Timing outweighs amount of rainfall in shaping population dynamics

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Article

Keywords: Climate variability, population dynamics, rainfall patterns, steppe grassland environment

Posted Date: October 14th, 2020

DOI: <https://doi.org/10.21203/rs.3.rs-90221/v1>

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Abstract

Climate variability has been widely documented to have bottom-up effects on the population dynamics of animals^{1,2}, but the mechanisms underlying these effects have been rarely investigated through field manipulative experiments that control for confounding factors³. Here, we examined the effects of different rainfall patterns (i.e. timing and amount) on the population size of Brandt's voles *Lasiopodomys brandtii* in semi-arid steppe grassland in Inner-Mongolia by conducting a 10-year (2010-2019) rainfall manipulation experiment in twelve 0.48 ha field enclosures. We found that moderate rainfall increase during the early rather than late growing season drove marked increases in population size through increasing the biomass of preferred plant species, whereas heavily increased rainfall produced no further increase in vole population growth. The increase in vole population size was more coupled with increased reproduction of overwintered voles and increased body mass of young-of-year than with better survival. Our results provide the first experimental evidence for the bottom-up effects of changing rainfall on the population growth of small mammals, and highlight the importance of rainfall timing on the population dynamics of wildlife in the steppe grassland environment.

Main Text

Changes in rainfall regime are occurring worldwide^{4,5} and have substantial consequences for vertebrate population dynamics, the species composition of communities and ecosystem functions and services^{6,7}. Both timing and amount of rainfall are recognized as major components that contribute synergistically to the population dynamics of wildlife through shaping plant primary productivity^{1,2}. However, it remains unclear whether changes in timing or amount of rainfall play the more dominant role in bottom-up regulation processes, despite their distinct and different effects on aboveground annual net primary productivity⁸. It is important to disentangle the independent effects of rainfall timing and amount to predict responses of species' populations and ecosystems to global climate change scenarios.

Three main factors interact to influence the dynamics of species' populations: bottom-up regulation by rainfall¹, top-down control by predators⁹, and interspecific competition¹⁰. Among rodents, for example, rainfall is well recognized to induce a bottom-up increase in abundance via increasing food availability, as observed in *Phyllotis darwini* and *Octodon degus* in South America^{11,12}, *Pseudomys hermannsburgensis* and *Mus domesticus* in Australia^{13,14}, *Spermophilus dauricus*¹⁵ and *Cricetulus barabensis*¹⁶ in East Asia, *Dipodomys merriami* in North America¹⁷ and *Mastomys natalensis* in Africa¹⁸. However, these observations are all based on the correlation between rodent abundance and precipitation; the mechanism underlying the bottom-up effects of precipitation on rodents through plant productivity is often assumed but has been rarely investigated (but see ref. ¹⁹). In addition, some studies have found neutral¹⁹⁻²¹ or even negative²²⁻²⁴ effects of rainfall on rodent abundance. These contradictory findings may be ascribed to the confounding effects of biotic factors (e.g. predation and interspecific competition) and abiotic factors (e.g. the flooding of burrows) in natural environments². To fully understand the bottom-up effects of rainfall on the population dynamics of target species, including the effects of

rainfall amount and timing, it is therefore necessary to exclude or control for confounding factors. Manipulative experiments provide a means to do this, but are very challenging even for species such as small rodents owing to the need for large-scale enclosures that prevent immigration/emigration of individuals and disturbance by predators.

We conducted a 10-year, large-scale, manipulative experiment to examine the bottom-up effects of changes in rainfall regime (including timing and amount; Fig. S1) on the population dynamics of Brandt's voles *Lasiopodomys brandtii* and the relative contribution of vital rates (i.e., survival, reproduction, and body growth) to population growth. In our study region in Inner Mongolia, an increase in annual rainfall, especially during the early growing season, can markedly enhance annual net primary productivity²⁵, with more rain in particular increasing the biomass of rye grass *Leymus chinensis*^{26,27}, a major and favored food source for Brandt's vole²⁸. Additional rainfall in the early growing season can provide a match between peak food resources and peak food requirements of young voles. Therefore, we hypothesized that rainfall would increase the population density of voles by enhancing the biomass of their preferred food species, and that rainfall increase in the early growing season would be of vital importance in triggering population increases, or outbreaks, of voles in arid steppe grassland.

We captured and marked a total of 18,452 Brandt's voles from 2010 to 2019. The population density of voles fluctuated dramatically between years (ranging from 59 to 667 voles/ha). The rainfall increase treatments showed various effects on the population density of Brandt's voles, depending upon the timing and amount of increased rainfall (Fig. 1a). In Phase 1 (2010-2015), the experimentally increased amount of rainfall was 50 mm and 100 mm (averaging 18% and 36% increase compared to the natural rainfall amount; termed the R50 and R100 treatments respectively; Table S1) and was evenly distributed throughout the growing season (Table S1). We found that allocating 50 mm and 100 mm evenly through the growing season to enclosures had no significant effect on either the biomass of preferred plant species or the population abundance of voles (Fig. 1a, 2a, Table S2). The high evaporation rate in the semi-arid study region could reduce the water-use efficiency of plants and weaken the positive effect of rainfall on food resources for voles, especially when the amount of rainfall increase is relatively low²⁹. This finding is similar to those of Carrier and Krebs (2002) who conducted a 5-yr rainfall manipulation in the Yukon Territory without varying the timing and magnitude of rainfall manipulation and not excluding predators and interspecific competition. They found little effect of rainfall increase on food resources for the boreal red-backed vole *Clethrionomys rutilus*¹⁹. The lack of a significant response of food availability to low rainfall increases may be the reason for the observed neutral effect of rainfall on the population density of *L. brandtii* and other small rodent.

In Phase 2 (2016-2018), we increased the amount of added rainfall to 130 mm and 260 mm (averaging 56% and 112% increase compared to the natural rainfall amount; termed the ER130 and ER260 treatments respectively; Table S1) and this time allocated more rainfall (61.5% of increased rain) to the early growing season (May-June; Fig. S1). As compared to the control group, the ER130 treatment displayed significant increases in both the biomass of preferred plant species (2016: $t = 2.27$, $P = 0.049$;

2017: $t = 3.05$, $P = 0.013$; 2018: $t = 3.07$, $P = 0.013$; Fig. 2a) and population density for all three years (2016: $t = 2.86$, $P = 0.018$; 2017: $t = 2.5$, $P = 0.034$; 2018: $t = 3.3$, $P = 0.01$; Fig. 1a; Table S2), whereas the ER260 treatment exhibited a substantial increase in the biomass of preferred plant species and vole density only in 2017 (both $P < 0.05$).

Previous studies have shown that increased rainfall can induce a sharp increase in the biomass of *L. chinensis* (main summer food for Brandt's voles)^{27,28}. Due to the high content of fructose and oligosaccharides in *L. chinensis*, increasing the intake of *L. chinensis* would alter the composition of the voles' gut microbiota, which could in turn increase the production of short-chain fatty acids, improve body growth and ultimately facilitate increases in population density²⁸. In addition, increased rainfall in the early growing season can promote vegetative sprouting. In the family Gramineae, sprouting produces a plant secondary metabolite (i.e. 6-methoxybenzoxazolinone; 6-MBOA) that can trigger the onset of reproduction in rodents such as the montane vole (*Microtus montanus*)³⁰ and the African multimammate rat (*Mastomys natalensis*)³¹. 6-MBOA has been detected in seedling *L. chinensis*; intraperitoneal injection of 6-MBOA into Brandt's voles also hastens the onset of reproduction by increasing serum levels of luteinizing hormone and testosterone and relative mRNA expression levels of reproduction-related genes (e.g. *StAR* and *CYP11a1*) in the testes of voles maintained under a short photoperiod³². Such regulatory pathways could explain the positive bottom-up effect of increased rainfall on Brandt's vole populations in the early growing season. The maximum population density of voles in the ER130 and ER260 treatment groups averaged 1.7 times and 1.5 times that of the control enclosures; although when the amount of rainfall was doubled, we found no further increase in the population density achieved by the ER260 compared to the ER130 groups. This result may be explained by the nonlinear response of net primary productivity to changes in annual rainfall³³. For example, in Phase 2, we found a significant increase in the biomass of all plant species in the ER130 treatment compared with that in the control, while there was no further increase in total plant biomass in the ER260 treatment compared with that in the ER130 treatment. In the extreme case, very high rainfall could cause flooding and drown voles in their shallow burrows (usually 30 cm below ground), leading to population collapse^{2,34}. The population density was lowest in 2015, a trough that was most likely caused by two successive intense thunderstorms that deposited over 30 mm rainfall in less than 2 hours on 22 June and 24 mm rainfall in less than an hour on 9 July during the breeding season. After the intense thunderstorms, we found many drowned young voles in the enclosures (Fig. S2b), confirming the harmful effect of extreme rainfall events on this vole population^{2,35}. The beneficial effect of rainfall through indirectly increasing food resources may be offset by the harmful influence of rainfall through direct burrow flooding, which may lead to a nonlinear effect of experimental rainfall increase on vole populations. The variation in annual natural rainfall was large at our study site (e.g. 512 mm in 2012, only 169 mm in 2017), and in turn influenced the effect size of our experimental rainfall increase on the vole populations. For example, in Phase 2, adding 260 mm rainfall during the growing season (ER260) significantly increased the vole population in 2017 when the natural rainfall during the growing season was relatively low (130.7 mm), but not in the years 2016 and 2018 that received 215 mm and 230 mm of rainfall during the growing season respectively.

Total rainfall in the early growing season (May and June) for plants has been increasing since 1970 in our study region (Fig. S3). In order to understand better the biological consequence of altered rainfall timing, in Phase 3 we fixed the total amount of added rainfall to 130 mm and allocated most water (61.5%) to the early growing season (ER130 treatment) and to the late growing season (LR130 treatment). This rainfall increase in ER130 treatment and LR130 treatment significantly increased both the biomass of the vole's preferred plant species and vole population density, compared with the control group (Table S2). Furthermore, the biomass of preferred plant species and population density of voles in the ER130 treatment were significantly higher than those in the LR130 treatment (both $P < 0.05$; Fig. 1a&2a). These results further confirm that rainfall increase in the early, not late, growing season can drive marked increases in the population density of voles. In the ER130 treatment, the enclosure received 120 mm of rainfall in total, including 40 mm of natural rainfall and 80 mm of artificial rainfall, during May and June 2019, and the mean population density of Brandt's vole went as high as 296 individuals per hectare, which is very close to the population density in years of population outbreaks (about 300-400 voles/ha). By reviewing meteorological records and literature, we found that there were 7 years when the amount of rainfall in May and June exceeded 120mm after 1970. Five of the 7 years with wet seasons in May and June were reported to have population outbreaks of Brandt's vole (> 300 individuals per hectare, Fig. S3), which is consistent with our manipulative results.

The response of reproduction and body growth of voles to increased rainfall depended on the rainfall treatment schedule (Fig. 1b, c). In Phase 1, there was no difference in either the total number of recruits or body mass of young-of-year (YOY) between the control, R50 and R100 treatment groups. In Phase 2, the total number of recruits in 2016, 2017 and 2018 increased significantly, by 71.8%, 87% and 167%, respectively, in the ER130 treatment compared with the control group (2016: $t = 3.68$, $P = 0.005$; 2017: $t = 4.3$, $P = 0.002$; 2018: $t = 3.5$, $P = 0.006$), while numbers in the ER260 treatment increased significantly only in 2017 ($t = 3.79$, $P = 0.004$). Voles also showed greater body mass in the ER130 group compared with the control group in October over all three years (2016: $t = 3.26$, $P = 0.01$; 2017: $t = 3.63$, $P = 0.006$; 2018: $t = 3.3$, $P = 0.009$), while those in the ER260 treatment showed increased body mass only in 2018 (2018: $t = 2.81$, $P = 0.02$). In Phase 3, the total number of vole recruited and their mean body mass were significantly greater in both the ER130 and LR130 groups compared with the control group (Fig. 1b, c, all $P < 0.05$). There was no difference in the total number of voles recruited or body mass between the ER130 and LR130 treatment groups (both $P > 0.05$).

Rainfall increase had cohort-specific effects on vole survival. For the overwintered cohort (i.e. founder population), survival increased after increased rainfall in 2010 (Phase 1), 2016 (Phase 2), and 2019 (Phase 3; Table S3; Fig. 3). However, there was no significant effect of rainfall increase on yearling survival (Fig. S4; Table S3). For the overwintered voles, initial body mass at the start of experiment was positively correlated with survival time across the breeding season, especially in 2010, 2013, 2016 and 2018 (Fig. 4). Overwintered females survived significantly longer than overwintered males in 2012, 2013, 2016-2018 (Fig. 4), whereas male yearlings had significantly higher survival than female yearlings in 2010 and 2019.

Population dynamics arise as a consequence of variations in population growth rates, which are determined by underlying demographic rates (survival, growth, reproduction). The relative contributions of different demographic rates to change in population growth rate vary among populations³⁶. Due to limited food resources in the natural environment, individuals must allocate resources in a balanced way to growth, reproduction and survival if fitness is to be maximized³⁷. At the population level, the trade-offs between survival versus growth and reproduction shape population fluctuations and species coexistence, but are constrained also by physiological limitations and ecological modes-of-life³⁷. According to the pace-of-life syndrome (POLS) hypothesis, individuals with a fast pace (fast growth rate, early reproduction and short lifespans) can be expected to allocate more investment in reproduction than in survival, while the opposite pertains for the slow-pace-of-life individuals³⁸. Small rodents are typically fast lifestyle species with relatively short lifespans, and may adopt a high-fertility/low-survival strategy to maximize fitness, especially in environments where resources arrive in short pulses. In our study, Brandt's vole responded consistently to the rainfall-induced increase in plant food resource, with populations rising due to increased fertility and individual growth rate and less to changes in survival rate, in accord with the POLS hypothesis.

In summary, we provide the first experimental evidence that rainfall can induce bottom-up effects on plant biomass that drive the population dynamics of small mammals, and in particular that the timing of rainfall is more important than the amount of rainfall in shaping these dynamics. Wet years, when > 120 mm rainfall during the growing season of May and June, can be used to predict population outbreaks of Brandt's voles in our study region. Globally, climate change is causing large variations in rainfall patterns. Understanding the response of animal populations to these changes is becoming more urgent for biodiversity conservation, wildlife management and pest or zoonotic disease control. Although our study was restricted to Brandt's vole in a steppe grassland ecosystem, changes in the rainfall pattern clearly drove large changes in the population dynamics of this rodent. Further experimental studies are now required on other species to reveal how the amount and timing of rainfall determine demographic processes, population fluctuations and changes in species distributions more generally.

Methods

Study area and experimental enclosures

This study was conducted at the Research Station of Animal Ecology (44°11'N,

116°27'E) in Inner Mongolia, China. This region is a steppe grassland that experiences a continental arid temperate climate, with a mean annual temperature of 3.4 °C, and mean annual precipitation of 259.2 mm (1980–2009 climate data from China Meteorological Administration). The small mammal community in this region consists mainly of Brandt's vole (*Lasiopodomys brandtii*), Daurian ground squirrels (*Spermophilus dauricus*), striped hamsters (*Cricetulus barabensis*), Mongolian gerbil (*Meriones unguiculatus*) and house mouse (*Mus musculus*).

In 2008, we constructed a set of 24 large outdoor enclosures (60 × 80 m each), each surrounded by a galvanized sheet metal wall extending 1 m underground and 1.4 m above ground. Wire mesh netting (mesh size: 1 cm) extending 50 cm above the sheet metal wall was welded onto the metal wall, and nylon netting (mesh size: 10 cm) was placed on the top of the enclosure (for details, see ref. ³⁹). The design of the enclosure was intended to prevent voles from emigrating or immigrating, as well as to exclude all mammalian and avian predators. To manipulate rainfall, a spraying irrigation system was built in each rainfall increase enclosure (see below) using steel pipe, and consisting of 30 two-meter-high rotating sprinklers arranged in a 5 × 6 array (Fig. S2a). Each sprinkler was pressure-regulated, allowing even application over each enclosure at a rate of approximately 5 mm h⁻¹. Water was delivered from a well into a storage tank (6 m × 3 m × 1.5 m) before transfer to the irrigation system with a pump.

Rainfall manipulation

Twelve enclosures were used for these manipulations, and were randomly assigned to control and two levels of rainfall increase treatment, with four replicates per treatment. There were three distinct phases for the rainfall manipulation experiment (Fig. S5). Phase 1 was conducted from 2010 to 2015 and was designed to test the effect of low and moderate amount rainfall increases (averaging 18% and 36% increases as compared to the natural rainfall amount; Table S1) on vole populations. In China, the 400 mm isohyet for the mean annual rainfall is considered as the boundary between semi-humid (> 400 mm) and semi-arid regions (200~400 mm), and also corresponds to the boundary between grassland and forest or farmland. Given that the mean annual rainfall in our study site was 259.2 from 1980 to 2009, the enclosures receiving the two levels of rainfall increase were set to receive in total 50 mm or 100mm of water (termed the R50 and R100 treatment groups, respectively) during the growing season (May-September), thus ensuring that the total amount of rain in our experiment was still less than 400 mm. By contrast, the control enclosures received only natural rain. The increased rainfall was evenly distributed bi-weekly throughout the growing season (Fig. S1) for a period of one or two hours each for the R50 and R100 treatment groups, respectively. Because we did not find significant differences in population abundance between the control and rainfall increase groups during Phase 1, we decided to increase the rainfall amount as well as to shift more rainfall to May and June (i.e. the early breeding season of voles) in the next phase. Phase 2 ran from 2016 to 2018 and aimed to examine the combined roles of timing shift and more rainfall (increases averaging 56% and 112% compared to the natural rainfall amount; Table S1) on vole populations. From 1980 to 2015, extreme rainfall events occurred frequently at our study site and the maximum annual rainfall was 511.7 mm in 2012. According to the maximum value of rainfall in our region, we increased the amount of added rainfall to 130 mm and 260 mm (termed the ER130 and ER260 treatment group; Fig. S1) and allocated more rainfall (61.5% of the total added rain) to the early growing season (May-June). In Phase 2, we found that rainfall increases of both 130 mm and 260 mm in May-June increased vole abundance but there was no difference between the 130 mm and 260 mm treatments, suggesting that excessive rainfall increase had no extra positive effect on vole density. Thus, we decided to further test the effects of rainfall timing on population density of voles by fixing the total amount of added rainfall to 130 mm in the next experiment. Phase 3 was designed to last

two years (2019-2020), but was disrupted in 2020 due to the coronavirus outbreak at the end of 2019 in China. In 2019, there were two rainfall increase treatments, with most water (61.5%) applied to enclosures in early growing season (termed the ER130 treatment group) or in late growing season (termed the LR130 treatment group; Fig. S1).

Animal trapping and vegetation survey

In April each year from 2010-2019, we conducted live-trapping for 7 consecutive days to remove all overwintered individuals in the enclosures, and then introduced fifteen (2010-2011) or thirteen (2013, 2015-2019) pairs of voles from the field into each enclosure to create a new founder population. The size of the founding population was the same in all enclosures, which helped to exclude the confounding factor of initial population size. Voles were given 10-15 days to acclimatize to their enclosure before the manipulative experiments started. In 2014, the overwintered individuals were not removed and continued to be observed for another year to test the carry-over effect of rainfall increase on vole populations. Capture-Mark-Recapture (CMR) was used to investigate the demography of vole populations biweekly (2010-2013) or monthly (2014-2019) from May to October. Each newly trapped vole was marked with a numbered aluminum ear tag (2010-2017) or implanted subcutaneously with a passive integrated transponder (PIT) tag (2018-2019). Information on sex, body mass, reproductive status, and family location was recorded before individuals were released at their capture sites. A vegetation survey was also conducted each month following the census of the vole population. We randomly selected five quadrats (1 × 1 m) in each enclosure, and measured the density (number of plants in each quadrat) and dry biomass of each plant species. For a more detailed description of the experimental procedure, see refs^{40 28 41}. Based on the relative preference index for each plant species consumed by Brandt's vole⁴¹, all plant species within enclosures were a priori categorized into two groups: preferred plant species (i.e. *Leymus chinensis*, *Setaria viridis*, *Agropyron cristatum* and *Medicago sativa*) and less preferred plant species (i.e. *Stipa krylovii*, *Lepidium apetalum*, *Corispermum declinatum*, *Carex tristachya*, *Cleistogenes squarrosa*, *Neopallasia pectinate*, and *Phlomis dentosa*).

Data analysis

The population density in each enclosure was estimated using the CMR data with Program CAPTURE⁴², and expressed as numbers per 0.48 ha (i.e. the size of the enclosures). Recruits were defined as individuals that were born in the current year. Because it was difficult to identify the exact birth date for each individual, we pooled yearlings together each year in our analysis. The total number of recruits and yearling body mass in October were compared between different rainfall treatments using analysis of variance. Differences in population density and biomass of food resources for voles between different rainfall treatments were analyzed with linear mixed models, with enclosure specified as random effect. All individuals in the enclosures were classified into two cohorts, overwintered and YOY, for analysis of survival. For overwintered voles (i.e. the population founders), survival analysis was performed using the Cox proportional hazards model to assess the effects of rainfall manipulation, sex and overwinter body

mass. For YOY, logistic regression was used to test the effects of rainfall manipulation and sex on the survival rate of YOY. All statistical analyses were performed using R⁴³, version 3.5.1.

Declarations

Author contributions

ZZ, XW, GL designed and lead the long-term study; XW, GL, BY, WW, XH, XZ, JZ, EB, XX, SH, YS, and JL collected data; ZZ and GL conceived the ideas for the paper and its structure; GL conducted the analyses; ZZ and GL wrote the manuscript; GW, AO, CK and CD modified the draft and commented on the manuscript.

Acknowledgments

We are indebted to the more than 100 people (including undergraduate students, graduate students and volunteers) who have participated in animal trapping and data collection over the last 10 years. This work was mainly funded by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB11050300), the State Basic Research Program of the Ministry of Science and Technology (2007CB109100), and the National Natural Science Foundation of China (31700344).

Competing interests

The authors have no competing interests to declare.

References

- 1 Ernest, S. K. M., Brown, J. H. & Parmenter, R. R. Rodents, plants, and precipitation: Spatial and temporal dynamics of consumers and resources. *Oikos* **88**, 470-482 (2000).
- 2 Brown, J. H. & Ernest, S. K. M. Rain and rodents: Complex dynamics of desert consumers. *Bioscience* **52**, 979-987 (2002).
- 3 Krebs, C. J. & Berteaux, D. Problems and pitfalls in relating climate variability to population dynamics. *Clim Res* **32**, 143-149 (2006).
- 4 IPCC. Climate change 2013: The physical science basis. Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change. *Cambridge, UK: Cambridge University Press* (2013).
- 5 Feng, X., Porporato, A. & Rodriguez-Iturbe, I. Changes in rainfall seasonality in the tropics. *Nat Clim Change* **3**, 811-815 (2013).
- 6 Paschalis, A. *et al.* Rainfall manipulation experiments as simulated by terrestrial biosphere models: Where do we stand? *Global Change Biol*, <https://doi.org/10.1111/gcb.15024> (2020).

- 7 McCarty, J. P. Ecological consequences of recent climate change. *Conserv Biol* **15**, 320-331 (2001).
- 8 Robertson, T. R., Bell, C. W., Zak, J. C. & Tissue, D. T. Precipitation timing and magnitude differentially affect aboveground annual net primary productivity in three perennial species in a Chihuahuan Desert grassland. *New Phytol* **181**, 230-242 (2009).
- 9 Krebs, C. J. *et al.* Impact of food and predation on the snowshoe hare cycle. *Science* **269**, 1112-1115 (1995).
- 10 Pimm, S. L., Rosenzweig, M. L. & Mitchell, W. Competition and food Selection: Field tests of a theory. *Ecology* **66**, 798-807 (1985).
- 11 Previtali, M. A., Lima, M., Meserve, P. L., Kelt, D. A. & Gutierrez, J. R. Population dynamics of two sympatric rodents in a variable environment: Rainfall, resource availability, and predation. *Ecology* **90**, 1996-2006 (2009).
- 12 Jaksic, F. M., Silva, S. I., Meserve, P. L. & Gutierrez, J. R. A long-term study of vertebrate predator responses to an El Nino (ENSO) disturbance in western South America. *Oikos* **78**, 341-354 (1997).
- 13 Dickman, C. R., Greenville, A. C., Beh, C. L., Tamayo, B. & Wardle, G. M. Social organization and movements of desert rodents during population "booms" and "busts" in central Australia. *J Mammal* **91**, 798-810 (2010).
- 14 Brown, P. R. & Singleton, G. R. Rate of increase as a function of rainfall for house mouse *Mus domesticus* populations in a cereal-growing region in southern Australia. *J Appl Ecol* **36**, 484-493 (1999).
- 15 Jiang, G. *et al.* Effects of ENSO-linked climate and vegetation on population dynamics of sympatric rodent species in semiarid grasslands of Inner Mongolia, China. *Canadian Journal of Zoology* **89**, 678-691 (2011).
- 16 Shuai, L. Y., Wang, L. Q., Yang, Y. P. & Zhang, F. S. Effects of density dependence and climatic factors on population dynamics of *Cricetulus barabensis*: a 25-year field study. *J Mammal* **101**, 507-514 (2020).
- 17 Beatley, J. C. Dependence of desert rodents on winter annuals and precipitation. *Ecology* **50**, 721-724 (1969).
- 18 Sluydts, V., Crespin, L., Davis, S., Lima, M. & Leirs, H. Survival and maturation rates of the African rodent, *Mastomys natalensis*: density-dependence and rainfall. *Integr Zool* **2**, 220-232 (2007).
- 19 Carrier, P. & Krebs, C. J. Trophic effects of rainfall on *Clethrionomys rutilus* voles: An experimental test in a xeric boreal forest in the Yukon Territory. *Canadian Journal of Zoology* **80**, 821-829 (2002).

- 20 Ernest, S. K. M. & Brown, J. H. Homeostasis and compensation: The role of species and resources in ecosystem stability. *Ecology* **82**, 2118-2132 (2001).
- 21 Magnusson, W. E., Layme, V. M. G. & Lima, A. P. Complex effects of climate change: Population fluctuations in a tropical rodent are associated with the southern oscillation index and regional fire extent, but not directly with local rainfall. *Global Change Biol* **16**, 2401-2406 (2010).
- 22 Valone, T. J. & Brown, J. H. Effects of competition, colonization, and extinction on rodent species-diversity. *Science* **267**, 880-883 (1995).
- 23 Thibault, K. M. & Brown, J. H. Impact of an extreme climatic event on community assembly. *P Natl Acad Sci USA* **105**, 3410-3415 (2008).
- 24 Tissier, M. L. *et al.* How maize monoculture and increasing winter rainfall have brought the hibernating European hamster to the verge of extinction. *Sci Rep-Uk* **6**, 25531(2016).
- 25 Peng, S. S. *et al.* Precipitation amount, seasonality and frequency regulate carbon cycling of a semi-arid grassland ecosystem in Inner Mongolia, China: A modeling analysis. *Agricultural and Forest Meteorology* **178**, 46-55 (2013).
- 26 Liu, Y. S., Pan, Q. M., Zheng, S. X., Bai, Y. F. & Han, X. G. Intra-seasonal precipitation amount and pattern differentially affect primary production of two dominant species of Inner Mongolia grassland. *Acta Oecologica* **44**, 2-10 (2012).
- 27 Bai, Y. F., Han, X. G., Wu, J. G., Chen, Z. Z. & Li, L. H. Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature* **431**, 181-184 (2004).
- 28 Li, G. L. *et al.* Host-microbiota interaction helps to explain the bottom-up effects of climate change on a small rodent species. *ISME J* **14**, 1795-1808 (2020).
- 29 Guo, Q. *et al.* Spatial variations in aboveground net primary productivity along a climate gradient in Eurasian temperate grassland: effects of mean annual precipitation and its seasonal distribution. *Global Change Biol* **18**, 3624-3631 (2012).
- 30 Berger, P. J., Negus, N. C., Sanders, E. H. & Gardner, P. D. Chemical triggering of reproduction in *Microtus montanus*. *Science* **214**, 69-70 (1981).
- 31 Leirs, H., Verhagen, R. & Verheyen, W. The basis of reproductive seasonality in *Mastomys* rats (Rodentia, Muridae) in Tanzania. *Journal of Tropical Ecology* **10**, 55-66 (1994).
- 32 Dai, X. *et al.* Reproductive responses of male Brandt's voles (*Lasiopodomys brandtii*) to 6-methoxybenzoxazolinone (6-MBOA) under short photoperiod. *Science of Nature* **103**, 29 (2016).

- 33 Knapp, A. K., Ciais, P. & Smith, M. D. Reconciling inconsistencies in precipitation-productivity relationships: Implications for climate change. *New Phytol* **214**, 41-47 (2017).
- 34 Jacob, J. The response of small mammal populations to flooding. *Mamm Biol* **68**, 102-111 (2003).
- 35 Lima, M., Ernest, S. K. M., Brown, J. H., Belgrano, A. & Stenseth, N. C. Chihuahuan Desert kangaroo rats: Nonlinear effects of population dynamics, competition, and rainfall. *Ecology* **89**, 2594-2603 (2008).
- 36 Coulson, T., Gaillard, J. M. & Festa-Bianchet, M. Decomposing the variation in population growth into contributions from multiple demographic rates. *J Anim Ecol* **74**, 789-801 (2005).
- 37 Healy, K., Ezard, T. H. G., Jones, O. R., Salguero-Gómez, R. & Buckley, Y. M. Animal life history is shaped by the pace of life and the distribution of age-specific mortality and reproduction. *Nature Ecology and Evolution* **3**, 1217-1224 (2019).
- 38 Ricklefs, R. E. & Wikelski, M. The physiology/life-history nexus. *Trends Ecol Evol* **17**, 462-468 (2002).
- 39 Li, G. L., Hou, X. L., Wan, X. R. & Zhang, Z. B. Sheep grazing causes shift in sex ratio and cohort structure of Brandt's vole: Implication of their adaptation to food shortage. *Integr Zool* **11**, 76-84 (2016).
- 40 Li, G. L. *et al.* Successive sheep grazing reduces population density of Brandt's voles in steppe grassland by altering food resources: A large manipulative experiment. *Oecologia* **180**, 149-159 (2016).
- 41 Yin, B. F. *et al.* Large manipulative experiments reveal complex effects of food supplementation on population dynamics of Brandt's voles. *Sci China Life Sci* **60**, 911-920 (2017).
- 42 Otis, D. L., Burnham, K. P., White, G. C. & Anderson, D. R. Statistical inference from capture data on closed animal populations. *Wildlife Monogr*, 1-135 (1978).
- 43 Team, R. C. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/> (2018).

Figures

Figure 1

Changes (means $\pm$ se) in population density, numbers of recruits and body mass of yearling Brandt's voles in 0.48-ha enclosures between different rainfall increase scenarios from 2010 to 2019. The asterisks denote significant overall treatment effects ($P < 0.05$) in some specific years. R50: 50 mm rainfall were added evenly throughout enclosures during the growing season; R100: 100 mm rainfall were added evenly throughout enclosures during the growing season; ER130: 130 mm rainfall were added during the growing season but with more rainfall allocated to the early growing season (May-June); ER260: 260 mm rainfall were added during the growing season but with more rainfall allocated to the early growing season. LR130: 130 mm rainfall were added during the growing season but with more rainfall allocated to the late growing season (July- September).

Figure 2

Changes (means $\pm$ se) in plant biomass (for plant species that are both preferred and less-preferred as food by Brandt's voles) between different rainfall increase scenarios from 2010 to 2019. The asterisks denote significant differences between different rainfall treatments.

Figure 3

Survival analysis of the population founders of Brandt's voles (i.e. overwintered individuals within 0.48-ha enclosures) during the plant growing season (May-October) under different rainfall addition scenarios

from 2010 to 2019. The asterisks denote significant differences in survival time between different rainfall treatments ($P < 0.05$).

Figure 4

Linking body mass and sex to survival time of the population founders of Brandt’s voles from 2010 to 2019. The asterisks denote significant differences.

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