > 10 years
  - Is data habitat-specific? ☐ yes ☐ no

Movement data

- ☐ Probability of Dispersal
  - Number years of data: ☐ 1 year ☐ 2-5 years ☐ 6-10 years ☐ > 10 years
  - Is data habitat-specific? ☐ yes ☐ no
- ☐ Dispersal distance
  - Number years of data: ☐ 1 year ☐ 2-5 years ☐ 6-10 years ☐ > 10 years
  - Is data habitat-specific? ☐ yes ☐ no
- ☐ Dispersal speed
  - Number years of data: ☐ 1 year ☐ 2-5 years ☐ 6-10 years ☐ > 10 years
  - Is data habitat-specific? ☐ yes ☐ no
- ☐ Individual movement paths (move lengths and turn angles)
  - Number years of data: ☐ 1 year ☐ 2-5 years ☐ 6-10 years ☐ > 10 years
  - Is data habitat-specific? ☐ yes ☐ no

<u>SEIBM Perception and Experience</u>

1) Have you used a spatially-explicit, individual-based model before? ☐ Yes ☐ No
2) Do you feel the ability to build a SEIBM would enhance your ability to manage threatened and endangered species on your installation? ☐ Yes ☐ No ☐ Maybe
3) Are you currently using a SEIBM to guide decisions regarding the management of your species of concern (if yes, skip to question 6)? ☐ Yes ☐ No
4) What factors would prevent you from considering use of a SEIBM to make management decisions? (check all that apply)
   - ☐ Lack the necessary data
   - ☐ Lack the resources to collect the necessary data
   - ☐ Inexperience with modeling
   - ☐ Question reliability of predictions
   - ☐ Types of questions SEIBMs address are not relevant to species being managed on this installation
   - ☐ Simpler tools are available that are adequate to help make management decisions (describe):
   - ☐ Other (describe):

5) What additional information would help you decide whether a SEIBM is a practical tool for habitat management?

6) Other comments or input for the researchers that develop SEIBMs?

Would you like to be notified about SEIBM tools and workshops when they are disseminated by our group? ☐ Yes ☐ No

Please save your changes and e-mail this form back to damiani@iws.org. Thank you for participating in this survey!

Appendix B. Written comments provided by managers in response to questions 4-6 in the "SEIBM perception and experience" section of the questionnaire.

QUESTIONS	MANAGERS' ANSWERS
4) Simpler tools available that are adequate to help make management decisions	Timber stand data
	We provide recruitment clusters in suitable habitat adjacent to existing, active clusters at a rate of 15% of active clusters. At the end of each breeding season, we create a 0.5-mile diameter buffer around the geographic center of each active cluster. If there is unoccupied suitable habitat between active clusters, those areas are prioritized to receive recruitment clusters. Secondly, we place recruitment clusters on the edges of occupied habitat to grow the population "out". This method has worked well for us. In 1997, we had 175 active clusters and 158 potential breeding groups (PBGs). The number of active clusters has increased an average of 5.2% per year, while PBGs have increased on average population on average 5.6% per year such that in 2016 we have 469 active clusters (a 168% increase since 1997) and 443 PBGs (a180% increase).
	Habitat assessment protocols
	Current surveying for this species is accepted by the USFWS and has provided everything we have needed to date to monitor and manage the species. However, if there is a better and/or less expensive way or another way that renders better results then I welcome that program.
4) What (other) factors would prevent you from considering use of a SEIBM to make management decisions?	Although we have a lot of data, some of it focuses on hatchlings and not adults and vice versa. Not all of it is incorporated into our GIS database.
	We are dealing with small areas and very low population numbers. The areas suitable for habitat restoration are limited so we usually make our decisions based on location to current occupied sites, topography of the drainage, and hydrology for the specific area
	Lack of necessary personnel to update constantly changing habitat conditions and animal movements
	I think SEIBMs would be a great tool for some species management programs that we are trying to establish. Unfortunately we do not have very much data and the data we do have is probably not adequate. I would be interested in learning more about what kind of data is necessary so that maybe we can start to set up survey work so that we are getting the proper data for species management programs that might benefit from an SEIBM.
	To an extent, the target sp. functions as an umbrella for native plants, other insects, other animal classes and ecological processes. SEIBM is resource-intensive, necessarily single-species, and thus might consume resources that could otherwise be used to increase understanding of larger ecological effects of restoration and maintenance actions...
	Military is not always willing to take models into consideration when making decisions. Particularly when it is ecologically based rather than based on military needs.
	There is a perception that the base can't do any habitat restoration without a major influx of birds. I don't think this is true, but I don't yet have the data to show yes or no. In the meantime, it's limited my ability to do restoration.
	SEIBMs may not be useful since all riparian habitat on base is important for the conservation of the species

Appendix B. (continued)

QUESTIONS	MANAGERS' ANSWERS
5) What additional information would help you to decide whether a SEIBM is a practical tool for habitat management?	Perhaps validation on a broad cast of species would improve confidence that models would work for particular managed species. Having a similar "model" type species already run would serve as a biologically useful comparison
	Information dissemination with successful projects
	A basic training on what SEIBMs can do would be beneficial
	Do you have SEIBMs already in use and approved by federal agencies? Since our species is federally listed as threatened under the ESA, all studies and management decisions based on modeling would have to be cleared through consultation with the U.S. Fish and Wildlife Service, and the U.S. Forest Service since the majority of our training and data collection is on their property
	The model will have to work at a very small scale. We generally work in 30x30 meter blocks
	Not sure - would need to learn more about SEIBMs.
	Is the model usable for the data that we have been collecting? What data do we need to collect to take advantage of the SEIBM?
	Costs of both modeling and collecting the required demographic and spatial information to drive SEIBM
	No further information is necessary and I believe that a SEIBM would be helpful in decision making
	Whether it could help with managing for high risk bird airstirke species, so managing in a way that favors lower risk species
	I would have a better understanding of the usefulness and application of SEIBMs if I could view a practical example
	Examples of projects where SEIBM has been applied and results
	Our annual site assessments and biennial GIS Mapping provides everything needed for anyone evaluating our program to date. Discussion of how SEIBM would be an improvement to what we are doing right now.
	Examples of other applications
	None. Seems like a really great tool
	I would have to evaluate the outcome to see if the outcome made "practical" sense
	Published papers or case studies using SEIBMs with species managed on this installation
	Is there a cost estimate to developing one of these with existing data?

Appendix B. (continued)

QUESTIONS	MANAGERS' ANSWERS
6) Other comments or input for the researchers that develop SEIBMs?	Great idea!
	Need to ensure enough data is available so robust and accurate outputs can be achieved. Objectives must be clear up front. Clearly defining objectives for model output is critical. Ability to ground truth is also critical. Ideally modelers would have close coordination with managers during development so those who would use the model understand how to interpret output.
	Most questions above are more suitable for the larger recovery team, as we've pretty much saturated potential sites we manage, so our local concerns revolve around how aggressively we can manage disturbance-maintained habitat, while maintaining population growth. Secondarily, improving viability and population size estimates.
	We use SEIBM to determine viability of our population, not so much for management purposes. We have a pretty good handle on management needs within our borders. I see user-friendly SEIBMs helping make decisions for landscape scale decisions, *e.g.* assessing the value of protecting habitat corridors between populations. Data needs of SEIBMs can be a challenge.
	For our installation I believe that SEIBM may be a useful tool.