Roles of human disturbance, precipitation, and a pathogen on the survival and reproductive probabilities of deer mice

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Abstract. Climate change, human disturbance, and disease can have large impacts on the dynamics of a species by affecting the likelihood of survival and reproduction of individuals. We investigated the roles of precipitation, off-road vehicle (ORV) alteration of habitat, and infection with Sin Nombre virus on the survival and reproductive probabilities of deer mice (*Peromyscus maniculatus*). We used generalized linear mixed models to estimate the effects of these factors and their interactions by fitting capture–recapture data collected seasonally from 2002 to 2007 at 17 sites in the Great Basin Desert of central Utah, USA. During periods with high precipitation, we found no difference in survival and reproductive probabilities between seasons, but during drier periods, we found a reduction of overwinter survival and fall reproductive activity. Precipitation also interacted with disturbance to affect survival probabilities and female reproduction; in periods with low precipitation, deer mice on highly disturbed sites had extremely low survival probabilities and low reproductive probabilities of females compared to those of individuals from low-disturbance sites. However, high precipitation ameliorated the effect of disturbance on both parameters. Deer mice from sites with high impact of ORV disturbance also had low survival over summer. Additionally, male reproductive probabilities were diminished on highly disturbed sites in both seasons; in contrast, they were reduced only in the fall on low-disturbance sites. Density had an overall negative effect on survival and reproductive probabilities of deer mice. For females, the negative effect on reproductive activity was amplified in highly disturbed sites. We found no effect of hantavirus infection on survival probabilities of deer mice. Overall, this study revealed complexity in the determinants of deer mouse survival and reproduction given by the effects of a number of significant interactions among explanatory variables. Thus, factors that may not appear to have a strong effect when investigated alone can still be influential by modulating the effect of a different factor.

Key words: deer mice; density dependence; Great Basin Desert, central Utah, USA; human disturbance; off-road vehicles; Peromyscus maniculatus; *precipitation; reproduction; seasonality; Sin Nombre virus; survival.*

Introduction

Ecologists have long investigated causes of fluctuations in animal populations and have reached the general consensus that species dynamics are affected by a combination of exogenous (density-independent) and endogenous (density-dependent) factors (Royama 1992, Berryman 1999, Turchin 2003). These factors can have nonlinear effects and interact in complex ways, often resulting in nonintuitive relationships and making it difficult to disentangle their individual roles. Ecological studies at large temporal and spatial scales are essential for revealing these complexities (Brown et al. 2001).

Naturally occurring drivers such as abiotic factors (Andrewartha and Birch 1954), predation (Lotka 1925, Volterra 1926), and competition (Nicholson 1954) are important in regulating animal populations. In addition, pathogens have long been proposed as having the potential to drive species dynamics (Anderson and May 1980); however, only recently have a few empirical studies demonstrated that even endemic pathogens, that is, pathogens that are always present in a population, can have significant effects on host populations (e.g., Burthe et al. 2008, Pedersen and Greives 2008, Vandergrift et al. 2008). The increased attention in recent years to understanding the influence of pathogens on population dynamics has probably been motivated by the increased discovery of emergent diseases, which are characterized by being caused by pathogens previously unrecognized or that are rapidly expanding in incidence or range (Jones et al. 2008, Plowright et al. 2008). Other phenomena that

have been the focus of more recent research are the effects of human-mediated alteration of natural conditions on species dynamics, including the impacts of climate change (e.g., Walther et al. 2002, Harley et al. 2006, Parmesan 2006), and habitat degradation and fragmentation (e.g., Henle et al. 2004, Cushman 2006, Banks et al. 2007). To better understand how species will respond to changing climatic conditions, increasing human disturbance, and emerging pathogens, it is necessary to evaluate the mechanisms driving population changes in a context-dependent manner.

In this study, we investigated how potential stressors including climate, human disturbance, and disease affect survival and reproductive probabilities of deer mice (Peromyscus maniculatus) in the Great Basin Desert, Utah. This system is an excellent one in which to investigate the impacts of multiple factors on survival and reproduction. First, deer mice are carriers of various pathogens (e.g., Sin Nombre virus (Childs et al. 1994), Borrelia burgdorferi (Burkot et al. 1999), and Schistosomatium douthitti (Schwanz 2006)). Second, the Great Basin Desert is a semiarid ecosystem with significant fluctuations in rainfall, a factor known to greatly influence small-mammal populations in other semiarid ecosystems (Jaksic 2001, Brown and Ernest 2002, Lima et al. 2003, 2006, Meserve et al. 2003, Letnic and Dickman 2006, Previtali et al. 2009). Additionally, much of the Great Basin Desert is commonly used by off-road vehicle (ORV) enthusiasts. This recent form of anthropogenic disturbance can have profound and long-lasting impacts on ecosystems processes by damaging vegetation, compacting soil, and polluting air and water (Dregne 1983, Webb 1983, Wilshire 1983, Wilderness Society 2006). As a semiarid habitat, the Great Basin is particularly vulnerable to the adverse impacts of ORVs, mainly because of the shallow root system of its plants and fragility of its soils (Dregne 1983, Wilshire 1983). ORVs are known to affect both behavior and hearing physiology of small mammals (Brattstrom and Bondello 1983). More importantly, the changes in habitat structure could increase predation rates and intraspecific competition, and could foster interspecific competition that results from an influx of heteromyid rodents into disturbed areas (Clay 2007).

We focused on the pathogen Sin Nombre virus (SNV), which is common in deer mice and is also the agent responsible for Hantavirus Cardiopulmonary Syndrome (HCPS) in humans (Hjelle et al. 1994). In deer mice, SNV causes a chronic infection that does not result in overt symptoms of illness under relatively benign conditions (i.e., ad lib food and water; Botten et al. 2000). However, under natural conditions, infected deer mice exhibit more severe pathological symptoms (Netski et al. 1999), as well as reduced growth rates (Douglass et al. 2007) and survival (Douglass et al. 2007, Adler et al. 2008). Additionally, there is indirect evidence suggesting that SNV can negatively affect reproductive output of female deer mice (Dearing et al.

2009). The discordance between laboratory and field studies may result from context-dependent virulence, in which hosts must be subjected to environmental stressors before an otherwise asymptomatic infection exerts negative effects (Brown et al. 2003). Laboratory studies and field experiments have shown that negative effects of pathogens are modulated by the availability of food and the condition of the individuals (e.g., Kristan and Hammond 2001, O'Brien and Dawson 2008, Pedersen and Greives 2008).

In this system, we expected precipitation to set the stage under which the negative effects of other potential stressors on survival and reproduction could be accentuated or ameliorated. Specifically, we predicted that under pressure from such stressors as extreme precipitation events, high anthropogenic disturbance, or high intraspecific competition, deer mice would have reduced survival and reproductive probabilities that would be further exacerbated by SNV infection.

METHODS

The study took place from May 2002 to September 2007 at 17 sites located in the Great Basin Desert in central Utah (Juab and Utah counties), USA. All sites were at least 700 m apart to minimize population overlap, with the maximum distance between sites being ~60 km to minimize various sources of large-scale geographic variation. Dominant vegetation in all sites consisted of big sagebrush (Artemisia tridentata) and Utah juniper (Juniperus osteosperma) on a sandy-clayish substrate. All sites were established on lands managed by the U.S. Department of Agriculture and the Bureau of Land Management.

Study sites differed in their degree of disturbance caused by ORVs, with impacts resulting primarily from the removal of shrubs and herbaceous plants leading to large areas of bare ground. To obtain a relative measure of disturbance for each site, we created an index based on the percentage of shrub cover and bare ground. Vegetation cover was measured at each site in every year except 2005 using the point intercept method, in which the tallest type of cover was recorded at 200 points located 0.5 m apart along 12 transects. At each point, vegetation was characterized as tree cover, shrub cover, litter, grass, or bare ground. Given that the vegetation cover data showed relatively little interannual variation, we calculated a disturbance index based on the cross-year mean of bare ground subtracted from the cross-year mean shrub cover estimation (see Appendix). For our analyses, we categorized sites with a negative value for this index (bare ground > shrub cover) as "high disturbance" and sites with a positive disturbance index (bare ground < shrub cover) as "low disturbance." The sites with the greatest levels of disturbance (i.e., most negative indices) had high ORV use and more than 40% bare ground and less than 10% shrub cover (Appendix). Sites that were protected from ORV use by a fence had 9.8–17.2% bare ground and >50% of shrub cover (Appendix).

The total annual (September–August) precipitation recorded at the closest meteorological station, Eureka, Utah (~20 km away from the study sites), was 272.9 ± 112.8 mm (mean ± SD; data from September 1990 to August 2007; *available online*).[7] Most of the precipitation occurred between the months of October and April. For the analyses, we used the total amount of precipitation recorded in the following two periods: spring–summer (from April to September) and fall–winter (from October to March).

Each year, small-mammal trapping was conducted in May–June (late spring) and September–October (early fall) for three nights during the new phase of the moon. Different numbers of sites were sampled in different years, with five of the 17 sites being sampled continuously throughout the study period (see Appendix). On each site, 148 Sherman live-traps were set in a web configuration consisting of 12 transects distributed across a 3.14 ha area. Traps were baited with oats and peanut butter and were provided with batting for insulation. Captured animals were identified to species and sex, marked with unique ear tags, and weighed. Blood (~0.1 mL) was collected from the retro-orbital sinus and stored at −80°C. Reproductive status of deer mice was also determined; individuals were classified as "reproductive" if they had descended testes, protruding nipples, or a perforate vagina. We used body mass as a surrogate for age; animals with body masses ≤14 g were classified as juveniles, whereas those >14 g were classified as adults. This mass-based age estimation is consistent with other deer mouse studies (e.g., Mills et al. 1997, Borucki et al. 2000, Douglass et al. 2001) and also corresponds to the mass at which individuals at our study sites begin to show signs of reproductive activity. All animal trapping and handling procedures followed guidelines for handling rodents potentially infected with hantaviruses (Mills et al. 1995) and were approved by the Institutional Animal Care and Use Committee at the University of Utah (IACUC #05-03011 and 08-02012).

We used an enzyme-linked immunosorbent assay (ELISA) to determine the presence of IgG antibodies against SNV nucleocapsid antigen in deer mouse sera (Feldmann et al. 1993, Otteson et al. 1996). Samples were considered positive if the optical density was more than three times greater than the negative control sera. Because SNV is a chronic infection, adult deer mice were classified as infected if they had antibodies against SNV. In juveniles, seropositivity may be due to the presence of maternal antibodies (Borucki et al. 2000) rather than their own infection, and thus we did not include them in the analyses.

Data analysis

We conducted two sets of analyses to independently investigate the effects of several factors on two response variables: survival and reproductive probabilities. First, as an indirect measurement of survival, we recorded whether individuals marked in initial captures were recaptured in a later season. This measurement is only a proxy of apparent survival because it does not account for differences in capture probabilities, nor does it discriminate between death and emigration from the site. However, this measurement provides information on the persistence of individuals in the population. Second, as a measurement of reproduction, we considered whether an individual was reproductively active or not at the time of capture. For individuals with captures in both the spring and the fall trapping sessions, we only used the record for the spring to avoid problems associated with lack of independence between observations.

These response variables were modeled as a function of individual characteristics (i.e., initial body mass and infection status (infected/uninfected)), and of environmental factors representing the prevailing conditions at the time of initial capture: i.e., season (across season for survival, and spring/fall for reproduction); seasonal precipitation (total mm recorded in the fall–winter period for overwinter survival and spring reproduction, and in the spring–summer period for over-summer survival and fall reproduction); deer mouse density (number of individuals per hectare); and degree of disturbance (high/low). Continuous explanatory variables were centered on the mean values (Gelman and Hill 2007). Males and females were analyzed independently for factors affecting reproductive activity, whereas in the analysis of survival, sex was used as an explanatory factor. Site identity was used as a grouping factor (random effect) to account for the lack of independence among observations from the same site. We fitted generalized linear mixed models (GLMM) with binomial errors and the logit link function to obtain restricted maximum likelihood parameter estimates using the procedure GLIMMIX in SAS 9.1.3 (SAS Institute 2005). For estimation, we used the restricted maximum likelihood method because it produces better estimates than full maximum likelihood when the number of higher level units is small (Flom et al. 2006). However, this method produces likelihoods that are not comparable across models, thus preventing the use of information criteria for model selection. Therefore, the approach that we used for model selection consisted of building a complex model that included the main effects of all the explanatory variables and the interactions between the variables that generated different environmental conditions for deer mice (i.e., the interactions between disturbance and precipitation, season, and density, and precipitation and season). We then eliminated the least significant term in a series of iterative steps. To investigate context-dependent effects of SNV on survival and reproductive probabilities, we fitted models with the interaction of infection status and any of the significant environmental terms. We finally
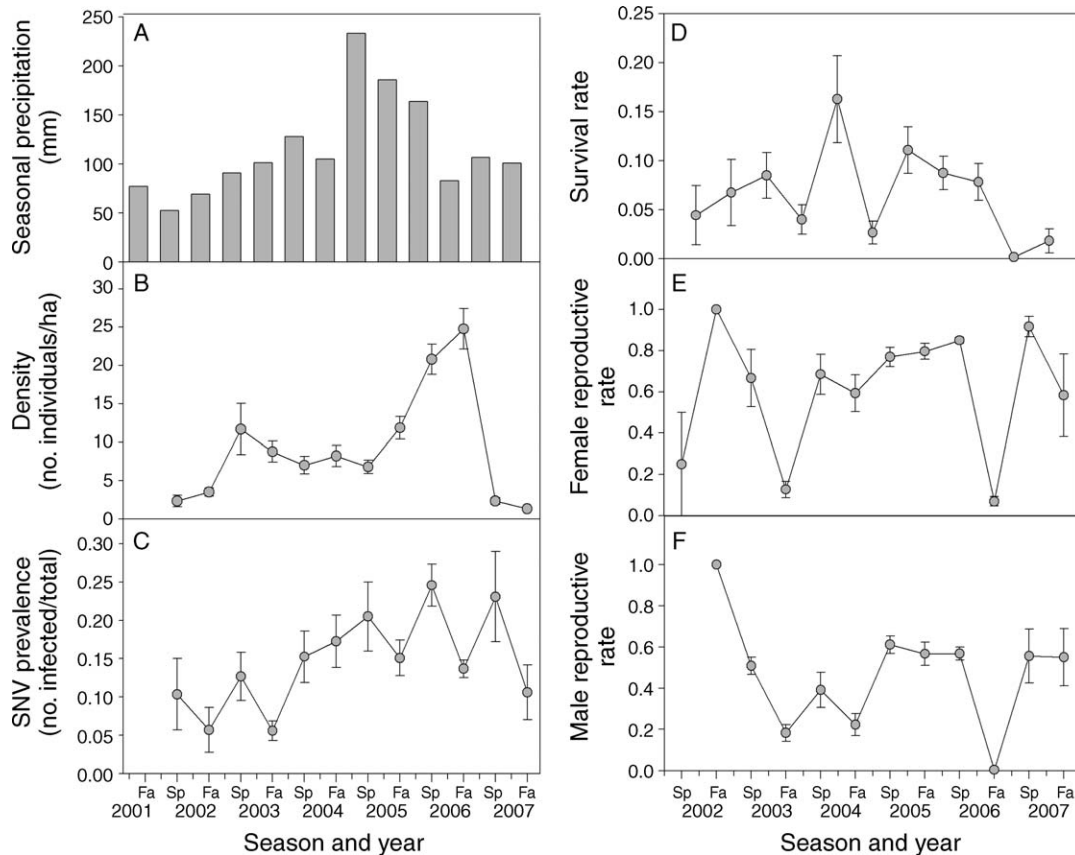
FIG. 1. (A) Total seasonal precipitation (fall–winter from October to March, and spring–summer from April to September) from Eureka, Utah, USA, near the study sites. (B) Density of deer mice *Peromyscus maniculatus* (mean ± SE) for the study sites sampled in each trapping session. (C) Seroprevalence of Sin Nombre virus in deer mouse populations (number of infected individuals/total number of individuals captured [mean ± SE]) for the different sites sampled in the spring (Sp) and fall (Fa) of each year from 2002 to 2007. (D) Survival rates (number of individuals recaptured at a later season/total number of individuals captured) over the winter (from October to May) and over the summer (from May to October). (E) Female reproductive rates (number of reproductively active females captured/total number of females captured) in the spring (May) and the fall (October). (F) Male reproductive rates (number of reproductively active males captured/total number of males captured) in the spring (May) and the fall (October).

arrived at a parsimonious model that included only significant terms ($P \leq 0.05$). We checked for evidence of overdispersion by calculating the ratio of the generalized chi-square value divided by the degrees of freedom, where a ratio greater than 1 was indicative of over-dispersion. From the final model, we calculated the effect on the probability of surviving or reproducing by back-transforming the estimates of the least-square means from the logit to the probability scale. Significant differences among categories were determined by adjusting for multiple comparisons using an approximation implemented in SAS and described by Kramer (1956).

RESULTS

Precipitation was highly variable across years (Fig. 1A); the fall–winter of 2004–2005 had almost twice as much precipitation as any of the previous periods, and precipitation remained high in the following two

periods. After this increase in precipitation, deer mouse populations increased in size, reaching their maximum density in the fall of 2006 with a mean of 25 individuals/ha. This represented a 10-fold increase from the mean density recorded in the spring of 2002 (Fig. 1B). Deer mouse populations then declined precipitously in the spring of 2007 to only 2 individuals/ha. Of the 939 individuals captured in the fall of 2006, only 2 were recaptured in the spring of 2007, making this the lowest survival rate recorded in the study (Fig. 1D). The proportion of reproductive females and males were also extremely low during the fall 2006 sampling session (Fig. 1E, F, respectively).

Prevalence of SNV also showed marked time and spatial variation. Spatial variation was characterized by some sites having zero or very low SNV seroprevalence across time (e.g., site 6; Appendix), while others had a greater SNV seroprevalence during most sampling periods (e.g., site 3; Appendix). These patterns resulted

TABLE 1. Coefficient estimates and significance of the parameters in the most parsimonious model for the probability of deer mice (*Peromyscus maniculatus*) surviving to a later season in the Great Basin Desert of central Utah, USA.

Parameter	Estimate	SE	df	t	P
Intercept	−1.90	0.17	15	−10.84	<0.01
Sex (female)	−0.48	0.16	2700	−3.04	<0.01
Density	−0.01	0.003	2700	−2.66	<0.01
Precipitation	−0.0004	0.002	2700	−0.22	0.83
Season (overwinter)	−1.08	0.19	2700	−5.53	<0.01
Disturbance (high)	−1.14	0.39	2700	−2.95	<0.01
Precipitation × disturbance (high)	0.012	0.004	2700	2.95	<0.01
Precipitation × season (overwinter)	0.012	0.003	2700	3.46	<0.01
Season × disturbance (overwinter and high)	0.99	0.41	2700	2.41	0.02

Notes: Estimates for categorical variables correspond to the category specified in parentheses with respect to a reference category (i.e., male for sex, over-summer for season, and low for disturbance). Site identification was used as a grouping (random) factor (estimated variance components ± SE = 0.09 ± 0.07).

in a large variance in mean seroprevalence within a single sampling period (Fig. 1C). Variation in SNV seroprevalence across time was also striking (Fig. 1C). In general, SNV seroprevalence was greater during the spring sampling periods, with prevalence in the springs of 2005, 2006, and 2007 being particularly high (Fig. 1C).

Survival

Marked deer mice were rarely recaptured at a later season, with the longest life span recorded being three consecutive seasons (i.e., 1.5 years). We analyzed data for a total of 2724 unique adult deer mice after removing individuals that were injured, hypothermic, or dead in the trap. Of these, 472 were infected with SNV. The proportion of adult individuals that were recaptured at a later season was similar among infected and uninfected individuals (0.072 and 0.071, respectively). Overall, the mean proportion of adult deer mice surviving fluctuated around 0.1 during the study period (Fig. 1D).

Dispersion parameters of the generalized linear mixed models were close to 1 (range in the generalized chi square/df = 0.93–0.95), indicating that there was no overdispersion. The most parsimonious model suggested that several factors affect the probability of deer mice surviving to a later season. This model included the influence of sex, deer mouse density, and the interactions between precipitation and both the degree of disturbance and season (Table 1). We found that males had a 1.5 times greater chance of surviving to a later season than females (least-square means ± SE = 0.06 ± 0.01 for males vs. 0.04 ± 0.01 for females; Table 1). Survival probabilities were also density dependent; as deer mouse density increased, survival probabilities declined (Table 1). Additionally, we found a significant interaction between precipitation and seasonality (Table 1). Precipitation had a positive effect on overwinter survival probabilities but it did not affect survival probabilities over the summer (Fig. 2A). There was also a significant interaction between precipitation and the degree of disturbance (Table 1). On high-disturbance sites, sur-

vival probabilities were extremely low in periods with low precipitation, but as precipitation increased survival probabilities increased. During periods with extremely high precipitation, survival probabilities on the high-disturbance sites reached the level of low-disturbance sites (Fig. 2B). In low-disturbance sites, precipitation did not affect survival probabilities (Fig. 2B). Finally, the interaction between disturbance and seasonality revealed that on low-disturbance sites, the probability of survival was affected by season; overwinter survival was less than half that of survival over summer (adjusted P < 0.01; Fig. 2C). In contrast, survival probabilities on high-disturbance sites were unaffected by season, being always low (adjusted P = 0.99; Fig. 2C). Furthermore, during the winter, survival probabilities did not differ between high- and low-disturbance sites (adjusted P = 0.99). Lastly, there was no significant effect of body mass or SNV infection status on the probability of surviving (P > 0.05).

Reproduction

A total of 2995 adult deer mice (1310 females and 1685 males) were used in the analysis of reproductive activity. The mean proportion of reproductively active females was generally high, ranging between 0.6 and 0.8, except for three seasons (spring 2002, fall of 2003, fall 2006; Fig. 1E). In contrast, we found marked temporal variation in the mean proportion of reproductively active males, with the fall 2003 and fall 2006 also being the sampling periods with the lowest rates (Fig. 1F).

We found that some factors influenced reproductive probabilities of male and female deer mice in a similar manner. For example, reproductive probabilities increased with increasing body mass of the individual (Table 2). In both sexes, we also found a significant relationship between SNV infection and reproductive activity (Table 2), with infected individuals being more likely to be reproductively active (least-square means ± SE = 0.60 ± 0.04 for uninfected females and 0.71 ± 0.06 for infected females, P = 0.05; and 0.30 ± 0.03 for uninfected males and 0.37 ± 0.04 for infected males, P =

0.03). The likelihood of being reproductively active was also influenced by the interaction between precipitation and seasonality (Table 2). Reproductive activity in the fall was highly affected by precipitation, being extremely low when precipitation was low and reaching an apex when the summer precipitation was highest (Fig. 3A, D). The effect of precipitation on spring reproductive probabilities was less pronounced, being nonexistent for females and slightly positive for males (Fig. 3A, D).

The remainder of the factors analyzed differentially affected the reproductive probability of male and female deer mice. For females, we found a significant interaction between precipitation and the degree of disturbance (Table 1). On high-disturbance sites, reproductive probabilities of females increased with precipitation, but on low-disturbance sites, precipitation did not affect their probability of being reproductively active (Fig. 3B). We also found a significant effect of the interaction between the degree of disturbance and deer mouse density (Table 2); the negative effect of density on reproductive probabilities was further exacerbated on highly disturbed sites (Fig. 3C). Density also had a negative effect on reproductive activity of males, but there was no significant interaction with the degree of disturbance (Table 2). Rather, the degree of disturbance interacted with season to significantly affect reproductive activity of males (Table 2). At low-disturbance sites, reproductive probabilities in the spring were higher than during the fall (adjusted $P < 0.01$) and were also greater than those of high-disturbance sites during either season (adjusted $P < 0.05$; Fig. 3E). In contrast, high-disturbance sites had low reproductive probabilities regardless of the season (Fig. 3E).

DISCUSSION

The factors governing the survival and reproduction of animals in nature are often complex and multifaceted. Precipitation, seasonality, predation, and density have been found to affect the vital rates of small-mammal species in semiarid habitats, (Lima et al. 2001a, b, Previtali 2006). The results of this study indicate that survival and reproductive probabilities of deer mouse populations in the Great Basin Desert were affected primarily by the interactions between factors. For instance, we did not find a significant effect of precipitation alone (i.e., as a main effect; Tables 1 and 2), but instead found that it played a major modulating role by changing the influence of both seasonality and disturbance. Specifically, during the wet year of 2005, we found no difference in survival probabilities of individuals tracked over winter vs. those individuals tracked over summer. In contrast, during drier years, survival of individuals over the winter was reduced to one-fourth that of individuals who survived over the summer. In dry years, this difference could be due to reduced insulation from low snowpack, thus resulting in higher overwinter mortality due to increased thermal stress. Likewise, individuals captured in the fall of a dry year
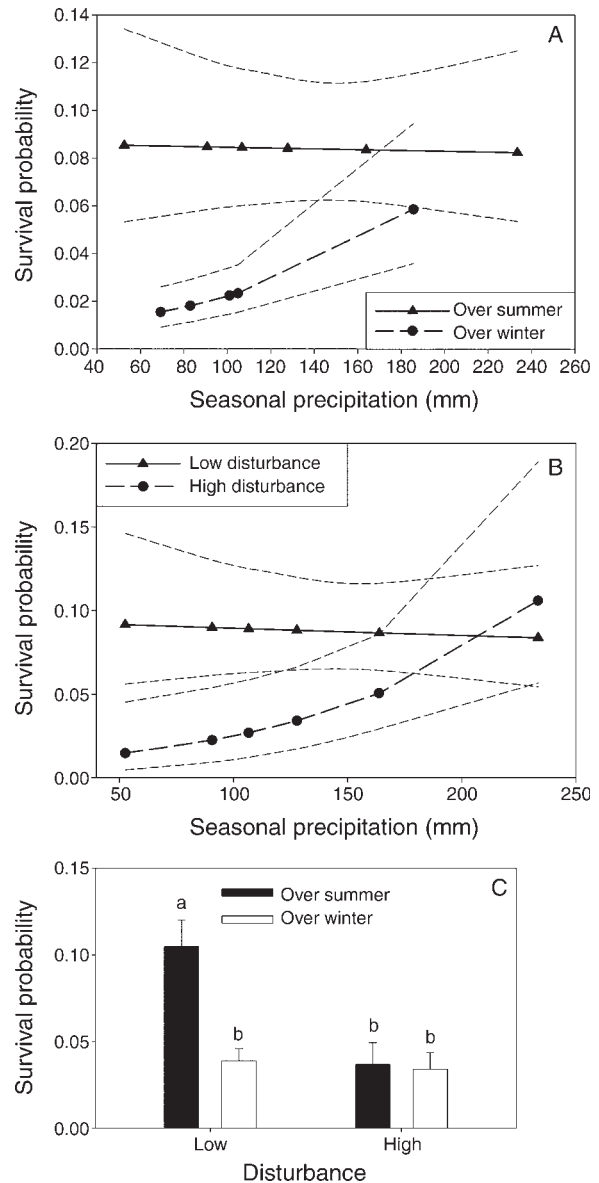

FIG. 2. Predicted survival probabilities according to the most parsimonious model, showing the effect of (A) the interaction between precipitation and season, (B) the interaction between precipitation and disturbance, and (C) the interaction between disturbance and seasonality. For interactions with a continuous variable, solid and long-dashed lines represent predicted values (over summer vs. over winter in panel A; low vs. high disturbance in panel B), and short-dashed lines are the 95% CI. For interactions between categorical variables (panel C), bars represent the least-square mean estimates + SE; lowercase letters indicate significant differences ($P < 0.05$) based on alpha level adjusted for multiple comparisons (see Methods: Data analysis). Model predictions for the effect of interactions with a continuous variable were obtained by controlling for the other factors in the model (e.g., season was modeled as spring, disturbance as low, sex as female, density was kept constant at its mean value of 17.3 individuals/ha, and the random variation due to site identification was removed).

TABLE 2. Coefficient estimates and significance of the parameters in the most parsimonious model for the probability of deer mice being reproductively active.

Parameter	Estimate	SE	df	t	P
Females					
Intercept	1.26	0.18	15	6.93	<0.01
Body mass	0.39	0.03	1285	13.24	<0.01
Infection status (infected)	0.54	0.28	1285	1.97	0.05
Precipitation	0.003	0.003	1285	0.86	0.39
Season (fall)	−1.13	0.18	1285	−6.13	<0.01
Disturbance (high)	−0.64	0.33	1285	−1.94	0.05
Density	−0.01	0.003	1285	−4.10	<0.01
Precipitation × season (fall)	0.02	0.004	1285	4.69	<0.01
Precipitation × disturbance (high)	0.01	0.005	1285	2.85	<0.01
Density × disturbance (high)	−0.02	0.01	1285	−2.13	0.03
Males					
Intercept	−0.15	0.19	15	−0.78	0.45
Body mass	0.24	0.02	1661	10.52	<0.01
Infection status (infected)	0.33	0.15	1661	2.15	0.03
Precipitation	0.005	0.002	1661	2.64	<0.01
Season (fall)	−1.03	0.16	1661	−6.56	<0.01
Disturbance (high)	−0.82	0.30	1661	−2.72	<0.01
Density	−0.02	0.003	1661	−7.25	<0.01
Precipitation × season (fall)	0.01	0.003	1661	5.35	<0.01
Disturbance × season (high and fall)	0.96	0.27	1661	3.58	<0.01

Notes: Estimates for categorical variables correspond to the category specified in parenthesis with respect to a reference category (i.e., low for disturbance, spring for season, and uninfected for infection status). Site identification was used as a grouping (random) factor (estimated variance components ± SE = 0.08 ± 0.1 for females and 0.18 ± 0.09 for males).

could be in poor physical condition and less likely to survive the winter than deer mice in a wet year. This potential difference in physical condition may also explain our finding that during the wet year, there were no seasonal differences in reproductive probabilities, whereas in drier years, reproductive probabilities in the fall were reduced to one-third of those in the spring. Reduced reproductive activity in the fall of years with low primary productivity could result from fewer young of the year reaching sexual maturity in the current breeding season (Taitt 1981, McAdam and Millar 1999; but see Gilbert and Krebs 1991) or from adults not being able to obtain the necessary energy or water to maintain reproduction (Nelson and Desjardins 1987, Nelson et al. 1992).

The combined effects of precipitation on survival and reproduction appear to drive the population fluctuations of deer mice at our study sites. We observed 10-fold differences in density between low and peak population sizes and these fluctuations appeared to follow changes in precipitation with a time lag (Fig. 1). Precipitation has been cited as an important driver of deer mouse population fluctuations in other ecosystems (Drost and Fellers 1991, Gillespie et al. 2008). Furthermore, Reed et al. (2007) found lower growth rates of grassland populations of deer mice during dry years, caused primarily by reduced survival of adults. In contrast, Kalcounis-Rueppell et al. (2002) found negative effects of precipitation on the survival of nestling and adult deer mice. These seemingly contradictory effects of precipitation on deer mice may result from the relative importance of direct (e.g., mortality resulting from

floods) vs. indirect effects (e.g., increases in primary productivity) in a particular season or population (Brown and Ernest 2002). In our system, increased precipitation resulted in high overwinter survival and prolonged reproductive activity, probably due to abundant snow cover during the winter and high primary productivity during the breeding season. We believe this to be the mechanism behind the population increase observed from fall 2005 to spring 2006. The abrupt decline in population size from fall 2006 to spring 2007 may be explained, in part, by a decrease in fall reproductive activity and overwinter survival (Fig. 1D–F), possibly caused by the unusually cold and dry winter of 2006–2007. During that winter season, minimum temperatures dropped below −20°C in November 2006 for the first time during the study period. January 2007 was characterized by minimum temperatures below −20°C for four consecutive days with no precipitation. Increased overwinter mortality is likely to have occurred under such harsh weather conditions. In addition, deer mouse densities were extremely high in fall of 2006 and density dependence may have contributed to the steep decline that followed. We found negative effects of deer mouse density on both survival and reproduction, suggesting that strong intraspecific competition during 2006 could have accentuated the negative effects of the cold and dry winter.

Precipitation also modulated the impacts of ORV disturbance on deer mouse survival and reproduction. In periods with low precipitation, deer mice on highly disturbed sites had extremely low survival probabilities and low reproductive probabilities of females compared
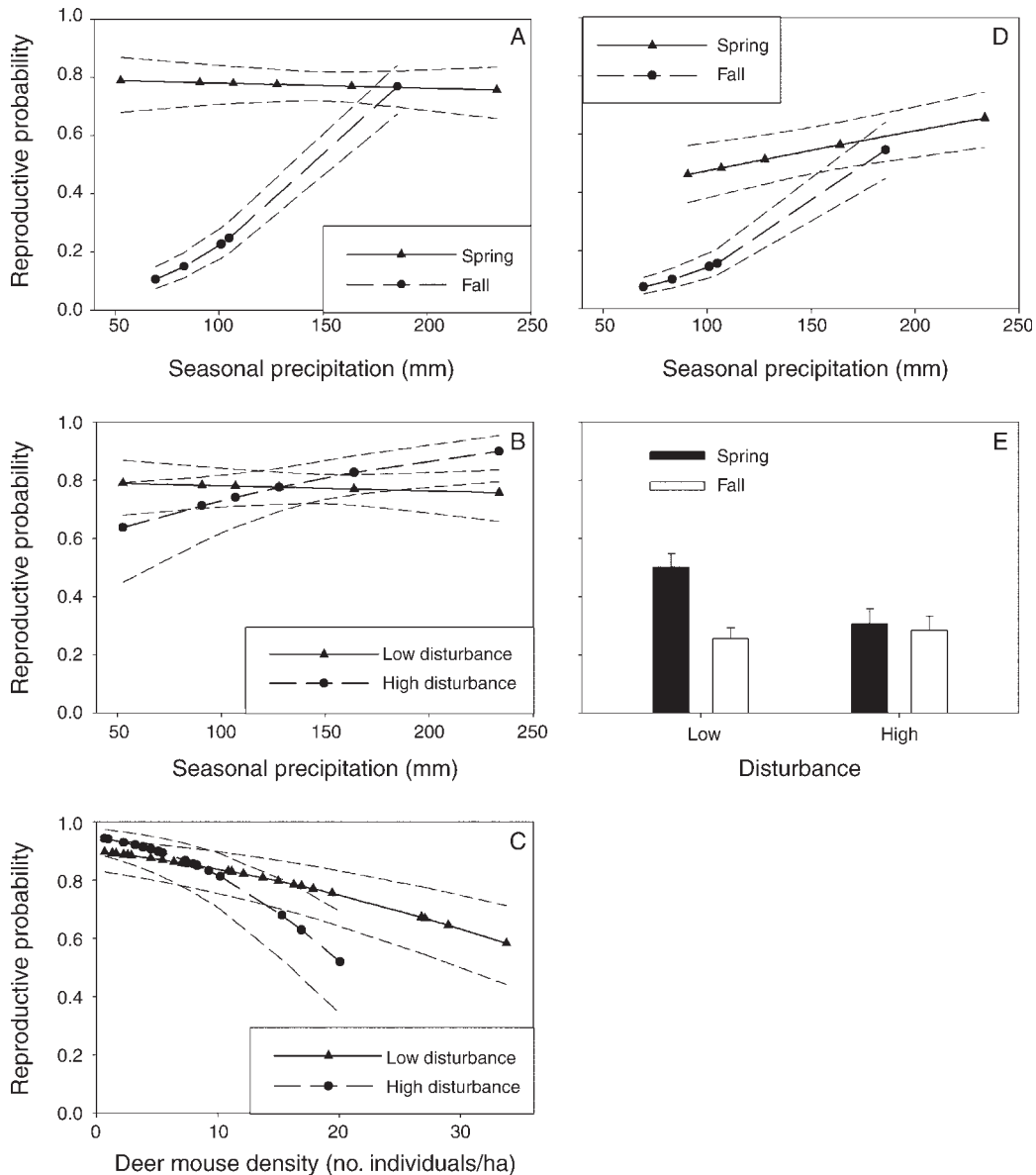
FIG. 3. Predicted reproductive probabilities according to the most parsimonious models for females and males, showing the effect of (A) the interaction between precipitation and season for females, (B) the interaction between precipitation and disturbance for females, (C) the interaction between disturbance and density for females, (D) the interaction between precipitation and season for males, and (E) the interaction between disturbance and seasonality for males (mean + SE; lowercase letters indicate significant differences based on alpha level adjusted for multiple comparisons). For interactions with a continuous variable (A–D), solid lines and long-dashed lines represent predicted values, and short-dashed lines are the 95% CI. For interactions between categorical variables, bars represent the least-square mean estimates + SE. Model predictions for the effect of interactions with a continuous variable were obtained by controlling for the other factors in the model (e.g., season was modeled as spring, disturbance as low, infection status as uninfected, density and precipitation were kept constant at their mean value of 17.3 individuals/ha and 132.2 mm, respectively, and the random variation due to site identification was removed).

to those of individuals from low-disturbance sites. However, high precipitation ameliorated the effect of disturbance on both parameters. The greater amount of shrub cover on low-disturbance sites may serve as a buffer from dry conditions, whereas on high-disturbance sites, the extensive bare ground may result in high evapotranspiration per unit area, especially during dry

climatic conditions. This microclimatic difference may feed back into plant and animal communities, resulting in lower food resources for deer mice and thus reduced survival in high-disturbance sites as precipitation decreases. This also could have resulted in the reduction in over-summer survival at highly disturbed sites. We also found that the impacts of ORV on deer mouse

reproductive probabilities were accentuated by seasonality and density dependence. In highly disturbed sites, we found a reduction of reproductive activity of males in the spring and a stronger negative effect of density on female reproductive probabilities. The potential mechanism for these effects could be due to lower availability and high competition for food and nesting resources in high-disturbance sites that limits reproduction relative to low-disturbance sites. Collectively, these negative effects of disturbance may explain why deer mouse density was lower on these sites than in sites with low levels of ORV disturbance (Lehmer et al. 2008).

SNV infection did not appear to influence survival of deer mice. However, for reproductive probabilities of both sexes, we found that the infection status of the individual had some predictive value. In both cases, the infected individuals were more likely to be reproductively active. We believe this effect to be due to reproductive individuals being more likely to be infected with SNV rather than an increase of reproductive activity driven by the pathogen. However, the lack of an effect of SNV infection on survival is surprising. Given that mounting an immune response is energetically costly (Demas et al. 1997), and that this could carry long-term consequences in chronic infections, we expected to find a negative effect of SNV infection on deer mice. Although a negative effect of hantavirus infection on survival and reproduction has been suggested for deer mice and bank voles (Douglass et al. 2001, Kallio et al. 2007, Adler et al. 2008, Dearing et al. 2009), results from the present study are not consistent with these previous studies. However, the low survival of deer mice between sampling periods in this study (<10%) makes it difficult to find small differences in survival. More frequent sampling would be necessary to detect the subtle changes in survivorship expected from an endemic pathogen (e.g., Burthe et al. 2008). We found a positive association between SNV infection status and the probability of being reproductively active for both males and females. We believe that this is probably due to reproductive individuals being more likely to be infected with SNV, rather than SNV infection accelerating reproductive activity.

Results of these analyses shed light on the processes underlying spatial and temporal patterns of deer mouse density; in broader terms, however, they emphasize the complexity that can be expected when analyzing the dynamics of species harboring infectious diseases, being affected by changing climatic conditions, or being subjected to increasing human alteration of their natural habitats. This study highlights the importance of the inclusion of interaction terms when modeling the determinants of a species' survival and reproduction. Factors that may not appear to have a strong effect when investigated alone can still be influential by modulating the effect of a different factor. Long-term studies that encompass spatial variability are key for

revealing the complexity in the mechanisms behind population fluctuations.

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APPENDIX

Sin Nombre virus prevalence and total deer mice captured at 17 sites that differed in their degree of disturbance caused by off-road vehicles (*Ecological Archives* E091-042-A1).