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Alpine grassland degradation intensifies the burrowing behavior of small mammals: evidence for a negative feedback loop

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Abstract

Globally, grassland degradation is an acute ecological problem. In alpine grassland on the Tibetan Plateau, increased densities of various small mammals in degraded grassland are assumed to intensify the degradation process and these mammals are subject to lethal control. However, whether the negative impact of small mammals is solely a result of population size or also a result of activity and behavior has not been tested. In this study, we use plateau pika as a model to compare population size, core area of colony, and the number of burrow entrances and latrines between lightly and severely degraded grassland. We test whether the alleged contribution of pika to grassland degradation is a result of increased population size or increased burrowing activities of individuals in response to lower food abundance. We found that grassland degradation resulted in lower plant species richness, plant height, and biomass. Furthermore, the overall population size of pika was not significantly affected by location in lightly and severely degraded grassland. However, pika core areas in severely grassland degradation were significantly larger and had significantly higher densities of burrows and latrines. Our study provides convincing evidence that habitat-induced changes in the behavior of small, burrowing mammals, such as pika, can exacerbate grassland degradation. This finding has significant implications for managing small mammals and restoring degraded grassland ecosystems.

Key words: burrowing behavior, grassland degradation, plateau pika, population size, small mammals

INTRODUCTION

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Grasslands, one of the most important ecosystems in the world, cover about 40% of the Earth's terrestrial surface (Bardgett *et al.* 2021). They are a dominant ecosystem that has significant economic value (Henkin *et al.* 2007). However, about 49% of grasslands globally have suffered degradation to various extents

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(Gang et al. 2014), resulting in an ecological problem challenging the ecosystem health and the livelihood of local people (Sneath 1998; Cease et al. 2012). This ecological crisis is particularly acute on the Qinghai-Tibetan Plateau (OTP) (Harris 2010; Li et al. 2013), where 90% of the grasslands have become degraded over the past half century (Cao et al. 2019). Overgrazing by livestock and global climate change have been recognized as the leading causes of grassland degradation (Sneath 1998). In addition, small burrowing mammals, such as prairie dog (Cynomys spp.) (Vermeire et al. 2004), plateau zokor (Eospalax bailevi) (Su et al. 2020), and plateau pika (Ochotona curzoniae) (Harris 2010), contribute to ongoing grassland degradation. These small mammals compete with livestock for food resources and their burrows cause extensive soil erosion (Vermeire et al. 2004; Pech et al. 2007; Su et al. 2020). Due to these negative impacts, they have been subject to lethal control over the past few decades (Smith & Marc 1999; Forrest & Luchsinger 2006; Su et al. 2020). However, controlling these small mammals has created further ecological problems, including a reduction in biodiversity (Bayless & Beier 2011; Wu & Wang 2017) and significantly reduced the infiltration rate of water affecting local ecohydrology (Wilson & Smith 2015).

It has been hypothesized that small burrowing mammals such as plateau pika prefer degraded grassland, and this preference results in larger populations when grasslands are degraded (Wangdwei *et al.* 2013). In turn, this causes further degradation. For instance, density of burrow entrances is commonly used to estimate the population size of small mammals (Johnson & Collinge 2004; Wei *et al.* 2020a). The high density of burrow entrances of pika observed in severely degraded grasslands led to the conclusion of a "population explosion" of pika in highly degraded grasslands (Harris 2010; Sun *et al.* 2015).

Food abundance is an important ecological factor influencing population and territory size of animals, and individuals often require larger territories as food abundance declines (Steury & Murray 2003; Marshall & Cooper 2004). Aboveground biomass and belowground biomass significantly decreased with the increase in the level of grassland degradation (Zhou *et al.* 2005; Bardgett *et al.* 2021), indicating a reduction in food resources. Reduced food then triggers small herbivores to compensate for low resources by enlarging their territory size, as seen in prairie dogs (*Cynomys gunnisoni*) (Verdolin 2007) and striped mice (*Rhabdomys pumilio*) (Schradin *et al.* 2010). It is unknown whether increased territory size in response to grassland degradation applies to plateau pika.

Predation pressure may also lead to behavioral changes of prey species (Mohr et al. 2003; Jermacz et al. 2017). For small mammals, burrow systems serve as important refuges against predators, especially in habitats with low vegetative cover (Deacon 2006). Small mammals usually build additional burrows for shelter where above ground refuges from predators is scarce, to minimize the predation risk (Blumstein et al. 2001; Wilson et al. 2012). It was proposed that pika's preference for open habitats with lower vegetative height and coverage (Wei et al. 2020b) is due to improved visibility and predator avoidance (Pang et al. 2021). However, in such open conditions, they may also be more easily detected by predators (Wheatley et al. 2020). Therefore, on severely degraded grasslands where pikas require larger territories to acquire enough food, they may build more extensive burrows with more burrow entrances, which may exacerbate grassland degradation.

Few studies have systematically tested the effect of grassland degradation on the burrowing behavior of small mammals, and it is unknown whether burrow density might be a reliable proxy for population density of small mammals under different grassland conditions (Severson & Plumb 1998; Magle *et al.* 2007; Qu *et al.* 2011). In addition, we do not know whether the aggravation of grassland degradation by small mammals is due to a perceived "population explosion" or due to animals' behavior, such as increased burrowing activities on degraded grassland due to limited food resources and increased predation.

To mitigate further grassland degradation and attempt to restore grassland ecosystems, it is crucial to understand the mechanisms of observed negative impacts of small mammals on grassland. In this study, we used pika as a model to test the effect of grassland degradation on ranging and burrowing behavior of pika. We compare population size, core area of colonies, and distribution of burrow entrances between lightly and severely degraded grasslands. This study will shed light on whether the aggravation of grassland degradation by pika is through increased population size or increased burrowing activities. We propose the following hypotheses:

- 1. In severely degraded grassland, we expect food abundance is reduced. Hence, we will observe reduced vegetation.
- If food abundance is reduced, we expect the population size of pikas in severely degraded grasslands to be smaller than that of lightly degraded grasslands.
- 3. If food abundance is reduced, we expect pika colonies require larger areas to obtain sufficient food. Hence, if population density is similar, we predict larger core areas of pika colony and subsequently smaller distances

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© 2023 The Authors. *Integrative Zoology* published by International Society of Zoological Sciences, Institute of Zoology/Chinese Academy of Sciences and John Wiley & Sons Australia, Ltd. between two core areas in severely degraded grass-lands.

4. In severely degraded grasslands, we assume higher predation rates; therefore, pika will require more burrow entrances to escape from predation. We hypothesize that the colonies in severely degraded grasslands will have more burrow entrances than lightly degraded grasslands.

MATERIALS AND METHODS

Study sites and animals

This study was conducted between 2019 and 2021 at the Qinghai Haibei National Field Research Station of Alpine Grassland Ecosystem ($37^{\circ}37'$ N, $101^{\circ}19'$ E, 3200 m a.s.l.), Qinghai–Tibetan Plateau, Qinghai Province, the People's Republic of China. The dominant species of the alpine meadow are *Stipa aliena* and *Kobresia humilis*. The mean annual air temperature is -1.2° C and precipitation 485 mm (Wang *et al.* 2021). The common burrowing small mammals inhabiting this site included plateau pika, plateau zokor, root vole (*Microtus oeconomus*), and Himalayan marmot (*Marmota himalayana*).

Plateau pika is an endemic small burrowing mammal on QTP and is considered to be a keystone species of alpine grassland ecosystem due to its critical role in maintaining grassland ecosystem biodiversity (Smith & Marc 1999; Wei et al. 2019). This social, small mammal lives in family groups (Qu et al. 2013) and occupies relatively stable territory on open habitats (Wei et al. 2020a; Smith & Dobson 2022). The main predators of pika included alpine weasel (Mustela altaica), Asia polecat (M. eversmanni), and upland buzzard (Buteo hemilasius) (Yin et al. 2017). Pikas are territorial and tend to guard their territory (Smith & Gao 1991). The burrows excavated by pika provide the necessary resource they need to withstand the harsh environment and, as a byproduct, provide the nesting habitats for many native birds and lizards (Smith & Marc 1999). The burrow systems also increase the habitat heterogeneity of the grasslands surface and alter soil physicochemical characters (Zhao et al. 2021).

Defining the level of grassland degradation

Long-term grazing has resulted in variable grassland degradation in this region (Zhao & Zhou 1999). To minimize the effects of other confounding factors (i.e. predator density, climate and altitude), we have used lightly degraded grassland site and severely degraded grassland site in the same area but with a 5-km distance in between. The two sites have similar environmental conditions and differ in the degree of grassland degradation. We had three 60 m \times 60 m replicate plots in each lightly and heavily degraded grassland, and the distance between the adjacent plots of each site was over 1 km. To quantify the degree of degradation (light and severe), we measured the plant species richness, above-ground biomass, and coverage of each species in three plots at each site. "Light" sites belong to a particular pastoralist and were only grazed in winter, so the grasslands were subject to low grazing pressure. "Severe" sites were shared among several pastoralists and were grazed year-round that resulted in higher grazing pressure.

Vegetation survey

In August 2019, five 0.5 m \times 0.5 m quadrats at 15-m intervals along the diagonal line in each plot were set up to survey the plant species richness (number of species present), plant height, and percentage coverage of each species (Liu *et al.* 2018; Dai *et al.* 2019). We harvested all the plants by species in each quadrat at ground level, dried the samples at 105°C for 10 min, and then further dried at 65°C for 48 h, before being weighed to obtain the biomass for each species (Ma *et al.* 2017).

Colony core area

A study by Wang and Dai (1990) proposed that pika use communal latrines to mark the colony territory. These latrines are depressions in the ground made by pika and where they deposit their feces. To identify the core area of pika colonies, we fed animals in each colony an artificial food containing colored acrylic beads. The small plastic beads we used is made of acrylic, also known as polymethyl methacrylate (PMMA). It is a non-toxic material in solid form and has been widely used in medical applications and has been proven to be safe, based on human and animal data (Becker et al. 2011; Shi et al. 2018). The diameter of beads we used is 1.5 mm, smaller than that of fecal pellets (diameter: 4 mm) of pika. This method has been used in recent wildlife studies (Buesching et al. 2016). The artificial food was composed of 300 g crushed rabbit feed (Beijing Keao Xieli Feed Co., Ltd. China) combined with 150 mL water and 400 acrylic beads. To test the palatability of the artificial food and whether pika fed on the artificial food produced feces containing the acrylic beads, we conducted a pilot trial in three plots at each site, during which 200 g of artificial food containing plastic beads was presented at the center of each plot in the morning and the latrines were checked the next day.

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The food provided was consumed and the fecal pellets containing colored beads were recovered. The artificial food had no visible adverse effect on pika's health.

To determine the core area of territory, we chose three adjacent colonies of pika in each plot. The area occupied by each colony was divided into three similar sized sections. A pile of feed (200 g) containing acrylic beads was placed near the burrow entrances in the center of each section. We used different bead colors for different colonies. The artificial food was provided for five consecutive days. From the sixth day, all latrines were checked and the latrines with fecal pellets containing colored beads were marked with a same-colored label. We also marked all burrows and latrines in each colony with numbered labels to determine whether the distribution of these varied between lightly and severely degraded sites.

An orthogonal coordinate system was built to analyze the relationship between each colony core area, where the corner point at the northeast of each plot was used as the origin point and the x axis was east-west direction and the y axis was north-south direction. We randomly chose three non-contiguous points in the center of a plot and measured the distance from each burrow and latrine in each colony to these three points. A trilateration algorithm was then used to calculate the coordinates of burrows and latrines (Oguejiofor *et al.* 2013).

To determine classification of an identified burrow or latrine into one colony or another, we used a k-nearest neighbor algorithm (KNN) (Cai *et al.* 2016). This algorithm was trained on our dataset of known latrines (latrines where a certain color bead was found and determined to belong to a certain colony). Unknown datapoints (latrines or burrows without bead data) were classified according to the classification of known points closest to them, based on Euclidean distance (as our *x* and *y* coordinates for each plot are in meters).

We contrasted the KNN colony classification with a colony classification done in situ. KNN classifications matched at least 90% of the time with in situ classifications in severely degraded plots, and 100% of the time in lightly degraded plots. In situ classification of severely degraded plots was challenging; thus, all analyses are presented with the KNN determined colonies.

Once we had calculated KNN colonies, we calculated the centroid for the three adjacent colonies (a colony cluster) in each plot and determined the Euclidean distances between centroid of adjacent colonies in each plot. To determine the core area of each colony, we calculated the area covered by borrow entrances and latrines in each colony using minimum convex polygon method (MCP) based on 100% MCP ranges (Jennrich & Turner 1969). Finally, as a measure for density burrow entrances, we calculated the within sum of squares for each cluster: the larger the within sum of squares the denser the burrow entrances is.

Colony size

A mark-recapture method was used to estimate the population size in each plot. A string noose method was used to capture individual pika (Dobson et al. 1998). The nooses were placed at burrow entrances, and once set, the site was monitored by two researchers scanning all burrow entrances constantly at approximately 20 m from the colony. Every 15 min, a researcher checked each noose to prevent captured pika not being seen by distant scanning. Once captured, the pika was removed from the noose and placed in dark cloth holding bags (25 cm long and 15 cm wide) to reduce stress before they were transferred into the anesthesia box ($30 \times 15 \times 15$ cm). Once under anesthesia (isoflurane; RWD life science Co., Ltd. China), we recorded sex, weight, head length, head width, and foot length. Finally, each pika was marked with a numbered metal ear tag and released back at the point of capture. Pikas were captured for two successive days at each site and the recapture was conducted 21 days after the initial capture. Recaptured pikas were only weighed and ID recorded. We estimated abundance of pika at each plot using the Lincoln-Peterson model (Moore et al. 2010). The animal experimental protocols were approved by the Institution of Animal Ethical and Welfare Committee of Lanzhou University (protocol number: CY-2019-0501).

Statistical analysis

We used generalized linear models (GLM) with a Gaussian distribution to determine potential differences in height, biomass, and species richness between sites with severe and light degradation. Height and biomass were both log-transformed to meet assumptions of normality and even distribution of residuals.

We examined differences in plant composition between the two sites: "Light" and "Severe" with non-metric multidimensional scaling (nMDS) based on Jaccard's distance matrix. This was followed by Ward's hierarchical cluster analysis, where we identified three main clusters in the dataset and characterized them based on the degree of degradation and species. We used INDVAL analysis to identify key species for each cluster (Hetherington-Rauth & Ramírez 2016).



Figure 1 Overall, sites with severe degradation had significantly lower vegetation height, biomass, and species richness than sites with light degradation. * indicates a significant difference with preference, between lightly and severely degraded sites (FDR adjusted P values < 0.01).

GLM was used to test for a difference in pika abundance between lightly and severely degraded sites. To determine whether distance between colony centers, colony density, or colony core area varied depending on degradation, we constructed a generalized linear mixed-effects model (GLMM) with plot and colony included as a random factor. Each of the distance, density, and core area was logged to meet assumptions of normality. Similarly, we constructed two GLMMs with underlying Poisson distribution to determine whether there was a difference in the counts of latrines or burrows between lightly and severely degraded sites. Plot and colony were included as random factors.

For all models, we calculated pairwise *P*-values adjusted for multiple comparisons using Bonferroni–Hochberg false discovery rate correction. We presented the conditional and marginal R^2 as a measure of goodness of fit. Model of best fit was assessed using AIC where appropriate.

All analyses and plots were performed using R version 4.2.0 (R Core Team 2018), including the "glmTMB" package for GLMM, the "lme4" package for GLM, the "lsmeans" package for Bonferroni–Hochberg false discovery rate correction, the "labdsv" package for INDVAL, the "performance" package for goodness of fit test, the "ggplot2" package for plotting all figures.

RESULTS

Vegetation composition on lightly and severely degraded grassland

The vegetation in severely degraded plots had significantly lower plant height, biomass, and species richness compared to plots in lightly degraded sites (Fig. 1, FDR adjusted *P*-values < 0.01). We found that plant community structure differed between severely degraded plots and lightly degraded plots (Fig. 2). Five plant species defined the two severely degraded clusters (Cluster 1: Ajuga lupulina and Lancea tibetica and Cluster 2: Hypecoum leptocarpum, Galium verum, and Aster diplostephioides; INDIC analysis *P*-values < 0.001), while 11 species defined the lightly degraded cluster (Euphrasia regelii, Morina kokonorica, Taraxacum mongolicum, Saussurea nigrescens, Comastoma pulmonarium, Ranunculus tanguticus, Stellaria alaschanica, Ajania tenuifolia, Tibetia himalaica, Stipa aliena, and Elymus nutans; INDIC analysis *P*-values < 0.001). The lightly degraded sites had a high abundance of various species such as S. aliena, E. nutans, T. himalaica, and T. mongolivum than the severely degraded sites (Fig. 3).

The effect of grassland degradation on pika population size

The abundance of pika in lightly degraded grasslands was higher than in severely degraded grasslands and the difference is not statistically significant (Fig. 4, FDR adjusted *P*-values = 0.85).

The effect of grassland degradation on core area of territory and burrow and latrine entrances

Our GLMM analysis suggested that colonies at severely degraded grasslands were closer to each other (Fig. 5a, FDR *P*-value < 0.0001), covered a larger area (Fig. 5b, FDR *P*-value = 0.001), and had denser burrow entrances and latrines, than lightly degraded

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Figure 2 Non-metric multidimensional scaling (nMDS) plot of plant species and abundance. Three distinct clusters were observed; cluster 1 and 2 for severely degraded plots and cluster 3 for lightly degraded plots (nMDS; stress value = 0.07).



Figure 3 Presence and abundance of indicator species (determined from indicator analysis) in three clusters determined by non-metric multidimensional scaling (nMDS). Two clusters pertain to severely degraded sites (cluster 1 and 2), and one to lightly degraded sites (cluster 3).

grasslands (suggested by larger within sum-of-squares; Fig. 5c, FDR *P*-value < 0.0001). KNN-cluster analysis consistently resulted in three distinct colonies for both lightly and severely degraded sites, but the colonies on lightly degraded plot were better separated, consistent with in situ surveys of colonies (Fig. 6).

The number of burrow entrances and latrines in severely degraded grassland were significantly higher than that of lightly degraded grassland (Fig. 7; FDR adjusted *P*-values < 0.001). Furthermore, the variance in burrow numbers was greater in severely, compared to lightly degraded sites.

DISCUSSION

By analyzing population size, core area of colony territory, and burrowing behavior, we found that greater grassland degradation was associated with increased burrowing activity by pika. In addition, we present, for the first time, evidence demonstrating that the contribution of pika to grassland degradation is likely due to a behavior response rather than population increases. While the impact of small mammals on grasslands has been recognized for a long time (Smith & Marc 1999; Zhang *et al.* 2003; Mary *et al.* 2010), we know little about underlying mechanisms of grassland degradation by small mammals, such





Figure 4 Pika abundance per plot between lightly and severely degraded grasslands.

as behavior responses. Our work seeks to improve this understanding.

Aboveground biomass, species richness, and plant height were significantly lower in severely degraded grasslands. This indicates a general reduction in food resources for small herbivores. Previous studies have demonstrated that overgrazing by livestock significantly decreases available food resources for small mammals, reflected in lower plant coverage and height (Steen et al. 2005; Foster et al. 2014). Our analyses of plant community structure show that the increase in the level of grassland degradation not only resulted in reduced plant biomass, but also altered the plant community structure. The dominant species in the lightly degraded grassland included S. aliena, E. nutans, T. mongolicum, O. ochrocephala, and O. kansuensis, all preferred food species of pikas (Wang et al. 1992; Liu et al. 2008). In contrast, severely degraded grasslands were dominated by A. lupulina and L. nanum, which are not preferred food species of pika (Wang et al. 1992; Liu et al. 2008). This may be because of overgrazing: Previous studies indicated that overgrazing often reduced the preferred food plants of small mammals (Yang *et al.* 2020). In our context, this modification may lead to a shortage of preferred food resources for pika in severely degraded grasslands. In addition, small herbivores typically prefer plant species with high nutritional value or low content of toxins (Li *et al.* 2021). Accordingly, more non-preferred plants mean lower food quality for pika, compounding the impact of overgrazing. Similar changes in the abundance of dominant species with different levels of degraded grassland had been recorded by previous studies in the same grassland ecosystem (Zhou *et al.* 2005; Guo *et al.* 2020).

Our study did not detect a significant difference in pika population size between lightly and severely degraded grasslands (Table S1, Supporting Information). Previous studies have reported that pika, being generalist foragers, feed on more than 40 plant species across different habitats and seasons (Wang *et al.* 1992; Liu *et al.* 2008). In harsh conditions, pika will decrease their metabolism and feed on yak feces to meet their energy needs (Speakman *et al.* 2021). These strategies may maintain local population size even with the limited food resources in

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Figure 5 Severely degraded sites had colonies that (a) were significantly closer to each other (Conditional R^2 : 0.941, Marginal R^2 : 0.768); (b) covered a significantly larger area (Conditional R^2 : 0.506, Marginal R^2 : 0.505); and (c) were significantly denser

than lightly degraded sites (Conditional R^2 : 0.944, Marginal R^2 : 0.539). All *P*-values are reported from generalized linear mixedeffects model (GLMM); ** indicates an FDR-adjusted *P*-value < 0.01; *** indicates an FDR-adjusted *P*-value < 0.0001.

severely degraded grasslands. In contrast, some previous studies found that the population size of pika was highest in severely degraded (Sun *et al.* 2015; Qian *et al.* 2021). However, these studies used burrow entrance density as proxies for the population size. We have demonstrated that pikas increase their burrow density in severely degraded grassland without increasing population size. Other studies have similarly indicated that the number of burrows may not be a reliable proxy for population size (Magle *et al.* 2007; Qu *et al.* 2011). Therefore, we propose that further investigation is needed to support the hypothesis that pika population increases with increasing grassland degradation.

On severely degraded grassland, pika markedly expanded their colony core areas; this resulted in a smaller distance and greater overlap between pika core areas in colonies. We propose that such an increase in core area is likely due to the shortage of food, as we, and others, report at degraded grassland sites (Schradin & Pillay 2006). Similar changes in territory size between habitats with different food abundance have been described for other small mammals (Harris & Leitner 2004; Quirici et al. 2010). Researchers have found that territories overlap when there are fewer food resources, such as in Mongolian gerbils (Wang et al. 2011). Here, we found that the spatial dispersion of pika varied, from a clumped distribution in lightly degraded grasslands, to an even distribution in severely degraded grasslands. Variation of pika spatial distribution between sites of different grazing pressure has been recorded in work by He et al. (2021).

The number of burrow entrances in severely degraded grasslands was significantly greater than that of lightly degraded grasslands. Predation risk strongly influences foraging decisions (food quality, quantity, activity time and distance) of small mammals (Bhattacharyya *et al.* 2015). The burrow system of small mammals provides an important refuge to escape from predators, especially in habitats with sparse vegetation (Karels & Boonstra 1999; Deacon 2006). Indeed, lower vegetation height and coverage increases predation risk resulting in higher predation losses of prey species (Wheatley *et al.* 2020). Thus, more burrow entrances are likely to enhance the chance to escape from predation of individual pika. This has been found in other burrowing herbivores, such as Vancouver Island marmot (Blumstein *et al.* 2001).



Figure 6 Distribution of burrows and latrines in each of the three plots and two sites, illustrating also the position of burrows and latrines within each colony. The dotted box indicates the 60×60 square meter plot.

There were significantly more latrines on pika core areas in severely degraded grasslands than in lightly degraded grasslands; a similar phenomenon has also been recorded in European rabbits (Ziege *et al.* 2016). Latrines of some animals are known to play an important role in information transfer (Ziege *et al.* 2016) and territory defense (Jordan *et al.* 2007). We speculate that an increase in the number of latrines in pika colony on severely degraded grassland may reflect increased competition between colonies due to reduced food resources (Stewart *et al.* 2001).

The increases in burrows and latrines we report associated with greater scarcity of food resources in severely degraded grasslands may lead to extensive soil erosion and further exacerbate degenerated conditions of grassland. To break this negative feedback cycle and maintain the vital ecosystem service of small mammals such as pika, a combination of reduced overgrazing by livestock and active restoration of grassland ecosystem and grassland vegetation will be required.

Small burrowing herbivorous mammals have been attributed to aggravating grassland degradation on QTP. Our study shows that, instead of an effect of population increase, the contribution of pika to grassland degradation is due to their behavioral response to degraded grassland conditions. Pika reacted to human-induced grassland degradation with a significant increase in colony core area and greater numbers of burrow entrances and latrines. Such behavioral changes likely contribute to the further deterioration of grassland conditions. A holistic approach, including reducing grazing levels and restoration of grassland vegetation cover, is required to bring back the positive ecosystem functions of native burrowing mammals. 7494877, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/1749-4877.12730, Wiley Online Library on [18/09/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons Licens

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Figure 7 Severely degraded sites had significantly more (a) burrows (conditional R^2 : 0.975; marginal R^2 : 0.916) and (b) latrines (conditional R^2 : 0.958; marginal R^2 : 0.925) than lightly degraded sites. *** indicates an FDR-adjusted *P*-value < 0.001, retrieved from a generalized linear mixed-effects model (GLMM).

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CONFLICT OF INTEREST

None of the authors have a conflict of interest.

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SUPPLEMENTARY MATERIALS

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1 The model structures for GLM and GLMM

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