The effect of seasonality, density and climate on the population dynamics of Montana deer mice, important reservoir hosts for Sin Nombre hantavirus

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Summary

1. Since Sin Nombre virus was discovered in the U.S. in 1993, longitudinal studies of the rodent reservoir host, the deer mouse (*Peromyscus maniculatus*) have demonstrated a qualitative correlation among mouse population dynamics and risk of hantavirus pulmonary syndrome (HPS) in humans, indicating the importance of understanding deer mouse population dynamics for evaluating risk of HPS.

2. Using capture–mark–recapture statistical methods on a 15-year data set from Montana, we estimated deer mouse survival, maturation and recruitment rates and tested the relative importance of seasonality, population density and local climate in explaining temporal variation in deer mouse demography.

3. From these estimates, we designed a population model to simulate deer mouse population dynamics given climatic variables and compared the model to observed patterns.

4. Month, precipitation 5 months previously, temperature 5 months previously and to a lesser extent precipitation and temperature in the current month, were important in determining deer mouse survival. Month, the sum of precipitation over the last 4 months, and the sum of the temperature over the last 4 months were important in determining recruitment rates. Survival was more important in determining the growth rate of the population than recruitment.

5. While climatic drivers appear to have a complex influence on dynamics, our forecasts were good. Our quantitative model may allow public health officials to better predict increased human risk from basic climatic data.

Key-words: rodent, small mammal, SNV, temporal variation, trophic cascade hypothesis

Introduction

It is becoming increasingly more apparent that climate can have significant impacts on infectious disease dynamics (Harvell *et al.* 2002; Patz *et al.* 2005). Understanding the influence of climatic drivers on disease emergence and incidence can help in forecasting and prevention and is becoming more urgent in this era of climate change. Climate can affect vector-borne diseases, such as malaria and dengue fever, by altering the abundance and/or distribution of vector hosts (Hopp & Foley 2003; Pascual *et al.* 2006), as well as the occurrence of water-borne diseases, such as cholera, through an increase in environmental reservoirs (de Magny *et al.* 2008). Less studied is the effect of climate on vertebrate reser-

voir hosts of zoonotic diseases, through changes in demography, distribution or abundance. One zoonotic pathogen for which climate appears to affect reservoir host demography is Sin Nombre hantavirus.

The main reservoir host for Sin Nombre virus (SNV), the primary etiologic agent of hantavirus pulmonary syndrome (HPS), is the deer mouse, *Peromyscus maniculatus*, an omnivorous generalist whose range spans most of North America. The first recognized outbreak of HPS in 1993 in the four corners region of the southwestern U.S. (where the states of Arizona, New Mexico, Colorado and Utah adjoin) was preceded by an El Niño Southern Oscillation (ENSO) event, which brought increased precipitation to this normally arid region. Parmenter *et al.* (1993) proposed a bottom-up trophic cascade hypothesis to explain the epidemic of HPS in which increased precipitation would lead to increased

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primary productivity, and greater abundance of preferred food items of the deer mouse. Increases in resources would allow the mice to survive and reproduce which would lead to higher population density. This increase in density has been hypothesized to lead to increased transmission and prevalence of SNV in the deer mice and therefore a greater chance of spillover to humans (Mills *et al.* 1999a; Yates *et al.* 2002). The length of the cascade leads to the prediction that there should be a delay between the climatic triggers and increased risk to humans.

Since the original outbreak in the Four Corners region, longitudinal studies sponsored by the U.S. Centres for Disease Control and Prevention (CDC) have monitored the population dynamics and infection status of rodent populations in the southwestern U.S. and Montana (Douglass *et al.* 1996, 2001; Mills *et al.* 1999b). Some of these studies have demonstrated a correlation among precipitation, rodent population size, prevalence of SNV antibody in rodent populations and consequent risk of HPS in humans (Abbott, Ksiazek & Mills 1999; Engelthaler *et al.* 1999; Mills *et al.* 1999a; Glass *et al.* 2000; Yates *et al.* 2002). A few novel studies have taken a more quantitative approach with satellite imagery (Glass *et al.* 2000, 2002). However, we still lack a clear understanding of how changing climatic conditions lead to changes in host demography (survival, maturation and birth rates) and increase the risk of disease outbreaks. Several recent studies have highlighted the importance of reservoir demography on human risk. Because hantaviruses cause chronic (often life-long) infection in their natural hosts, antibody is often used as a marker of infection (Mills *et al.* 1999b). Madhav *et al.* (2007) demonstrated delayed density dependence in antibody prevalence, and Calisher *et al.* (2001) demonstrated that populations with an older age structure have higher antibody prevalence.

Reservoir demography can be affected by both density-dependent and density-independent processes. Understanding both processes and their interaction may be needed to fully understand reservoir demography and what leads to outbreaks. There is now a broad consensus that both density-dependent and density-independent factors are important in population ecology, but their relative importance may vary among and within species (Higgins *et al.* 1997; Lewellen & Vessey 1998a; Lima *et al.* 2001; Merritt, Lima & Bozinovic 2001). This is illustrated by the wealth of studies of population dynamics of rodents. Northern Fennoscandian rodent populations, for example, undergo regular cycles thought to be due to delayed density dependence mediated by specialist predators and competition (Stenseth, Bjornstad & Falck 1996). These populations are therefore thought to be predominantly under density-dependent controls. In contrast, populations of the muroid genera *Peromyscus* in North America and its sister genus, *Apodemus*, in Eurasia, while showing evidence of density-dependent competition for space (e.g., Saitoh, Bjornstad & Stenseth 1999), are significantly influenced by external drivers. These drivers include large scale climatic oscillations (Brown & Heske 1990; Glass *et al.* 2002; Stapp & Polis 2003) and more local scale fluctuations

in productivity such as acorn mast (Wolff 1996; Ostfeld *et al.* 2006; Shimada & Saitoh 2006) and periodic emergence of insects (e.g., cicadas and gypsy moths; Elkinton, Liebhold & Muzika 2004; Marcello, Wilder & Meikle 2008).

As there is no effective treatment or vaccine for HPS, the most effective strategy is prevention. As human risk is linked to mouse density and demography, to understand what leads to spillover, we need to dissect deer mouse population dynamics to determine the relative contributions of endogenous and exogenous factors. A quantitative understanding of how environmental factors affect mouse demography and human risk may allow public health officials to better predict outbreaks and more effectively target prevention strategies.

Using a capture–mark–recapture data set spanning 15 years (Douglass *et al.* 1996, 2001), we evaluated the seasonal and interannual variation in survival, maturation rates and recruitment rates and explored the relative importance of environmental vs. density-dependent factors on deer mouse demography and dynamics. Because the bottom-up trophic cascade model postulates a delayed response to climate, we carefully evaluated evidence of lagged effects of climatic drivers. We then formulated a population model including climatic drivers to capture the key dynamics of this system and tested its predictive capabilities. Through our capture–mark–recapture analyses, we discovered a high level of predictability to the dynamics once key environmental drivers and their lags were taken into account.

Materials and methods

STUDY SITE AND FIELD METHODS

Long-term studies of deer mice have been conducted in Cascade County, central Montana since June of 1994. The study site is grassland supporting an active cattle ranch where deer mice typically account for over 85% of the small mammal assemblage (Douglass *et al.* 2001). It is a highly seasonal environment which receives about 36 cm of precipitation a year, mostly in spring. Often this spring precipitation is in the form of snow, which may persist for 2–3 months or last only a few days, depending on wind and temperature. Temperatures also fluctuate widely; one January it may be −37 °C and next year 10 °C, and temperatures in the summer may range from 1 °C in the morning to 35 °C in the afternoon.

Live trapping was conducted for three consecutive nights each month on two grids (*c.* 1 mile apart) from June 1994 to May 2009. Grids consisted of 100 trap stations equally spaced (10 m apart) in a square of 0·81 ha with one Sherman live trap per station. As the mouse abundances on the two grids were significantly correlated (Pearson's product moment correlation test on minimum number alive (MNA); $R = 0.77$, $P < 0.001$), we analysed the capture histories from the two grids jointly. Each captured mouse was tagged with a uniquely numbered ear-tag, its breeding status, body mass and presence of scars noted, and a blood sample taken to test for hantavirus antibody. For a detailed description of the field methods see Douglass *et al.* (1996).

CLIMATIC AND VEGETATION DATA

Climatic data, including mean temperature and summed precipitation, were obtained from the Western Regional Climate Centre

(http://www.wrcc.dri.edu). Data were collected from a meteorological tower < 1 km from the study site (Cascade 20 SSE, Station number 24 1557). Normalized difference vegetation indices (NDVI) for the study area from 2000 to 2004 were obtained from MODIS satellite data (http://www.modis.ornl.gov/modis/index.cfm).

ESTIMATING DENSITY AND DEMOGRAPHIC PARAMETERS

Models were formulated from capture–mark–recapture data from June 1994 to 2004 and were tested against data through May 2009. These data were used to estimate density and demographic rates. Individuals were classified into age classes at each capture occasion based on mass according to the definitions of Fairbairn (1977): juveniles < 14 g, subadults > 14 and < 17 g, and adults > 17 g. For the purposes of this study, we combined juveniles and subadults, because they represent the non-reproductive portion of the mouse population, hereafter called juveniles. For analysis, the data for the three consecutive trapping days were collapsed into one primary trapping occasion, which resulted in 127 monthly primary trapping occasions for the demographic rate analyses, from June 1994 to December 2004, and 180 monthly occasions for the density analysis, through May 2009. We did not use robust design models (Pollock 1982) because the data for the secondary occasions were not recorded for most of the study. Goodness-of-fit tests were performed on both the multistrata capture histories (stratum for each age class) and the single stratum histories (without separating juveniles and adults) (Pradel, Wintrebert & Gimenez 2003), as implemented in U-CARE (Choquet et al. 2005).

The POPAN formulation (Schwarz & Arnason 1996) of Jolly-Seber models (Jolly 1965; Seber 1965) was used to estimate population density, as implemented in program MARK (White & Burnham 1999). We estimated survival (S) and maturation (Ψ) probabilities using multistrata models (Nichols et al. 1992) and recruitment rates (f) using Pradel models (Pradel 1996), as implemented in program MARK. We evaluated the appropriateness of including covariates (age class, month, season, year, precipitation, temperature, density, including at several lags) using quasi-Akaike's information criterion (QAICc). Covariates were included in models by altering the design matrix using RMark (Laake 2007), a package for the R software (R Development Core Team, 2005) with an interface to program MARK. The demographic parameters were essentially modelled as a function of these covariates assuming multinomial errors and a generalized linear framework (McCullagh & Nelder 1989). The link function was logit for the recapture, survival and maturation analyses, and log for recruitment. In the capture history data, survival is confounded with emigration and births are confounded with immigration, so the parameters estimated here are 'apparent survival' (hereafter called survival) and recruitment.

For the three demographic parameters, we initially explored a basic set of models, which included constant, age class dependent, monthly, seasonal, yearly and fully time-dependent models, without density and environmental covariates. A large suite of models was subsequently tested, to test for significant seasonality, density dependence and climatic forcing, including those containing covariates for month, temperature and precipitation deviation from monthly means and density, at various time lags. We looked at precipitation and temperature lags up to 6 months; such lags have been shown to affect both grassland primary productivity and small mammal abundance (Perry 1976; Collins & Weaver 1978; Lewellen & Vessey 1998b). Models were ranked based on their QAICc values.

We also estimated seniority probabilities (γ) for our best model to explore the possible contribution of survival vs. recruitment on the population growth rate (Nichols et al. 2000). Seniority probability (γ) is the probability that an individual in the population at the current time step was also there at the previous time step, equivalent to reversing the capture histories and calculating survivorship (Pradel 1996). From the seniority estimates (γ), we can determine the relative contribution of survivors and new recruits to the population growth rate, λ, equivalent to elasticities (Caswell & Trevisan 1994). If γ is < 0·5, then recruitment is more important. If γ is > 0·5, survivorship is more important.

POPULATION MODEL

To simulate the mouse population dynamics, we developed a discrete-time population model with monthly time steps. The model is:

$$N_{t+1} = (S[s, c, d] + f[s, c, d]) \times N_t \qquad \text{eqn 1}$$

where N is mouse abundance, and t is time in months, therefore N_{t+1} and N_t refer to the mouse abundance in the next month and the current month, respectively. S is the probability of survival to the next month, and f is the recruitment rate per individual at month t. Both parameters may be a function of covariates, $[s,c,d]$: season (or month), climate and density. To test the predictive power of the model, we used the Pearson's product moment correlation between abundance predicted by the model 4 months ahead (parameterized from the data through 2004) and MNA or Jolly-Seber abundance estimates (for the full time series through May 2009), using the following equation:

$$\begin{aligned} Npred_{t+4} = {} & (S_t + f_t) \times (S_{t+1} + f_{t+1}) \times (S_{t+2} + f_{t+2}) \\ & \times (S_{t+3} + f_{t+3}) \times Nobs_t \end{aligned} \qquad \text{eqn 2}$$

where $Npred$ is the predicted abundance and $Nobs$ is the observed abundance. We use both MNA and Jolly-Seber estimates because we feel neither is ideal. The MNA estimates do not account for low trappability, whereas the Jolly-Seber estimates were calculated using program MARK and are not fully independent of the demographic rate estimates. Robust design models would give population estimates with minimal sampling correlation to vital rates (Kendall & Pollock 1992); however, the secondary trapping information was not recorded for most of the study. We compared the different population estimates for dates in which we had the additional data, from August 2004 to May 2009, and found that the population estimates using a closed robust design gave estimates very similar to MNA (Pearson's product moment correlation, $R = 0.93$); see (Fig. S1, Supporting information and Table S1, Supporting information). Formulating the population model from the demographic estimates and comparing the output to the data allows us to test the accuracy of the estimates and test the predictive power of the model.

Results

There was a total of 4288 captures representing 2036 individuals on the two grids over the study period from June 1994 to December 2004 and 5930 captures representing 2770 individuals over the study through May 2009. Minimum number known alive (MNA) as well as Jolly-Seber estimates of abundance were used as indices of population density (Fig. 1).
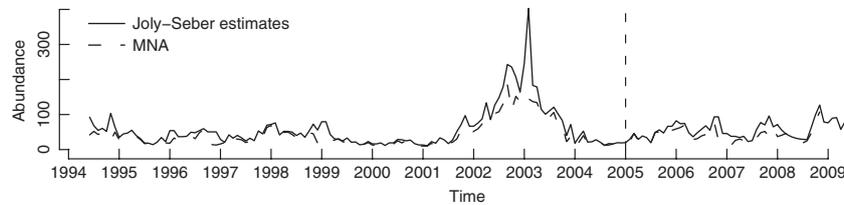
Fig. 1. Monthly abundance of the deer mouse population from two trapping grids in Cascade county, Montana, represented as minimum number known alive (MNA) and Jolly-Seber estimates.

Goodness-of-fit tests on the fully time-dependent mark–recapture statistical models revealed some evidence of lack-of-fit ($P < 0.001$). There appeared to be a significant number of transients seen (animals that were passing through the study site en route to other locations; $\chi^2 = 189.2$, d.f. = 114, $P < 0.001$) as well as some trap-dependence (i.e. 'trap-happy' animals; $\chi^2 = 318.5$, d.f. = 102, $P < 0.001$). To accommodate the lack-of-fit, we estimated the correction factor, $\hat{c}$, for the QAICc. (As $\hat{c}$ or lack-of-fit increases, models with fewer parameters are favoured.) $\hat{c}$ was calculated to be 1·796 for the single stratum capture history data and 1·28 for the multistrata data.

DEMOGRAPHIC RATES

First, we explored the basic suite of mark–recapture models for the demographic rates that did not include covariates (i.e. density, precipitation and temperature). For recapture probability (P), the fully time-dependent and age class dependent model (i.e. $P \sim age\ class + time$) was the most parsimonious (Table S2, Supporting information). For survival and maturation probabilities, models calculating a separate probability for each month were the best models (according to

QAICc values) in the basic suite of models (Table 1), demonstrating that seasonality is important for these demographic parameters. For recruitment rates, the year model (an estimate for each of the eleven years of trapping) was the best model (Table 2). To explore if precipitation, temperature and/or density could explain some additional variation, we evaluated a large suite of candidate models (Tables S3 and S4, Supporting information), including covariates, such as precipitation and temperature variables as well as density, at several time lags.

The most parsimonious models were

$$\mathrm{logit(Survival}_t) \sim \mathrm{month} \times \mathrm{Prcp}_{t-5} + \mathrm{month} \times \mathrm{Temp}_{t-5}$$
$$+ \mathrm{month} \times \mathrm{Prcp}_t + \mathrm{month} \times \mathrm{Temp}_t$$

$$\mathrm{logit(Maturation}_t) \sim \mathrm{month}$$

$$\mathrm{log(Recruitment}_t) \sim \mathrm{month} \times \mathrm{sum(Prcp}_{t\,\mathrm{through}\,t-4})$$
$$+ \mathrm{month} \times \mathrm{sum(Temp}_{t\,\mathrm{through}\,t-4})$$

where Prcp is precipitation, Temp is temperature, $t-5$ indicates 5 months previously, t indicates the current month, etc., and × indicates the interaction of two terms in the model

Table 1. The basic set of statistical models tested for variation in survival (S) and maturation (Ψ) probabilities, along with the most parsimonious model with covariates, using multistrata models in program MARK

Model	Number of estimable parameters	QAICc	Weight	QDeviance
$S(\sim \mathrm{month} \times P_{t-5} + \mathrm{month} \times T_{t-5}$ $+ \mathrm{month} \times P_t + \mathrm{month} \times T_t)\ \Psi(\sim\mathrm{month})$	211	8056·6	1	3408·9
$S(\sim\mathrm{month})\ \Psi(\sim\mathrm{month})$	163	8079·9	0	3537·1
$S(\sim\mathrm{age\ class} + \mathrm{month})\ \Psi(\sim\mathrm{month})$	164	8081·9	0	3536·9
$S(\sim\mathrm{year})\ \Psi(\sim\mathrm{month})$	162	8087·3	0	3546·6
$S(\sim\mathrm{age\ class} \times \mathrm{month})\ \Psi(\sim\mathrm{month})$	175	8088·3	0	3519·4
$S(\sim\mathrm{age\ class})\ \Psi(\sim\mathrm{month})$	153	8137·4	0	3616·1
$S(\sim\mathrm{month})\ \Psi(\sim\mathrm{year})$	161	8138·5	0	3600·0
$S(\sim\mathrm{time})\ \Psi(\sim\mathrm{month})$	277	8142·7	0	3346·2
$S(\sim\mathrm{year})\ \Psi(\sim\mathrm{year})$	160	8145·5	0	3609·1
$S(\sim\mathrm{time})\ \Psi(\sim 1)$	255	8221·5	0	3475·1
$S(\sim\mathrm{month})\ \Psi(\sim\mathrm{time})$	391	8395·7	0	3330·6

P and T denote precipitation and temperature, respectively; $t-5$ indicates 5 months previously; t indicates the current month; time denotes the full time-specific variation with 126 values estimated, one for each capture occasion; month denotes 12 values estimated, one for each month of the year; age class denotes two values estimated, one for juveniles and one for adults; a one denotes no time-specific variation, which is a single value estimated for all capture occasions; and × indicates the interaction of two terms as well as the individual terms. For all models capture probabilities were $P(\sim\mathrm{age\ class} + \mathrm{time})$ accounting for 127 parameters. QAICc is the estimated quasi-Akaike's information criterion, using the correction factor, $\hat{c} = 1\cdot28$, to adjust for lack-of-fit. Weight gives the statistical weight of that model compared to the other candidate models.

Table 2. The basic set of statistical models tested for variation in recruitment rates (*f*), along with the most parsimonious model with covariates, using Pradel models

Model	Number of estimable parameters	QAICc	Weight	QDeviance
$f(\sim \text{month} \times P_{t \to t-4} + \text{month} \times T_{t \to t-4})$	175	15 232·3	1	1765·7
$f(\sim \text{year})$	150	15 259·4	0	1846·8
$f(\sim \text{time})$	265	15 334·3	0	1667·5
$f(\sim \text{season})$	143	15 587·9	0	2190·3
$f(\sim \text{month})$	151	15 591·1	0	2176·3
$f(\sim 1)$	140	15 603·2	0	2212·1

$P_{t \to t-4}$ and $T_{t \to t-4}$ denote the sum of precipitation and the sum of temperature, respectively, from the current month through 4 months previously; time denotes the full time-specific variation with 126 values estimated, one for each capture occasion; month denotes 12 values estimated, one for each month of the year; year denotes 11 values estimated, one for each year of the study; season denotes four values estimated, one for each of the seasons; and a one denotes no time-specific variation, which is a single value estimated for all capture occasions. For all models capture probabilities, *P*, were fully time-dependent, and survival probabilities, φ, were monthly, i.e. φ (~month) *P* (~time), accounting for 131 of the parameters. QAICc is the estimated quasi-Akaike's information criterion, using the correction factor, $\hat{c} = 1\cdot796$, to adjust for lack-of-fit. Weight gives the statistical weight of that model compared to the other candidate models.

(as well as the individual terms). (Tables 1 and 2 show these models in relation to the basic suite of models, and Tables S3 and S4, Supporting information show all the models considered.) Precipitation, temperature and seasonality were important factors explaining variation in survival and recruitment rates. Climatic variables important in determining survival were precipitation and temperature in the current month and 5 months previously, whereas the sum of precipitation over the last 4 months and the sum of temperature over the last 4 months were important for recruitment rates. Full equations are given in the Appendix S1, Supporting information (eqns A1–3). These survival and recruitment models did significantly better (had a lower QAICc value) than the best model in the basic suite of models that did not consider covariates (Tables 1 and 2). Survival did not appear to be age specific (i.e. models which estimated a separate survivorship for juveniles and adults had higher QAICc values than those which did not). For comparison, we found that NDVI for the study area from 2000 to 2004 was best explained by month, precipitation 2 months ago, and temperature 3 months ago, and their interactions.

The estimates of monthly population growth rates (*S* + *f*) ranged from 0·51 to 2·10 with a mean overall growth rate (λ) of 1·02 (standard deviation (SD) = 0·27). Seniority estimates (γ) for our mouse population ranged from 0·23 to 1·0, with a mean of 0·66 (SD = 0·15), suggesting considerable variability in the importance of recruitment vs. survivorship. However, for 110 out of 126 months, γ was > 0·5, indicating that most often, survivorship is more important than recruitment in determining the growth rate of the mouse population.

Table 3. The effect of precipitation (Prcp) and temperature (Temp), occurring during the given season, on recruitment (*f*) 0–4 months later and survival (*S*) 5 months later based on the most parsimonious MARK models

| Season	Effect on demographic rates	
	More Prcp	Warmer Temp
Early spring	↓*f*	↓*f*, ↓*S*
Late spring	↓*f*, ↓*S*	↓*f*, ↑*S*
Early summer	↑*f*, ↓*S*	↑*f*, ↓*S*
Late summer	↑*f*, ↑*S*	↑*f*, ↑*S*
Early fall	↑*f*, ↑*S*	↑*f*, ↑*S*
Late fall	↑*f*, ↑*S*	↑*f*, ↑*S*
Early winter	↑*f*, ↑*S*	↓*f*, ↑*S*
Late winter	↓*f*	↓*f*, ↑*S*

Up and down arrows indicate an increase or decrease, respectively, in recruitment rate or survival probability. Precipitation had mixed to no effect on survival late winter and early spring. The effects were reversed for less precipitation and cooler temperatures.

Seasonality was important for all three demographic rates. Under mean precipitation and temperature conditions, survival was highest in December and January, decreased in the early spring and slowly increased through the summer and fall. Recruitment generally increased through the spring, peaked in the summer, and declined through the fall with another small peak in January. Maturation was low in late fall, increased to a peak in spring, and declined through mid summer with another small peak during late summer. For survival and recruitment rates, the interactions between month and the climatic variables were important, meaning that precipitation and temperature had different effects in different months.

From these models, we can describe some likely general trends of the effect of precipitation and temperature on demographic rates. The effects of precipitation and temperature on recruitment rates and survival 5 months into the future were fairly consistent across seasons and between other similar models (Figs S2 and S3, Supporting information). Recruitment rate was positively correlated with cooler temperatures December through June, warmer temperatures July through October, less precipitation from February to May, and more precipitation July to December (Table 3 and Fig. S3, Supporting information). More precipitation occurring from August to January, less precipitation February and May to July, higher temperatures September to February, and May and June, and lower temperatures April and July to August were positively correlated with Survival 5 months in the future (Table 3 and Fig. S2, Supporting information).

POPULATION MODEL

The above models are more parsimonious than all the other models tested based on QAICc-rankings. It is however important to ask the extent to which they have predictive power relative to long-term population dynamics. To investigate this, we combined the demographic estimates from the
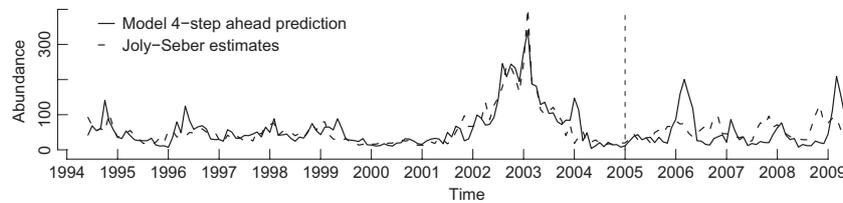
Fig. 2. Four-step-ahead predictions simulated using demographic parameters estimated in MARK for the best models for survival and recruitment, along with the Jolly-Seber population estimates.

best models with our population model (eqn 1), and predicted the abundance for each time point. We used the estimates from the mark–recapture models to predict abundance for the data that was not used in the mark–recapture analysis (January 2005 to May 2009). We did four-step-ahead predictions (eqn 2) and then compared the model results with our density indices (MNA and Jolly-Seber estimates), over the study period.

The recruitment rates predicted in this manner contained a few values that were unreasonably high (>1000). These abnormally large values corresponded to several December months. Because of low trappability, the data were particularly sparse for several of the December months, resulting in a large standard error for the β coefficient for the effect of precipitation for December. In order to correct for this sparseness in the data, we averaged the recruitment rates for the Decembers of 1994–2003, and used this average, $f = 0.27$, for the recruitment rate for December 2004, 2005, 2006 and 2008.

The simulated abundance from the population model predicted 4 months ahead (eqn 2) for the sample data (June 1994–December 2004) was highly correlated to MNA ($R = 0.85$) and to Jolly-Seber estimates ($R = 0.89$) (Fig. 2). The model did not fit the out-of-sample data as well ($R = 0.26$), though the correct range in abundance was predicted. For the whole time series, the model was correlated to the data with $R = 0.79$ for Jolly-Seber estimates and $R = 0.77$ for MNA. The data points for which there was the biggest discrepancy were winter months and these are the months when the data is the sparsest.

Discussion

The objective of our study was to evaluate the importance of seasonality, population density and climate on population dynamics of the deer mouse and formulate population models that can describe the dynamics and forecast abundance. A large amount of the variation seen in the population dynamics of the deer mouse was explained by seasonality, precipitation, and temperature, confirming the greater importance of density-independent forces, and lending significant predictability to this system. Given the current and previous months' precipitation and temperature, we were able to reasonably predict population dynamics several months in advance.

Several studies of the effect of food supplementation, acorn masting or periodical cicadas on *Peromyscus* found an increase in population density with increased food availability (Gilbert & Krebs 1981; Hansen & Batzli 1978; Marcello *et al*. 2008; Shimada & Saitoh 2006; Smith 1971; Sullivan & Sullivan 2004; Taitt 1981; Yunger 2002), suggesting that many *Peromyscus* populations may be limited by food or at least high quality food. Increasing food items such as the introduced biocontrol agent, gall flies, for knapweed, caused an increase in deer mouse population density in Montana and increased SNV antibody prevalence (Pearson & Callaway 2006), although other areas in Montana have shown significant increases in density without knapweed (Douglass *et al*. 2001). If deer mouse populations are often limited by food, increasing primary productivity may increase population density, either directly through an increase in seeds, nuts and fruits, or indirectly through insects.

The time lags between changes in environmental variables and changes in demographic rates indicated by our models (0–5 months) are consistent with those for primary productivity. NDVI was best explained by precipitation at a 2-month lag and temperature at a 3-month lag. So, there was another few months after primary productivity was affected until mouse demography was affected. This lag might be due to time for plants to set seed, for insects to respond, and for mice to reproduce and for their progeny to enter the trappable population. As environmental variables appear to affect primary productivity and deer mouse demography with a time lag, our study lends support to a bottom-up trophic phenomenon. However, the relationship for our system is not as simple as the more-rain-equals-more-food-equals-more-mice hypothesis. The effects of precipitation and temperature depend on the month and for some months were not as we had predicted; higher temperatures and more precipitation during the summer through early winter (not in the spring) were correlated to increased survival and recruitment. Previous studies have shown that spring precipitation best predicts grass production, but fall-through-summer precipitation better predicts total forage production (Noller 1968; Whitman & Hausge 1972). Our results are not unlike those reported for deer mouse populations in Colorado where populations responded favourably to rainfall during warm periods, but crashed when high rainfall occurred during cold periods (Calisher *et al*. 2005; Mills 2005).

In our analysis, juvenile survival was not significantly different from adult survival. Conventional wisdom is that *Peromyscus* juveniles have a higher mortality rate than adults (Terman 1968; Myers & Master 1983). We speculate that the juveniles we captured had already survived the period of high mortality (in the nest or while dispers-

ing) before entering the trappable population. The finding that recruitment is affected by environmental factors from the current month through 4 months previously suggests that we are detecting a combination of immigration and *in situ* reproduction, since gestation and growth of off-spring before leaving the nest would take *c.* 2 months. The small peak in recruitment in January under mean environmental conditions is most likely due to immigration, given the well known seasonality in reproduction in the deer mouse (Douglass *et al.* 2001).

Our population model formulated with the most parsimonious MARK models for survival and recruitment accounted for most of the variation seen in mouse abundance for the sample data, but a significant amount of unexplained variation was seen in the out-of-sample data. Some of this reduction in the correlation coefficient can be explained by the restricted range of mouse abundances observed during the out-of-sample period. (As is well known, the statistical R is both a function of the overall predictability of any given system and the range of observed values along the abscissa.) If we, for example consider the in-sample predictability of abundances that covers the range of the out-of-sample forecast (0–100 individuals), the in-sample *R* is reduced by about half to 0·46, more comparable to our out-of-sample predictability of 0·26. There were a large number of models tested, so it is possible that some associations could occur by chance. However, for the recruitment analysis, most models containing precipitation and temperature (whatever the lag) did better than time varying, monthly or yearly models, suggesting a real effect of the environmental factors. There may be a number of sources for the remaining unexplained variation. Our models did not consider predation, parasitism or interspecific competition – all factors that have been implicated in deer mouse demography (Grant 1971, 1972; Kaufman & Kaufman 1989; Pedersen & Greives 2008). Furthermore, some of the covariates may have nonlinear influences on demographic rates other than those implied by the logit- and log-links associated with the mark–recapture formalism. We also did not consider time lags longer than 6 months; there is evidence that precipitation can have lagged effects of up to 2 years, perhaps by increasing soil moisture or altering nutrient cycling rates (Perry 1976). Delayed density dependence of longer lags has been implicated in certain small rodents. However that is typically associated with cyclic populations of voles and lemmings and has not been reported for *Peromyscus* or *Apodemus* (see, for example, Saitoh *et al.* (1999) for a sympatric comparative analysis). Acorn mast (Elkinton *et al.* 1996; Jones *et al.* 1998) and knapweed (Pearson & Callaway 2006) have been shown to affect *Peromyscus* abundance but were not found at our study site. Another possibility is that environmental factors operated differently during the first part of the study than the last. The inability of the model to predict abundance well for the out-of-sample data suggests that more data collection is necessary to fully understand climatic influences on deer mouse population dynamics. The uncertainty in the winter months seems to be particularly important.

Understanding what leads to changes in deer mouse abundance is important for predicting Sin Nombre virus epizootics. Hantaviruses are directly transmitted and thought to have density-dependent transmission (Madhav *et al.* 2007), therefore, mouse abundance affects the possibility and size of epizootics. Several previous studies have suggested qualitative correlations between environmental factors and deer mouse population dynamics. Our study quantitatively described this correlation through changes in demographic rates. While it is true that we found the link to be complex, a significant amount of the variability seen in mouse abundance can be predicted from climatic drivers. This is encouraging because it suggests that armed with a more precise understanding of the links and time lags between climatic conditions and deer mouse increases, we may be able to better predict epizootics. This particular model may not apply to the southwestern U.S., because the climate and habitat types are quite different; a separate analysis may be needed for each region of concern. We are currently testing the model to determine its applicability to other field sites in Montana with different habitat types (i.e. sagebrush and pine forests) and formulating an epidemiological model, with the aim to relate environmental forcing to number or proportion of individuals infected. A better understanding may allow public health officials to enhance HPS prevention strategies, as well as help scientists predict possible effects of climate change on hantavirus-host dynamics.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Equations for mark-recapture models.

Figure S1. Population abundance estimates including minimum number alive (MNA), Jolly-Seber, and closed robust design estimates from August 2004 to May 2009.

Figure S2. The effect of precipitation and temperature 5 months previously on survival in the current month from the model $Survival_t \sim month \times Precipitation_{t-5} + month \times Temperature_{t-5} + month \times Precipitation_t + month \times Temperature_t$. The x-axis gives precipitation deviation (in inches) from the summed monthly mean (i.e. -2 means 2 in below average for that month). The different coloured lines represent different mean temperatures for the month (in °F), again deviation from monthly mean (i.e. $T = 10$ indicates the mean temperature for the month is 10°F above average).

Figure S3. The effect of the summed precipitation and temperature over the last 4 months (t through $t-4$) on recruitment rate in the current month from the model $Recruitment_t \sim month \times sum(Precip_{t\ through\ t-4}) + month \times sum(Temp_{t\ through\ t-4})$.

Figure S4. The effect of precipitation and temperature in the current month on survival from the model $Survival_t \sim month \times Precipitation_{t-5} + month \times Temperature_{t-5} + month \times Precipitation_t + month \times Temperature_t$.

Table S1. Statistical models tested using closed robust design models.

Table S2. Statistical models tested for variation in recapture rates (P), using multistrata models.

Table S3. Ranking of multistrata MARK models for survival (S), capture probability (P), and maturation probability (Psi).

Table S4. Ranking of Pradel MARK models for recruitment rate (f) (and survival, Phi, and capture probability, P).

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