

# The role of spatial structure in the collapse of regional metapopulations

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**Abstract.** Many wildlife populations are either naturally, or as a result of human land use, patchily distributed in space. The degree of fragmentation—specifically the remaining patch sizes and habitat configuration—is an important part of population dynamics. Demographic stochasticity is also likely to play an important role in patchy habitats that host small local populations. We develop a simulation model to evaluate the significance of demographic stochasticity and the role fragmentation plays in the determination of population dynamics and the risk of extinction of populations on habitat patches. Our model is formulated as a Markov-chain stochastic process on a finite, spatially explicit array of patches in which probability of successful dispersal is a function of interpatch distance. Unlike past work, we explicitly model local population dynamics and examine how these scale up to the entire population. As a test case, we apply the model to the American pika (*Ochotona princeps*) population living on the ore dumps in the ghost mining town of Bodie, California. This population has been studied nearly continuously for over four decades and has been of conservation concern as the southern half of the population declined precipitously beginning in 1989. Our model suggests that both the specific configuration of habitat and landscape heterogeneity are necessary and sufficient predictors of the eventual extinction of the southern constellation of patches. This example has important implications, as it suggests that fragmentation alone can lead to regional extinctions within metapopulations.

**Key words:** American pika; Bodie; dispersal; local extinction; metapopulation; *Ochotona princeps*; population viability analysis; spatial heterogeneity; spatial structure.

## INTRODUCTION

Many populations naturally occur in spatially heterogeneous or fragmented habitats (Levin 1992). There are two important aspects of habitat fragmentation: it alters the size of individual habitat patches and increases the isolation of populations on those patches (Fahrig 2003). It is often difficult to disentangle these two processes from one another, and each process can in turn affect population dynamics (Swihart et al. 2003). Smaller patch sizes increase extinction risk through demographic stochasticity (Diamond 1984, Harrison 1991), while decreased connectivity due to isolation between habitats can decrease population persistence (Hastings and Botsford 2006, Villard and Metzger 2014).

In order to study the effects of fragmentation, metapopulation theory is a natural first choice. A metapopulation is a network of spatially distinct patches (i.e., subpopulations) connected to each other via dispersal (Hanski and Gilpin 1991, Harrison 1991). A metapopulation is distinct from a spatially distributed population or a mainland-island configuration, as each patch within a metapopulation has a high probability of going extinct at any given time (Harrison 1991). In nature, true metapopulations are probably rare (Fronhofer et al. 2012), but their tractability allows for the study of spatial processes. Metapopulation structure also depends on the specific species of interest. For example, Olivier et al. (2009) note that small mammals, as opposed to large mammals, are more likely to meet all the criteria of classic metapopulations.

The first-generation metapopulation models involved spatially implicit processes (Levins 1969, 1970). From these

models Levins (1969, 1970) showed that in order to ensure metapopulation persistence, rates of colonization must exceed those of extinction. There have been extensions of these spatially implicit models, but their simplicity prevents them from being applied to real systems (Hanski et al. 1996).

Spatially realistic metapopulation models (Hanski 1998, 2001) have been developed to overcome these challenges. A large class of these models are termed stochastic patch occupancy models (SPOMs; Hanski and Ovaskainen 2003). SPOMs are spatially explicit because they assume connectivity between patches is distance-dependent and the extinction probability of any given patch is related to patch size (Hanski and Ovaskainen 2003). These models have been used to investigate the effects of stage-structure and correlated extinctions (Sutherland et al. 2012) on metapopulation dynamics. These models have also been extended to account for false absences and imperfect detection (Risk et al. 2011, Sutherland et al. 2014).

More system-specific SPOMs have been built to understand the interaction between spatial structure and disease (Heard et al. 2015, Penczykowski et al. 2015), the dynamics of metapopulations following reintroductions (Chandler et al. 2015), and for predicting species range shifts under climate change (Mestre et al. 2017). SPOMs are typically implemented by estimating model parameters (e.g., colonization and extinction rates) using presence-absence data (Moilanen 2004). A fitted model can then be simulated to explore how colonization and extinction rates affect overall metapopulation dynamics. Of course, colonization and extinction rates reflect the amalgamation of individual processes (e.g., birth, death, movement) that interact with the properties of the environment, such as the configuration of suitable habitat.

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SPOMs tend to prioritize model simplicity in lieu of specific mechanisms by not explicitly modeling local population dynamics (Hanski and Ovaskainen 2003). Local population dynamics refer to explicit birth and death processes as well as dispersal. These simplified models have been explored for two reasons. First, parameterization of a more detailed model would require detailed life-history information and long-term census data, as opposed to only snap-shots of occupancy data. Second, building models that incorporate local population dynamics are often computationally intensive to run. However, local population dynamics have been found to be important in describing overall metapopulation dynamics (Pellet et al. 2007, Sutherland et al. 2014). For example, Ozgul et al. (2009) built a spatially structured matrix model that explicitly included local demography. They showed that local population dynamics were more important than dispersal for determining overall metapopulation dynamics, especially in the short term. Despite this work, most of our understanding of metapopulation dynamics is from models that ignore local population dynamics.

Here, we extended prior SPOM approaches (Hanski and Ovaskainen 2003, Sutherland et al. 2014) and the work of Ozgul et al. (2009) to develop a stochastic, spatially explicit metapopulation model that, unlike most previous work, explicitly models local population (within-patch) dynamics by tracking abundance instead of occupancy. Our goal was not to use the model to estimate connectivity and extinction parameters like much of the metapopulation literature. Instead, we sought to parameterize a model with independent field estimates and then to use the model to understand how habitat configuration interacts with local population dynamics to determine overall metapopulation dynamics. Modeling these local population dynamics as stochastic processes allows for the extinction of not only individual patches, but also the entire metapopulation.

This approach required a metapopulation system with long-term census data on discrete habitat patches and knowledge of life-history parameters. Therefore, we explored the model by examination of one of the best-known and documented mammalian metapopulation systems, that of the American pika (*Ochotona princeps*) at Bodie, California (Smith 1974a, 1980, Peacock and Smith 1997, Smith and Gilpin 1997, Moilanen et al. 1998, Smith and Nagy 2015). This population has been studied semi-continuously for over four decades with corresponding census data coupled with investigations on reproduction, dispersal, and mortality. The system presented a unique opportunity to study fragmentation and metapopulation dynamics for two reasons. First, although Bodie is a fragmented landscape, habitat loss has not occurred there; this allows us to separate the two processes, which is typically difficult to do in practice (Fahrig 2003, Villard and Metzger 2014). The habitat is fragmented in such a way that the heterogeneity in patch sizes and patch configuration may be particularly important in determining overall metapopulation dynamics. Second, a significant fraction of the patches in one region collapsed midway through the study. We use our modeling approach to explore explanations for this collapse of nearby patches, not simply extinction of individual patches. Thus, this investigation goes beyond previous metapopulation models that examine only extinction-colonization dynamics and instead addresses the

interaction between local population dynamics and habitat configuration. Our robust data set allows us to run in silico, or virtual, experiments (Zurell et al. 2010) to tease apart the effects of habitat configuration and patch heterogeneity on overall metapopulation dynamics.

## METHODS

### Model

We modeled a spatially explicit population as an array of patches without explicitly assuming that the population is indeed a metapopulation. In other words, we do not make specific assumptions regarding the frequency of recolonization or extinction events, or if patch dynamics are asynchronous (Hanski 1991). Instead, we built a simulation model from the ground-up and examine how local processes may scale up to the entire population. Each patch has a time-invariant number of territories (patch carrying capacity). This creates heterogeneity in the patch size variable. We modeled population sizes on individual patches instead of a correlate such as patch size (Moilanen 2004, Robles and Ciudad 2012, Sutherland et al. 2014).

Our simulation model incorporates several important stochastic processes. We do not use the model to estimate its underlying parameters. Instead, we parameterize each stochastic process using previously collected information on life-history traits (See *Model parameterization of American pikas* and Appendix S1). Here, we detail a general model that could be used for any spatially and stage-structured population (Fig. 1; Appendix S1). This framework also includes the potential for stochastic collapse of patch and regional populations.

The model is stochastic and stage-structured with neonate, juvenile, and adult classes. We incorporate demographic

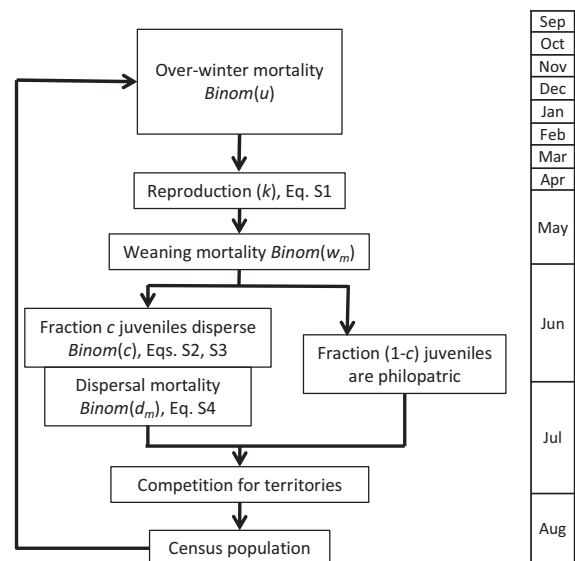


FIG. 1. Schematic of simulation approach. The flowchart depicts each year on each occupied patch in the model. The details of the simulation are given in Appendix S1.

stochasticity (Melbourne and Hastings 2008) into our model by assuming adults produce offspring independently drawn from a fixed distribution (Appendix S1: Eq. S1). This distribution could be from field data of litter sizes. These neonates endure some probability of mortality according to a binomial process (Appendix S2). Surviving neonates are then classified as juveniles.

The number of dispersers is stochastic and is given by a binomial distribution with a mean dispersal propensity (Appendix S1: Eq. S2). Only juveniles are allowed to disperse in our model, but this is not a strict assumption. Juvenile dispersal from their natal patch to nearby patches is a function of distance; juveniles disperse according to a multinomial process (Appendix S1: Eq. S3). All philopatric (non-dispersing) juveniles search for territories on their natal patches. We further assume that dispersal probability and success are distance-dependent. We model dispersal mortality as a binomial process (Appendix S1: Eq. S4). Field measurements of dispersal could be used to obtain a transition matrix of dispersal probabilities specified for each patch.

After dispersal, juveniles compete for territories. If there are fewer juveniles than unoccupied territories, all individuals can obtain a territory. However, if the number of juveniles is greater than the number of unoccupied territories, a competition function is included. Any juveniles with a territory after the dispersal stage are then deemed to be adults. At this point in the model, we census the population (at the end of the breeding season). Adults have an over-winter survival probability determined by a binomial process (Appendix S1: Eq. S5). Individuals that survive winter are able to reproduce the following spring, starting the yearly cycle over again. This is essentially a hybrid of models for each season (White and Hastings 2018). Expanded methods and further details on model development and parameterization are given in Appendix S1.

#### *Study area and census methods*

American pikas are habitat-specific to piles of broken rock bordered by suitable vegetation for foraging, and at Bodie, Mono County, California (38.19–38.22 N; –118.99 to –119.01 W), they occupy ore dumps from prior mining activity (total area of 10 km<sup>2</sup>) that dot the open Great Basin Sage plant community. The ore dumps vary in size and spatial configuration (Appendix S1: Fig. S1), thus present a natural laboratory to explore metapopulation processes.

Severaid (1955) studied the pikas at Bodie in the late 1940s and observed that they had occupied every ore dump, regardless of size or degree of isolation, but that the average stable population was never equal to the carrying capacity of the habitat. Smith (1974a) initiated our study at Bodie in 1969, making the same observation as Severaid. In 1972, Smith (1974a) conducted the first complete census of 76 isolated ore dumps and 3 samples of continuous ore dump areas. This census was repeated in 1977 (Smith 1980) with the same general results, except that there was a high degree of turnover (extinction of pika populations on ore dumps or recolonization of ore dumps that were not occupied in 1972). Empirical investigation of the Bodie pika metapopulation was renewed with additional censuses in 1989 and 1991 (Smith and Gilpin 1997, Moilanen et al. 1998). These censuses found a general collapse in populations

in the southern half of the study area. Annual or bi-annual censuses of the Bodie metapopulation were continued from 1992 to 2010, thus resulting in 15 1-yr intervals and three 2-yr intervals from 1989 to 2010, and 21 total censuses beginning in 1972 (Smith and Nagy 2015). The time series is sufficient in length to study long-term population trends (White 2018).

Each of the censuses of pika occupancy on ore dumps at Bodie (from 1972–2010) was conducted in the same manner and mostly with the same personnel, thus with high inter-observer and inter-year reliability (details in Smith 1974a, 1980, Smith and Gilpin 1997, Smith and Nagy 2015). Each ore dump was examined thoroughly in late summer (the time of highest potential occupancy) by looking for the characteristic sign left by American pikas: fresh small dark green round scats (normally deposited in clusters) and fresh green caches of vegetation (haypiles) stored by pikas during summer to serve as a source of food over winter (Smith and Weston 1990).

#### *Model parameterization of American pikas*

Characteristics of the biology of American pikas make them ideal for a study of metapopulation dynamics. Pikas are obligate rock-dwelling animals and the ore dumps that they occupy at Bodie have remained virtually unchanged since pika investigations were initiated there, thus reducing variance in habitat availability (but see Smith and Nagy 2015). Pikas are individually territorial, territory size is equivalent between males and females, and there is little variance in territory size (Smith and Weston 1990); thus, on any ore dump it is possible to determine accurately the potential maximum population size (carrying capacity of each patch). Average distance between territory centers on patches with more than one pika at Bodie is 21.8 m (Smith 1974b). Sex ratio is near 1:1, and territory replacement is usually by an animal of the same gender as the previous occupant, particularly in saturated populations (Smith and Ivins 1983a).

Demographically, pikas are relatively long-lived for a small (125–175 g) mammal, and there is no fecundity-age regression; average litter size is equivalent among all adult-aged females (Millar 1974, Smith 1978). Pika mothers initiate 2 litters per year, but normally only one is successfully weaned (Millar 1974, Smith and Ivins 1983b). Average mortality of adults at Bodie was 37% (average  $q_x$  values of 1- to 4-yr-old pikas) or 36% (based on percentage yearlings; Smith 1978). Average litter size from collected pregnant females averaged 3.3 young (Smith 1978).

Both intra- and inter-population (patch) dispersal are highly restricted in American pikas (Smith 1974a, 1987, Peacock 1997, Smith and Nagy 2015, Castillo et al. 2016). At Bodie, over our span of censuses, vacant ore dumps as close as 300 meters from a source of potential dispersers appeared essentially isolated due to the inability of pikas to disperse that distance across the open sagebrush habitat (Smith 1974a, 1980, Smith and Gilpin 1997).

#### *Model analysis*

We initialized simulations with Bodie-specific parameter values (Table 1) and the initial 1972 census data. We simulated the model 1,000 times for 39 yr (until 2010),

TABLE 1. Notation and interpretations of model parameters, their default values, ranges, and sources for the American pika (*Ochotona princeps*) at Bodie, California.

Parameter	Definition	Default	Range	Source
$k$	Mean litter size	3.3	0–3.68	Smith (1978)
$c$	Mean dispersal propensity	0.25		Smith (1987)
$r$	Maximum dispersal distance (m)	300		Smith (1974b)
$w_m$	weaning mortality probability	0.48		Appendix S2
$d_m$	Dispersal mortality probability	0.61		Appendix S2
$u$	Over-winter mortality probability	0.37	0.2–0.5	Smith (1978)

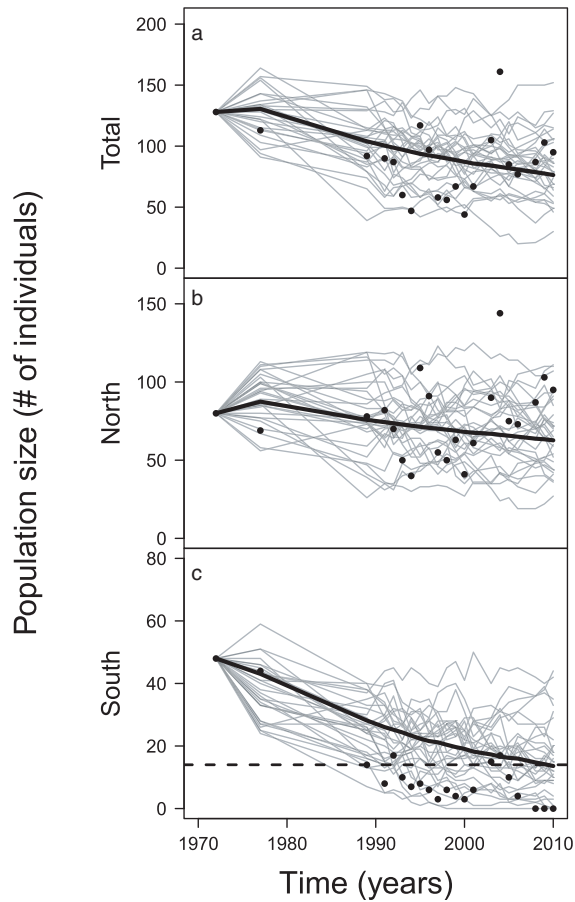


FIG. 2. Simulated time series of 50 typical runs for (a) total population size, (b) population size of individuals in the north, and (c) population size of individuals in the south. The black circles are data from the field. The dashed horizontal line in (c) is the collapse threshold as defined in the main text.

representing the time-frame of our fieldwork (Fig. 2). We used the specific patch heterogeneity and configuration at Bodie (Appendix S1: Fig. S1). We measured five model outputs for comparison to field data: mean population size, variance in population size, patch recolonization rate, patch extinction rate, and the percent of occupied patches (Appendix S3). We evaluated sensitivity of each measurement to variations in our model parameters (Appendix S4: Figs. S1–S5).

We also measured time to collapse of the southern region (Fig. 3). We defined time to collapse of the southern region as the year when the total regional population size dropped

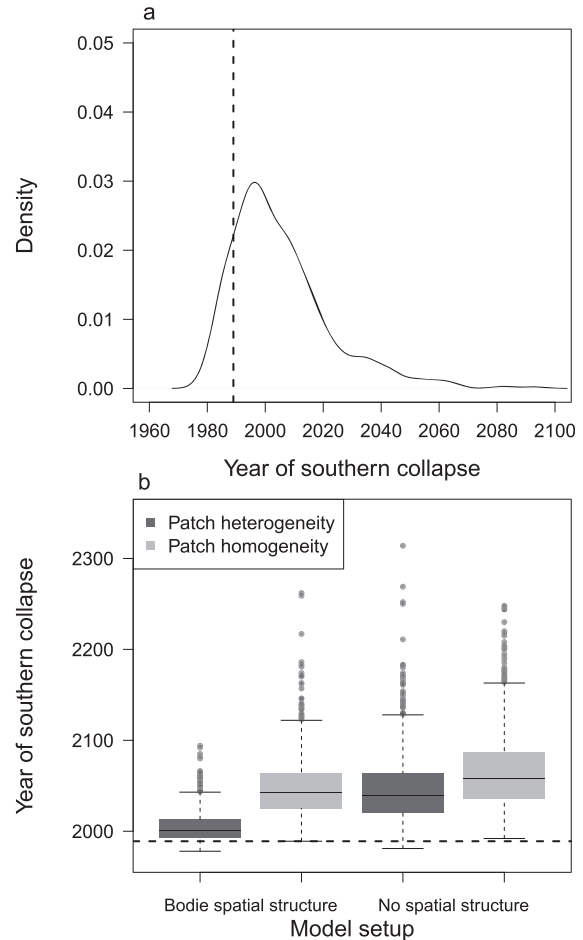


FIG. 3. (a) Frequency of times to collapse of the southern region (for model of actual Bodie spatial structure and heterogeneity). Southern collapse is the first time the southern area drops below 14 individuals in total abundance. The actual Bodie site reached this threshold after 1989. (b) Year of southern half of Bodie collapse for four different model scenarios. These represent a  $2 \times 2$  full factorial design to assess the effects of Bodie’s spatial structure and the heterogeneity in number of territories per patch (patch heterogeneity). The dashed horizontal line is the year the southern half of Bodie actually collapsed. The individual points designate simulation runs where the time to southern collapse was 1.5 times above the upper quartile or below the lower quartile.

below a quasi-extinction threshold (Ginzburg et al. 1982) of 14 pikas. We chose this threshold because by 1989 the southern region contained only this many pikas, and it has yet to recover. Although some individuals were censused in the

south after 1989, no individuals have been observed there since 2006 (Smith and Nagy 2015).

We modified our model to test two scenarios. First, we examined aspects that may have been responsible for the observed extirpation of pikas on all patches in the southern constellation. Second, we compared different scenarios to determine the relative effects of spatial structure and patch size heterogeneity. To do this, we ran additional simulations, including demographic stochasticity, with a  $2 \times 2$  full factorial design. We examined the effect of spatial structure, at Bodie (the configuration of patches, thus the type of dispersal possible) and the heterogeneity of number of territories on patches. This process generated four different scenarios: (1) the actual Bodie spatial structure and heterogeneity in patch sizes; (2) Bodie's spatial structure and homogeneous patches (same number of territories per patch); (3) no spatial structure (i.e., global dispersal) and heterogeneous patches; and last, (4) no spatial structure and homogeneous patches.

## RESULTS

### *Collapse of the southern region*

By the year 1989, pika populations on most of the southern patches were extinct (Figs. 2, 3) and have remained so ever since (Smith and Nagy 2015). We ran simulations forward from 1972 and examined if, and when, the southern region would collapse. Most simulations "post-dicted" a southern collapse near the year 1989, although with a skewed distribution (Fig. 3a).

To examine the cause of the southern collapse, we simulated the model with different spatial structures. We used a fully crossed factorial design to determine the effects of spatial structure, including two factors: the specific configuration of fragmented habitat and patch size heterogeneity. We found that both aspects of spatial structure were necessary components to explain the observed population dynamics of pikas at Bodie (Fig. 3b; Appendix S3: Table S1). Only when we included both patch configuration and patch size heterogeneity did our model predict a collapse of the southern half of Bodie on a similar time scale to field observations (Fig. 3b). In addition, only the model incorporating both the specific Bodie patch configuration and patch size heterogeneity predicted other aspects of population dynamics, including regional patch occupancy (Appendix S3: Table S1).

### *Population dynamics*

To assess general performance of the model, we compared simulation outputs to census data of the whole Bodie population. Previous work suggests that the northern and southern patches are largely dynamically decoupled (Smith and Gilpin 1997, Moilanen et al. 1998). Therefore, we ran simulations with the two areas connected via dispersal, but censused the two regions separately (Fig. 2). Our model produces results similar to census data for mean population size and the percent of occupied patches for the entire population (Appendix S3: Table S1). Further, the model predicts total abundance over time for both the northern and southern regions of Bodie (Fig. 2). However, the model poorly predicts several years (e.g., 1994 and 2004) with particularly

high or low abundance. Consequently, the model also underestimates inter-annual variance in total abundance (Appendix S3: Table S1).

### *Extinction risk*

To assess risk of extinction of the Bodie population under current conditions, we projected our best-fit model, with realistic spatial structure and patch size heterogeneity, into the future. We ran 1,000 replicates of our best-fit model starting from 1972 conditions to estimate the probability of extinction over a 300-yr time horizon. These results suggest that probability of extinction is relatively low over the next 100 yr and increases linearly thereafter (Fig. 4).

## DISCUSSION

We built a stochastic, spatially structured metapopulation model. Unlike past work using SPOMs, we took a different approach. We explicitly modeled local population dynamics using a framework more akin to Ozgul et al. (2009) and other matrix models. We were able to model local population dynamics because we had detailed natural history information and long-term census data. Our approach differs from Ozgul et al. (2009) because we incorporate demographic stochasticity and density-dependence. Typically, SPOMs use occupancy data to estimate model parameters, including connectivity and extinction rates (Hanski and Ovaskainen 2003). Both of these parameters are simply compositions of other processes. For example, extinction risk is a correlate for the combined effects of demographic stochasticity, local abundance, and environmental stochasticity. Because we explicitly modeled local population dynamics, we were able to examine how the specific habitat configuration and heterogeneity in patch sizes can cause the collapse of an entire region of a metapopulation. We were also able to apply our model to better understand the dynamics of a specific population of the American pika.

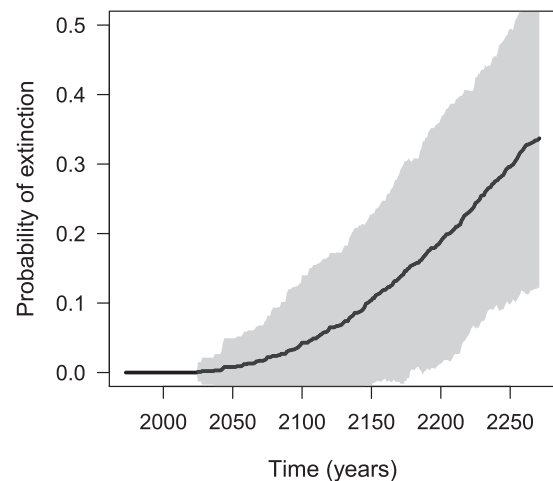


FIG. 4. Probability of extinction for the entire Bodie American pika (*Ochotona princeps*) population at different time points in the future starting from the year 1972. The light grey bands are 95% confidence intervals generated from 1,000 simulations.

Previous work on metapopulations has emphasized the role of recolonization and extinction rates in determining overall metapopulation persistence (Hanski et al. 1995, Howell et al. 2018). This approach goes back to Levin's original "rule" that recolonization has to be greater than extinction for metapopulation persistence. Recent work has shown the importance of habitat configuration, dispersal ability, and habitat quality to inform metapopulation dynamics (Eaton et al. 2014, Sutherland et al. 2014, Howell et al. 2018). Typically, this work has examined recolonization and extinction rates of individual patches. We ask an additional question about extinction. What can cause an entire constellation, or nearby collection of patches, of a metapopulation to go extinct? We found that demographic stochasticity alone was insufficient to drive an entire constellation to extinction (Fig. 3b). Individually, neither habitat configuration nor heterogeneity in patch sizes could explain such a collapse. However, when demographic stochasticity, habitat configuration, and patch heterogeneity were all included in the model, a constellation collapse occurred quickly (Fig. 3b). This result contrasts with the approach of Moilanen et al. (1998). They used an incidence function model, a specific type of SPOM, to address the same question. They concluded that a simple model, with only habitat configuration and patch heterogeneity, was insufficient to explain such a constellation collapse. They argue that instead you need some form of regional stochasticity. Clinchy et al. (2002) used simulation models to conclude that "extinction disks" could be responsible for a constellation collapse. These are events of correlated extinctions of local populations. Although their explanation was feasible, it was not mechanistic. Instead our model includes specific birth, death, and dispersal processes that interact with the specific habitat configuration to explain the extinction of an entire constellation.

#### *Bodie pika population*

We chose the Bodie pika metapopulation because it is one of the most well-studied mammalian metapopulations (Smith and Nagy 2015). The simplified nature of the conditions at Bodie makes it an ideal case study for studying the general nature of metapopulation dynamics. For example,

we are able to ignore potential landscape effects (Howell et al. 2018) on colonization dynamics, because the matrix between patches is inhospitable and relatively homogeneous.

We tested our model by first initializing it with census data from 1972, simulating forward in time, and then comparing the output to Bodie census data from the past four decades. Our model correctly "post-dicts" mean population size, overall patch occupancy, and total population size relatively well from 1972 to 2010 (Fig. 3; Appendix S3: Table S1). At first glance, the entire population looks to be in decline (Fig. 2a), but decomposing the dynamics into northern and southern areas illustrates that, while the southern subpopulation declined between 1972 and 1989, the northern subpopulation remained stable (Fig. 2b, c).

With a fully parameterized model, we then asked two questions about the Bodie pika population specifically. First, what drove the southern constellation to extinction? Habitat configuration and patch heterogeneity by themselves fail to explain the extinction of the southern constellation (Fig. 3b; Appendix S3). However, when both the actual Bodie spatial structure and patch heterogeneity are included, the model accurately predicts the timing of the southern constellation collapse observed in the field. Because a simple model, which includes only demographic stochasticity, spatial structure, and patch level dynamics, correctly predicts extinction of the southern area, it is not necessary to invoke more complicated explanations, including correlated predation episodes, global climate change, or habitat destruction, to explain field observations of pika occupancy at Bodie (Smith and Nagy 2015, Table 2). We are not claiming these processes have no effect, simply that they are not necessary to explain the major aspects of the Bodie population dynamics, especially the southern constellation collapse.

Is the Bodie pika population at risk of near-future extinction like some other recent Great Basin pika populations (Beever et al. 2011, Nichols et al. 2016, Millar et al. 2018)? To address this question, we used the simulation model to project future extinction risk over the next several hundred years for the entire Bodie pika population (Fig. 4; Appendix S7: Fig. S1). These projections support the conclusion that in the shorter term (one century), extinction caused solely by demographic stochasticity, with no environmental forcing, is unlikely. However, over timescales of a few

TABLE 2. Hypotheses for why the southern constellation of American pikas (*Ochotona princeps*) at Bodie may have gone extinct.

Hypothesis	Support	Reference
Demographic stochasticity	No support. Model with only demographic stochasticity does not predict extinction of southern constellation	This study, Fig. 3b
Spatial structural characteristics	Support. Our modeling work supports hypothesis that the combined effects of habitat configuration and patch heterogeneity can cause large extinction events	This study, Fig. 3b
Correlated extinction events	No support. This hypothesis posits that nearby patches can go extinct simultaneously because of stochastic events (e.g., weasel predation on several nearby patches). Our model supports a simpler, more mechanistic explanation for the extinction event	Clinchy et al. (2002)
Climate change	No support for this hypothesis based on past work. There is no difference in climate between the northern and southern constellations	Smith and Nagy (2015)
Change in patch quality	No support. Smith and Nagy (2015) suggested 15 patches in the southern region may no longer be suitable pika habitat. Our work suggests that removing these 15 patches from simulations does little to change overall metapopulation dynamics (Appendix S6: Fig. S1)	Smith and Nagy (2015); Appendix S6

centuries, extinction caused by demographic stochasticity becomes a more significant threat even though large patches are present in the north (Fig. 4; Appendix S7; Fig. S1). This supports the view of Millar et al. (2018) that pika populations within the Great Basin Desert can persist, despite warm summer temperatures.

#### Open questions

Although our simulation model correctly predicts mean population size, patch occupancy, and total abundance through time for both the northern and southern areas, as well as the timing of the collapse of the southern constellation, it has one obvious, but instructive, failure—it captures only 46% of the variance observed in the field (Appendix S3; Table S1). This underestimate of the variance results primarily from poor predictions for 2 yr: 1994 and 2004. Some of this variation, particularly the 2004 yr, may have resulted from differences in census personal between years. Alternatively, these extremes may have been caused by a variety of factors in those years, such as winter snowpack, summer temperature, plant productivity, or the timing of late-season snowstorms. Future field work on American pikas is needed to determine how factors such as these may influence annual survivorship.

Most of the parameters in our model were estimated independently as part of past studies (Table 1). However, we had to use the model itself to estimate both dispersal mortality and weaning mortality. Future field studies should try to quantify both of these parameters.

A key question remains open—why did the south not go extinct prior to 1990? The habitat configuration or patch heterogeneity has not changed since the 1940s indicating the south could have gone extinct sooner. It is possible that warmer temperatures have increased juvenile mortality rates during dispersal (Smith and Nagy 2015). Not surprisingly, simulations with higher dispersal mortality rates tend to predict earlier extinction of the southern constellation (Appendix S4; Fig. S2).

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.2546/supinfo>

## DATA AVAILABILITY

Code used in this paper and the supporting information are available at <https://doi.org/10.5281/zenodo.1451853>.