

PREDICTION OF *PEROMYSCUS MANICULATUS* (DEER MOUSE) POPULATION DYNAMICS IN MONTANA, USA, USING SATELLITE-DRIVEN VEGETATION PRODUCTIVITY AND WEATHER DATA

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ABSTRACT: Deer mice (*Peromyscus maniculatus*) are the main reservoir host for Sin Nombre virus, the primary etiologic agent of hantavirus pulmonary syndrome in North America. Sequential changes in weather and plant productivity (trophic cascades) have been noted as likely catalysts of deer mouse population irruptions, and monitoring and modeling of these phenomena may allow for development of early-warning systems for disease risk. Relationships among weather variables, satellite-derived vegetation productivity, and deer mouse populations were examined for a grassland site east of the Continental Divide and a sage-steppe site west of the Continental Divide in Montana, USA. We acquired monthly deer mouse population data for mid-1994 through 2007 from long-term study sites maintained for monitoring changes in hantavirus reservoir populations, and we compared these with monthly bioclimatology data from the same period and gross primary productivity data from the Moderate Resolution Imaging Spectroradiometer sensor for 2000–06. We used the Random Forests statistical learning technique to fit a series of predictive models based on temperature, precipitation, and vegetation productivity variables. Although we attempted several iterations of models, including incorporating lag effects and classifying rodent density by seasonal thresholds, our results showed no ability to predict rodent populations using vegetation productivity or weather data. We concluded that trophic cascade connections to rodent population levels may be weaker than originally supposed, may be specific to only certain climatic regions, or may not be detectable using remotely sensed vegetation productivity measures, although weather patterns and vegetation dynamics were positively correlated.

Key words: Deer mice, hantavirus, MODIS, *Peromyscus*, prediction, satellites, trophic cascade.

INTRODUCTION

Hantavirus pulmonary syndrome (HPS) was first identified in North America in the spring and summer of 1993. Initial cases were clustered in the Four Corners region of the southwestern United States, where origins of the disease were traced to an unrecognized, directly transmissible rodent-borne hantavirus (Nichol et al., 1993; Childs et al., 1994) later named Sin Nombre virus (SNV; genus *Hantavirus*, family *Bunyviridae*). Sin Nombre virus is believed to be transmitted to humans from the infected host (the deer mouse, *Peromyscus maniculatus*) through inhalation of aerosols of secretions and

excretions, through direct contact with these substances, or via rodent bite (Peters et al., 2006). Rodent-borne hantaviruses are well known in Europe and Asia (Plyusnin et al., 2001) and have recently been identified in most countries in South America (Mattar and Parra, 2004; Pini, 2004) as well as Panama (Bayard et al., 2004).

The 1993 HPS outbreak is attributed to atypical climatic conditions associated with the 1991–92 El Niño Southern Oscillation, including heavy spring and summer precipitation in 1991/1992 and a mild winter in 1992 (Parmenter et al., 1993; Hjelle and Glass, 2000). A bottom-up trophic cascade hypothesis is proposed

as a likely explanation for the timing and location of the outbreak (Glass et al., 2000; Yates et al., 2002; Glass et al., 2007). Trophic cascades are interactions among organisms from different levels within a food web (e.g., producers, consumers, and predators) that result in changes in abundance and biomass across trophic levels (Pace et al., 1999). In moisture-limited temperate terrestrial systems primary-level trophic cascades can be initialized by precipitation, followed by an increase in ecosystem productivity (growth of grasses, seeds, leaves, nuts, and subsequently insects) stimulated by recharged soil moisture. Increased primary and secondary productivity and mild seasonal temperatures can promote high rates of reproduction and survival in rodent reservoir populations through extension of the reproductive period and favorable overwintering conditions (Abbott et al., 1999; Mills et al., 1999). Thus the trophic cascade hypothesis may help explain interannual increases in deer mouse populations. In addition, trophic cascade-mediated changes in reservoir population density may influence the prevalence of infection within populations through regulation of rate of pathogen transmission and probability of infection. When populations are large and densely distributed (e.g., following irruption events), greater frequency of rodent-to-rodent contact may increase the probability of virus transmission to susceptible individuals (Mills et al., 1999; Root et al., 1999; Douglass et al., 2001; Glass et al., 2007; Wesley et al., 2010). These processes can result in increasing prevalence of infection in high-density host populations in a delayed-density-dependent manner, following seasonal time lags (Madhav et al., 2007; Kallio et al., 2010). A recent analysis of long-term trapping data from sites in Arizona, Colorado, Montana, and New Mexico found a statistically significant positive relationship between prevalence of hantavirus antibodies (a marker of infection) and deer mouse population

density, when data were aggregated across multiyear sampling periods (Calisher et al., 2007).

Although identifying and quantifying environmental variables associated with increasing reservoir abundance has been identified as a key component of developing a predictive model of human risk (Mills et al., 1999), to date no successful generalized predictive model for HPS has been developed. Douglass et al. (2001) suggested that predictive models for SNV-related disease may be developed by relating changes in reservoir populations to fluctuations in plant productivity. Although studies have quantified some relationships between rodent population density and landscape and climate variables (Lima et al., 1999; Ernest et al., 2000; Langlois et al., 2001; Brown and Ernest, 2002), few studies have been conducted in a manner useful for broad-scale modeling and prediction.

We hypothesized that trophic cascade dynamics should be resolvable via a combination of weather and vegetation productivity data; these data should in turn serve as predictors of inter- and intra-annual rodent population dynamics. Applying the trophic cascade hypothesis as the basis for predicting disease risk in reservoir and human populations suggests that increased precipitation and biotic productivity trigger establishment of large reservoir populations with high rates of pathogen transmission. Such conditions maximize the probability of encounters between humans and infected rodents (Fig. 1). We assumed that human risk of hantavirus exposure is strongly related to the probability of contact with infected deer mice, as demonstrated by studies that indicated higher rodent densities at likely exposure sites than at nonexposure sites (Childs et al., 1995; Crowcroft et al., 1999), although other exposure risk factors have been identified, including hand plowing, cleaning of outbuildings, and other activities that served to aerosolize rodent excreta (Zeitz et al., 1995; Crowcroft et al., 1999).

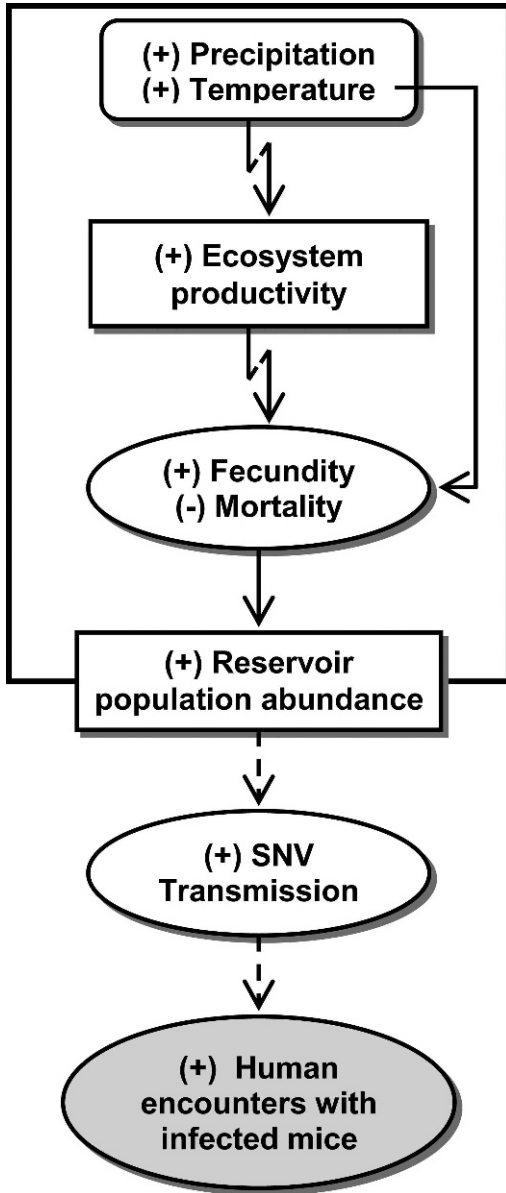


FIGURE 1. Flow diagram of the trophic cascade hypothesis for predicting risk of transmission of Sin Nombre virus (SNV) in its rodent reservoir (deer mouse, *Peromyscus maniculatus*) population and from deer mice to humans. Temperature and precipitation are driving variables that influence rate processes (ovals) and system states (boxes). Symbols in parentheses represent direction of flow at each step, broken arrows indicate time lags in response, and dashed arrows indicate probability relationships. The outer bounding box defines those processes directly related to rodent population abundance, while rate processes outside of the box are those related to reservoir infection levels and transmission to humans.

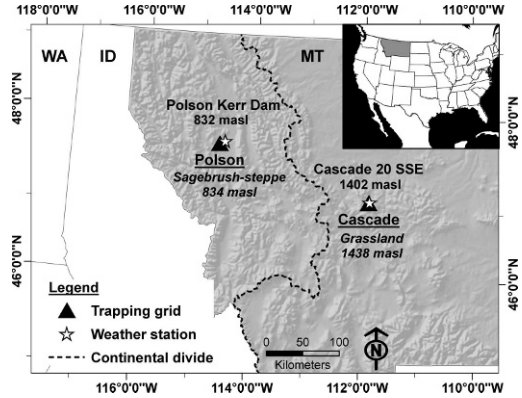


FIGURE 2. Cascade and Polson, Montana, USA, rodent trapping sites and associated weather stations. MT = Montana; ID = Idaho; WA = Washington; masl = meters above sea level.

MATERIALS AND METHODS

Study area

We assessed rodent populations, weather trends, and vegetation productivity at two ecologically and climatically distinct sites in Montana, USA (Fig. 2). The eastern site, Cascade, is a grassland ecotype east of the Continental Divide (46°59.3'N, 111°35.3'W, elevation 1,438 masl), with monthly mean temperatures of 13.3 C in January and 34.3 C in July and annual precipitation of 36.7 cm (average values 1971–2000). The Polson site is a sage-steppe ecotype west of the Continental Divide (47°38.4'N, 114°20.7'W, elevation 834 masl), with monthly mean temperatures of 14.7 C (January) and 37.4 C (July) and annual precipitation of 34.0 cm.

Rodent population data

We used longitudinal, mark-recapture trapping data for deer mice from live-trapping grids at the Cascade and Polson sites (Fig. 2), 1994–2007, to test whether gross primary productivity (GPP) derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) and temperature and precipitation variables were useful predictors of rodent population levels. These and other sites are maintained as long-term study areas for monitoring changes in hantavirus reservoir populations and associated environmental variability (Douglass et al., 2001). We chose to use data from the Cascade and Polson trapping sites because these two have the longest period of overlap with the 2000–06 MODIS GPP data. We selected a single trapping grid per site based on the highest

deer mouse captures during 2000–06 ($n=2,651$ at Cascade, $n=3,471$ at Polson) and used data from these grids consistently throughout the analyses. We used only one of three available grids in the analysis because grids were co-located within the spatial extent of our remote sensing data and did not exhibit markedly different trends in rodent abundance.

Rodents were live-trapped for three consecutive nights per month on each 1-ha grid, for 12 mo annually at Cascade and 6 mo per year (May–October) at Polson. Grids consisted of 10×10 -trap arrays of 100 live-capture traps (H. B. Sherman Live Traps, Tallahassee, Florida, USA) spaced at 10-m intervals. A comprehensive description of trapping methods is provided by Douglass et al. (2001). Population data were available as minimum number alive (MNA). The MNA metric accounts for the current monthly population as the sum of all animals captured during that period, plus the number of individuals that were not captured during the current period but were captured during at least one previous and one subsequent trapping period (Chitty and Phipps 1966).

We have no evidence that repeated sampling affected our population abundance estimates. Potential trap effects were minimized by sampling for only three nights per month and removing traps between sampling periods. Douglass et al. (2003) compared effects of removal of deer mice from trapping areas with capture and release methods and found that although removal resulted in an increase in recruitment and more overall captures over time, population sizes of trapped and released mice remained constant. Further, the monthly sampling interval is ideal for detecting shifts in abundance. Carver et al. (2010) found that sampling less frequently resulted in an underestimation of monthly MNA by 10–20% and detection of fewer annual highs and lows in MNA.

Bioclimatology

Monthly weather observations were obtained from National Climatic Data Center weather stations (NCDC, 2008) co-located with trapping sites (Fig. 2). The Cascade 20 SSE weather station is located 1.6 km north-east of the Cascade trapping site, and the Kerr Dam weather station is located approximately 8.4 km northeast of the Polson trapping site. Meteorologic elements included in the analysis were total monthly precipitation, departure from monthly precipitation normals, minimum and maximum monthly temperatures, mean

monthly temperature, and total monthly snowfall.

Remote sensing

The majority of epidemiologic or wildlife studies that incorporate remotely sensed data for vegetation monitoring have used spectral vegetation indices such as the Normalized Difference Vegetation Index, a vegetation greenness measure based on the contrast between red (absorbed by green plants) and infrared (reflected by green plants) reflected energy (Boone et al., 2000; Viel et al., 2006; Glass et al., 2007; Luis et al., 2009; Cao et al., 2011). We were interested in testing whether rodent dynamics are linked with variability in vegetation biomass and abundance, rather than vegetation phenology or greenness, and so chose to use remotely sensed GPP to estimate terrestrial vegetation production and resource availability at our study sites. Primary productivity is the rate at which light energy is converted to plant biomass, and GPP is the sum total of the converted energy without accounting for plant respiration costs. The GPP data set, produced from the MODIS sensor onboard the NASA Earth Observing System Terra and Aqua satellites, is the first continuous satellite-based data-set monitoring global vegetation productivity. Unlike other available vegetation sensors MODIS incorporates daily bioclimatology and carbon cycling logic in its vegetation productivity estimations, and MODIS GPP data are biome specific (Hansen et al., 2000). We obtained MODIS 8-day GPP for 3-km-by-3-km matrices centered over the midpoint of each 1-ha trapping grid. We averaged GPP over the pixels in the matrix and gap-filled across 8-day periods to produce a monthly site GPP estimate, measured as grams of carbon fixed by vegetation per square kilometer per month.

Data analysis

In an attempt to develop a model that could accurately predict deer mouse population levels using weather and plant productivity data, we used the Random Forests (RFs) technique (Breiman, 2001), a model that is known for its accuracy, resistance to overfitting, and ability to handle large numbers of predictor variables. Random Forests is an ensemble model that forms many simple models, or decision trees, and then aggregates (averages) their predictions. Briefly, a large number (B) of bootstrap samples of the data are drawn, and a single binary regression tree is fitted to each bootstrap sample (De'ath and Fabricius, 2000). The only modification to the standard tree algorithm is that at

each node only a subset of the predictor variables is selected to search for the optimal binary split. Predictions are made by averaging the values of each individual tree. The principal parameters in this model are the number of models, or trees, that are tested (*ntree*) and the number of variables selected at each node of each tree (*mtry*). For all models we used *ntree* = 1000. All models were run using the random-Forest package in the R software environment (R Development Core Team, 2010).

Bootstrapping provides a convenient method for independently evaluating the accuracy of the fitted model. Although typically a data partitioning method such as cross-validation might be employed, in the case of RFs, due to the bootstrapping procedure, each observation has been used in the construction of only approximately two thirds of the decision tree “forest.” Hence for each model, approximately one third of the data was not used in its construction and was considered “out-of-bag.” We aggregated predictions from only those models for which a particular observation was out-of-bag and used these predictions to calculate the out-of-bag (OOB) error estimate.

Due to the irregular collection of data at the Polson site and location of the Cascade and Polson trapping grids in distinct biomes, we considered the data for each site separately. Because several of the initial suite of model weather predictor variables were highly correlated we used a subset: departure from normal temperature (DPNT), departure from normal precipitation (DPNP), total snowfall (TSNW), and mean temperature (MNTM), all measured monthly (Fig. 3).

Previous research suggests that rodent populations may respond to weather and plant productivity changes in a time-lagged manner (Ernest et al., 2000; Brown and Ernest, 2002; Thibault et al., 2010; Cao et al., 2011). For example, Ernest et al. (2000) found significant correlations between rodent density and previous-season precipitation and plant cover at a long-term study site in a Chihuahuan desert ecosystem in southern Arizona, and a recently developed model using data from the Cascade, Montana, trapping site identified temperature and precipitation 5 mo previous as important factors for deer mouse survival (Luis et al., 2009). To account for potential lagging we included predictor variables of 3-, 6-, and 12-mo lags. For instance, at month *i* we included the average of each predictor variable for the months (*i*-1, *i*-2, *i*-3), (*i*-5, *i*-6, *i*-7), and (*i*-11, *i*-12, *i*-13), which represent the 3-, 6-, and 12-mo lags for each predictor variable. Lagging methods reduce the size of the data set somewhat; by including the lagged variables

we omitted the first 13 mo of data, since we did not have values for the lagged variables for these months. As mentioned previously, the MODIS GPP data set is available for fewer years than the rodent and weather data sets, minus an additional 13 mo for lag transformation of variables. We fitted separate models to consider each case.

Given the poor fit of our models to the continuous data set, we developed a second set of models based on classified, rather than continuous, data values. Although classification results in a loss of information, thresholding can reduce the amount of “noise” in a variable enough so that a model can find a signal. We transformed the continuous response variable MNA to a binary discrete variable by thresholding at seasonal quantiles. Each response value y_i was converted to a 0 or 1 according to whether it lay below or above the 75th quantile value for months in the same season. Seasons were assigned as winter (Dec./Jan./Feb.), spring (Mar./Apr./May), summer (June/July/Aug.), and fall (Sept./Oct./Nov.). Our goal was to see if the RF models could accurately identify unusually large MNA values relative to the season. The 75th quantile was chosen as the largest quantile possible without the binary response variable becoming too imbalanced in our judgment (far more zeros than ones). Then the RF models were repeated using this binary discrete variable as the response.

Finally, we investigated the relationship between MODIS GPP and the locally recorded weather variables at our sites. The MODIS-based vegetation productivity estimates incorporate meteorologic data as a critical input, though measured on a much coarser scale than the local weather data included as predictors in our analysis (Zhao et al., 2006). We expected that if the MODIS GPP data were successfully measuring vegetative production at our study sites, they should display some correlation with our more locally measured climatic variables. If not, MODIS GPP was likely not capturing vegetative productivity dynamics at our sites and hence ought not to be related to deer mouse populations using trophic cascade logic. To test this relationship we fit a RF model using MODIS GPP as a response variable and local weather variables as predictors, including the 3-, 6-, and 12-mo time lags.

RESULTS

We fit two regression models each for the Cascade and Polson trapping sites, one

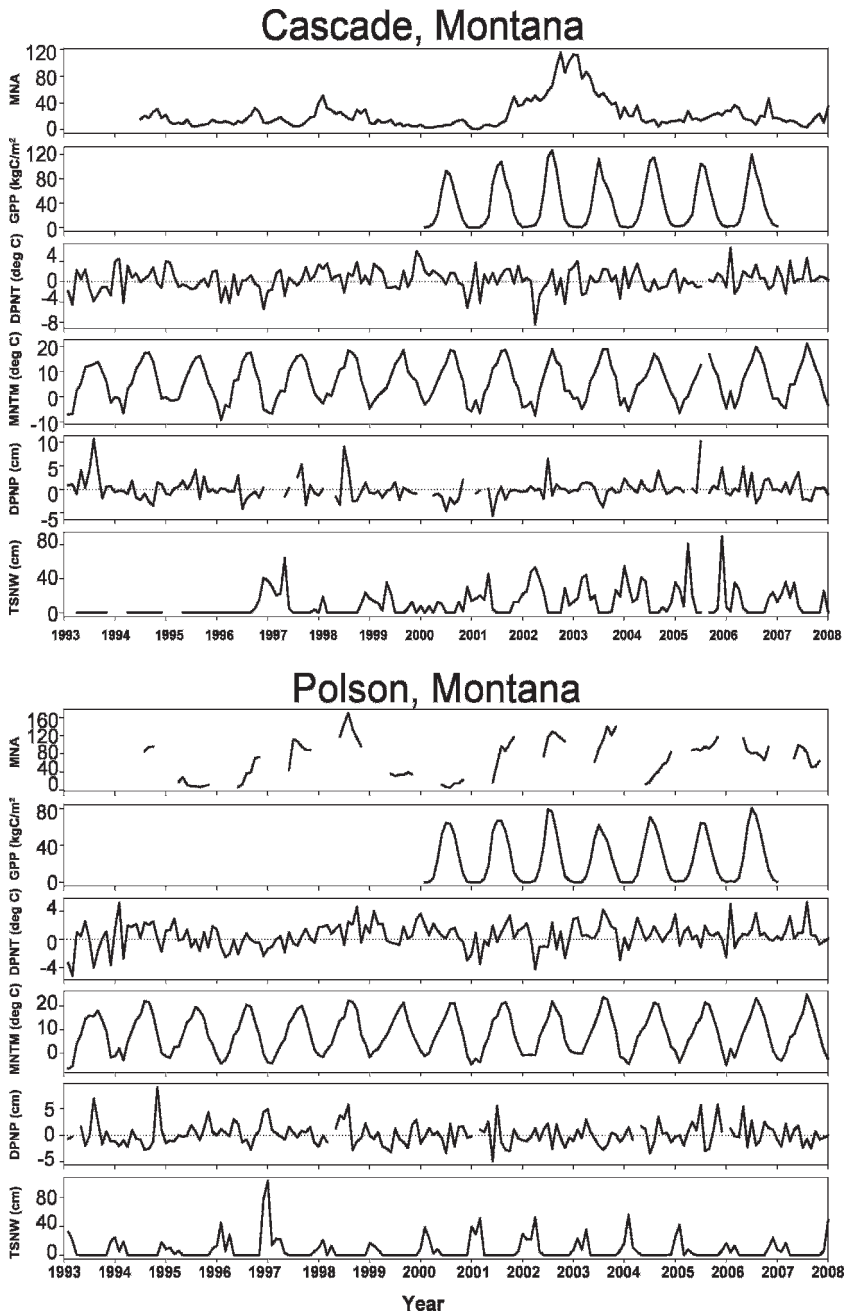


FIGURE 3. Time series plots for data from Cascade and Polson, Montana trapping sites. Quantities displayed are MNA (minimum number of mice alive), GPP (vegetation gross primary productivity), DPNT (departure from normal temperature), MNTM (mean temperature), DPNP (departure from normal precipitation), and TSNW (total snowfall). Missing data values are indicated by broken lines. The MODIS GPP data set was available only for a portion of the time series.

TABLE 1. Results for all random forest (RF) models. Mean squared error (MSE) and percentage variation explained values apply to RF models based on continuous minimum number of mice alive (MNA) response variables. Out-of-bag (OOB) error and baseline error values represent results from RF models based on discrete binary MNA response variables. Where OOB error values are less than baseline error values the model performed more poorly than naïve baseline predictions.

RF model	MSE	% variation explained	OOB error	Baseline error
Cascade: weather only	401.90	18.93	0.220	0.250
Polson: weather only	1593.10	6.74	0.276	0.252
Cascade: weather and GPP	686.00	11.69	0.333	0.252
Polson: weather and GPP	1,518.20	0.46	0.289	0.311

with the MODIS GPP data and one without. For models that included MODIS GPP we had 84 observations and 15 predictor variables (including lags), and for models using only weather predictors we had 163 observations and 12 predictor variables. The out-of-bag mean squared error and percentage of the variability explained for each model are shown in Table 1. As illustrated in Figure 4, all of these models fit poorly; the best model (Cascade, using weather data only) explained around 18% of the variation in

MNA, and the worst (Polson, using weather and GPP) explained practically none of the variation.

Our classified models, for which we employed a thresholding technique to identify unusually large MNA values relative to season, performed poorly as well. The out-of-bag error rates and the baseline error for each model are shown in Table 1. The baseline error is the error we would observe in the case of a null model that predicts every observation to be the majority class. In all cases, the RF models' ability to distinguish between months with high or low rodent reservoir population levels was poor. For example, for the Cascade model, using weather data only, a naïve baseline prediction that says that *every* month will have relatively high rodent reservoir populations will have an error rate of around 25%. The actual OOB error rate for this RF model was 22%. Two of the models (Cascade, using weather only; Polson, using weather and GPP) performed worse than the baseline model. In addition, there was no consistent set of predictor variables across the models tested with regard to either variable type (e.g., temperature or precipitation) or time lag, regardless of study site or type of model (Table 2).

In contrast, our RF model using MODIS GPP as a response variable and local weather variables as predictors, including the 3-, 6-, and 12-mo time lags, fit well, explaining 86% of the variation in MODIS GPP (Fig. 5). In addition the model identified MNTM (and its 6- and

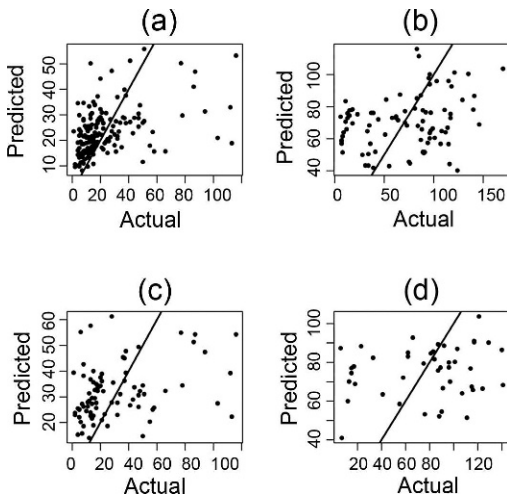


FIGURE 4. Fitted versus actual minimum number alive (MNA) values for each random forest (RF) model, using both weather predictors and MODIS gross primary productivity (GPP). Plots are (a) Cascade, Montana, USA, with weather only; (b) Polson, Montana, with weather only; (c) Cascade with weather and GPP; (d) Polson with weather and GPP. If a model fits well, points should cluster near the line.

TABLE 2. Top five predictor variables for continuous and classified random forest (RF) models that included gross primary productivity (GPP). Variable names are departure from normal temperature (DPNT) and precipitation (DPNP), total snowfall (TSNW), and mean temperature (MNTM); numbers are time lags in months. Ranking is based on decrease in predictive accuracy (continuous) and decrease in Gini index (classified). In each case the measure of importance is calculated from a random permutation of the values for each predictor variable, and the degree to which this degrades the predictive accuracy of the model is the measure of importance.

Cascade		Polson	
Continuous	Classified	Continuous	Classified
DPNT6	DPNT12	DPNP12	DPNP3
TSNW6	MNTM3	DPNT3	DPNT3
DPNT12	TSNW6	DPNP3	DPNT
DPNT	DPNT6	DPNT6	DPNP6
MNTM12	DPNT3	DPNP	MNTM

12-mo lags) as the most important predictors of GPP; and the TSNW variable also held a fair degree of predictive power. Scatter plots of GPP versus the six most important variables in the RF model are shown in Fig. 6.

DISCUSSION

Despite our use of RFs, a powerful and flexible modeling technique that has a strong history of predictive accuracy, and despite attempting to model MNA levels

in a variety of fashions (regression vs. classification, with and without time lags), none of the models we fit displayed a significant predictive ability. In general our findings suggest that MODIS GPP and weather data, at least over the time period of our analysis, can provide limited predictive information regarding deer mouse population levels at Cascade and Polson. These results, in turn, suggested that using these same predictor variables

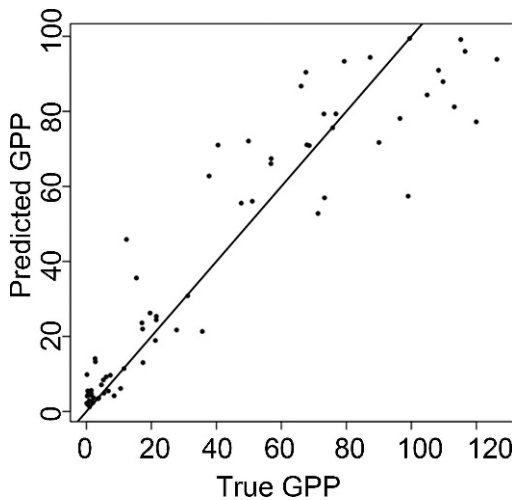


FIGURE 5. Actual (true) versus predicted gross primary productivity (GPP) from a random forest (RF) model in which local weather station variables explained about 86% of the variability in GPP at two rodent trapping sites in Montana, USA.

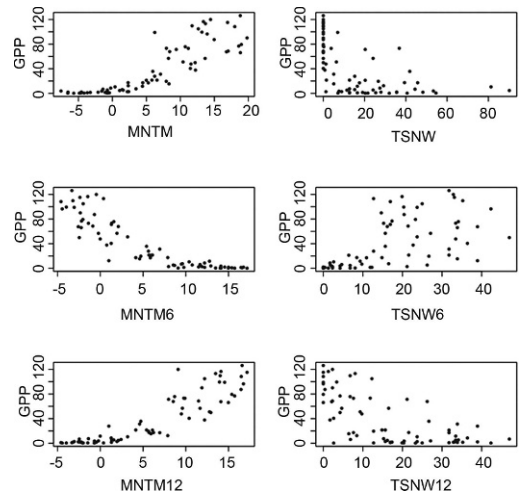


FIGURE 6. Scatterplots of MODIS gross primary productivity GPP versus the six most important weather predictor variables from a random forest (RF) model. The model predicts MODIS GPP using the locally measured climate variables MNTM (mean temperature) and TSNW (total snowfall), with 6- and 12-mo time lags.

to develop a generalized model for HPS risk in humans, as called for in previous studies, may not be feasible. An international team of forecasters attempting to use weather variables to predict a longer but overlapping MNA time series at the Cascade site came to a similar conclusion (Yaffee et al., 2008). Although temperature, precipitation, and snowfall were predictors in our models, they explained so little of the variance that we had no confidence that the relative importance of the variables reflected signal rather than noise.

We posit several potential explanations for the results of our modeling experiment. First, resource-consumer relationships can exhibit nonlinear or chaotic behavior that may confound simple bottom-up regulation, as defined by the trophic cascade hypothesis (Brown and Ernest, 2002). In addition, the trophic cascade hypothesis, although proposed as an explanatory mechanism for rodent population irruptions in the southwestern United States (Parmenter et al., 1999; Glass et al., 2000; Glass et al., 2002) may apply only within arid ecosystems where water is a clear limiting factor in plant growth, and monsoonal precipitation patterns, common across the southwestern United States, have been found to be strong drivers of biotic cascades.

Thibault et al. (2010) note that the consequences of precipitation-driven increases in primary productivity on consumers have not been well explored in nonarid environments. Water is less limiting at our Montana study sites than in desert ecosystems (Nemani et al., 2003), and precipitation patterns are not monsoon driven. Thus, vegetation communities and rodent populations may exhibit less sensitivity to changes in timing and amount of rainfall. Our local, fine-scale weather variables were poor predictors of MNA at both sites but successfully predicted GPP, suggesting that coarse-scale GPP weather inputs are appropriately tracking site temperature and precipita-

tion. If, as generally hypothesized, temperature and precipitation are key drivers of rodent population fluctuations via trophic cascades (Glass et al., 2000), we would expect that both the MODIS GPP data and our local weather data would have successfully predicted patterns in rodent abundance. Thus we suggest that the application of a rainfall-based trophic cascade hypothesis as a broad-scale explanation for increases in deer mouse population density and subsequent HPS risk may not be universally appropriate, especially in temperate ecosystems.

Second, MODIS GPP may have insufficiently characterized resource availability at our study sites either because of inaccuracies in the data product or differences in scale between GPP and deer mouse habitat characteristics. Comparisons of MODIS GPP with ground-based productivity estimates across multiple biomes have demonstrated that MODIS data tended to be underestimates at low-productivity sites and overestimates at high-productivity sites, although they captured seasonal variation in a manner consistent with ground-based measures (Turner et al., 2005, 2006). Our MODIS GPP predictors are averages of a 9 km² (900 ha) area as compared with the 1-ha rodent trapping grids. Thus, the remotely sensed data may not have resolved vegetative productivity at a spatial scale that influences deer mouse populations. Further, MODIS GPP does not capture elements of landscape structure such as fragmentation, dispersal corridors, shrub cover, and vegetation community composition that have been cited as important habitat characteristics for deer mice (Root et al., 1999; Langlois et al., 2001). The MODIS GPP also does not measure nonvegetative food sources such as arthropods, which have been noted to provide an important dietary component for deer mice and potentially alter their habitat selection (Jameson, 1952; Pearson et al., 2000).

As noted by Turchin (2003) and others, density-dependent processes may influence

rodent demography. Population fluctuations that result from a combination of exogenous (density-independent, such as weather and resource availability) and endogenous (density-dependent, such as predation and competition) factors may exhibit nonlinear behavior and confound attempts to develop generalized prediction models. For example, although Luis et al. (2009) modeled deer mouse population survival and recruitment at the Cascade site using climate predictors, the authors noted that other important exogenous or endogenous factors likely influenced temporal population variation, including resource-based factors such as primary productivity.

Many researchers have recognized the need for generalized models capable of predicting temporal and spatial risks of epidemics (Epstein, 1999; Patz and Lindsay, 1999). Whereas vegetation productivity is hypothesized to be an important driver for increases in population density of hantavirus reservoir species, our study and others' suggest that additional processes regulate reservoir populations (Abbott et al., 1999; Calisher et al., 1999; Mills et al., 1999). Although deer mouse population dynamics are likely, in part, influenced by changes in resource abundance, there seems to be no single, easily detectable, consistent driver of the temporal variation in populations observed at our and others' study sites. Further research is required to more fully elucidate the causes of reservoir population variability, including examination of intra-annual relationships among variables, predation and competition, minimum and maximum thresholds in temperature, precipitation, resource abundance, and other landscape factors that influence the fecundity, mortality, distribution, dispersal, and abundance of reservoir species. Models that improve predictability of reservoir population abundance through incorporation of complex and nonlinear controls will be very useful tools for identifying disease risks for human populations, particularly in the

context of projected climate changes that are likely to significantly alter continental patterns of precipitation, temperature, and vegetation distribution (Parmesan and Yohe, 2003; Parmesan, 2006; Christensen, 2007; Iverson et al., 2010).

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