

DEMOGRAPHIC RESPONSE OF A GRASSLAND RODENT TO ENVIRONMENTAL VARIABILITY

AARON W. REED,* GLENNIS A. KAUFMAN, AND BRETT K. SANDERCOCK

Division of Biology, Kansas State University, Manhattan, KS 66506, USA

Present address of AWR: Natural History Museum and Department of Ecology and Evolutionary Biology, Dyche Hall, 1345 Jayhawk Boulevard, University of Kansas, Lawrence, KS 66045, USA

We used stage-structured matrix population models, derived from 3 years with disparate levels of precipitation, to assess the potential effects of climate change on annual population growth (λ) of deer mice (*Peromyscus maniculatus*). Populations of deer mice increased during a year of normal precipitation ($\lambda = 1.69 \pm 0.02 SE$) and a wet year ($\lambda = 1.03 \pm 0.02$), but declined in a dry year ($\lambda = 0.34 \pm 0.02$). Life-table response experiment analyses indicated that reduced survival of adults in the dry year, and reduced survival of pups and juveniles in the wet year, exerted the greatest influence on variation in population growth. Stochastic models that projected populations of deer mice for a 50-year period predicted that populations would not be able to persist if mean annual precipitation was reduced $\geq 11\%$ by increasing the frequency of dry years. Furthermore, the stochastic population growth rate declined more quickly when the probability of a normal year was reduced, simulating increased variability in rainfall, relative to other scenarios examined. Our stochastic models indicate that a relatively small reduction in mean precipitation could result in substantial population declines of *P. maniculatus* in the mixed-grass prairie of central North America.

Key words: climate change, deer mouse, life-table response experiment, matrix model, *Peromyscus maniculatus*, prairie, stochastic model

Anthropogenic change to the environment, specifically the addition of CO₂ and other greenhouse gases to the atmosphere, is predicted to have significant consequences for global climates (Smith et al. 2005). Change in global climate patterns, in turn, likely will affect the distribution and abundance of plant and animal populations (McLaughlin et al. 2002; Stenseth et al. 2002). Efforts to assess organismal response to climate change primarily have examined geographic shifts in range distributions, or temporal changes in the timing of life-cycle events (Hughes 2000; Root et al. 2003). In the case of small mammals, most investigators have examined changes in geographic distribution as a response to changes in plant communities (Brown et al. 1997; Cameron and Scheel 2001). Animal populations might incur negative effects of climate change through changes in demographic rates before the signature of climate change is apparent in plant communities (Boyce et al. 2006). Environmental variability can directly influence demographic rates such as reproduction (Bolger et al. 2005), recruitment (Lima et al. 2001), and survival (Barbraud

and Weimerskirch 2001) that can lead to changes in population growth rate and reduce the likelihood of population persistence.

Among the possible consequences of climate change in central North America is a reduction in soil moisture, caused by increased evaporation and decreased precipitation during the growing season (Smith et al. 2005), and by alteration of the temporal distribution of rain events (Easterling et al. 2000). Decreased water availability associated with climate change is predicted to lead to significant, rapid changes in aboveground net primary productivity in the grasslands of central North America (Izaurre et al. 2005; Knapp and Smith 2001). Over temporal scales < 1 year, the abundance of some small mammal species was related positively to productivity in grassland systems (Whitford 1976). The numerical responses of small mammals to long-term reductions in precipitation that may be associated with climate change are unclear. Further, the effect of decreased aboveground net primary productivity on demographic parameters, and therefore rates of population change, is unknown because most previous studies have assessed only total population numbers.

Reduction in abundance or extinction of small mammal species is likely to have substantial impacts on ecosystem processes. In temperate grasslands, rodents are significant seed and egg predators and directly affect grassland plants and birds through their foraging activities (Bradley and Marzluff 2003;

* Correspondent: awreed@ku.edu

Hoffmann et al. 1995). Rodents are a significant prey item in the diets of mammalian and avian predators (Brillhart and Kaufman 1994; Huebschman et al. 2000). Furthermore, rodents can affect nutrient cycling through urine deposition and physical disturbance of soils (Clark et al. 2005; Sirotiak and Huntly 2000). Loss of numerically dominant rodents in prairie ecosystems would have important consequences on population dynamics of other trophic levels, community structure, and ecosystem processes.

In this study, we examined the population dynamics of the deer mouse (*Peromyscus maniculatus*) in the mixed-grass prairie ecosystem. We used stage-classified matrix models derived from 3 years of natural variation in annual precipitation to assess changes in population growth (Sauer and Slade 1987). Based on the known effects of precipitation on aboveground net primary productivity, seed production, and invertebrate biomass, we predicted that population growth rates of *P. maniculatus* would be positively correlated with annual precipitation. Second, we used retrospective analyses based on life-table response experiment methods to assess the relative contribution of demographic rates to differences in annual population growth. Deer mice are short-lived mammals and we predicted that variation in fecundity rates would make the greatest contributions to seasonal and annual differences in population growth (Oli and Dobson 2003). Last, we used stochastic models to assess the effect of changes in total precipitation and variability in precipitation on the population viability of deer mice in mixed-grass prairie ecosystems. We predicted that population growth rates would decline with a simulated decrease in average precipitation, but that the rate of decline would be dependent on the manner in which average precipitation was decreased.

MATERIALS AND METHODS

Demographic data for *P. maniculatus* were collected from 1986 to 1988 in native mixed-grass prairie near Lucas, Kansas, (39°04'N, 98°28'W; Lincoln County). The dominant vegetation at the site consisted of bluestem–grama prairie with a mix of perennial grasses including blue grama (*Bouteloua gracilis*) and big bluestem (*Andropogon gerardii*). Annual precipitation (data from National Atmospheric and Oceanic Administration weather station, Lake Wilson, Kansas) averaged 680 mm (1961–1990; 30-year $SD = 165.7$ mm). A total of 711 mm of precipitation was recorded in 1986 (z -score = 0.19; hereafter “normal”), 834 mm in 1987 ($z = 0.93$; hereafter “wet”), and 493 mm in 1988 ($z = -1.13$; hereafter “dry”).

Small mammals were sampled on a 10.8-ha grid consisting of 480 stations with a single Sherman live trap (H. B. Sherman Traps, Inc., Tallahassee, Florida) at each station (Kaufman 1990). Traps were baited with rolled oats and peanut butter. Alternate lines of the grid were trapped biweekly over 2-day sampling periods from March to October during 1986–1988. Small mammals were identified to species, weighed, and sex was determined by examining external genitalia. Reproductive condition was ascertained through palpation of the abdomen and inspection of external genitalia. Individuals were marked

by toe-clips and ear tags. Artificial burrows were used to collect data on reproduction and winter survival (Kaufman 1990; Kaufman and Kaufman 1989). Burrows were constructed of polyvinyl chloride pipe (25 cm height and 20.3 cm diameter) with a single 2.5-cm-diameter pipe leading to the soil surface from the nest chamber. Within the boundaries of the grid, 100 burrows were placed in a stratified random manner. Burrows were checked every 7–10 days throughout the year from July 1986 to January 1989. Adults and pups were captured by hand within burrows. Pups were weighed, their sex was determined, and they were marked by toe-clips (if possible) or by injecting a small amount of India ink in appendages to identify individuals until toe-clipping and ear-tagging were possible. Field methods followed guidelines recommended by the American Society of Mammalogists at the time of the field study (Ad Hoc Committee for Acceptable Field Methods in Mammalogy 1987).

We synthesized demographic data for *P. maniculatus* with a female-only, stage-classified matrix model based on a post-breeding census (Sauer and Slade 1987). We did not detect regression of any individuals into a smaller size class during the study and did not include transitions for regression in our population model. The population of *P. maniculatus* was divided into 4 stages by body mass, as follows: pups: ≤ 5 g, juveniles: 5 g to < 10 g, small adults: 10 g to < 15 g, and large adults: ≥ 15 g. Each individual was assigned to a stage at 1st capture in each time period. Because of sparse sample sizes and within-year variability, we grouped demographic data by 2-month intervals (hereafter, “periods”). The field data were then used to parameterize the following projection matrix:

$$\begin{pmatrix} 0 & 0 & F_3 & F_4 \\ G_{12} & S_{22} & 0 & 0 \\ 0 & G_{23} & S_{33} & 0 \\ 0 & 0 & G_{34} & S_{44} \end{pmatrix}, \quad (1)$$

where F is fecundity, G is the transition between stage classes, S is survival without transition into the next stage class, and subscripts indicate stage class at time t and time $t + 1$.

We used data from both livetrapping and burrow monitoring to estimate demographic parameters for each 2-month period. Only 2 of 390 animals (on 1 occasion each) were not captured in consecutive periods. Therefore, we used simple proportions, and not mark–recapture statistics, to calculate survival and growth probabilities. Variance of the binomial distribution was used to estimate variability of probability estimates ($\text{Var}(p) = p(1 - p)/n$). Survival probabilities (σ) were calculated as the proportion of individuals surviving from time t to $t + 1$. Growth into a new stage (γ) and pregnancy probabilities (ψ) were calculated conditional upon survival. Birth rates (β) were calculated as the average number of female offspring per pregnant female per period. Immigration (ι) was included as a per capita rate for each size class, except pups, during each period (Sandercock and Beissinger 2002). An individual was considered an immigrant if it was unmarked at the beginning of a period. Because artificial burrows were not established until July 1986, survival and fecundity of pups for the first 2 periods of 1986 were calculated in a different manner. Survival

of pups was calculated as the number of new juveniles captured during time $t + 1$ divided by the expected number of pups born during time t . The expected number of pups (fecundity) was calculated using mean litter size from the rest of the year multiplied by the proportion of pregnant females.

The 5 demographic rates (σ , γ , ψ , β , and ι) then were used to parameterize the matrix model (Table 1). All analyses of projection matrices were performed using MATLAB (version 7; MathWorks Inc., Natick, Massachusetts). We estimated period-specific population growth rates by calculating the dominant eigenvalue of each 2-month matrix. To compare demographic parameters among years, we used life-table response experiment analysis. The life-table response experiment is a retrospective examination of how demographic parameters differed between treatments (i.e., years), as well as the contributions of those differences to the population growth rate. We used a fixed-effect analysis to assess the changes in parameters between the wet and dry years compared to the normal year as a baseline reference year:

$$\Delta\lambda = (a_{ij}^N - a_{ij}^W) \times S_{ij|A^+}, \tag{2}$$

where a_{ij}^N is the transition value in the normal year, a_{ij}^W is the corresponding transition in either the wet or dry year, and S_{ij} is the sensitivity of this transition calculated from the mean matrix A^+ (Caswell 2000). We did not conduct life-table response experiment analyses for the January period because sampling did not begin until March 1986.

We multiplied matrices from six 2-month periods in sequential order to calculate a single projection matrix for each year (Caswell 2001). We then calculated the dominant eigenvalue for these matrices as our estimate of annual population growth rate and used bootstrap resampling (200 iterations) to calculate 95% confidence intervals (95% CIs).

Annual matrices were used to assess population response to changes in precipitation. Transitions were not temporally autocorrelated so we used each matrix as an independent observation. Although we used 3 years of demographic data, our study years represent the range of variation in annual precipitation present in the mixed-grass prairie and are a reasonable representation of the response of *P. maniculatus* to variability in precipitation. We projected populations of deer mice for 50 years by randomly drawing an independent, identically distributed series of annual matrices. We used initial probabilities (0.18 for wet year, 0.69 for normal, and 0.13 for dry) that corresponded to the observed frequency of these levels of precipitation based on the 30-year mean for the site. We then projected the population by postmultiplying a population vector and the random series of projection matrices. We then calculated a maximum-likelihood estimate of the stochastic growth rate ($\log \lambda$ —Caswell 2001). Projections were repeated for 10,000 replicates to obtain the geometric mean stochastic growth rate and the 95% CIs.

We modeled 3 possible scenarios of regional climate change. First, we modeled “gradual drying” by reducing the probability of both wet and normal years by 0.01 each and increasing the probability of a dry year by 0.02. Second, we modeled “rapid drying” by reducing the probability of a wet year by 0.02 with

TABLE 1.—Formulae used to calculate transition probabilities and fecundities for matrices, where σ is survival within a stage, ι is the per capita immigration rate, γ is probability of growing into the next stage, β is the number of female offspring per pregnant female, and ψ is the conditional probability of a female being pregnant. Subscripts indicate transitions between stages where p = pup, j = juvenile, sa = small adult, and la = large adult.

Parameter	Formula
F_3	$\sigma_{sa}\beta_{sa}\psi_{sa}$
F_4	$\sigma_{la}\beta_{la}\psi_{la}$
G_{12}	σ_p
S_{22}	$(1 + \iota_j)\sigma_j(1 - \gamma_j)$
G_{23}	$(1 + \iota_j)\sigma_j\gamma_j$
S_{33}	$(1 + \iota_{sa})\sigma_{sa}(1 - \gamma_{sa})$
G_{34}	$(1 + \iota_{sa})\sigma_{sa}\gamma_{sa}$
S_{44}	$(1 + \iota_{la})\sigma_{la}$

a concomitant increase in the probability of a dry year. After the probability of a wet year was decreased to 0.0, we decreased the probability of a normal year by 0.02. Last, we modeled “increased variability” by reducing the probability of a normal year and increasing that of a dry year by 0.02 with the likelihood of a wet year fixed at 0.18. Each scenario decreased the nominal mean precipitation by approximately 0.3% per replicate. For each scenario, we continued to reduce mean precipitation until the 95% CI of the stochastic growth rate no longer included 0 (equivalent to $\lambda = 1$) for 2 successive simulations.

RESULTS

During 1986–1988, 390 female deer mice were captured and marked on the study area. Overall, the patterns of population growth were similar in each year (Fig. 1), with seasonal peaks in λ occurring in March–April and in September–October. However, period-specific λ differed among years, exceeding $\lambda = 1$ in 4 of 5 periods of the normal year, but only 2 of 6 periods in the wet year, and 0 of the 6 periods in the dry year. The pattern of population growth in the wet year was similar to that of the dry year, except during the September–October period when the population grew rapidly ($\lambda = 1.6$). Confidence intervals for the annual population growth rates, calculated from the composite matrices for the normal ($\lambda = 1.69$; 95% CI = 1.65–1.73), wet (1.03; 0.99–1.07), and dry years (0.34; 0.30–0.38) did not overlap.

Contribution values of the life-table response experiment analysis were positive in most 2-month periods, indicating better demographic performance by deer mice in the year of normal precipitation than other years (Fig. 2). The largest positive contribution values ($c > 0.1$) were recorded for the growth of small adults (G_{34}) and survival of large adults (S_{44}), especially during the first 3 periods. Growth of pups (G_{12}) and survival of juveniles (S_{22}) also had positive values, but mainly during March and July and in comparison to the wet year. The largest negative contribution values were observed for growth of juveniles (G_{23}) and survival of small adults (S_{33}), but only during March. Contribution values were negative for fecundity

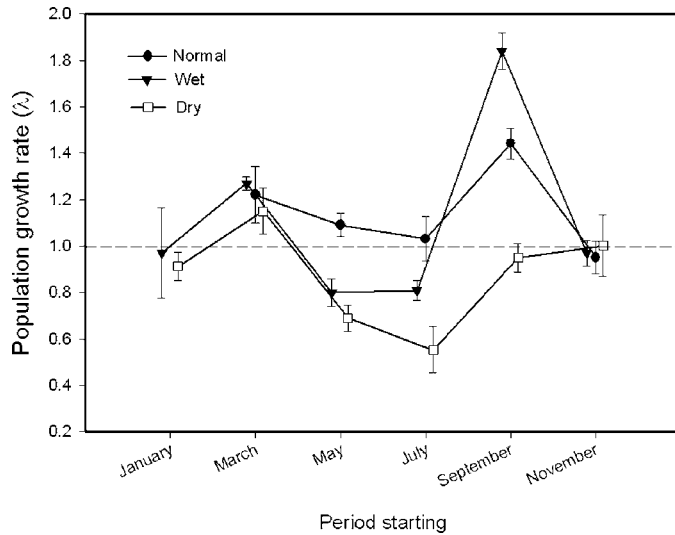


FIG. 1.—Period-specific population growth rates ($\lambda \pm SE$) for a population of the deer mouse (*Peromyscus maniculatus*) near Lucas, Kansas, in normal, wet, and dry years. The dashed line represents $\lambda = 1$. Each period represents data collected during 2 months (e.g., March period consists of data collected in March and April).

(F_3, F_4) and a few other demographic rates during September and November of the wet year, presumably as the result of late-season breeding by deer mice.

The stochastic models predicted a marked decrease in population growth rate as the frequency of dry years increased (Fig. 3). For all scenarios, the stochastic growth rate decreased below 0 if the frequency of a dry year was >0.45 , indicating that the population would not persist for a 50-year period. However, the pattern of decline differed among the 3 scenarios. In the rapid-drying scenario, the stochastic growth rate declined at a relatively slow rate until the probability of a wet year was 0, at which point the stochastic growth rate declined more rapidly as the probability of a normal year was reduced. The stochastic growth rate declined more quickly in the gradual-drying scenario relative to the rapid-drying scenario. The stochastic growth rate declined most rapidly in the increased-variability scenario and the population was predicted to be unable to persist when the frequency of dry years exceeded 0.33, which corresponds to an 11% decrease in mean annual precipitation.

DISCUSSION

Climatic variability had strong effects on both seasonal and annual population growth rates of *P. maniculatus*. Population growth rates, both seasonal and annual, were highest in a year of normal precipitation and lowest in a dry year. Annual population growth rate was intermediate in a wet year, as were seasonal rates, with the exception of the September period. A fixed-effect life-table response experiment analysis indicated that growth of individuals and survival, particularly of the large size classes, contributed most to high population growth rates in the normal year relative to both the wet and dry years. Finally, stochastic models revealed that population viability of

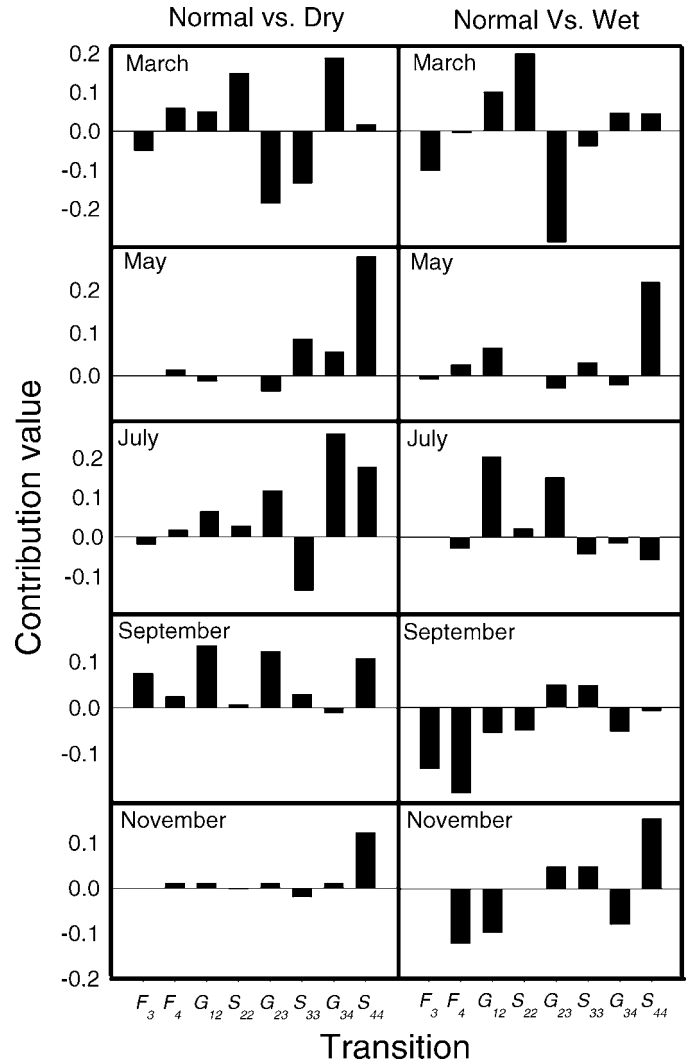


FIG. 2.—Life-table response experiment analyses that compare parameters in normal year and dry year and normal year with wet year during five 2-month sample periods. Sample periods are March–April, May–June, July–August, September–October, and November–December. Labels on x axis represent transitions. Positive values indicate an advantage in the normal year for a given parameter.

P. maniculatus would likely be reduced under the 3 scenarios of increased variability and intensity of precipitation.

We predicted that precipitation would affect populations of *P. maniculatus* indirectly through impacts on primary productivity and changes in resource availability. Primary productivity in temperate grasslands is related directly to rainfall (Sala et al. 1988), and seed production and invertebrate biomass are in turn related directly to primary productivity (Knapp and Seastedt 1986; Siemann 1998). Changes in resource availability were not measured but likely would affect demographic parameters of *P. maniculatus* (e.g., fecundity and survival), resulting in high population growth rates in favorable years and low population growth rates in unfavorable years. The annual model predicted that the population would decline precipitously during the dry year ($\lambda = 0.34$). Contrary to our expectations, the

observed population growth rate was stationary ($\lambda = 1.03$; 95% CI included 1) in the wet year. Increased intensity of precipitation events may have negated the positive effects of increased amount of precipitation on population growth rate of *P. maniculatus*, both indirectly and directly. Direct effects of intense precipitation on *P. maniculatus* included decreased survival and recruitment caused by flooding. Eight extreme rainfall events (>3.75 cm/24 h) flooded some artificial burrows, and presumably natural burrows, during the wet year (1987), resulting in litter abandonment (Kaufman 1990). Reproductive failures combined with low pup and juvenile survival contributed to the low population growth rates in some seasonal periods. Low population growth was not an artifact of our sampling design because immigration onto the site, an indirect measure of broadscale fecundity, also was reduced during this year. Indirectly, the population could have been affected through reduced aboveground net primary productivity in the wet year. Intense rainfall events do not recharge soil moisture (Fay et al. 2002; Knapp et al. 2001), resulting in lower aboveground net primary productivity that would likely affect demographic rates in a manner similar to that of a drought year.

A rich body of theory exists on the relative influence of vital rates on population growth rates in mammals (Gaillard and Yoccoz 2003; Oli and Dobson 2003; Promislow and Harvey 1990; Stearns 1983). Generally, one would expect changes in fecundity to have the greatest effect, and survival of adults the least effect, on population growth rate of short-lived mammals during the reproductive season (Oli and Dobson 2003). Moreover, survival should have the greatest effect on population growth rate during the nonreproductive season (Lima et al. 2003). We expected to observe greater reproduction in periods with high population growth rates relative to those with low population growth rates, particularly in those periods of active reproduction (March–September). In contrast to these predictions, our analyses indicated that survival had the greatest influence on the population growth rate of *P. maniculatus* in all seasons. The difference between our results and theoretical predictions might be due to differences in analytical procedures. Predictions of the relative influence of fecundity and survival tend to be based on prospective analyses (e.g., elasticity—Oli and Dobson 2003), which examine the effect of small changes in demographic parameters on future population growth rates. Our life-table response experiment analyses were retrospective and assessed the observed changes in demographic parameters between time periods and the effect of this change on the population growth rate. Prospective and retrospective analyses address different questions but may have complementary results (Coulson et al. 2005). Further, vital rates that have the greatest impact on future population growth (i.e., high elasticities) may have the least variability (Gaillard and Yoccoz 2003). Retrospective analyses assess the difference in vital rates among treatments, in this case years, and estimate the effect of that difference on the population growth rate by using the sensitivities of each vital rate. Vital rates with low variability likely would be similar among years and, therefore, have little effect on variation in population growth rates among years.

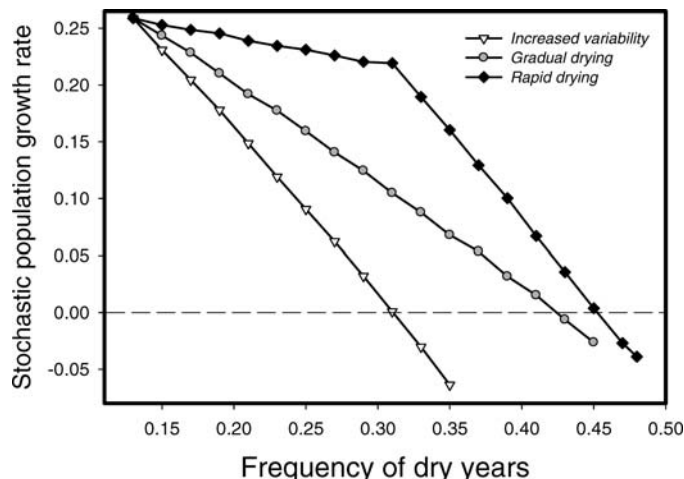


FIG. 3.—Geometric mean of stochastic growth rate ($\log \lambda$) with decreasing precipitation. Error bars were too small to represent on graph. Dashed line indicates the population growth rate necessary for population persistence (equal to $\lambda = 1$).

Our stochastic models indicated that a relatively small decrease in mean precipitation is likely to affect the long-term population viability of *P. maniculatus* in the mixed-grass prairie of central North America. Moreover, the variability in precipitation, and not only total rainfall, will affect the population dynamics of *P. maniculatus*. Tallgrass prairie plants are clearly sensitive to patterns of change in precipitation because aboveground net primary productivity was lower in experimental treatments with increased variability and intensity of rainfall events relative to simply decreased amount of precipitation (Fay et al. 2002; Knapp et al. 2002). Further, changes in the variance of precipitation have been shown to impact some mammal populations without a change in mean precipitation (Saltz et al. 2006). Our research suggests that the pattern of change in precipitation also will affect the demographic response of small mammals in grasslands. When we reduced precipitation by 1st reducing the probability of a year with above-average rainfall, and then the probability of a year with average precipitation (rapid drying), the stochastic population growth rate declined relatively slowly, indicating that the population would persist with a relatively high frequency of drought years. Persistence likely was due to the higher frequency of normal years, the year with the highest rate of population growth, being fixed in the model for the first 10 simulations. However, when we reduced only the probability of a year with average precipitation (increased variability), which simulated an increase in the frequency of extreme weather events, the stochastic growth rate declined quickly past the extinction threshold.

Although our stochastic model indicates that populations of *P. maniculatus* would not persist with decreasing precipitation, a more likely outcome would be either a change in the dispersion of *P. maniculatus* or a subspecific range shift in the Great Plains. The deer mouse is the most abundant and widespread small mammal species in the mixed-grass prairie of central North America and can be found in nearly every habitat

(Kaufman et al. 2000). Our models are based on a single 10.8-ha patch that, although representative of mixed-grass prairie, may not describe the population dynamics of *P. maniculatus* in all habitat patches. One possible outcome of the reduced precipitation associated with climate change could be a more patchy distribution of *P. maniculatus* across the landscape. The taxon might become locally extinct in habitats similar to the study area, but persist in other habitats. A similar pattern has been observed in populations of *P. maniculatus* in Michigan and has been attributed to climatic change (Myers et al. 2005). Our study area also lies near the boundary of 2 subspecies of *P. maniculatus*. *P. m. bairdii* occurs on the study area, whereas *P. m. luteus* occurs <50 km to the west of it in the shortgrass prairie (Hall 1981). With climate change, the border between these subspecies might shift to the east. That is, as abundance of *P. m. bairdii* decreases, it might be replaced by *P. m. luteus*, a subspecies that is better adapted to xeric grasslands.

Our study complements previous investigations of the effects of climate change on vertebrate populations. Several research groups have predicted that the ranges of common small mammals will change with changes in floral communities (Brown et al. 1997; Cameron and Scheel 2001) or due to physiological constraints (Humphries et al. 2002; Root et al. 2003). Our study extends this previous work by showing that changes in demographic rates associated with decreased precipitation might lead to localized extinction independent of any changes in plant communities or physiological constraints. The demographic mechanisms of population response to climate change should receive greater attention in the future.

ACKNOWLEDGMENTS

We were supported by the Division of Biology, Kansas State University, during preparation of this manuscript. We thank N. A. Slade and 2 anonymous reviewers for helpful comments on earlier drafts of this manuscript.

LITERATURE CITED

- AD HOC COMMITTEE FOR ACCEPTABLE FIELD METHODS IN MAMMALOLOGY. 1987. Acceptable field methods in mammalogy: preliminary guidelines approved by the American Society of Mammalogists. *Journal of Mammalogy* 68, supplement:1–18.
- BARBRAUD, C., AND H. WEIMERSKIRCH. 2001. Emperor penguins and climate change. *Nature* 411:183–186.
- BOLGER, D. T., M. A. PATTEN, AND D. C. BOSTOCK. 2005. Avian reproductive failure in response to an extreme climatic event. *Oecologia* 142:398–406.
- BOYCE, M. S., C. V. HARIDAS, C. T. LEE, AND NCEAS STOCHASTIC DEMOGRAPHY WORKING GROUP. 2006. Demography in an increasingly variable world. *Trends in Ecology and Evolution* 21:141–148.
- BRADLEY, J. E., AND J. M. MARZLUFF. 2003. Rodents as nest predators: influences on predatory behavior and consequences to nesting birds. *Auk* 120:1180–1187.
- BRILLHART, D. E., AND D. W. KAUFMAN. 1994. Temporal variation in coyote prey in tallgrass prairie of eastern Kansas. *Prairie Naturalist* 26:93–105.
- BROWN, J. H., T. J. VALONE, AND C. G. CURTIN. 1997. Reorganization of an arid ecosystem in response to recent climate change. *Proceedings of the National Academy of Sciences* 94:9729–9733.
- CAMERON, G. N., AND D. SCHEEL. 2001. Getting warmer: effects of global climate change on distribution of rodents in Texas. *Journal of Mammalogy* 82:652–680.
- CASWELL, H. 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. *Ecology* 81:619–627.
- CASWELL, H. 2001. *Matrix population models: construction, analysis, and interpretation*. 2nd ed. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.
- CLARK, J. E., E. C. HELLGREN, J. L. PARSONS, E. E. JORGENSEN, D. M. ENGLE, AND D. M. LESLIE. 2005. Nitrogen outputs from fecal and urine deposition of small mammals: implications for nitrogen cycling. *Oecologia* 144:447–455.
- COULSON, T., J. M. GAILLARD, AND M. FESTA-BIANCHET. 2005. Decomposing the variation in population growth into contributions from multiple demographic rates. *Journal of Animal Ecology* 74: 789–801.
- EASTERLING, D. R., G. A. MEEHL, C. PARMESAN, S. A. CHANGNON, T. R. KARL, AND L. O. MEARNES. 2000. Climate extremes: observations, modeling, and impacts. *Science* 289:2068–2074.
- FAY, P. A., ET AL. 2002. Altered rainfall patterns, gas exchange, and growth in grasses and forbs. *International Journal of Plant Sciences* 163:549–557.
- GAILLARD, J. M., AND N. G. YOCOZ. 2003. Temporal variation in survival of mammals: a case of environmental canalization? *Ecology* 84:3294–3306.
- HALL, E. R. 1981. *The mammals of North America*. 2nd ed. John Wiley & Sons, Inc., New York. Vol. 2.
- HOFFMANN, L. A., E. F. REDENTE, AND L. C. MCEWEN. 1995. Effects of selective seed predation by rodents on shortgrass establishment. *Ecological Applications* 5:200–208.
- HUEBSCHMAN, J. J., P. W. FREEMAN, H. H. GENOWAYS, AND J. A. GUBANYI. 2000. Observations on small mammals recovered from owl pellets from Nebraska. *Prairie Naturalist* 32:209–217.
- HUGHES, L. 2000. Biological consequences of global warming: is the signal already apparent? *Trends in Ecology & Evolution* 15: 56–61.
- HUMPHRIES, M. M., D. W. THOMAS, AND J. R. SPEAKMAN. 2002. Climate-mediated energetic constraints on the distribution of hibernating mammals. *Nature* 418:313–316.
- IZAURREALDE, R. C., A. M. THOMSON, N. J. ROSENBERG, AND R. A. BROWN. 2005. Climate change impacts for the conterminous USA: an integrated assessment—part 6. Distribution and productivity of unmanaged ecosystems. *Climatic Change* 69:107–126.
- KAUFMAN, D. W., G. A. KAUFMAN, AND B. K. CLARK. 2000. Small mammals in native and anthropogenic habitats in the Lake Wilson area of north-central Kansas. *Southwestern Naturalist* 45: 45–60.
- KAUFMAN, G. A. 1990. Population ecology, social organization, and mating systems in the deer mouse (*Peromyscus maniculatus bairdii*) in mixed-grass prairie in Kansas. Ph.D. dissertation, Kansas State University, Manhattan.
- KAUFMAN, G. A., AND D. W. KAUFMAN. 1989. An artificial burrow for the study of natural populations of small mammals. *Journal of Mammalogy* 70:656–659.
- KNAPP, A. K., J. M. BRIGGS, AND J. K. KOELLIKER. 2001. Frequency and extent of water limitation to primary production in a mesic temperate grassland. *Ecosystems* 4:19–28.
- KNAPP, A. K., ET AL. 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science* 298:2202–2205.

- KNAPP, A. K., AND T. R. SEASTEDT. 1986. Detritus accumulation limits productivity of tallgrass prairie. *BioScience* 36:662–668.
- KNAPP, A. K., AND M. D. SMITH. 2001. Variation among biomes in temporal dynamics of aboveground primary production. *Science* 291:481–484.
- LIMA, M., R. JULLIARD, N. C. STENSETH, AND F. M. JAKSIC. 2001. Demographic dynamics of a neotropical small rodent (*Phyllotis darwini*): feedback structure, predation and climatic factors. *Journal of Animal Ecology* 70:761–775.
- LIMA, M., N. C. STENSETH, H. LEIRS, AND F. M. JAKSIC. 2003. Population dynamics of small mammals in semi-arid regions: a comparative study of demographic variability in two rodent species. *Proceedings of the Royal Society of London, B. Biological Sciences* 270:1997–2007.
- McLAUGHLIN, J. F., J. J. HELLMANN, C. L. BOGGS, AND P. R. EHRLICH. 2002. Climate change hastens population extinctions. *Proceedings of the National Academy of Sciences* 99:6070–6074.
- MYERS, P., B. LUNDRIGAN, AND B. VANDE KOPPLE. 2005. Climate change and the distribution of *Peromyscus* in Michigan: is global warming already having an impact? Pp. 101–125 in *Mammalian diversification: from chromosomes to phylogeography* (a celebration of the career of James L. Patton) (E. A. Lacey and P. Myers, eds.). University of California Press, Berkeley.
- OLI, M. K., AND F. S. DOBSON. 2003. The relative importance of life-history variables to population growth rate in mammals: Cole's prediction revisited. *American Naturalist* 161:422–440.
- PROMISLOW, D. E. L., AND P. H. HARVEY. 1990. Living fast and dying young—a comparative-analysis of life-history variation among mammals. *Journal of Zoology* 220:417–437.
- ROOT, T. L., J. T. PRICE, K. R. HALL, S. H. SCHNEIDER, C. ROSENZWEIG, AND J. A. POUNDS. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421:57–60.
- SALA, O. E., W. J. PARTON, L. A. JOYCE, AND W. K. LAUENROTH. 1988. Primary production of the central grassland region of the United States. *Ecology* 69:40–45.
- SALTZ, D., D. I. RUBENSTEIN, AND G. C. WHITE. 2006. The impact of increased environmental stochasticity due to climate change on the dynamics of asiatic wild ass. *Conservation Biology* 20:1402–1409.
- SANDERCOCK, B. K., AND S. R. BEISSINGER. 2002. Estimating rates of population change for a neotropical parrot with ratio, mark–recapture and matrix methods. *Journal of Applied Statistics* 29:589–607.
- SAUER, J. R., AND N. A. SLADE. 1987. Size based demography of vertebrates. *Annual Review of Ecology and Systematics* 18:71–90.
- SIEMANN, E. 1998. Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology* 79:2057–2070.
- SIROTNAK, J. M., AND N. J. HUNTLY. 2000. Direct and indirect effects of herbivores on nitrogen dynamics: voles in riparian areas. *Ecology* 81:78–87.
- SMITH, S. J., A. M. THOMSON, N. J. ROSENBERG, R. C. IZAURRALDE, R. A. BROWN, AND T. M. L. WIGLEY. 2005. Climate change impacts for the conterminous USA: an integrated assessment—part 1. Scenarios and context. *Climatic Change* 69:7–25.
- STEARNS, S. C. 1983. The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. *Oikos* 41:173–187.
- STENSETH, N. C., A. MYSTERUD, G. OTTERSEN, J. W. HURRELL, K. S. CHAN, AND M. LIMA. 2002. Ecological effects of climate fluctuations. *Science* 297:1292–1296.
- WHITFORD, W. G. 1976. Temporal fluctuations in density and diversity of desert rodent populations. *Journal of Mammalogy* 57:351–369.

Submitted 5 April 2006. Accepted 18 December 2006.

Associate Editor was John A. Yunker.