Wildl. Biol. Pract., 2016 June 12(1): 1-11
doi:10.2461/wbp.2016.12.1

ORIGINAL ARTICLE

RAPID ASSESSMENT AND EXTINCTION PREDICTION USING STOCHASTIC MODELING OF THE ENDANGERED AMARGOSA VOLE

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Keywords
Diffusion model;
Environmental stochasticity;
Global climate change;
Mojave Desert;
Population viability analysis;
Rapid assessment;
Stochastic extinction analysis.

Abstract

The Amargosa vole, *Microtus californicus scirpensis*, is an endangered microtine rodent obligately found in marshes near the Amargosa River, Mojave Desert in California. There are very few data to inform modeling and adaptive management. If interventions are postponed until data are available, the vole could go extinct in the interim, making a more flexible modeling approach imperative. The voles face threats from environmental and demographic stochasticity, Allee effects, inbreeding, genetic drift, intense predation, and disease. The modeling approach used here is based on diffusion methods for time series of population size constrained by a carrying capacity, focusing on environmental stochasticity and the probability that the variance in population growth could allow the population to encounter the lower "absorbing" boundary and go extinct. We parameterized the model with Amargosa vole data that stand as Bayesian "priors" for carrying capacity, until more data can be obtained and allow us to refine a more accurate estimate. There are no multiple-year time series data or data for most demographic characteristics of the Amargosa vole, forcing us to look to California vole time series as a Bayesian prior. Our analysis indicated expected 20-24 years to extinction and 4-5% probability of extinction in one year due to environmental stochasticity: the real time could even be shorter if there is significant demographic stochasticity. Implementation of management based on best available modeling will be crucial to avert this risk. This modeling approach also has merit for other species in urgent need of management even in the face of early projects lacking mature data sets.

Introduction

The Amargosa vole (*Microtus californicus scirpensis* Kellogg 1918) is a rare rodent found only near Tecopa, Inyo County, California [1]. Although the first reports were from a collection in 1891 from the "Amargosa River (near the Nevada line), Inyo County" [2], soon began reports of extinction, rediscovery, and extinction again, testimony that the vole has been rare throughout recent history. The vole is federally and State of California endangered under the Endangered Species Act [3]. Despite listing, there has been only sporadic research since 1997 [4]. A collaborative group of

Published by: Portuguese Wildlife Society.

researchers undertook two pulses from 2012-2014 of mark-recapture efforts to estimate demographic characteristics [5,6]. Survival rate was only 0.347/month favoring larger males, much lower than the 0.83/month in the 1990s [6]. Densities range from 2-60 individuals/ha.

Voles are restricted to small, isolated marshes surrounded by harsh alkali flats, totaling about 30 ha of suitable habitat with numbers from several hundreds to no more than a thousand individuals [7]. The most densely occupied patch was a marsh around an Artesian well accidentally dug in 1967 (Marsh 1). Less than half of available habitat is occupied, small patches have very low vole density, and wetlands in Marsh 1 recently collapsed from excessive water loss following landscape manipulation and drought. There is very limited gene flow among subpopulations, inbreeding, and genetic bottlenecking [8](Conroy, UC Berkeley unpub. data), and a significant threat of endemic, epidemic, or catastrophic disease is synergistic with genetic loss and anthropogenic habitat challenges [5,9]. Voles compete with sympatric native and non-native rodents and there may be apparent competition among rodents mediated by disease. Predation on Amargosa voles is intense from at least 27 species of birds, snakes, amphibians, and mammals (A. Roy, CDFW, unpub. data). Finally, some of the marshes are also adversely affected by invasive non-native plants such as *Tamarisk* sp. (Otahal, BLM, unpub. data).

The already extremely small Amargosa vole population is highly fragmented and experiences wide fluctuations in size. Demographic and environmental stochasticity could cause its rapid extinction by means of any of the mechanisms described above. Future management could perhaps avert extinction if we understood the magnitude of the risk, for example by reducing disease or stabilizing habitat. Yet we lack even two full years of demographic data and have minimal knowledge of basic life history upon which to base population projections. Nevertheless, population viability analysis (PVA) is required for conservation management [10,11]. Commonly PVAs are done using Leslie or Lefkovich matrices but such methods typically require extensive data and don’t readily lend themselves to cyclicity, environmental and demographic stochasticity, and important biotic and abiotic forces (such as the unanticipated release of water from Marsh 1) that change population trajectories.

Rather, here we apply a diffusion-based modeling approach to Amargosa vole data. Diffusion methods based on population size time series can capture population vulnerability due to environmental stochasticity and such methods (sometimes called “diffusion approximation methods”) have strong theoretical foundations and tools for working with “corrupted data” have been produced [12] as well. The model is mathematically simple and equations can be solved to directly answer how T_e depends on the data. If, as in the case of Amargosa voles, few census data are available, we can start the analysis using Bayesian priors for population growth rates from related species and then improve accuracy by incorporating target species data as they become available [13]. Our goals were to: 1) highlight key variables that would likely contribute to Amargosa vole extinction, 2) determine whether or not data were available for these variables or whether proxy data would serve, and 3) use diffusion analysis-based modeling to predict how long before the Amargosa vole population would likely go extinct without changes to environmental stochastic forces that impact it.

Methods

This study relies on results from diffusion analysis of $\ln N_t$ [13] to predict persistence of the Amargosa vole population. Such analysis assumes that the basic relationship between N_0 and N_t applies even when N_t is small and that the residuals are independently and identically distributed [14]. The set of N_t is a time-series of annual population sizes measured at their lowest point (this nadir can occur at a different time each year). Using $\ln N_t$ eliminates some common variation in N which would violate assumptions of diffusion analysis. Density-dependence is imposed by a carrying capacity K. A local population is extinct when the pooled reproductive value of all females < 1. Following [15] Equation 18, expected time to extinction $T_e(n_0) = 2n_0(k-n_0/2)/v_r$, where n_0 is $\ln(N_0)$ and k is ln(K). The few demographic data available for Amargosa voles show a 1:1 male:female sex ratio and provide an estimate of density at two marshes (Marshes 1 and 17) from which we calculated range-wide N by multiplying by the available 30 ha [5,6]. K is the total calculated number of voles during the time of year when there are the fewest voles.

Variance in *r* (per capita growth rate), v_r, is calculated from a time series of N. Environmental stochasticity causes v_r but we correct v_r to v_{re} for temporal autocorrelation (ρ). We assume that the expected value of *r* (r_d) = 0, i.e. there is no secular trend in rates. We also assume initially that demographic stochasticity is far outweighed by environmental stochasticity [16]. Because there are no data on inter-annual variability in *r* for Amargosa voles, we cautiously used Bayesian prior estimates from California voles which have similar gestation periods of about 21 days, time to weaning in about 14 days, a post-partum estrus allowing for a litter to be conceived shortly after parturition, reproductive maturity in 3 weeks for females and 6 weeks for males, and a mean litter size of 4-5 [1,17,18]. California vole populations are regulated by an interplay of seasonally abundant resources promoting reproduction, predation, and then over-predation plus loss of food resources [19,20]. Spacing behavior and social interactions, sometimes mediated by pheromones, also influence vole demography [21]. We used time series from California voles on Brooks Island in the San Francisco Bay for 5 years (designated "Brooks") [20], two sites in Mendocino County for 21 years ("Mendocino1" and "Mendocino2") [22], and Richmond, Alameda County for 7 years ("Richmond") [23,24]. We also examined values from the western harvest mouse, *Reithrodontomys megalotis* which is marsh-dependent when in the Chihuahuan Desert ("Chihuahua") [25].

Results

Initial recapture data of Amargosa voles in two marshes yielded estimated densities from 2-60 individuals/ha, which yields a range-wide N varying from as low as 50 to almost 2000 (Fig. 1). In the second pulse of trapping beginning in October 2013, there was dramatically higher N, characteristic of other vole "boom and bust" dynamics [23]. Winter temperatures are very harsh and bulrush quality is poor during that season. Thus the second year of data reflected considerably reduced numbers in fall into winter. In the first year of trapping, a ceiling was apparent at approximately 200 animals. In the second year, despite the intense transient increase in calculated N, the sharp downward turn suggests that the true ceiling is still very low, from 200-400 individuals.

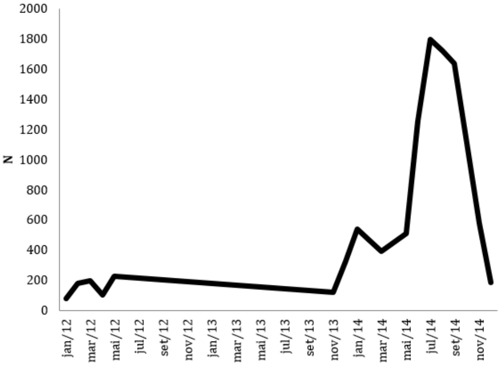

Figure 1: Time series of population size estimates for Amargosa voles during intensive trapping for demographic assessment. Data from June 2012-Sept. 2013 are interpolated as no trapping was conducted during that period.

Characteristics of other rodent times series are summarized in Table 1 and Fig. 2. Among the studies of California voles excluding Amargosa voles, ρ was negative for the Mendocino1, Richmond, and Chihuahua time series and positive for Mendocino2 and Brooks. Correcting v_r for ρ (temporal autocorrelation) yields values of vr_e from 0.72-1.52. The harvest mouse vr_e was lower than all voles and was not used in further analysis.

Table 1: Characteristics of published time series of population sizes (N) for California vole populations and a population of western harvest mice (see text for details and citations). Full references are given in text. ρ (temporal autocorrelation), v_r (variance in population growth), and vr_e (v_r corrected for temporal autocorrelation) are used in diffusion-based extinction analysis of Amargosa voles; estimates of carrying capacity (K) and expected value of the per capita growth rate (median r_d) are provided for comparative purposes with Amargosa voles.

	Mendocino1 California vole	**Mendocino2 California vole**	**Brooks California vole**	**Richmond California vole**	**Chihuahua Harvest mouse**
Lowest N	0	0	20	1	1
Highest N	50	40	75	50	34
Length of time series (years)	21	21	5	7	11
Magnitude of fluctuation (voles)	50	40	3.75	50	34
Evidence of periodicity	2 10yr periods, yr 5 N anomalously high	1.5 10yr + periods, less abrupt crash, high N at yr 5	Possibly 1 period, yr 2 max	Not clear	Not clear, gradual increase
ρ	-0.43	0.05	0.24	-0.52	-0.49
v_r	1.8	0.67	0.74	4.75	1.74
vr_e	0.72	0.74	1.21	1.52	0.59
K (voles)	16 (apparent from plot of data	16 (from plot)	75	32	Not clear
r_d median	0.06	0	-0.26	0.28	0.05

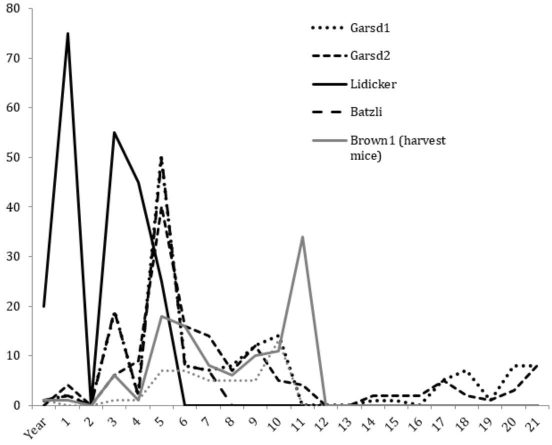

Figure 2: Time series of population sizes (N) for populations of California voles in northern California and western harvest mice in the Chihuahuan desert. Full references are given in text.

In order to understand how different inputs of vr_e and N_0 would affect the estimates of T_e, we plotted T_e across the range of different N_0 for a mid-value vr_e (1.3) observed in California vole time series and across the range of vr_e for a moderate N_0 (100 females) observed for Amargosa voles (Figs. 3a and 3b). These plots reveal that there is a sharp decline in predicted extinction as population size increases at very low levels, and correspondingly, increasing variance in *r*, associated with environmental stochasticity, precipitously increases risk of extinction of Amargosa voles. We performed diffusion-based analyses of expected Amargosa vole persistence given population size and *r* estimates obtained from our data. These data ranged from the low N_0 of 15 females seen in Marsh 1 to the more moderate sizes we anticipate rangewide with K of 150 females (with the initial simplistic assumption that habitat is fully saturated and N_0 = K). We used vr_e across the full range reported in the literature for California voles (Table 2). In the worst case scenario of high vr_e in a small population, then T_e = is as low as 5 years. At best with data available for voles, using the notably low vr_e seen by Garsd, the population could be expected to persist 35 years. Because T_e is an exponential random variable with expected value = 5-35 years, then there is a 1/5-1/35, or 2.9-30% probability of going extinct in one year.

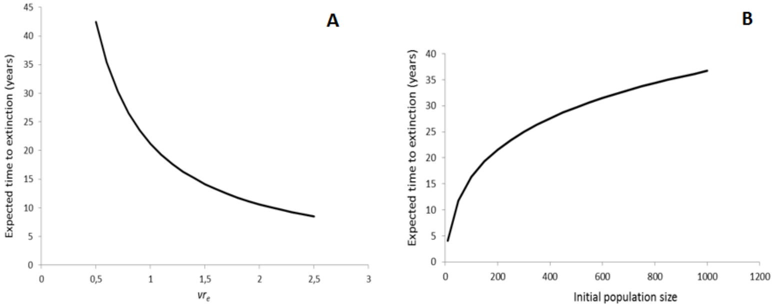

Figure 3: *A*. Estimates of T_e across a range of different N_0 for a mid-value vr_e (1.3) observed in California vole time series. *B*. Estimates of T_e across a range of vr_e for a moderate N_0 (100 females) observed for Amargosa voles.

Table 2: Expected time to extinction of a population of Amargosa voles across a range of population sizes using Bayesian prior estimates of vr_e from California voles in published studies. See text for details.

	Low population size (15 females)	**Moderate population size (150 females)**
Low vr_e (0.7, Mendocino 1 and 2)	10.5	35.9
Moderate vr_e (1.2, Brooks)	6.1	20.9
High vr_e (1.5, Richmond)	4.9	16.7

Discussion

Viability analyses of populations are widely necessary for endangered species management. Microtine rodent biology would seem to lend itself straightforwardly to PVA, with high fecundity, short generation and life spans, ease of trapping (although studies in California voles show diminished trapping success during population growth phases [26]), and dependable seasonality. However, there are few or no data on Amargosa vole territoriality, dispersal, home range size, habitat and food constraints, among other factors. Amargosa vole population dynamics lack stationarity: intrinsic growth rate, monthly mortality rate, and dispersal capacity have changed over the last few decades [4,6,8]. PVA for such an endangered species must at least address environmental stochasticity, which is reportedly the most important contributor to extinction risk [16]. Amargosa voles are subject to spatially and temporally autocorrelated environmental stochasticity because of: their dependence on small habitat patches in one hydrogeomorphic basin, a drought across most of California from 2012-2015 likely exacerbated by climate change, water-seeking exotic *Tamarix*, water diversion, railroad construction and floods, fire, disease, road management, development, and human and pet dog access into marshes for recreation [3].

All California vole time series we examined showed boom and bust cycles, regionally correlated environmental stochasticity, and seasonality. Temporal autocorrelation across the series varied from positive to negative, so we are not confident that we have accurately captured ρ for the present model and regard estimating actual ρ values for Amargosa voles as an important priority. Inaccurate estimates of N could increase negative temporal autocorrelation and overestimate T_e, which we addressed by using vr_e rather than v_r. The relationship of T_e and v_r is such that, if for example Amargosa vole v_r is actually twice as high as the values we used, then T_e is actually half as long, but as for all Bayesian analyses, any additional data we obtain from Amargosa voles can be used to increase the precision of the estimates.

Predicted T_e is less sensitive to K than it is to v_r because of the use of ln(K) and because it appears in the numerator. Use of some form of K is required to provide a reflecting boundary and impose density-dependence. However, our data show two very different dynamical regimes across fragments of two years, consistent with other microtines with swings over orders of magnitude in N seasonally, annually, super-annually, and irregularly. Seasonal and annual cycles occur in northern California voles because reproduction increases after a lag following rainfall and emergence of wet season vegetation [1]. Population cycling is thought to be due in part to predator recruitment following high vole numbers, overconsumption of voles, and vole population crashes [19]. We focused our model, and the estimation of extinction risk, on the lowest N which occurs at the most vulnerable time of the year. Irregular and superannual cycles induced by over-predation by specialist predators, lack of available food resources, depletion of micronutrients, chaos, disease, and others [27-29] are poorly addressed by diffusion or matrix models.

Of great concern is the likelihood that we are overestimating K because N is estimated from density at the best habitat patch and we added all isolated local subpopulations into one N, when in reality, small local patches have accelerated probabilities of extinction. Some literature suggests that the Amargosa vole population is a classical metapopulation [3,4,8,30,31] although we neither detected migration to confirm this nor found sufficient genetic structure to allow us to infer colonization (C. Conroy, UC Berkeley, pers. comm.). Since water began to recede at the end of the Pleistocene, patches have become smaller and more isolated [33], leaving only 25 marshes or marsh fragments, each from 0.1 to 19.5 ha, in the Tecopa area (A. Roy, CDFW, pers. comm.) with only half showing evidence of occupation by voles. Dispersal among patches is blocked by a railroad grade, roads, parks, and alkali flats. Flow of animals when it occurs is generally in the direction of spreading floodwater and smaller and more isolated patches serve as population “sinks”. Anecdotes suggest that flooding is less common and the water table lower than a few decades ago. Moreover, all patches share a single hydrogeomorphic basin subject to regionally correlated stochasticity that would serve to nullify some of the possible benefits of a true Levins metapopulation [34]. Even in thriving California vole populations, there was regionally-correlated stochasticity, with both the Richmond and Tilden populations (separated by 10 km) undergoing crashes such that voles were no longer detected at the sites for months to years. Both nearby populations also had anomalously high N at year 5 [35]. Our model incorporates regional stochasticity but not metapopulation dynamics. Our analysis also did not include genetic drift [32], which may be warranted because Amargosa voles are already so deeply bottlenecked that drift now may be relatively low. Results suggest that it is important to develop more sensitive genetic markers structure, attempt to observe migration, manage habitat to increase connectivity, and apply metapopulation modeling if warranted.

General theory predicts the greater influence of environmental relative to demographic stochasticity for most species [16]. However, demographic stochasticity is a serious threat to voles if by chance subpopulations overrepresent reproductively senescent voles, sex ratio becomes unproductively skewed, and other characteristic features of demographic stochasticity occur. Older voles are less fecund yet predominantly older individuals are being recaptured [6]. Moreover, the voles in some marshes are now almost certainly below Allee thresholds [36] which occurs in some California vole family groups that show behavioral avoidance of each other [1] and laboratory studies showing that sibling mating is inhibited [37]. Clearly, demographic stochasticity is a risk and the diffusion approach emphasizes environmental stochasticity. Because of this, the predicted T_e should be interpreted as a *maximum* time before extinction might be expected. If indeed demographic stochasticity is found to play an important role, then there is even less time left to conserve this species.

Benefits of matrix models are familiarity [38], emphasis on reproduction and mortality-driven impacts on population size, and the ability to incorporate stochasticity [39]. Matrix PVA models commonly assume stable age structure and although Amargosa vole age structure is skewed, we may assume it is stable. However, because matrix-based PVA obtains future population estimates by multiplying the dominant eigenvalue, i.e. the *mean* of the population growth rate, matrix-based PVAs cope poorly with populations which are not stable around a mean growth rate, often because they are very small or highly variable, or have secular trends in λ or year-to-year correlation. Backwards analysis of the fit of matrix-based PVAs to real population outcomes reveals that short data sets considerably overestimate T_e especially in variable environments [40]. Yet small, highly impacted, poorly studied, declining, and variable populations are often those most in need of PVA as indeed are Amargosa voles.

In this study, we incorporated current population density estimates of Amargosa voles, evidence of "boom and bust" dynamics, population regulation, variance in population growth, and regional stochasticity into a diffusion analysis-based model to predict time to extinction, where some of the needed variables were estimated as Bayesian priors from time series of California vole populations. With high vr_e in a small population, then T_e = is as low as 5 years and there is a 3-30% probability of Amargosa voles going extinct in one year. This model synthesizes our best knowledge as a baseline for understanding impacts of management on population sustainability. Many readers are accustomed to matrix approaches but such models have important limitations; most importantly, the needed extensive data for Amargosa vole modeling will not be available for years. The Amargosa vole population has a secular trend downwards but also high variability, and is challenged by demographic and regionally-correlated environmental stochasticity. The variability in this population is a hallmark for the exceedingly high risk it has for extinction. Implementation of management based on best available modeling [41] is crucial to avert this risk.

Acknowledgements

We thank Russ Scofield, Chris Otahal, and Mickey Quillman at BLM, Robert Klinger of the USGS, Deana Clifford, Steve Torres, and Scott Osborn at CDFW, and Erin Norden, Chris Kofron, and Brian Croft at USFWS for facilitating logistics and data collection and Tammy Branston, Austin Roy, Caitlin Ott-Conn, Michael Cleaver, Steven Anderson, Paul Maier, Jonathan Clark, Amanda Poulsen, and Anna Rivera for contributions in the field. We also would like to thank members of the Tecopa and Shoshone communities, Shoshone Village, and the Amargosa Conservancy for support. This work was funded by the Bureau of Land Management, California Department of Fish and Wildlife, UC Davis Center for Vectorborne Disease, and UC Davis Wildlife Health Center.

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