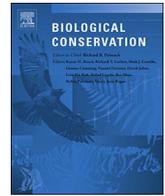




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Viability analysis for multiple populations

Seth J. Wenger^{a,*}, Douglas R. Leasure^a, Daniel C. Dauwalter^b, Mary M. Peacock^c, Jason B. Dunham^d, Nathan D. Chelgren^d, Helen M. Neville^b^a University of Georgia, 203 D.W. Brooks Drive, Athens, GA 30602, United States^b Trout Unlimited, 910 West Main Street #342, Boise, ID 83702, United States^c University of Nevada, Reno, Department of Biology, Reno, NV 89557, United States^d US Geological Survey, 3200 SW Jefferson Way, Corvallis, OR 97331, United States

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ABSTRACT

Many species of conservation interest exist solely or largely in isolated populations. Ideally, prioritization of management actions among such populations would be guided by quantitative estimates of extinction risk, but conventional methods of demographic population viability analysis (PVA) model each population separately and require temporally extensive datasets that are rarely available in practice. We introduce a general class of statistical PVA that can be applied to many populations at once, which we term multiple population viability analysis or MPVA. The approach combines models of abundance at multiple spatial locations with temporal models of population dynamics, effectively borrowing information from more data-rich populations to inform inferences for data-poor populations. Covariates are used to explain population variability in space and time. Using Bayesian analysis, we illustrate the method with a dataset of Lahontan cutthroat trout (*Oncorhynchus clarkii henshawi*) observations that previously had been analyzed with conventional PVA. We find that MPVA predictions are similar in bias and higher in precision than predictions from simple PVA models that treat each population individually; moreover, the use of covariates in MPVA allows for predictions in minimally-sampled and unsampled populations. The basic MPVA model can be extended in multiple ways, such as by linking to a sampling and observation model to provide a full accounting of uncertainty. We conclude that the approach has great potential to expand the use of PVA for species that exist in multiple, isolated populations.

1. Introduction

Perhaps the single most interesting and important question in conservation biology is: “why do some small populations decline to extinction while others persist?” If this question could be reliably addressed for species of interest, managers would have the information necessary to strategically focus actions on populations most at risk. Conservation theory and empirical observations have produced rules of thumb on the minimum number of individuals (Frankham et al., 2014; Franklin, 1980; Traill et al., 2007) or minimum habitat extent (e.g., Hilderbrand and Kershner, 2000; Robbins et al., 1989) required for a viable population, but there are numerous examples of populations that defy these rules (Peterson et al., 2014; Shoemaker et al., 2013). Smallness alone is an insufficient predictor of risk; it is also critical to understand the factors that correlate with population declines and stochasticity, and thus extinction (Caughley, 1994).

A holistic understanding of the causes of population declines, and

ultimately the processes contributing to extinction of small populations, is particularly important for species in highly fragmented habitats (Fagan and Holmes, 2006; Gilpin and Soule, 1986) — a category that covers many imperiled species of conservation interest. Examples include the island fox (*Urocyon littoralis*) in the Channel Islands (Kohlmann et al., 2005), “mountain island” species such as pika (*Ochotona* spp.; Beever et al., 2003), and water-associated species in arid landscapes (Kodric-Brown and Brown, 1993). For such species, the relative viability of individual populations is of fundamental concern to managers who must make hard decisions regarding the allocation of limited resources to prevent population and species extinctions. Ideally, such decisions would be guided by data-driven estimates of extinction probabilities under alternative scenarios of management action (or inaction) and varying environmental conditions, such as future climates.

Population viability analysis (PVA) is a class of analytical approaches that yields probabilistic estimates of population viability (or extinction) over specified time horizons (Beissinger and McCullough,

* Corresponding author at: Seth Wenger, University of Georgia, River Basin Center, 203 D.W. Brooks Drive, Athens, GA 30602-5017, United States.

E-mail addresses: swenger@uga.edu (S.J. Wenger), dleasure@uga.edu (D.R. Leasure), ddauwalter@tu.org (D.C. Dauwalter), mpeacock@unr.edu (M.M. Peacock), jdunham@usgs.gov (J.B. Dunham), nchelgren@usgs.gov (N.D. Chelgren), hneville@tu.org (H.M. Neville).

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2002; Morris and Doak, 2002). However, traditional PVAs require temporally extensive demographic data (e.g. survival, reproduction, and maturation rates), and have generally been limited to populations that have been the focus of long-term monitoring programs. Such datasets are unusual for imperiled species, and it is particularly rare to have long-term data for every population of interest, which is required to evaluate relative risk and to target management actions effectively. Some traditional PVA approaches also require data from marked and tracked individuals; such data are generally expensive to collect.

One alternative is to use a species distribution modeling approach (Elith and Leathwick, 2009) or abundance modeling approach (e.g., Royle, 2004) to identify spatial or spatiotemporal environmental covariates to explain presence or abundance. These covariates allow projection of occurrence or abundance across broad geographies and under alternative management and climate conditions. However, they generally do not consider temporal population dynamics or density dependence, and are often made at the scale of the sampling unit rather than the full population. Thus, as typically employed they cannot provide estimates of population viability.

2. A multiple population viability model

We propose that statistical methods of modeling presences or abundances in space can be married with statistical time-series models of populations to provide a data-driven approach to population viability analysis that can be applied to many populations simultaneously. The method has four defining characteristics:

1. Some population parameters are shared among populations. One or more of these parameters are influenced by covariates that vary in space and in time (or both) so they can be used to describe spatial differences among populations as well as temporal fluctuations within populations.
2. Populations are modeled as autoregressive, meaning that abundance at one point in time depends in part on the abundance in a previous time step, as in a traditional PVA. A mechanism to account for density dependence should be included in most cases.
3. Modeling is at the scale of the full population, not the sampling unit. Counts must either be scaled to the full population before modeling, or (better yet) scaled to the full population during modeling via an observation model and a sampling model directly linked to a process model.
4. As a statistical method it is driven by empirical data, which sets it apart from simulation-based methods that usually rely on a mix of literature values and expert opinion.

Previously introduced methodologies have incorporated some of these characteristics, but we know of no published approaches with all four. Clark and Bjørnstad (2004) introduced Bayesian methods to fit flexible state-space time series models that could account for hidden states, missing values, observation errors and other complexities, but applied them to only one population at a time. Zipkin et al. (2014) used a Bayesian modeling framework to extend the open N-mixture model (Dail and Madsen, 2011) to account for stage-structured time series population data. Kanno et al. (2015) further developed this to model abundance at multiple locations with density dependence as a function of climate covariates, but analysis was at the scale of the sampling unit rather than full populations, and the focus was not on viability.

We build on these antecedents to introduce a simple Bayesian multiple population viability analysis process model, or MPVA. While previous studies (Berliner, 1996; Clark and Bjørnstad, 2004; Staples et al., 2004; Zipkin et al., 2014) have emphasized the importance of linking population models to observation models to remove bias associated with incomplete detection, for the sake of simple exposition we focus here on the process model. We discuss methods for linking to observation and sampling models later.

To develop the model we assume a dataset collected from multiple isolated populations p , at least some of which have been sampled at sequential time steps t . Because our focus is on the process model, we assume that the population estimate for each population at each sampling occasion N_{pt} is known without error. We assume at least one covariate X_{pt} with a value corresponding to each sampling occasion. A traditional way to analyze such a dataset might be to use Poisson regression in a generalized linear modeling framework:

$$N_{pt} \sim \text{Poisson}(\bar{N}_{pt}) \quad (1)$$

$$\log(\bar{N}_{pt}) = \beta_0 + \beta_1 X_{pt} \quad (2)$$

Such a model would probably not meet assumptions, as repeat samples of individual populations would not be independent. This could be corrected by including a random intercept for population identity, making it a multilevel model (Gelman and Hill, 2007; Raudenbush and Bryk, 2002). Alternatively, one could make the model explicitly autoregressive by making the population at the current time step dependent on the previous time step:

$$\log(\bar{N}_{pt}) = \log(N_{pt-1}) + \beta_0 + \beta_1 X_{pt} \quad (3)$$

The above applies to $N_{pt-1} > 0$, as the outcome $N_{pt} = 0$ is deterministic when $N_{pt-1} = 0$; this caveat also applies to all subsequent forms of this equation. Eq. (3) is simply an exponential growth model where the intrinsic population growth rate r is a linear function of covariate X . It can be rewritten as:

$$\log(\bar{N}_{pt}) = \log(N_{pt-1}) + r_{pt} \quad (4)$$

$$r_{pt} = \beta_0 + \beta_1 X_{pt} \quad (5)$$

While valid, the model lacks a term for density dependence, which means that populations are unbounded and could grow exponentially to infinity in projections.

One can solve this with a simple density dependence term:

$$\log(\bar{N}_{pt}) = \log(N_{pt-1}) + r_{pt} \left(1 - \frac{N_{pt-1}}{K_p} \right) \quad (6)$$

This is now a form of the Ricker model (Ricker, 1954) in which the realized population growth rate approaches the intrinsic growth rate r_{pt} when populations are small, but declines as populations approach carrying capacity K_p . We chose the Ricker model because it is simple, it has been widely used in both theoretical and applied ecology (May, 1974; Clark, 2007; Morris and Doak, 2002; Dail and Madsen, 2011; Kanno et al., 2015), and it has a linear form amenable to covariates on rates of recruitment and density-dependent mortality (Hobbs and Hooten, 2015). However, many other formulations are possible; the Gompertz model in particular has been shown to have desirable properties (Dennis and Taper, 1994). In our example K_p is indexed by population, indicating that each population has a unique carrying capacity that is constant through time. Carrying capacity could be allowed to vary temporally as a function of covariates, but we have found that when both r and K are allowed to vary spatio-temporally, the model can suffer identifiability issues (i.e. there are multiple optima).

A solution is to reformulate the Ricker equation using the term ϕ (φ) to represent r/K , the strength of density dependence (Hobbs and Hooten, 2015). One can include spatio-temporal covariates on both r and φ :

$$\log(\bar{N}_{pt}) = \log(N_{pt-1}) + r_{pt} - \varphi_{pt} N_{pt-1} \quad (7)$$

$$r_{pt} = \beta_0 + \beta_1 X_{pt} \quad (8)$$

$$\varphi_{pt} = \gamma_0 + \gamma_1 X_{pt} \quad (9)$$

In this formulation, φ represents the reduction in population growth rate associated with adding a single individual to last year's population, and will be a small positive number—generally much < 1 but > 0 . The

prior can be specified in various ways—as a beta, a lognormal, a gamma, or as a logit-normal (we use the latter in our example below). One problem, though, is that the value of φ is likely to be much less for a population occupying 1000 km² than a population occupying 10 km². To accommodate multiple populations with varying spatial extents, we use population density instead of abundance as our covariate for density-dependence:

$$\log(\bar{N}_{pt}) = \log(N_{pt-1}) + r_{pt} - \varphi_{pt} \frac{N_{pt-1}}{A_p} \quad (10)$$

where A_p is the area available to population p . With this adjustment, φ is now the change in growth rate associated with adding one individual *per unit area* to last year's population, which is comparable among populations occupying different spatial extents. Traditional demographic models (e.g. logistic or Ricker models) do not need to make this adjustment because they are only evaluating a single population at a time, but it is critical for MPVA.

At this stage the only error term in the model is Poisson, which can be interpreted as demographic stochasticity when incorporated into a Ricker model (Melbourne and Hastings, 2008). Residual environmental stochasticity can be added as normal error (note that throughout this article we specify the normal distribution with mean and variance, σ^2 , which is equivalent to the inverse of precision, τ). We specify normal error because it is a traditional choice for overdispersion in Poisson regression (Kery and Schaub, 2012), but many other specifications are possible (note that since the normal error is applied to the logged abundance, this is lognormal error on the original scale).

$$N_{pt} \sim \text{Poisson}(\bar{N}_{pt}) \quad (11)$$

$$\log(\bar{N}_{pt}) = \log(N_{pt-1}) + r_{pt} - \varphi_{pt} \frac{N_{pt-1}}{A_p} + \varepsilon_{pt} \quad (12)$$

$$r_{pt} = \beta_0 + \beta_1 X_{pt} \quad (13)$$

$$\varphi_{pt} = \gamma_0 + \gamma_1 X_{pt} \quad (14)$$

$$\varepsilon_{pt} \sim \text{normal}(0, \sigma^2) \text{ OR } \varepsilon_{pt} \sim \text{normal}(0, \sigma_i^2). \quad (15)$$

The stochasticity term σ^2 could be assumed to be constant among populations (as shown here) or to vary at the population level σ_i^2 (i.e., be a population-level random effect). It is also possible to include population-level random effects on r and φ in lieu of (or in addition to) covariates. This allows populations to differ in r and φ in unexplained ways, although in the absence of covariates estimates of these terms for unsampled or minimally sampled populations will be noisy estimates around the mean.

This model can be fit using freely available Bayesian software such as WinBUGS (Lunn et al., 2000) or JAGS (Plummer, 2003). Prediction of population viability can be made concurrent with model fitting by including additional years of unknown future abundance (specified as “NA”) at the end of the input file for N . An alternative to making predictions within the Bayesian software is to reconstruct the model in R (or other programming language) with the parameter estimates sampled from the posterior densities produced by the model fitting process. Typically tens or hundreds of thousands of simulations are run, and viability is calculated as one minus the frequency of extinction. As in traditional PVA, it is possible to set a quasi-extinction threshold, or one can simulate the number of females and declare an extinction if the population reaches zero females or zero males.

A critical step is selecting appropriate covariates for r and φ . As for any model, the covariates should reflect the best scientific understanding of the species' biology and its relationship with the environment. Covariates on r should include variables that affect growth rate (recruitment) as well as those that affect mortality. Lagged effects (e.g., temperature in a prior year) may make sense for modeling recruitment, particularly when N excludes young/juvenile stages. Covariates on φ

should include those hypothesized to affect carrying capacity, and potentially other covariates. In practice it can take some hard thinking to determine which covariates should be placed on each term.

3. Application to Lahontan cutthroat trout

We illustrate the method with Lahontan cutthroat trout (*Oncorhynchus clarkii henshawi*), a fish listed as threatened under the U.S. Endangered Species Act (Coffin and Cowan, 1995). The species is endemic to the endorheic Lahontan basin, which encompasses a large portion of northwest Great Basin desert and eastern flanks of the Sierra Nevada Range in western North America (Behnke, 1992). Most extant populations of Lahontan cutthroat trout occur within small isolated streams or stream networks (Neville et al., 2016; Neville et al., 2006) that are fragmented due to stream intermittency and habitat suitability related to climatic factors (Dunham et al., 1999; Warren et al., 2014), and further constrained by impacts of human land and water use and interactions with nonnative trout (Coffin and Cowan, 1995). As the climate in the region warms, regional shifts in the probability of drought (Diffenbaugh et al., 2015) and associated wildfires (Westerling, 2016) are also on the rise, leading to increased threats to native fishes including Lahontan cutthroat trout (Dunham et al., 2003a; Schultz et al., 2017).

Previously, Peacock and Dochtermann (2012) conducted traditional population viability analyses of 10 isolated and three interconnected populations of Lahontan cutthroat trout in northeastern Nevada (Fig. 1). Each population had been sampled annually for five to ten years between 1993 and 2002. Fish were sampled at 6 to 30 sites per population using multiple-pass removal sampling with a backpack electrofisher. Fish of age zero were identified based on length-frequency histograms and excluded from analysis. Abundance of fish age one and greater was estimated using the Zippin estimator (Zippin, 1958) in the program MicroFish (van Deventer, 1989), averaged across sites, and then extrapolated to the full population extent for each stream. They used these abundances to calculate population growth rates and 100-year extinction probabilities for each population, based on a quasi-extinction threshold of 50 individuals. They summarized relative extinction probability for each population as low, medium or high using 100-yr extinction probabilities of < 0.5, 0.5–0.9, and > 0.9, respectively.

We used the dataset of Peacock and Dochtermann (Table 1; yearly data are shown in Table A1 in the Supplementary Material) to construct a MPVA model for Lahontan cutthroat trout. To illustrate how the model allows for viability estimates at sites with little data, we added two populations that had been sampled in only one or two years during the same 10-year period by the Nevada Department of Wildlife: Toe Jam Creek and Fourth Boulder Creek. We modeled the three interconnected populations (East Marys, West Marys, Marys River Basin) as if they were isolated, since our purpose here was to provide an illustration of the method. For population area, we used the occupied lengths reported by Peacock and Dochtermann. For Toe Jam Creek and Fourth Boulder Creek we used the “conservation population” delineations of the US Fish and Wildlife Service 2009 review of the sub-species' status (United States Fish and Wildlife Service (USFWS), 2009).

We specified two very similar MPVA models that differed only in how they treat residual stochasticity (σ^2). The first (MPVA1), shown here, models σ^2 as a random effect, which means that each population's stochasticity is drawn from a common distribution, constraining the degree to which they can differ.

$$N_{pt} \sim \text{Poisson}(\bar{N}_{pt})$$

$$\log(\bar{N}_{pt}) = \log(N_{pt-1}) + r_{pt} - \varphi_{pt} \frac{N_{pt-1}}{A_p} + \varepsilon_{pt}$$

$$r_{pt} = \beta_0 + \beta_1 \text{temp}_{pt} + \beta_2 \text{spring}_{pt} + \beta_3 \text{springlag}_{pt}$$

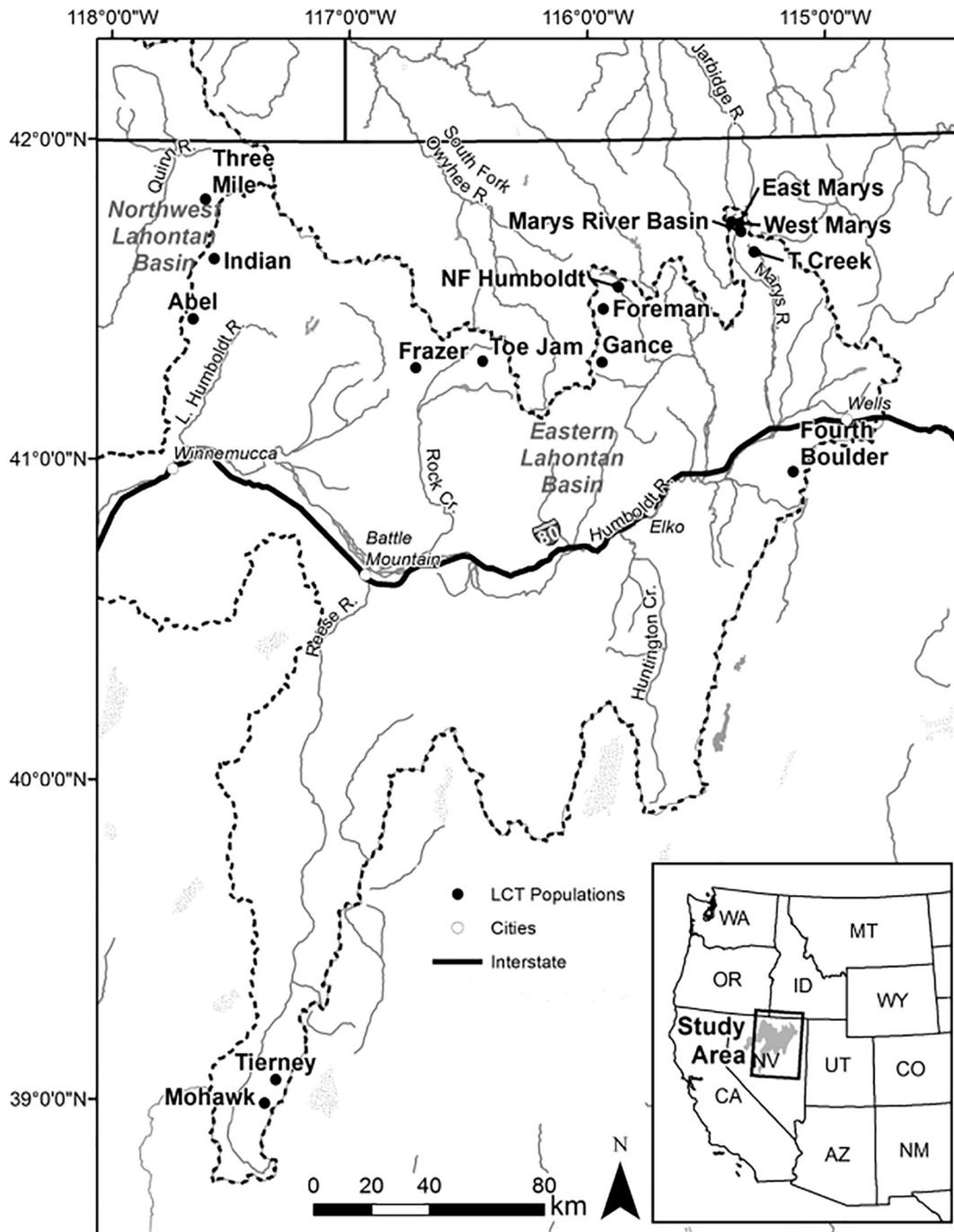


Fig. 1. Eastern Lahontan Basin in northern Nevada, U.S.A., and location of study populations of Lahontan cutthroat trout (“LCT”).

$$\varepsilon_{pt} \sim \text{normal}(0, \sigma_p^2); \sigma_p^{-2} \sim \text{gamma}(\alpha, \beta); \text{logit}(\varphi_p) \sim \text{normal}(\mu, \sigma^2);$$

$$\mu \sim \text{uniform}(-9, -3); \sigma^2 \sim \text{uniform}(0, 100); \alpha, \beta \sim \text{gamma}(.001, .001); \beta_{0,1,2,3} \sim \text{normal}(0, 100)$$

The second (MPVA2) is the same except that σ^2 is estimated independently for each population, with vague priors. Both rely the Ricker model of density dependence, which is a common choice for modeling salmonids (e.g., Elliott, 1985; Myers et al., 1998). For simplicity, we included covariates on r only, and assumed φ was distinct for each population using a random effect with mean and variance estimated from the data. We used three spatio-temporally-varying climate-related covariates on r_{pt} : stream temperature (temp), spring flow magnitude (spring) and spring flow magnitude in the previous year

(springlag). Mean August temperature was extracted from the NorWeST dataset (Isaak et al., 2016). We hypothesized that excessively high temperatures in this desert environment could lead to mortality (Dunham et al., 2003b). Spring flow magnitude was calculated as the annual maximum 7-day flow during the season of spring runoff (March–July) for each population’s most-downstream segment, using outputs from the Variable Infiltration Capacity macroscale hydrologic model run by the University of Washington (<https://cig.uw.edu/datasets/wus/>) and downscaled to NHDPlus stream segments using the methods of Wenger et al. (2010). We included flow magnitude for the current year as well as flow magnitude with a one-year lag, as earlier modeling efforts using this dataset by Ray et al. (2007) suggested that high flows in the current year may cause mortality (reduced growth rate from last year) but that high flows in the previous year may

Table 1
Population names, mean density (fish/km), and length (km) for 15 Lahontan cutthroat trout populations.

Population name	Years sampled (n)	Mean density (fish/km)	Length (km)
East Marys River	1993 to 2001 (9)	155.7	5.90
West Marys River	1993 to 2002 (10)	170.6	6.00
Marys River Basin Cr	1993 to 2002 (10)	147.4	5.10
Frazer Cr	1993 to 2002 (10)	617.2	3.54
Gance Cr	1993 to 2002 (10)	245.2	8.55
Foreman Cr	1993 to 1999 (7)	376.3	5.93
Abel Cr	1996 to 2002 (7)	131.6	2.00
Indian Cr	1996 to 2002 (7)	323.4	1.77
Mohawk	1996 to 2001 (6)	245.7	4.70
NF Humboldt River	1996 to 2002 (7)	199.7	19.00
T Cr	1994 to 2002 (9)	251.0	9.98
Three Mile Cr	1996 to 2000 (5)	400.4	6.76
Tierney Cr	1993 to 2001 (6)	56.2	13.00
Toe Jam Cr	1996, 2002 (2)	156.3	17.13
Fourth Boulder Cr	2001 (1)	204.8	4.17

increase recruitment to adulthood in the following year (increasing growth rate). We standardized covariates by subtracting the mean and dividing by the standard deviation.

To compare MPVA to traditional PVA methods, we additionally constructed two simplified models. The first (“Simple1”) is equivalent to modeling each population individually, with density dependence:

$$N_{pt} \sim \text{Poisson}(\bar{N}_{pt})$$

$$\log(\bar{N}_{pt}) = \log(N_{pt-1}) + r_p - \varphi_p N_{pt-1} + \varepsilon_{pt}$$

$$\varepsilon_{pt} \sim \text{normal}(0, \sigma^2); \varphi_p \sim \text{uniform}(0, 1); r_p \sim \text{normal}(0, 1E4); \sigma^2$$

$$\sim \text{uniform}(0, 100)$$

The second version (“Simple2”) is identical but removes the term for density dependence ($\varphi_p N_{pt-1}$). There are no covariates in either model (covariates are rarely used in traditional count-based PVA, nor could their coefficients be readily estimated without long time series, since each population is modeled independently). Despite the names, Simple1 and Simple2 both include more parameters than MPVA1, since each population is modeled individually (Table 2). When applied to 13 populations, Simple1 has 27 parameters and Simple2 has 14 parameters, whereas MPVA1 has 7 (although three of these represent random effects, which can have an effective number of parameters greater than their nominal value; Bolker et al., 2009). MPVA2 has 18 parameters. Note that because each population is independent, the models cannot be run for Toe Jam and Fourth Boulder, which were only sampled once (Toe Jam) or twice (Fourth Boulder and therefore had insufficient time series to support model parameterization. The essential characteristics of all four models are shown in Table 2.

We implemented each model in the Bayesian software JAGS (Plummer, 2003). We specified vague priors for all stochastic parameters and ran the model for the 10-year period for which we had data (1993–2002). We used five chains with a 10,000 iteration burn-in period followed by 250,000 sampling iterations, using a thinning factor of 25, resulting in a net 50,000 samples for estimating posterior

Table 2
Essential characteristics of the two MPVA models and the two “simple” models.

Model name	Populations modeled jointly, with covariates?	Density dependence?	Residual stochasticity parameterization	Number of parameters
MPVA1	Yes	Yes	Random effect by population	7 ^a
MPVA2	Yes	Yes	Independent by population	18
Simple1	No	Yes	Independent by population	27
Simple2	No	No	Independent by population	14

^a Three parameters represent random effects.

distributions. We conducted forecasts concurrent with model fitting by adding an additional 100 years, with covariates for each year randomly sampled from the 10 years of historical covariate data (note that since the forecasts are concurrent with model fitting, there are a net 50,000 samples used for prediction). We started the forecasting simulations for each population using the final year's observed value for that population. In every year we randomly estimated the number of females based on a 1:1 sex ratio by drawing from a binomial distribution ($p = 0.5$, $N =$ number of individuals) and declared a population to be extinct if that number dropped to zero or was equal to the total number of individuals (i.e., no females or all females). This approach could overestimate extinction, however, because trout have overlapping generations and a population potentially could be maintained with no adults at all, as long as there are still juveniles that can survive into adulthood. For MPVA2 we could not forecast Toe Jam and Fourth Boulder concurrent with model fitting, so we made post-hoc predictions by reconstructing the forecast code in R and drawing from the posterior parameter estimates. The full models and details on all settings are provided in supplementary material. We compared model in-sample performance on the basis of absolute error, bias, and precision.

4. Results

All models passed Gelman-Ruben convergence diagnostics. Of the covariates we tested with MPVA, we found no relationship with temperature (perhaps because the sites do not span a sufficient gradient; see Discussion), a possible weak negative response to spring flow, and a positive response to spring flow in the prior year (Table 3). The intercept on r was positive and corresponded to an average growth rate (when N is near zero) of $\exp(0.4) = 1.49$ in MPVA1, with all covariates at their mean values. The mean estimate of φ was 0.0015. This corresponds to an average carrying capacity ($K = r/\varphi$) of 267 fish per km.

A plot of predicted vs. observed densities shows reasonable fit for all models (Fig. 2), considering that trout populations have been shown to undergo large, unpredictable fluctuations (Dauwalter et al., 2009; Dochtermann and Peacock, 2010; Platts and Nelson, 1988), although there was a general tendency to over-predict low-densities and under-predict high densities. For MPVA1 mean absolute prediction error was 653 individuals, with a bias of -148 and a precision (expressed as a mean 90% credible interval width) of 4620 individuals (Table 4). For MPVA2 results were very similar, though precision was slightly worse. The two simple models also had similar performance to MPVA, except that precision was worse, especially for Simple1 (Table 4). It's important to note that the low bias of the simple models is expected, given that each population is fitted individually. The advantage of MPVA (particularly MPVA1) is that it achieves comparable bias with fewer parameters, and furthermore can be used for prediction in additional locations. However, predictions for Tierney and Three Mile Creeks from Simple1 appeared unreliable due to very imprecise estimates of growth rate that allowed populations to rise very high in population forecasts before crashing to extinction.

The estimates of 100-yr extinction probabilities ranged from 7.5% to 21.8% for MPVA1 and 2.7% to 52.9% for MPVA2 (Table 5). Extinction rates for Simple1 and Simple2 were much higher: 12.6%–85.1% for Simple1 and 34.4%–73.6% for Simple2 (Table 5).

Table 3
Means and 80% credible intervals of posterior parameter estimates from Lahontan cutthroat trout MPVA models.

Variable	MPVA1			MPVA2		
	10%	Mean	90%	10%	Mean	90%
B0 Intercept	0.12	0.40	0.67	0.14	0.46	0.77
B1 temperature	-0.18	-0.02	0.13	-0.20	-0.06	0.008
B2 springlag	0.03	0.16	0.29	0.001	0.11	0.21
B3 spring	-0.23	-0.09	0.05	-0.18	-0.07	0.004
Mean phi	0.0004	0.0015	0.0036	0.0006	0.0015	0.0041

Among MPVA1 results, the highest extinction risk was associated with Abel Creek, which had both a low density and a small spatial extent; as the smallest overall population, its relatively low viability makes sense. In contrast, the Simple2 model gave Abel Creek the lowest extinction probability of any of the populations, and Simple1 gave it an intermediate extinction probability (Table 4). The reason for the difference is that estimates of extinction risk from Simple1 and Simple2 are determined by the observed growth rate and stochasticity in Abel Creek alone, whereas MPVA1 projections assume that year-to-year variability is partly explainable by covariates and remaining stochasticity is treated as a random effect, with some influence from the overall mean of the stochasticity across all populations. Since the short seven-year data series for Abel Creek has low stochasticity and a slight upward trend (Table A1, Supplementary Material), extinction risk is low in the simple models (relative to other populations, not to MPVA estimates). MPVA2, which explains some variability using covariates but which estimates residual stochasticity for each population separately, is intermediate in behavior. Like Simple1 and Simple2, MPVA2 shows N.F. Humboldt as having the highest extinction probabilities, as this population has the highest stochasticity.

The higher extinction probabilities for Simple1 and Simple2 compared to MPVA are in large part due to the higher uncertainties in these

Table 4
Mean absolute prediction error, bias, and precision for the MPVA and “simple” models. Numbers are in units of fish of age 1 +.

Model	Mean absolute prediction error	Bias	Precision (mean 90% credible interval)
MPVA1	653	-148	4620
MPVA2	646	-136	5390
Simple1	626	-196	18,707
Simple2	775	-32	12,900

Table 5
100-Year extinction probabilities of Lahontan cutthroat trout populations from MPVA1, MPVA2, Simple1, Simple2, and Peacock and Dochtermann (2012).

Population name	MPVA1	MPVA2	Simple1	Simple2	P & D Extinct.
East Marys River	14.1	30.1	55.6	48.5	Low
West Marys River	11.5	17.1	28.8	39.9	Low
Marys River Basin Cr	17.5	35.5	64.7	58.6	Mod
Frazer	16.4	14.1	12.6	45.5	Mod
Gance	14.0	23.1	45.1	50.5	Mod
Foreman	7.5	3.5	16.3	57.8	Mod
Abel	21.8	12.0	23.9	34.4	Low
Indian	13.2	11.9	37.8	62.3	High
Mohawk	9.0	2.7	14.9	40.0	Low
NF Humboldt	20.4	52.9	85.1	87.1	High
T Creek	9.0	4.4	14.1	70.3	High
Three Mile	13.5	14.1	*	66.6	High
Tierney	11.8	20.5	*	73.6	High
Toe Jam	19.1	21.4	-	-	-
Fourth Boulder	20.2	22.9	-	-	-

*Estimates are unreliable; see text.

model predictions. With these types of models, higher stochasticity in a population forecast translates to higher extinction probability (Morris and Doak, 2002). The extinction rate classes reported by Peacock and

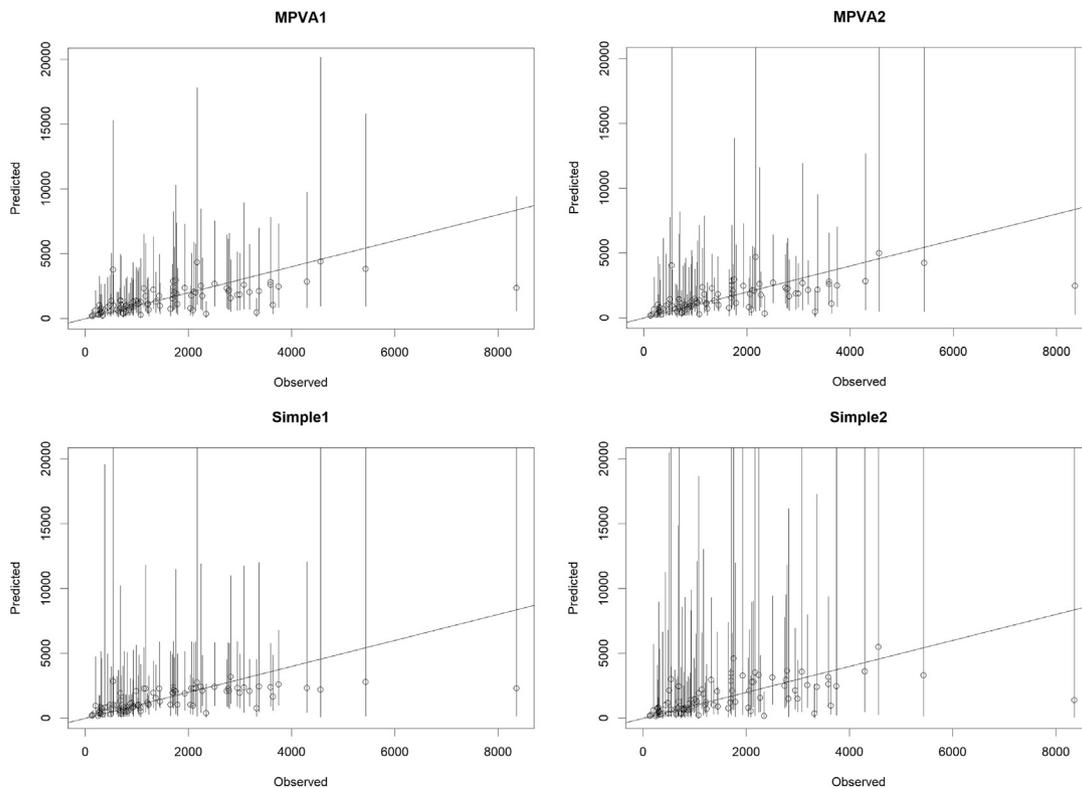


Fig. 2. Predicted vs. observed densities for each population at each sampling event under MPVA and the Simple1 and Simple2 models. Circles show medians; lines show 95% credible intervals. The diagonal line is the 1:1 line. The extent of the Y axis is defined by MPVA1; the upper ends of some intervals are truncated for the other three models.

Dochtermann (2012) are broadly consistent with those of the Simple2 model. Since Peacock and Dochtermann set a quasi-extinction threshold of 50, as a test we reran Simple2 with an equivalent threshold. We then found that our results exactly matched those that they reported, which is expected since Peacock and Dochtermann used a density-independent exponential growth model (Morris and Doak, 2002) that is equivalent to Simple2. One problem with such a model is that its population predictions are unbounded by carrying capacity; as a result some of our forecasts from Simple2 rose to unrealistically high numbers. Morris and Doak (2002) point out that violations of the model's assumption of density independence can render its results "extremely inaccurate."

5. Discussion

We have introduced an approach for assessing the viability of multiple populations that has several advantages over existing PVA methods. First, this approach borrows information from other populations, and as such allows estimation of viability for populations with insufficient data for conventional PVA. Accordingly, MPVA can even make predictions for populations with few to no observations. Second, as a statistical modeling approach, it is inherently empirical; biological expertise is needed to determine model structure and reasonable covariates, but MPVA does not depend on parameters set from the literature or expert opinion. Third, it allows proper accounting of uncertainty, although to take advantage of this fully the process model should be coupled to an observation and sampling model. We return to this shortly.

The use of covariates opens the door to numerous practical applications. If climate-related variables are used as covariates, it is possible to use outputs from general circulation models to generate projections of viability under future climate conditions. The covariate parameter estimates from the fitted model provides an empirical basis for the climate effect, without the need for additional assumptions about the climate-organism response (except for the assumption that the climate-organism response remains within the bounds of existing observations). Similarly, if habitat-related variables are used as covariates, it is possible to test the benefits of restoration or management actions that alter these habitat conditions. Finally, modeling invasive species presence or density as a covariate can allow exploration of the influence of this factor and the benefits of invasive species control. In all these cases, however, it is necessary to have populations that span a gradient of the predictor variable of interest in order to estimate the associated parameters. If all of the extant populations are in a narrow climatic band, it may not be possible to estimate a temperature effect (in fact, this is likely the reason for the lack of effect in our example). Similarly, to estimate the effect of an invasive species the distribution of its densities should have good representation across a broad range. Locations where the focal species has gone extinct as a result of the invasion will strongly inform parameter estimates. Consideration of statistical representation of populations is therefore critical.

A potential downside to MPVA is that a sudden downward trend in a monitored population that might indicate a risk to persistence will not necessarily translate to a substantial decline in predicted viability for that population, especially if it is due to a factor that is not included as a model covariate. Because MPVA borrows information from other populations, any one data point has reduced leverage compared to a simple single-population model. Accordingly, when there is particular interest in individual populations that are the subject of long-term monitoring, it is reasonable to fit both MPVA and single-population models, using outputs of both in evaluating risk. In our example, MPVA ranked Tierney Creek as having a low extinction risk, whereas the simple models assigned it a high risk due to a marked localized decline. In reality this population went extinct, likely due to invasive brook trout *Salvelinus fontinalis*, a factor not included in our MPVA model.

Ideally, the MPVA process model should be linked with an observation and sampling model to allow for full accounting of

uncertainty. Berliner (1996) described hierarchical Bayesian time-series models that included a model of the data generating process (e.g. fish surveys) plus a model of the underlying process of interest (e.g. fish population dynamics). Following Hobbs and Hooten (2015), the data model can be further subdivided into an observation model and a sampling model. The observation model estimates detection probability and the underlying true abundance at a site or plot, while the sampling model scales multiple abundance estimates to the full region of inference (in this case, a defined population). The three models can be linked in a hierarchical fashion: the observation model yields an estimate of site-scale abundance, which feeds into the sampling model of population-scale abundance, which in turn feeds into the process model that estimates inter-annual changes in populations. In our example, our dataset was based on an external observation model (Zippin), extrapolated to the full sample extent. We treated the resulting estimate of abundance as if it had been known precisely. Thus, uncertainty from the first two levels was ignored. The alternative is to code an internal multi-pass estimator as the observation model, link this to a sampling model that assumes the reaches sampled are representative of the overall population extent, and use the estimates of latent total abundance in each year to fit the process model. This hierarchical approach allows for realistic propagation of all sources of uncertainty into estimates of persistence, and more realistic estimates of extinction probability. We have created several versions of such a model, but the code and model behavior is complex and well beyond the scope of this article, which aims to present the core process model with sufficient detail. The full model is the subject of a manuscript in preparation.

Any version of MPVA will be data demanding (though much less so than conventional PVA applied to numerous populations), both in terms of in-situ species observations and covariates to explain differences in those species observations among populations and years. A couple of decades ago, these models would have been of theoretical interest only, but we are optimistic that the required data are now available for many taxa of interest. First, there is an increasingly diverse and accessible array of remotely sensed data products from NASA and other providers that can serve as useful covariates across broad study domains (Dauwalter et al., 2017). These in turn have been used to develop numerous secondary and tertiary data products, such as the NorWeST stream temperature dataset used in our example. Second, there is a largely untapped resource out there for biotic data, at least within the US: state agency data collections. The Nevada Department of Wildlife alone has over 5000 records of collections targeting Lahontan cutthroat trout since the early 1980s. Other states have comparable or larger datasets for other species of interest.

Existing sampling regimes are generally not optimized for generating data for MPVA analysis, however. MPVA is autoregressive, and at least some populations need to be sampled in sequential years in order to fit a model. Many agencies use rotating panel designs, visiting a site every five years or so (Larsen et al., 2001; Urquhart et al., 1998). While there are advantages to such an approach, the lack of data for back-to-back years may make it difficult to estimate model parameters. We are currently conducting simulation studies to determine how important such data are, and the tradeoffs of different types of sampling designs in terms of identifying covariate effects and in predicting viability using MPVA models.

We presented MPVA as a blend of spatial distribution/abundance models and temporal population dynamics models that are empirical statistical approaches. In contrast, conservation prioritization has historically relied on non-empirical methods to support decision-making in data-deficient locations. These span a gradient of complexity. One end of the spectrum is occupied by spatial ranking methods that rely on indirect indicators of population status and habitat quality (O'Grady et al., 2004), such as Trout Unlimited's Conservation Success Index (Williams et al., 2007). The scores used in such indices are often derived from the same types of variables that serve as covariates in an MPVA or species distribution model, but they are usually parameterized by a mix

of expert opinion and past study results. At the other end of the model complexity spectrum are spatially-explicit population simulation programs such as RAMAS-Metapop (Akçakaya and Root, 2002), CDMetaPOP (Landguth et al., 2017), and Hexsim (Schumaker, 2011). These are also non-empirical, which is both their strength and weakness: they can provide estimates of viability in the absence of data, but those estimates can vary greatly depending on how the user chooses to set parameters (and such models may have many, many parameters). MPVA is similar in that it estimates extinction risk, but these estimates are based on empirical data.

We are beginning to explore variations on MPVA. Age- or stage-structured MPVA models are a natural extension, and for species with appropriate datasets such models may offer dramatic improvements over the simple form presented here. Connected populations are another obvious extension, but estimating movement among populations represents a major challenge. Highly connected populations may also be of lower interest because viability will tend to be much higher than for isolated populations, and for classical metapopulations with extinction-colonization dynamics existing methods such as the incidence function method (Hanski, 1994) may be more practical. It may be useful to incorporate catastrophes into an MPVA, particularly where there is the possibility for linking to models of catastrophe risk. However, since most catastrophes are stochastic and uncommon, it may be difficult to estimate their effects from empirical data alone (Mangel and Tier, 1994). Hybrid empirical/simulation models may be required. Finally, spatial error structure could be a valuable addition to future MPVA models, especially for populations that are clustered. This would move MPVA into the realm of dynamical spatio-temporal models (Cressie and Wikle, 2011). In our MPVA example, we used spatio-temporal covariates to account for spatial autocorrelation induced by key environmental drivers, but we did not account for residual spatial autocorrelation. This was largely to keep the models simple, as anisotropic (directional) covariance functions based on stream distance and flow direction introduce significant model complexity (Ver Hoef et al., 2006).

6. Implications for Lahontan cutthroat trout

Our purpose here was to use the Lahontan cutthroat trout dataset as an illustration, not to make conservation recommendations, but we nevertheless provide some context for our results. Of the covariates we tested, we found a positive effect of high flows in the preceding year, suggesting that these flows increase survival and recruitment to the adult stage (our data excluded young-of-year), possibly by stimulating increased productivity. We found no effect of temperature among the populations we examined, perhaps because they do not span a sufficient gradient. We found that 100-year extinction rates from MPVA were much lower than those produced by the simple models, which represent traditional PVA approaches. We also found substantial differences in the rank ordering of extinction risk, although all models agreed that the North Fork Humboldt population was at high risk. We caution that this is a small dataset, and we are in the process of conducting an analysis on a much larger dataset, the results of which will be reported separately. However, our preliminary findings are enough to suggest that managers should be cautious in relying too heavily on traditional PVA methods in the management of Lahontan cutthroat trout, or other similar species. In fact, a population-specific prediction from a PVA of any kind (including MPVA) would benefit from an interpretation by experienced field biologists with knowledge of the system, and should be considered in the context of other available information.

7. Conclusions

Morris and Doak (2002) suggested that a first rule to using PVA is to let the available data guide the type of PVA to perform. Historically, assessing the viability of data-deficient populations necessitated the use

of approaches that required literature values or expert opinion. Here we show that MPVA presents a data-driven alternative that can provide reasonable viability estimates for poorly-sampled populations, as long as there are sufficient data from other populations to estimate covariate effects. We argue that the resulting estimates of viability are an appropriate basis for decisions on the allocation of scarce resources for imperiled species that occur in multiple isolated populations.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2017.10.006>.

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