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Moderate density of small mammalian herbivores facilitates livestock growth by improving vegetation composition in grasslands

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eLife Assessment

This **important** study provides evidence that plateau pikas, at moderate densities, can facilitate yak nutrition by suppressing a poisonous plant, offering a helpful perspective on reciprocal interactions between small mammal ecosystem engineers and large herbivores. The evidence is **solid**, supported by a manipulative field experiment and appropriate measurements of intermediary ecological processes, although some claims about density dependence, competition, and stress-gradient mechanisms are not fully supported by the experimental design. The work will be of interest to ecologists, conservation biologists, and rangeland managers, particularly those studying grassland herbivore interactions and livestock management on the Qinghai-Tibetan Plateau.

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Abstract

Small mammals and large herbivores have co-evolved in grasslands for millions of years, yet how they interplay remains unclear. On the Qinghai–Tibetan Plateau, plateau pikas (*Ochotona curzoniae*) are often considered pests that compete with livestock at high densities. Using field experiments, we show that pikas facilitate yaks (*Bos grunniens*) below a moderate density threshold (~200 active burrows/ha). By selectively clipping tall poisonous forbs, especially *Stellera chamaejasme*, pikas reduced their cover by two-thirds, increased the abundance and protein content of palatable grasses and sedges, improved yak foraging efficiency, and enhanced weight gain by up to 67%. These results provide the first empirical evidence of a density-dependent transition from antagonism to facilitation between small and large herbivores. They highlight how moderate populations of ecosystem-engineering small mammals can sustain both biodiversity and pastoral productivity in rangelands.

Introduction

Both large and small mammalian herbivores are keystone species in grasslands worldwide, exerting profound impacts on ecosystem structure and functions (1-6). They have co-evolved with grasslands and with each other over millions of years, but how these mammals co-exist remains poorly understood (6-10). By sharing food and other resources, guilds of different herbivore species can participate in varied interactions ranging from negative (competition) to positive (facilitation) for one or more of the species (11-14). However, such interactions often are assumed to be highly asymmetric: large herbivores have been demonstrated to affect the abundance, diversity, and demography of small mammals (15-20), whereas the potential for reverse effects has received little attention (10,21-23).

Small mammals, including pikas, voles, prairie dogs, pocket gophers, and other small herbivores, are not only primary consumers but also key ecosystem engineers in many grasslands (6,9,24-26). Through their feeding, clipping, and burrowing activities they profoundly alter vegetation and soil properties, with potential cascading effects on co-occurring large herbivores (6,10,21-23). In rangelands and other less productive ecosystems, small herbivorous mammals are often considered to be pests because their population outbreaks can lead to competition with livestock for food (27-29). Despite this, the stress gradient hypothesis predicts that the direction of interspecific interactions should shift as environmental stress changes (30). Specifically, a competition-facilitation balance between species may transition with population density: facilitation should occur when species populations are at low density, while competition should occur when densities are high; such density-transitions may promote community stability and productivity (31,32). Despite such expectations, it remains unclear whether the competitive effects of outbreaks of small herbivorous mammals on larger herbivores diminish or even shift to facilitation when the smaller species are at lower, non-outbreak levels. Livestock grazing currently uses ~77% of global agricultural land, and sustains billions of people worldwide (33). A critical assessment of small mammals' impacts on livestock production is urgently needed to guide management for both production and biodiversity conservation.

The Qinghai-Tibetan Plateau supports approximately 14 million yaks (*Bos grunniens*), forming one of the world's most extensive pastoral systems (34). These herds are vital to pastoral livelihoods and key ecosystem functions across the region's 2.5 million km² expanse (35). The dominant small mammal species—plateau pika (*Ochotona curzoniae*)—is an iconic keystone species that commonly coexists with yaks, and is the focus of long debate on whether its impact of yaks is positive or negative (9,36-38). In regions with high population densities (e.g., over 500 active burrows/ha), plateau pikas can suppress livestock production by heavily consuming nearly all plant species foraged by yaks, leading to extensive poisoning campaigns targeted at eradicating these small mammals (37-39). At low and moderate densities of pikas (e.g., below 200 active burrows/ha), however, competition for food is mitigated and dietary partitioning can occur: yaks graze selectively on monocotyledonous plants such as grasses and sedges (40,41), whereas pikas prefer to clip and feed on the leaves of dicotyledonous plants (42,43). Thus, whether plateau pikas and yaks compete for pasture largely depends on their diets and population densities.

In line with global trends in weed invasions in rangelands (44), intensive livestock grazing and other human disturbances have facilitated grassland degradation on the Qinghai-Tibet Plateau, creating opportunities for the proliferation of toxic weeds (45). Among these, the wolf poison *Stellera chamaejasmehas* become a predominant species, now covering approximately 20 million hectares, as it outcompetes palatable grasses and sedges while thriving under grazing pressure

(46). The expansion of poisonous plants on the Qinghai-Tibetan Plateau poses a dual threat to livestock, either by causing direct toxicity (47) or by reducing forage availability through competition with palatable species for light and soil nutrients (45,46). However, plateau pikas may indirectly benefit yak foraging by selectively clipping large plants (48,49), especially those poisonous forbs such as *S. chamaejasme* (37) (Fig. 1)—a behavior that reduces predation risk (50,51) but also suppresses these competitors, potentially enhancing the quality and quantity of desirable grasses and sedges. Despite these plausible interactions, empirical studies directly testing such interactions remain scarce.

Here, we experimentally assess how a moderate population density of pikas (~200 active burrows ha^{-1}) affects yak performance in an alpine ecosystem of the Qinghai–Tibetan Plateau. We hypothesized that, at moderate densities, plateau pikas facilitate yaks by suppressing tall poisonous forbs, thereby increasing the abundance and nutritional quality of palatable grasses and sedges during the growing season (June–August). Specifically, we predicted that (i) pika clipping reduces poisonous plant cover; (ii) this enhances the availability and quality of palatable forage (i.e., grasses and sedges) for yaks; (iii) yaks increase their foraging efficiency in the presence of pikas; and (iv) these cascading effects ultimately improve yak weight gain (Fig. 1). To test these predictions, we first conducted two field surveys to examine diet partitioning between pikas and yaks, and the associations among pika density, *Stellera* abundance, and yak grazing activity. We then performed an in-situ field experiment using 150 × 150 m fenced enclosures to test the interactive effects of pikas and Stellera on yak body growth and the underlying mechanisms driving these effects.

Results

In the field surveys, we found that pikas and yaks have distinct diets: pikas very frequently clipped but did not eat large, poisonous *Stellera* plants and fed mostly on other forbs, whereas yaks strongly preferred grasses and sedges (Fig. 2A,B, table S1,2), supporting findings of previous studies (40-43). We also found that the cover abundance of Stellera was associated negatively with the density of active pika burrows ($R^2 = 0.39$, $P < 0.001$; Fig. 2C) and with yak foraging activity, as indicated by dung density ($R^2 = 0.43$, $P < 0.001$; Fig. 2D).

In the manipulative field experiment, pika removal led to a 90% reduction in the number of active burrows per hectare, with 182.9 (SE ± 24.5) burrows/ha in pika-present plots compared to 19.0 (SE ± 1.6) burrows/ha in the pika-removed plots (Fig. 3A, table S3). In the presence of *Stellera*, yaks co-occurring with pikas showed daily weight gains 67% greater than those in the no-pika treatment, but such effects disappeared once *Stellera* was removed (Fig. 3B, table S3,4). Notably, yak weight gain showed a hump-shaped relationship with pika density, with the highest growth at ca. 220 active burrows/ha, after which, yak growth decreased linearly as pika density increased ($R^2 = 0.75$, $P < 0.001$; Fig. 3C).

In the presence of *Stellera*, pikas suppressed the cover abundance of this forb by two-thirds (Fig. 3D, table S3,4), which led to increases of 118% and 18% in cover abundances of co-occurring grasses and sedges, respectively (Fig. 3E,F, table S3,4). These shifts in vegetation composition also improved the nutritional value of the total available forage for yaks, with increases of 15% in crude protein (CP) content and 6% in acid detergent fibre (ADF) content in the pika + *Stellera* treatment compared with the *Stellera* only treatment (Fig. 3G,H, table S5,6). Pikas and *Stellera* had no interactive effects on abundance of sedges, forbs, and neutral detergent fibre (NDF) of total forage for yaks (Fig. 3F,I, fig. S1, table S3,5). These results suggest that pikas facilitate yak growth by suppressing poisonous plants, increasing both the availability and quality of food for the livestock.

Pika-yak facilitation was also linked to improved foraging efficiency in yaks when grazing alongside pikas. Bite rate (i.e., the number of bites taken on plants per hour) and bites/step ratio (i.e., the number of bites taken on plants per step) are two key indicators of foraging efficiency in large herbivores (52). In the presence of *Stellera*, sedge bite rate and sedge bites per step of yaks significantly increased by 48% and 89%, respectively (Fig. 4A,C, table S7,8), and grass bite rate and grass bites per step increased similarly by 41% and 80% (Fig. 4B,D, table

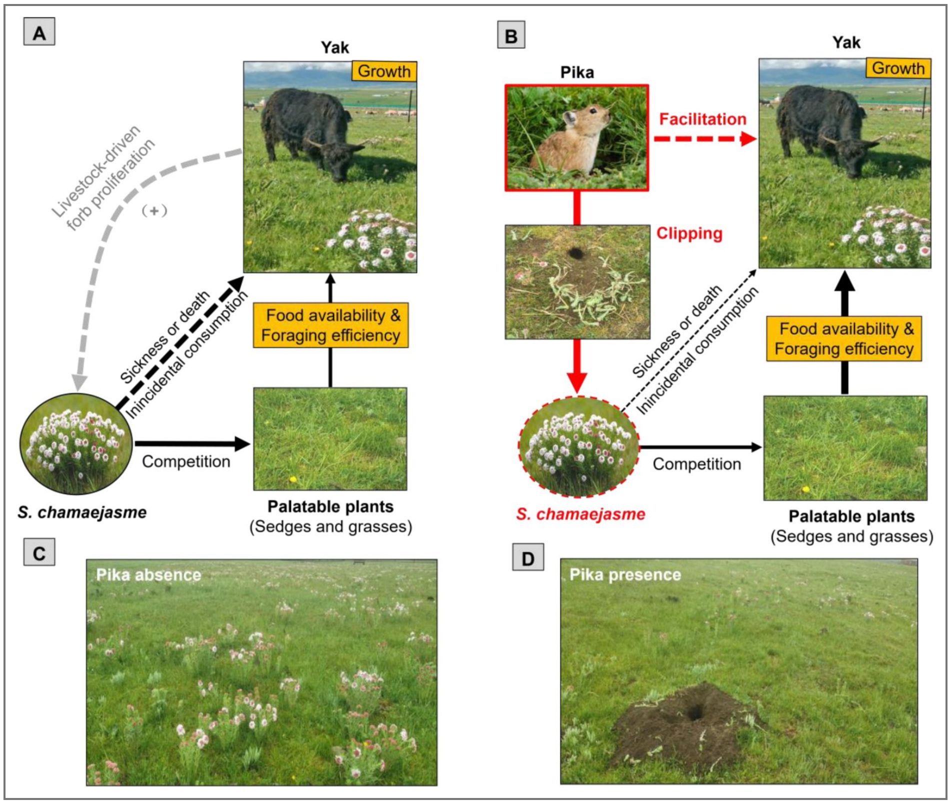

Figure 1. **Conceptual diagram of the hypothesized facilitative effects of pikas (*Ochotona curzoniae*) on yak (*Bos grunniens*) growth performance on the Qinghai-Tibetan Plateau.**

(**A**) In the absence of pikas, the poisonous forb *Stellera chamaejasme* exerts strong negative effects on the growth of yaks by outcompeting palatable grasses and sedges, thereby reducing forage availability and foraging efficiency. (**B**) In the presence of pikas, clipping of *Stellera* suppresses its abundance, mitigating its negative impact and promoting yak growth. Grey dashed line and "+" indicate livestock grazing promotes the proliferation of the poisonous forbs by suppressing palatable grasses and sedges. Black dashed lines indicate negative effects of poisonous plants on yaks, black solid lines indicate competition between plant groups, and red solid lines indicate pika suppression of *Stellera*. Line thickness represents the relative strength of putative species interactions. (**C**, **D**) show pika clipping activity and its effect on *Stellera* abundance at the study site.

Credits: Xiaona Zheng (photographs).

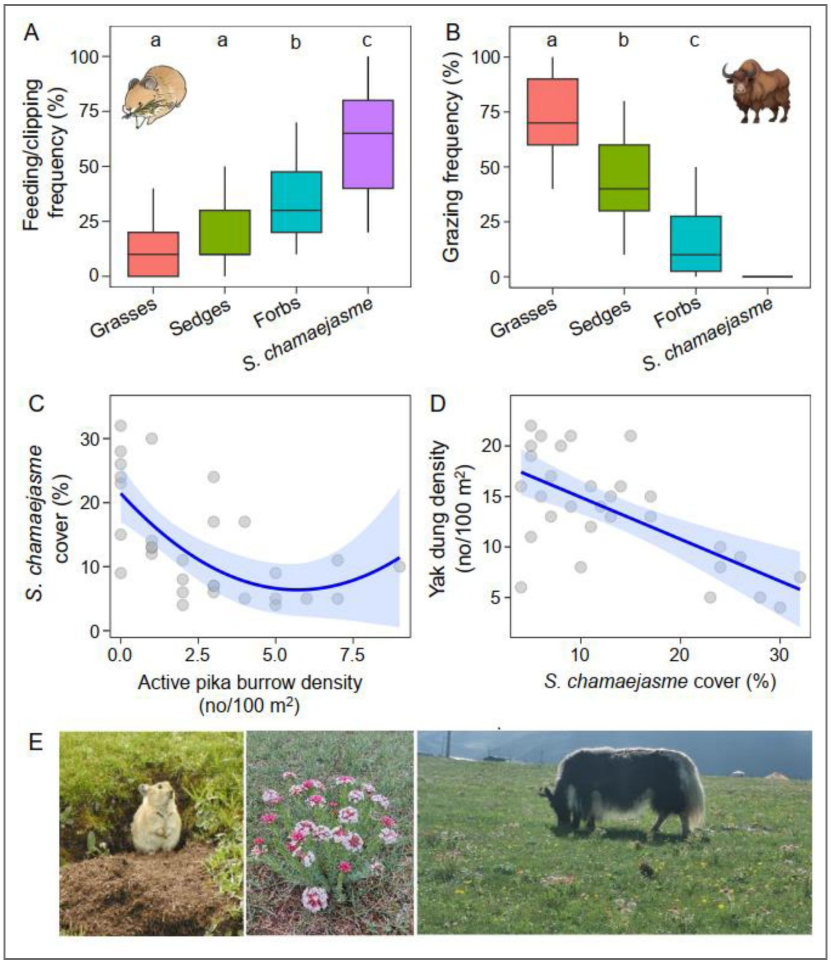

Figure 2. **Diet selection of pikas and yaks and their potential interactions mediated by poisonous plants based on field surveys in July 2021.**

(**A**) Feeding and clipping frequencies of pikas, and (**B**) grazing frequencies of yaks on grasses, sedges, forbs, and *Stellera* across 10 2 × 2 m plots and 10 250 m transects, respectively. (**C**) Relationship between active pika burrow density and *Stellera* cover, and (**D**) between *Stellera* cover and an index of yak grazing activity (dung density) in 30 10 × 10 m plots. (**E**) Photographs showing (left to right) a pika at its burrow entrance, flowering *Stellera*, and a yak grazing among *Stellera* plants. Different letters above bars indicate significant differences at $P < 0.05$. Credits: Xiaona Zheng (photographs).

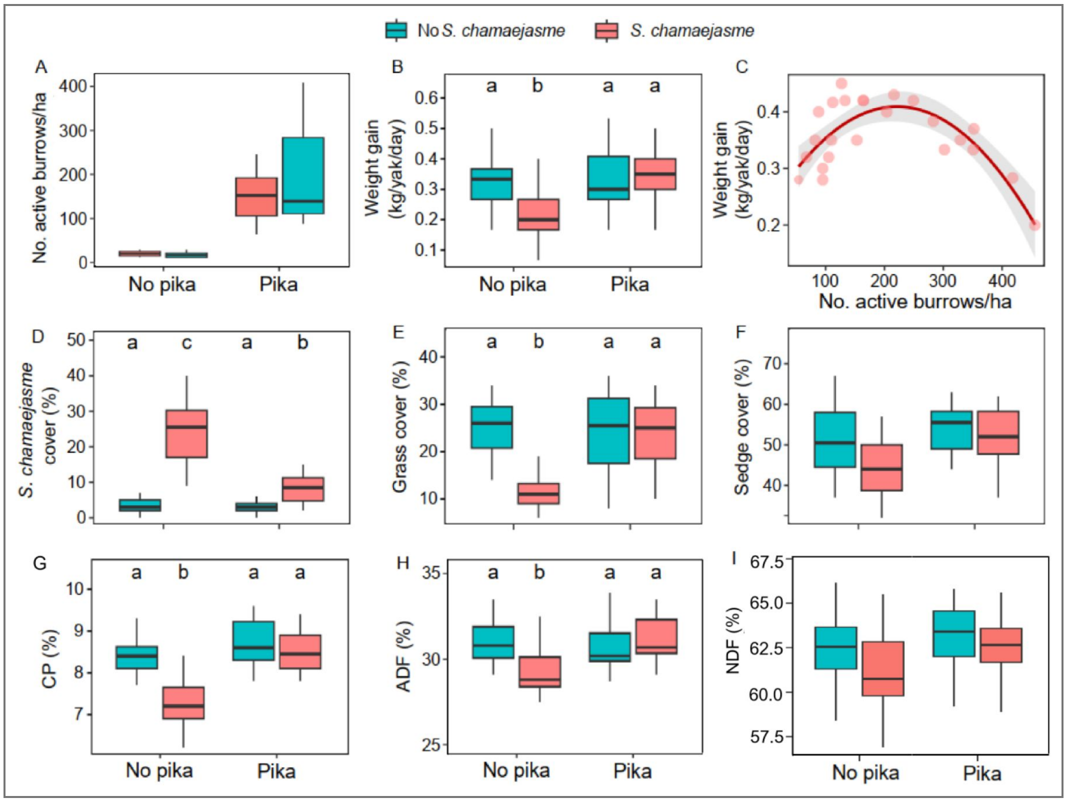

Figure 3. **Combined effects of two-year (2022–2023) pika and *Stellera* removal treatments on yak growth, forage quantity, and quality in the field manipulative experiment.**

(**A**) Pika density (indicated by active burrow density), (**B**) yak weight gain, (**C**) relationship between pika density and yak weight gain, (**D**) *Stellera* cover, (**E**) grass cover, (**F**) sedge cover, (**G**) crude protein (CP) content, (**H**) acid detergent fibre (ADF) content, and (**I**) neutral detergent fibre (NDF) of total forage (dry mass basis). Average values from both years were used in analyses, yielding one data point per 150 × 150 m plot. Significant interactions between pikas and *Stellera* were evaluated using post hoc tests; means not sharing letters differ significantly. For panels (**A**) and (**F**), only main effects were significant (table S3). Error bars indicate ± SE.

S7,8), when yaks occurred with compared without pikas. These enhancements in yak foraging efficiency can be attributed to the decline in cover of the poisonous *Stellera* (Fig. 3D), which removed a grazing deterrent and improved access by yaks to palatable food items. Pikas and *Stellera* had no interactive effects on yaks' foraging efficiency on forbs (fig. S2, table S7).

Discussion

By combining field surveys and manipulative experiments, we have demonstrated that pikas—when occurring at moderate density—can benefit yak body growth by suppressing large poisonous plants and increasing the availability of palatable forage in the Qinghai-Tibetan Plateau. Our findings thus quantify the beneficial impacts of small mammals that, during outbreak years, are often considered as pests and competitors with livestock for food (1,37-39). These observations support predictions of a density-dependent transition in competition-facilitation interactions by Zhang (2003) (31) and provide new insights into how small and large herbivores co-exist in nature.

Ecosystem engineering is a key mechanism driving interspecific facilitation (24,53,54). Engineering activities of one herbivore species can indirectly benefit another by either increasing access to food resources or ameliorating abiotic conditions in particular habitats (11,12,40,55). In our system, the selective clipping activities of pikas greatly suppressed the abundance of large poisonous forbs (Fig. 3D), and increased both the quantity and quality of yaks' palatable food plants (Fig. 3E-H). These improvements in food availability and nutrition for yaks can be attributed to the release of grasses and sedges from competition with the forbs for limiting above- and below-ground resources, including light, soil moisture and nutrients (45,46). Pika-induced increases in food resources, along with fewer foraging barriers for yaks after poisonous forb removal by pikas, together increased foraging efficiency (Fig. 4) and thus facilitated weight gain by yaks (Fig. 3B). In addition to increasing food resources, the removal of poisonous plants by pikas may also benefit yaks by reducing the risk of incidental consumption (45,46), which can cause biochemical or physiological stresses in yaks that lead to sickness or even death (47).

Our results add to a growing list of studies that highlight the importance of small mammal impacts on large herbivores. In grasslands of the North American Great Plains, for example, black-tailed prairie dogs (*Cynomys ludovicianus*) can alter growing-season forage quality and quantity both on and off their colonies, exerting either competitive or facilitatory impacts on daily forage intake rates and mass gain of cattle (10,22,23,56). By contrast, in drought years on the Mongolian mountain steppes, overlap in use of forage grasses (*Stipa krylovii* and *Agropyron cristatum*) can lead to competition for food between Mongolian pika (*Ochotona pallasi*) and goats, sheep, and cattle, with potential negative impacts on livestock production (57). Given the ubiquity of small mammals, and their ability to strongly modify plant and soil properties via herbivory and ecosystem engineering, the impacts of small mammals on co-occurring large herbivores may be complex, resulting in either positive or negative outcomes which would benefit from further investigations.

The classic stress gradient hypothesis predicts an increase in the intensity of facilitation as environmental conditions become increasingly stressful (30), and this has been widely documented in plant communities (58,59). In contrast to this prediction, however, we found that facilitation between herbivores tends to occur in less (i.e., low- or moderate-density of pikas), rather than in more stressful environments (during pika population outbreaks). In an examination of wild ungulate-cattle interactions in African savannas, it has also been found that herbivore facilitation is greater in wet than in dry seasons (12). Similar facilitation was also reported between migratory grazers (14), between prairie dogs and cattle (23), and between snails and caterpillars (60) in habitats with moderate, but not limited resource levels. Our results, along with these prior studies, therefore suggest a different competition-facilitation balance in herbivore communities compared to those exhibited in plant communities (58,59). These observations also highlight the importance of population density in regulating competition-facilitation transitions in species interactions (31). More studies should performed to understand how herbivore interactions may change in strength and direction along stress gradients, which is key to predicting how herbivore communities assemble under global change.

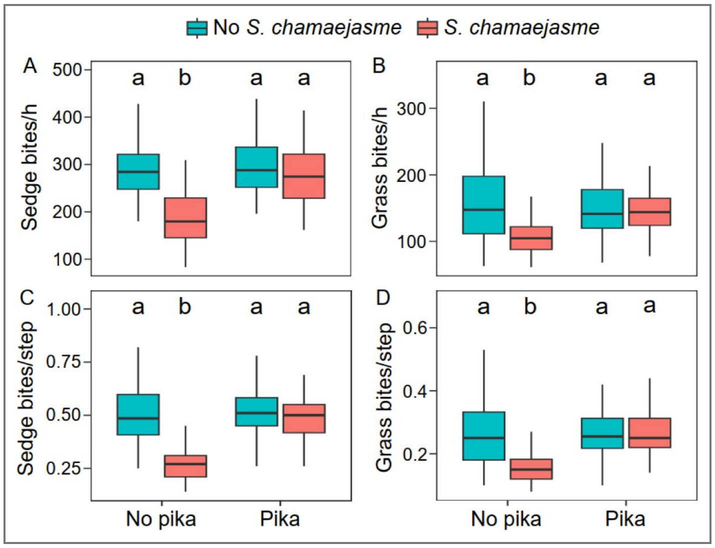

Figure 4. **Combined effects of two-year (2022–2023) pika and *Stellera* removal treatments on yak foraging efficiency in the field manipulative experiment.**

(**A**, **B**) Bite rates and (**C**, **D**) bites per step for sedges and grasses, respectively. Mean values from both years were used for analysis (one data point per 150 × 150 m plot). Significant interactions between pikas and *Stellera* were evaluated using post hoc tests; means not sharing letters differ significantly. Error bars indicate ± SE.

Our results reveal the importance of wild small herbivores in counteracting livestock grazing-induced vegetation imbalance in rangelands. Small herbivores have comparatively high metabolic demands and small gut capacities and often prefer dicotyledonous plants (e.g., forbs) with high concentration of nutrients (61-62). In contrast, larger herbivores such as livestock prefer monocotyledonous plants (e.g., grasses) because they can tolerate low plant nutrient contents but require a greater quantity of food (61-62). The coexistence of the small and large herbivores is therefore can lead to an "compensatory effect" on grass and forb biomass that helps to maintain a balance and diverse plant community (62), with importance consequences for ecosystem functioning and services. In our system, the widespread of *Stellera* across the Qinghai-Tibetan Plateau is itself a product of long-term grazing pressure, which suppresses palatable grasses and sedges while releasing unpalatable, stress-tolerant forbs (45,46). The pika's selective clipping of forbs helps promoting graminoid recovery, benefiting not only livestock production but may also other key rangeland functions (e.g., carbon storage and nutrient cycling) (41). Such modification effects of small herbivores, especially those colonial and hyper-abundant ones (e.g., rodents and insects), on large grazers' ecological functions may be more common and importance than previously perceived (7,55,63,64).

Collectively, our experiments provide empirical evidence that small mammals can facilitate large herbivores through altering vegetation properties. By suppressing tall poisonous forbs, plateau pikas improved forage composition and quality, increased yak foraging efficiency, and ultimately boosting yak weight gain. These findings overturn the dominant perception that small mammals act purely as rangeland pests (*27-29,37-39*) and reveal that small-bodied herbivores can contribute positively to pastoral systems when maintained at moderate densities. Our study examined pika–yak interactions only during the summer period, when food resources are most abundant. Whether such facilitative effects weaken or even shift toward competition under more stressful conditions—for example, when forage becomes limited during autumn or winter—remains to be tested.

Crucially, these insights carry direct policy relevance. Current rangeland management practices often rely heavily on rodenticides and other toxic compounds, leading to widespread small-mammal eradication (27-29,37-39). Our findings show that coexistence when small herbivorous mammals at low to moderate densities can enhance both livestock production and biodiversity. Recognizing and managing such facilitatory interactions between herbivore guilds supports international goals to integrate biodiversity conservation with food security and climate adaptation.

Rangeland policy should therefore move beyond pest eradication toward ecologically based management (28) that regulates herbivore populations through ecosystem processes and habitat managements. Such an approach embraces the full spectrum of herbivores—from rodents to megafauna to livestock—as contributors to multifunctional landscapes in the Anthropocene (67,68).

Materials and Methods

All pika and yak manipulations were carried out in accordance with the Law of the People's Republic of China on the Protection of Wildlife (1988).

Study system and background

We conducted the study at a grazing grassland in Menyuan County, Qinghai Province, China (37o48' N, 101o56' E, 3200 m a.s.l.). The site is located in the northeast Qinghai-Tibetan Plateau and has continental cold/humid climate conditions, with a summer rainy season and a winter dry season. The mean annual temperature is 4.2°C, and rainfall was 750 mm. The vegetation is typical of alpine meadows. The grassland is dominated by sedges such as *Kobresia* spp. (e.g., *K. humilis* and *K. graminifolia*), subdominant species include grasses such as *Elymus* spp. (i.e., *E. nutans*), *Festuca* spp. (e.g., *F. ovina*), and *Stipa* spp. (i.e., *S. aliena*), and companion species of forbs such as *Potentilla* spp. (e.g., *P. anserina* and *P. multifida*) and *Medicago ruthenica*. In recent decades, the poisonous *Stellera chamaejasme* forb, commonly named wolf poison, which is toxic to livestock, has encroached and has become a dominant plant owing to human disturbances and climate changes, competing with forage plants for shared resources such as light, soil water, and nutrients (45,46).

The plateau pika (*Ochotona curzoniae*) is a small (body length ca. 120-190 mm, and body weight ca. 110-170 g) lagomorph endemic to and dominant in the alpine meadows of the Qinghai-Tibetan Plateau (69). When populations outbreak, pika population densities can reach over 500-1000 active burrows per hectare (37-39). However, our study grassland hosts a moderate density (ca. 100-300 active burrows per hectare) of plateau pikas during the forage growing seasons (June to August), providing us with an ideal opportunity to investigate the effects of non-outbreak pika density on yak performance. Pikas live in social groups, breed during the warm summer and have lifespans about 120-250 days (69). The plateau pika is a keystone species due to the feeding, forb-clipping, and burrowing activities of individuals that exert profound effects on soils, plants, and other animals in the meadows (70). By selectively feeding on and clipping large dicotyledonous plants such as forbs (42,43), pikas occupy a different plant-food utilization niche compared with domestic livestock such as yaks and sheep, which often prefer monocotyledonous plants such as grasses and sedges (40,41). Besides pikas, other small mammals such as rabbits and zokors occur rarely in the area.

Tibetan yak (*Bos grunniens*) is the major ruminant species on the Tibetan rangelands due to the species' excellent adaptability and production performance (34). It is estimated that about 14 million domestic yaks live on the Tibetan Plateau, providing local herdsmen with daily necessities like meat, milk, wool, skins, fuel and economic benefit (35). In our study site, the grassland has been managed by pastoralism of domesticated yaks for years, and the grazing intensity is mainly controlled by pastoral practice.

Field survey #1: Diet preferences of pikas and yaks

In July (peak growing season) 2021, we investigated the diet/clipping selection of pikas and yaks in the study site. For pika feeding/clipping preferences, we randomly selected 10 2 m × 2 m plots separated by at least 100 m from each other in the study site. A large cage enclosure 1.5 m high and 2 m × 2 m bottom surface area, covered with a 5 × 5 mm plastic mesh window screen, was assigned to each plot. We then captured pikas nearby and placed one adult into each enclosure, allowing each animal to freely feed/clip plants within the cage for 20 min before it was released. We then laid out a 2 m linear transect in each cage plot consisting of 10 0.2 × 0.2 m quadrats. If vegetation had been consumed (i.e., plant tissues were removed and digested) or clipped (i.e., plant tissues were cut down and lay on the ground surface), we assigned that quadrat a value of one for that vegetation group (i.e., *Stellera*, sedges, grasses, and forbs); if there was no sign of consumption, a value of zero was assigned. Values assigned for each vegetation group were summed for the transect and divided by 10 to obtain a frequency of feeding/clipping use ranging from 0% to 100% (64). To document yak diet preferences, we placed 10 1 × 1 m quadrats on the ground at approximately 20 m intervals along 10 250 m transects that were randomly located on fresh grazing paths of yaks. We recorded and calculated how frequently different plant groups were grazed by yaks using the same methods as above.

Field survey #2: Associations among pikas, poisonous plants, and yak activities

In July 2021, we investigated the potential ecological interactions among pikas, poisonous plants, and yaks in the study site. We firstly selected 30 10 m × 10 m plots separated by at least 200 m from each other in the study site. The site was grazed by yaks at low to moderate intensity (i.e., 0.5-1.5 animal units/ha), with varying abundance of pikas and wolf poison *Stellera* forbs. Within each plot, we then assessed the abundance of pikas and *Stellera*, and foraging activities of yaks. We visually counted the number of active burrows (hole entrances characterized by clear openings, fresh soil or pika feces) to indicate pika abundance. For poisonous plant abundance, we visually estimated the percentage of the ground surface covered by *Stellera* in four 1 m × 1 m quadrats within each plot. For yaks, we recorded the number of dungs present in each plot, which is regarded a good measure for assaying grazing pressure in grasslands (71).

Field manipulative experiment: Interactive effects of pika and poisonous plants on yak performance

Experimental design.—In May 2022, we established four replicate blocks of experimental plots, for a total of 16 plots in a large area with similar plant community composition and pika densities (table S9). The site had not been disturbed by human activities (e.g., grazing or mowing) for two years prior to the initiation of the study. Each block had the following 2 × 2 factorial design: presence of pikas and poisonous plants, pikas only, poisonous plants only, and where neither pikas nor poisonous plants was present. Plot treatments were randomly assigned within each block. Minimum distances between the four replicate blocks of plots were 200 – 300 m. Each of the four plots in a replicate block was separated by 50 m, and each plot was 150 × 150 m. To avoid edge effects, we sampled plant, pika, and yak variables within the 100 × 100 m area at the center of each plot.

At the start of experimental treatments each year, we obtained 32 yak steers aged 2 years and weighing 115 kg ± 7.8 (SD) from adjacent and/or nearby pastures, and randomly grouped them into 16 herds of two yaks each. We then randomly allocated these yak herds to the 16 experimental plots (one herd/plot), creating a light to moderate grazing intensity recommended by local government guidelines, which often allow yak to maximize their growth rates (72). Electric fencing was used to confine yaks within the experimental plots. To align with their local grazing habits, yaks were allowed to graze daily in the experimental plots between 08:00 and 18:00, after which the animals were removed from the plots and housed in shelters overnight without feeding. All yaks had free access to fresh water and a mineral-lick block (Cangzhou Leysin Biotechnology Co., Ltd, Cangzhou, China) during the experimental period. Yak grazing under this regime continued for two growing seasons (June to August) in 2022 and 2023.

Pika treatments.—We installed exclosures to control pika populations in the plots. Initially, pikas were present on all plots, and the treatments with pika absence were implemented by removing pikas and preventing recolonization by fencing using an iron sheet around the perimeter of the plots. The iron sheet extended 0.60 m aboveground to prevent pikas jumping in or out, and was buried 1.5 m below the soil surface to deter animals from burrowing underneath.

In May 2022, after the establishment of the iron sheet fences, the pika exclusion treatments were initiated by removing pikas from the allocated experimental plots. Pikas were trapped using live traps and relocated elsewhere in the study site. Pika activities (e.g., number of active burrows) in the experimental plots were monitored monthly (June to August) thereafter, and pikas entering the exclosure plots were removed as necessary to maintain the exclusion treatments.

Poisonous plant treatments.—For the experimental plots without poisonous plants, we clipped and removed *Stellera* forbs using garden clippers. To simulate the clipping activities of pikas, we clipped only those large *Stellera* forbs with a height exceeding 20 cm, as these are often preferred by pikas and can exert significant impacts on the plant community and on yak grazing behaviors (Z.Z., field observations). We removed these poisonous plants once a month from June to August. For the experimental plots with poisonous plants, *Stellera* forbs were left intact.

Yak body growth and grazing activity.—During the growing seasons (June to August) in 2022 and 2023, we recorded the initial and final body weights (Weighbridge, Shanghai Jiujin Electronics Apparatus Co. Shanghai, China) of yaks each month to calculate their average daily weight gain. Each month, we also observed the grazing activities of each yak for six 2-hour focal periods. During these observations, we recorded the number of bites that the yaks took on different forage plant groups (i.e., sedges, grasses, and forbs) and the number of steps they took. The foraging efficiency of yaks on each plant group (bites/step) was calculated as the number of bites on specific plant group/the total number of steps during the observations (52).

Forage quantity and quality.—From June to August, along with the measurements of yak behavior and attributes as described above, we assessed how the food resources of yaks changed in the experimental plots each month. To assess forage quantity, we randomly assigned ten 1 × 1 m quadrats spaced at least 10 m from each other, and recorded the percentage of the ground surface covered by each plant group (i.e., *Stellera*, sedges, grasses, and forbs). To assess forage quality, forage samples were collected to quantify their nutritive values. To obtain a sample of forage apparently consumed by yaks, we tracked and observed yak foraging activities along their grazing paths, and used the hand-plucking technique to collect the corresponding plants species and tissues that were consumed by animals (73). Forage sub-samples from different plant species and tissues were pooled into a single forage sample within each plot, which was then dried at 60 ° C for 48 h in a forced-air drying oven, milled using a 1-mm mesh, and stored in plastic bags for subsequent analyses.

We analysed forage samples for crude protein (CP), acid detergent fibre (ADF), and neutral detergent fibre (NDF). Total nitrogen content was determined by the Kjeldahl method (2300; Foss Tecator AB, Hoganas, Sweden) using selenium as the catalyst, and CP was calculated as 6.25 × nitrogen. ADF and NDF were analysed with an automatic fibertec apparatus (M6, Foss Tecator AB, Hoganas, Sweden) by the method of Van Soest et al. (1991) (74).

Statistical analyses

All data were analyzed using linear models, generalized linear mixed models, or generalized additive models, with the choice of model and statistical family guided by the structure and distribution of the data. Post-hoc comparisons were conducted only when the pika × *Stellera* interaction term was significant. For the 2021 field surveys, we fitted generalized linear mixed models with plot and month as random effects. We then used generalized additive mixed models for the cover abundance of *Stellera* and active pika burrow density, with plot as a random effect, and linear regression models for dung density and *Stellera* cover. For the field manipulation experiments in 2022 and 2023, we constructed generalized linear mixed models with the dependent variables regressed against the interactive effect of pika and *Stellera* treatments, while including block, year, and month as random effects to capture the hierarchical structure of the data. Models assumed Gaussian, beta (for proportions), or Tweedie (for non-normal data) distributions, selected based on data type and model fit. A significance threshold of $P = 0.05$ was applied, with Tukey-HSD or Sidak post-hoc tests used where appropriate. All data management, modeling, and visualization approaches were carried out in R, with dependencies managed using *renv*. The main modeling packages were *glmmTMB* and *mgcv*, with *DHARMa* used for model diagnostics. Data management relied on the *tidyverse* suite of packages. A complete record of package versions is available in the renv.lock file in the repository Zenodo (75): *https://doi.org/10.5281/zenodo.18290921*.

Supplementary Materials

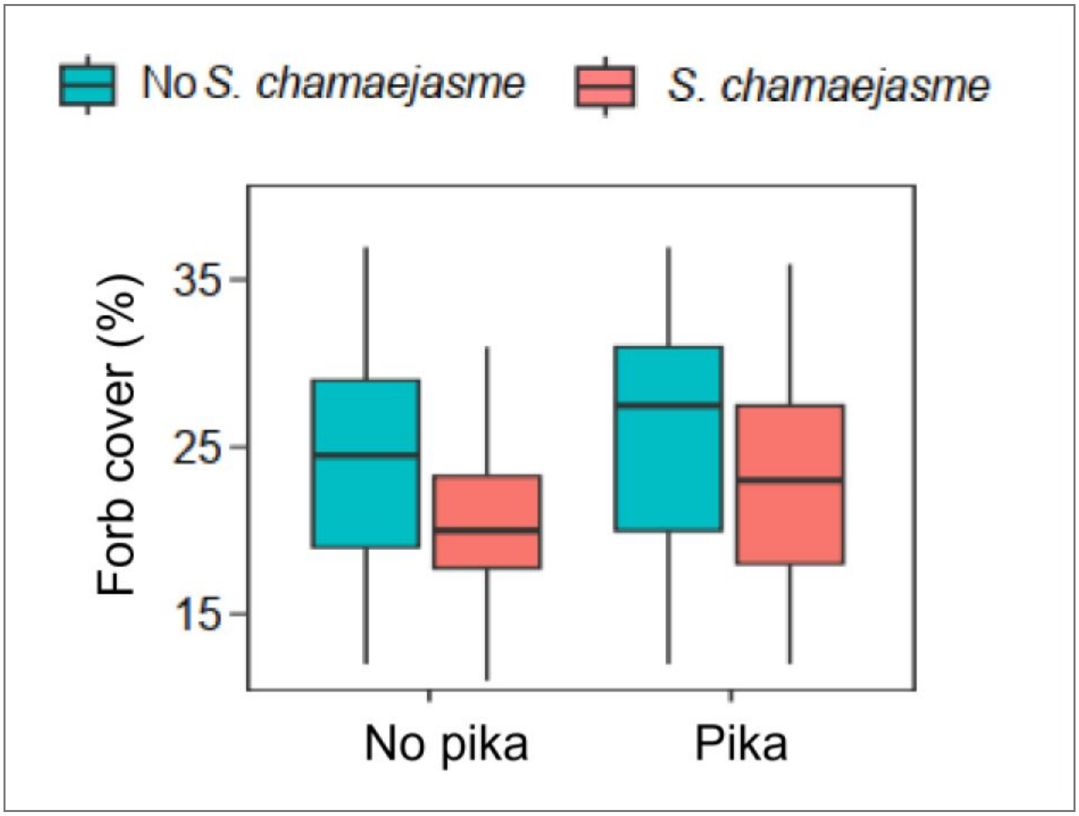

Figure S1. Combined effects of two-year (2022–2023) pika and *Stellera* removal on forb cover in the field manipulative experiment. The average values of each variable in the two years were used for statistical analysis, providing a single data point for each variable in each 150 × 150 m plot. Error bars represent ± SE.

Figure S2. Combined effects of two-year (2022–2023) pika and *Stellera* removal on foraging efficiency of yaks in the field manipulative experiment.

(**A**) bite rates and (**B**) bites per step of yaks for forbs, respectively. The average values of each variable in the two years were used for statistical analysis, providing a single data point for each variable in each 150 × 150 m plot. Error bars represent ± SE.

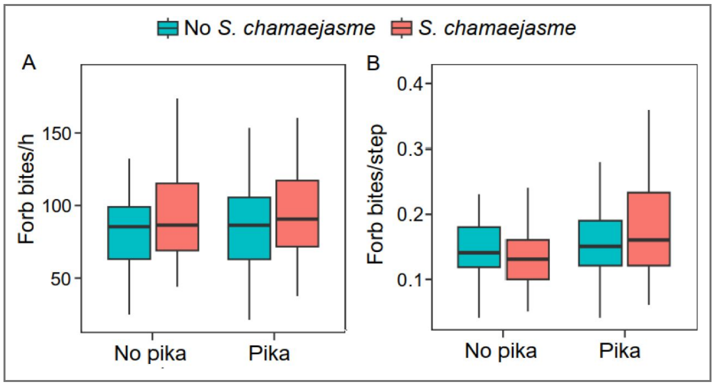

Table S1. Model summary for diet and clipping selections of pikas and yaks in the field surveys in July 2021.

Effect	Term	Estimate	SE	Statistic	*P*
		Pika feeding/clipping			
Fixed	(Intercept)	36.33	3.24	11.23	**<0.001**
Fixed	Grasses	-21.67	4.39	-4.94	**<0.001**
Fixed	*S. chamaejasme*	23.67	4.39	5.39	**<0.001**
Fixed	Sedges	-18.67	4.39	-4.25	**<0.001**
Random	Plot	<0.001	NA	NA	NA
Random	Month	1.58	NA	NA	NA
Random	Residual	17.00	NA	NA	NA
		Yak grazing			
Fixed	(Intercept)	16.33	3.23	5.05	**<0.001**
Fixed	Grasses	58.00	4.24	13.68	**<0.001**
Fixed	Sedges	29.00	4.24	6.84	**<0.001**
Random	Transect	3.83	NA	NA	NA
Random	Month	<0.001	NA	NA	NA
Random	Residual	16.42	NA	NA	NA

Contrast	**Estimate**	**SE**	**df**	***t* ratio**	***P***
Pika feeding/clipping					
Forbs−Grasses	21.67	4.39	113.00	4.94	**<0.001**
Forbs−*S. chamaejasme*	-23.67	4.39	113.00	-5.39	**<0.001**
Forbs−Sedges	18.67	4.39	113.00	4.25	**<0.001**
Grasses−*S. chamaejasme*	-45.33	4.39	113.00	-10.33	**<0.001**
Grasses−Sedges	-3.00	4.39	113.00	-0.68	0.90
S. chamaejasme−Sedges	42.33	4.39	113.00	9.64	**<0.001**
Yak grazing					
Forbs−Grasses	-58.00	4.24	84.00	-13.68	**<0.001**
Forbs−Sedges	-29.00	4.24	84.00	-6.84	**<0.001**
Grasses−Sedges	29.00	4.24	84.00	6.84	**<0.001**

Table S2. Model contrasts for diet and clipping selections of pikas and yaks in the field surveys in July 2021.

Effect	Term	Estimate	SE	Statistic	*P*
	Pika burrow density				
Fixed	(Intercept)	20.21	17.10	1.18	0.24
Fixed	Pika	149.67	22.01	6.80	**<0.001**
Fixed	*S. chamaejasme*	−2.42	22.01	−0.11	0.91
Fixed	Pika × *S. chamaejasme*	28.42	31.13	0.91	0.36
Random	Block	14.20	NA	NA	NA
Random	Month	<0.001	NA	NA	NA
Random	Residual	76.24	NA	NA	NA
	Yak weight gain				
Fixed	(Intercept)	0.32	0.03	10.80	**<0.001**
Fixed	Pika	0.01	0.01	0.74	0.46
Fixed	*S. chamaejasme*	−0.11	0.01	−7.70	**<0.001**
Fixed	Pika × *S. chamaejasme*	0.13	0.02	6.63	**<0.001**
Random	Block	0.01	NA	NA	NA
Random	Year	0.01	NA	NA	NA
Random	Month	0.05	NA	NA	NA
	***S. chamaejasme* cover**				
Fixed	(Intercept)	−3.44	0.26	−13.39	**<0.001**
Ffixed	Pika	−0.11	0.22	−0.49	0.62
Fixed	*S. chamaejasme*	2.25	0.17	12.91	**<0.001**
Fixed	Pika × *S. chamaejasme*	−1.15	0.25	−4.58	**<0.001**
Random	Block	0.16	NA	NA	NA
Random	Year	0.17	NA	NA	NA
Random	Month	0.24	NA	NA	NA
	Grass cover				
Fixed	(Intercept)	−1.11	0.10	−11.58	**<0.001**
Fixed	Pika	−0.09	0.10	−0.90	0.37

Table S3. **Model summary for interactive effects of pikas and *S. chamaejasme* on pika burrow density, yak weight gain, *S. chamaejasme* cover, grass cover, sedge cover, and forb cover in the field manipulative experiment in 2022-2023.**

Fixed	*S. chamaejasme*	−0.88	0.11	−7.76	**<0.001**
Fixed	Pika × *S. chamaejasme*	0.90	0.15	5.97	**<0.001**
Random	Block	0.13	NA	NA	NA
Random	Year	<0.001	NA	NA	NA
Random	Month	0.02	NA	NA	NA
		Sedge cover			
Fixed	(Intercept)	0.02	0.08	0.32	0.75
Fixed	Pika	0.12	0.08	1.50	0.13
Fixed	*S. chamaejasme*	−0.27	0.08	−3.51	**<0.001**
Fixed	Pika × *S. chamaejasme*	0.19	0.11	1.77	0.08
Random	Block	0.08	NA	NA	NA
Random	Year	<0.001	NA	NA	NA
Random	Month	0.06	NA	NA	NA
		Forb cover			
Fixed	(Intercept)	−1.12	0.11	−10.56	**<0.001**
Fixed	Pika	0.05	0.10	0.50	0.62
Fixed	*S. chamaejasme*	−0.22	0.10	−2.21	**0.03**
Fixed	Pika × *S. chamaejasme*	0.09	0.14	0.65	0.52
Random	Block	0.10	NA	NA	NA
Random	Year	0.09	NA	NA	NA
Random	Month	<0.001	NA	NA	NA

Table S3. (continued)

Contrast	Estimate	SE	df	*t* ratio	*P*
Yak weight gain					
No pika+No *S. chamaejasme*−Pika+No *S. chamaejasme*	−0.01	0.01	184.00	−0.74	0.88
No pika+No *S. chamaejasme*−No pika+*S. chamaejasme*	0.11	0.01	184.00	7.70	**<0.001**
No pika+No S. chamaejasme−Pika+*S. chamaejasme*	−0.03	0.01	184.00	−2.42	0.08
Pika+No *S. chamaejasme*−No pika+*S. chamaejasme*	0.12	0.01	184.00	8.44	**<0.001**
Pika+No *S. chamaejasme*−Pika+*S. chamaejasme*	−0.02	0.01	184.00	−1.68	0.34
No pika+*S. chamaejasme*−Pika+*S. chamaejasme*	−0.14	0.01	184.00	−10.12	**<0.001**
***S. chamaejasme* cover**					
No pika+No *S. chamaejasme*−Pika+No *S. chamaejasme*	NA	0.24	Inf	NA	0.96
No pika+No *S. chamaejasme*−No pika+*S. chamaejasme*	NA	0.02	Inf	NA	**<0.001**
No pika+No S. chamaejasme−Pika+*S. chamaejasme*	NA	0.07	Inf	NA	**<0.001**
Pika+No *S. chamaejasme*−No pika+*S. chamaejasme*	NA	0.02	Inf	NA	**<0.001**
Pika+No *S. chamaejasme*−Pika+*S. chamaejasme*	NA	0.06	Inf	NA	**<0.001**
No pika+*S. chamaejasme*−Pika+*S. chamaejasme*	NA	0.46	Inf	NA	**<0.001**
Grass cover					
No pika+No *S. chamaejasme*−Pika+No *S. chamaejasme*	NA	0.11	Inf	NA	0.81
No pika+No *S. chamaejasme*−No pika+*S. chamaejasme*	NA	0.27	Inf	NA	**<0.001**
No pika+No S. chamaejasme−	NA	0.11	Inf	NA	0.90

Table S4. Model contrasts for pika burrow density, yak weight gain, *S. chamaejasme* cover, and grass cover in the field manipulative experiment in 2022-2023.

Table S4. (continued)

Pika+*S. chamaejasme*					
Pika+No *S. chamaejasme*– No pika+*S. chamaejasme*	NA	0.25	Inf	NA	**<0.001**
Pika+No *S. chamaejasme*– Pika+*S. chamaejasme*	NA	0.10	Inf	NA	1.00
No pika+*S. chamaejasme*– Pika+*S. chamaejasme*	NA	0.05	Inf	NA	**<0.001**

Table S5. Model summary for interactive effects of pikas and *S. chamaejasme* on crude protein (CP) %, acid detergent fibre (ADF) %, and neutral detergent fibre (NDF) % of total forage in the field manipulative experiment in 2022-2023.

Effect	Term	Estimate	SE	Statistic	*P*
		CP			
Fixed	(Intercept)	−2.39	0.02	−107.03	**<0.001**
Fixed	Pika	0.03	0.02	1.88	0.06
Fixed	*S. chamaejasme*	−0.15	0.02	−8.72	**<0.001**
Fixed	Pika × *S. chamaejasme*	0.13	0.02	5.45	**<0.001**
Random	Block	0.01	NA	NA	NA
Random	Year	<0.001	NA	NA	NA
Random	Month	0.03	NA	NA	NA
		ADF			
Fixed	(Intercept)	−0.82	0.03	−32.36	**<0.001**
Fixed	Pika	0.01	0.02	0.46	0.65
Fixed	*S. chamaejasme*	−0.06	0.02	−3.14	**<0.001**
Fixed	Pika × *S. chamaejasme*	0.08	0.03	2.84	**<0.001**
Random	Block	0.03	NA	NA	NA
Random	Year	<0.001	NA	NA	NA
Random	Month	0.03	NA	NA	NA
		NDF			
Fixed	(Intercept)	0.51	0.02	27.44	**<0.001**
Fixed	Pika	0.03	0.03	1.03	0.30
Fixed	*S. chamaejasme*	−0.05	0.02	−2.03	**0.04**
Fixed	Pika × *S. chamaejasme*	0.02	0.04	0.61	0.54
Random	Block	0.01	NA	NA	NA
Random	Year	<0.001	NA	NA	NA
Random	Month	<0.001	NA	NA	NA

Contrast	Estimate	SE	df	*t* ratio	*P*
CP					
No pika+No *S. chamaejasme*–Pika+No *S. chamaejasme*	NA	0.02	Inf	NA	0.24
No pika+No *S. chamaejasme*–No pika+*S. chamaejasme*	NA	0.02	Inf	NA	**<0.001**
No pika+No S. chamaejasme–Pika+*S. chamaejasme*	NA	0.02	Inf	NA	0.91
Pika+No *S. chamaejasme*–No pika+*S. chamaejasme*	NA	0.02	Inf	NA	**<0.001**
Pika+No *S. chamaejasme*–Pika+*S. chamaejasme*	NA	0.02	Inf	NA	0.61
No pika+*S. chamaejasme*–Pika+*S. chamaejasme*	NA	0.01	Inf	NA	**<0.001**
ADF					
No pika+No *S. chamaejasme*–Pika+No *S. chamaejasme*	NA	0.02	Inf	NA	0.97
No pika+No *S. chamaejasme*–No pika+*S. chamaejasme*	NA	0.02	Inf	NA	**<0.001**
No pika+No S. chamaejasme–Pika+*S. chamaejasme*	NA	0.02	Inf	NA	0.54
Pika+No *S. chamaejasme*–No pika+*S. chamaejasme*	NA	0.02	Inf	NA	**<0.001**
Pika+No *S. chamaejasme*–Pika+*S. chamaejasme*	NA	0.02	Inf	NA	0.82
No pika+*S. chamaejasme*–Pika+*S. chamaejasme*	NA	0.02	Inf	NA	**<0.001**

Table S6. Model contrasts for crude protein (CP) % and acid detergent fibre (ADF) % of total forage in the field manipulative experiment in 2022-2023.

Effect	Term	Estimate	SE	Statistic	*P*
		Grass bites/h			
Fixed	(Intercept)	151.72	7.49	20.25	**<0.001**
Fixed	Pika	−0.80	8.61	−0.09	0.93
Fixed	*S. chamaejasme*	−45.34	8.61	−5.27	**<0.001**
Fixed	Pika × *S. chamaejasme*	43.95	12.17	3.61	**<0.001**
Random	Block	4.78	NA	NA	NA
Random	Year	5.17	NA	NA	NA
Random	Month	0.00	NA	NA	NA
Random	Residual	42.16	NA	NA	NA
		Sedge bites/h			
Fixed	(Intercept)	5.65	0.04	138.78	**<0.001**
Fixed	Pika	0.04	0.04	0.92	0.36
Fixed	*S. chamaejasme*	−0.42	0.05	−8.71	**<0.001**
Fixed	Pika × *S. chamaejasme*	0.35	0.06	5.51	**<0.001**
Random	Block	0.04	NA	NA	NA
Random	Year	0.02	NA	NA	NA
Random	Month	0.03	NA	NA	NA
		Forb bites/h			
Fixed	(Intercept)	4.39	0.07	65.12	**<0.001**
Fixed	Pika	0.07	0.07	1.06	0.29
Fixed	*S. chamaejasme*	0.13	0.07	1.90	0.06
Fixed	Pika × *S. chamaejasme*	−0.04	0.10	−0.44	0.66
Random	Block	0.06	NA	NA	NA
Random	Year	0.00	NA	NA	NA
Random	Month	0.05	NA	NA	NA
		Grass bites/step			
Fixed	(Intercept)	−1.01	0.08	−13.16	**<0.001**
Fixed	Pika	0.02	0.09	0.19	0.85
Fixed	*S. chamaejasme*	−0.60	0.10	−6.28	**<0.001**

Table S7. **Model summary for interactive effects of pikas and *S. chamaejasme* on yak bite rate (bites/h) and the bite to step ratio (bites/step) for grasses, sedges, and forbs in the field manipulative experiment in 2022-2023.**

Fixed	Pika × *S. chamaejasme*	0.67	0.13	5.15	**<0.001**
Random	Block	0.03	NA	NA	NA
Random	Year	0.06	NA	NA	NA
Random	Month	0.00	NA	NA	NA
Sedge bites/step					
Fixed	(Intercept)	0.04	0.14	0.28	0.78
Fixed	Pika	0.08	0.12	0.67	0.50
Fixed	*S. chamaejasme*	−0.95	0.12	−7.61	**<0.001**
Fixed	Pika × *S. chamaejasme*	1.01	0.17	5.83	**<0.001**
Random	Block	0.17	NA	NA	NA
Random	Year	0.08	NA	NA	NA
Random	Month	0.06	NA	NA	NA
Forb bites/step					
Fixed	(Intercept)	−1.76	0.09	−18.74	**<0.001**
Fixed	Pika	0.06	0.09	0.64	0.52
Fixed	*S. chamaejasme*	−0.05	0.09	−0.49	0.63
Fixed	Pika × *S. chamaejasme*	0.24	0.13	1.83	0.07
Random	Block	0.11	NA	NA	NA
Random	Year	0.00	NA	NA	NA
Random	Month	0.07	NA	NA	NA

Table S7. (continued)

Contrast	Estimate	SE	df	*t* ratio	***P***
Grass bites/h					
No pika+No *S. chamaejasme*– Pika+No *S. chamaejasme*	0.80	8.61	184.00	0.09	1.00
No pika+No *S. chamaejasme*– No pika+*S. chamaejasme*	45.34	8.61	184.00	5.27	**<0.001**
No pika+No *S. chamaejasme*– Pika+*S. chamaejasme*	2.19	8.61	184.00	0.25	0.99
Pika+No *S. chamaejasme*– No pika+*S. chamaejasme*	44.54	8.61	184.00	5.18	**<0.001**
Pika+No *S. chamaejasme*– Pika+*S. chamaejasme*	1.39	8.61	184.00	0.16	1.00
No pika+*S. chamaejasme*– Pika+*S. chamaejasme*	−43.15	8.61	184.00	−5.01	**<0.001**
Sedge bites/h					
No pika+No *S. chamaejasme*– Pika+No *S. chamaejasme*	NA	0.04	Inf	NA	0.80
No pika+No *S. chamaejasme*– No pika+*S. chamaejasme*	NA	0.07	Inf	NA	**<0.001**
No pika+No S. chamaejasme– Pika+*S. chamaejasme*	NA	0.04	Inf	NA	0.94
Pika+No *S. chamaejasme*– No pika+*S. chamaejasme*	NA	0.08	Inf	NA	**<0.001**
Pika+No *S. chamaejasme*– Pika+*S. chamaejasme*	NA	0.05	Inf	NA	0.45
No pika+*S. chamaejasme*– Pika+*S. chamaejasme*	NA	0.03	Inf	NA	**<0.001**
Grass bites/step					
No pika+No *S. chamaejasme*– Pika+No *S. chamaejasme*	NA	0.09	Inf	NA	1.00
No pika+No *S. chamaejasme*– No pika+*S. chamaejasme*	NA	0.17	Inf	NA	**<0.001**
No pika+No S. chamaejasme–	NA	0.08	Inf	NA	0.79

Table S8. **Model contrasts for yak bite rate (bites/h) and the bite to step ratio (bites/step) on grasses and sedges in the field manipulative experiment in 2022-2023.**

Table S8. (continued)

Pika+*S. chamaejasme*					
Pika+No *S. chamaejasme*– No pika+*S. chamaejasme*	NA	0.18	Inf	NA	**<0.001**
Pika+No *S. chamaejasme*– Pika+*S. chamaejasme*	NA	0.08	Inf	NA	0.88
No pika+*S. chamaejasme*– Pika+*S. chamaejasme*	NA	0.05	Inf	NA	**<0.001**
Sedge bites/step					
No pika+No *S. chamaejasme*– Pika+No *S. chamaejasme*	NA	0.11	Inf	NA	0.91
No pika+No *S. chamaejasme*– No pika+*S. chamaejasme*	NA	0.32	Inf	NA	**<0.001**
No pika+No S. chamaejasme– Pika+*S. chamaejasme*	NA	0.10	Inf	NA	0.66
Pika+No *S. chamaejasme*– No pika+*S. chamaejasme*	NA	0.35	Inf	NA	**<0.001**
Pika+No *S. chamaejasme*– Pika+*S. chamaejasme*	NA	0.11	Inf	NA	0.96
No pika+*S. chamaejasme*– Pika+*S. chamaejasme*	NA	0.04	Inf	NA	**<0.001**

Table S9. **Summary statistics from generalized linear mixed effects models testing for pre-treatment differences in response variables representing plant community composition (cover by group) and diversity in designated mesocosm locations, as measured in 2021 prior to initiation of pika (±) and *S. chamaejasme* (±) treatments.**

	Pika		*S. chamaejasme*		Pika × *S. chamaejasme*	
	F^*	*P*	F^*	*P*	F^*	*P*
S. chamaejasme cover	0.53	0.519	0.75	0.451	0.30	0.620
Grass cover	0.95	0.402	0.69	0.467	0.01	0.930
Sedge cover	0.08	0.801	0.11	0.760	0.60	0.494
Forb cover	0.70	0.464	0.01	0.950	0.24	0.659
Species richness	3.08	0.177	1.28	0.340	0.02	0.902
Pika burrow density	0.14	0.737	0.85	0.426	0.05	0.842

* df = 1 and 3.

Data availability

A complete record of package versions is available in the renv.lock file in the repository Zenodo (75): *https://doi.org/10.5281/zenodo.18290921* .

Additional information

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Peer reviews

Reviewer #1 (Public review):

Summary:

This is important and significant work because it helps describe the complexity of interactions between system components where two herbivores interact with vegetation. Whereas other studies have shown that the larger ungulate (yaks, Bos grunniens, in this case) can facilitate the abundance and population growth of the smaller (the semi-fossorial lagomorph, Ochotona curzoniae, plateau pika hereafter), this study flips the tables and shows that, at least under some conditions, moderate densities of the plateau facilitate the nutritional condition of yaks.

The study was not designed to investigate the reasons that pikas clip Stellera chamaejasme. That said, based on other studies and general knowledge of the ecology of these pikas, it is likely that they clip (although do not eat) this plant because its relatively large size hinders predator detection. This species of pika does better where vegetation height is low than where it is higher.

Strengths:

Notably, the strong inference the authors can claim for their results is supported by the careful experimental design. A weaker paper would have simply noted correlations between pika burrow density and yak feeding efficiency without experimental removal. This paper, to its credit, not only used experimental removals but also documented the various intermediary results that support the ultimate conclusions. The statistical approaches used appear to be appropriate. (Readers are encouraged to read the full Materials and Methods, which are available in the Supplementary Materials section.)

Weaknesses:

Although the study was well designed and executed, and its conclusions appear strongly supported, readers interested in the management implications of the Qinghai-Tibetan Plateau should be mindful of its limitations. First, the study site, at approximately 3,200 m elevation, was relatively low by Qinghai-Tibetan Plateau standards. Stellera chamaejasme becomes less common at elevations > 4,000 m, where a majority of livestock grazing occurs. Thus, it would be instructive to learn, through follow-up studies, whether similar facilitation occurs where unpalatable (and mildly poisonous) species in such genera as Astragalus, Oxytropis, and Thermopsis replace S. chamaejasme as the problematic plant for pastoralists. Second, the authors make no mention of wild ungulates, so it is unclear what, if any, role they may have played in this system. At least one study in Qinghai Province, albeit at a slightly higher elevation, showed that not only pikas, but also Tibetan gazelles (Procapra picticaudata), which were commonly observed on grazed pastures, grazed more frequently on some dicots avoided by domestic sheep than did the livestock themselves (Harris et al. 2015). It would also be instructive to learn if similar facilitation as observed here applied to the other principal livestock species in the area, domestic sheep (which are often herded together with smaller numbers of domestic goats). Finally, as suggested by this study, the interactions between all components of the system are complex and interactive. If pika facilitation of yak nutrition at the densities documented results in herders increasing yak density, might the increased herbivory from the domestic animals provide the conditions for the pika population to increase beyond the densities observed here, and thus toward the levels where facilitation yields to competition?

Citation:

Harris RB, Wang, WY, Badinqiuying , Smith AT, Bedunah DJ (2015) Herbivory and Competition of Tibetan Steppe Vegetation in Winter Pasture: Effects of Livestock Exclosure and Plateau Pika Reduction. PLoS ONE 10(7): e0132897. doi:10.1371/journal.pone.0132897

https://doi.org/10.7554/eLife.111340.1.sa2

Reviewer #2 (Public review):

Summary:

This study uses a combination of field sampling and manipulative experiments to test for facilitative impacts of pikas on yaks via suppression of a poisonous forb. The authors found that, when Stellera forbs were present, yak weight increases over the growing season were greater in the presence of pikas compared to in their absence. This occurred because, although pikas do not consume Stellera, they clip it and use it in nest/burrow construction, thereby decreasing its relative abundance in the plant community. Thus, overall, the study contributes to our understanding of how herbivores of different size classes indirectly affect each other via the use of shared resources.

Strengths:

It is well known that large herbivores on grasslands impact smaller animals, but the reciprocal interaction is rarely tested. Thus, this study asks a valuable question, and the experiment is well-designed to test it. The authors also do a good job of demonstrating the potential conservation impacts of their research.

Weaknesses:

What the authors tested is really cool, but their claims go far beyond what they can say based on their experimental design. For example, the authors claim to show that pika impacts on yaks display density-dependent transitions from competition to facilitation. However, their experiment only looked at the presence (at moderate densities) and absence of pikas, and they only tested for facilitation, not competition.

The paper would also benefit from changes to the framing in the introduction and discussion. For example, the authors pitch the work as a test of the stress-gradient hypothesis. However, there is no abiotic stress gradient in the study, which is an essential component of the SGH. They also pitch the work in terms of density dependence, but there is no significant variation in population densities beyond the presence-absence binary. The paper would be stronger if they focused their framing around the literature on facilitative interactions across mammals of different size classes, especially indirect facilitation via use of shared resources, which is what this paper is really about.

Finally, the paper has significant weaknesses in the experimental and statistical methodology. Most importantly, there are inconsistencies in what is visualized in the figures compared to the model results. For example, the results section in several places notes a lack of significant interaction terms in the model but shows interactions in the p-values on the figures. The authors also plot smoothed lines rather than their model results and then draw interpretations from those lines that cannot be tested in the models that they used. There are also missing details that are important for model interpretation, including the distributions used and the sample sizes. Another major concern with experimental design is in the forage nutrient analyses. The authors picked plants along a grazing trail, then measured nutrient content without standardizing based on plant species, so any differences across treatments could be because of what they happened to grab rather than overall forage quality.

https://doi.org/10.7554/eLife.111340.1.sa1

Author response:

> ***eLife Assessment***
>
> *This important study provides evidence that plateau pikas, at moderate densities, can facilitate yak nutrition by suppressing a poisonous plant, offering a helpful perspective on reciprocal interactions between small mammal ecosystem engineers and large herbivores. The evidence is solid, supported by a manipulative field experiment and appropriate measurements of intermediary ecological processes, although some claims about density dependence, competition, and stress-gradient mechanisms are not fully supported by the experimental design. The work will be of interest to ecologists, conservation biologists, and rangeland managers, particularly those studying grassland herbivore interactions and livestock management on the Qinghai-Tibetan Plateau.*

Thank you very much for these positive assessments of our work, below we provided the point-by-point responses to the comments from the 2 peer reviewers, and we hope these revisions are satisfied.

> ***Reviewer #1 (Public review):***
>
> *Summary:*
>
> *This is important and significant work because it helps describe the complexity of interactions between system components where two herbivores interact with vegetation. Whereas other studies have shown that the larger ungulate (yaks, Bos grunniens, in this case) can facilitate the abundance and population growth of the smaller (the semi-fossorial lagomorph, Ochotona curzoniae, plateau pika hereafter), this study flips the tables and shows that, at least under some conditions, moderate densities of the plateau facilitate the nutritional condition of yaks.*
>
> *The study was not designed to investigate the reasons that pikas clip Stellera chamaejasme. That said, based on other studies and general knowledge of the ecology of these pikas, it is likely that they clip (although do not eat) this plant because its relatively large size hinders predator detection. This species of pika does better where vegetation height is low than where it is higher.*
>
> *Strengths:*
>
> *Notably, the strong inference the authors can claim for their results is supported by the careful experimental design. A weaker paper would have simply noted correlations*

> *between pika burrow density and yak feeding efficiency without experimental removal. This paper, to its credit, not only used experimental removals but also documented the various intermediary results that support the ultimate conclusions. The statistical approaches used appear to be appropriate. (Readers are encouraged to read the full Materials and Methods, which are available in the Supplementary Materials section.)*

We appreciate these positive comments on our work.

> *Weaknesses:*
>
> *Although the study was well designed and executed, and its conclusions appear strongly supported, readers interested in the management implications of the Qinghai-Tibetan Plateau should be mindful of its limitations. First, the study site, at approximately 3,200 m elevation, was relatively low by Qinghai-Tibetan Plateau standards. Stellera chamaejasme becomes less common at elevations > 4,000 m, where a majority of livestock grazing occurs. Thus, it would be instructive to learn, through follow-up studies, whether similar facilitation occurs where unpalatable (and mildly poisonous) species in such genera as Astragalus, Oxytropis, and Thermopsis replace S. chamaejasme as the problematic plant for pastoralists.*

Agree! We will acknowledge this limitation in the Discussion, by adding the paragraph below (see the Third point):

“Despite of these, several questions remain deserve further investigation. First, our study examined pika–yak interactions only during the summer period, when food resources are most abundant. Whether such facilitative effects weaken or even shift toward competition under more stressful conditions—for example, when forage becomes limited during autumn or winter—remains to be tested. Second, if pika facilitation of yak nutrition at the densities documented results in herders increasing yak density, might the increased herbivory from the domestic animals provide the conditions for the pika population to increase beyond the densities observed here, and thus toward the levels where facilitation yields to competition (Yang et al., 2026)? Third, our study site located at approximately 3,200 m elevation, was relatively low by Qinghai-Tibetan Plateau standards. *Stellera* becomes less common at elevations > 4,000 m, where a majority of livestock grazing occurs. It would be instructive to learn, through follow-up studies, whether similar facilitation occurs where unpalatable (and mildly poisonous) species in such genera as *Astragalus*, *Oxytropis*, and *Thermopsis* replace *Stellera* as the problematic plants for pastoralists (Lu et al., 2012; Li and Zhao, 2025). Finally, it is unclear whether similar facilitation as observed here applied to the other principal livestock species in the area, such as domestic sheep and goats.”

> *Second, the authors make no mention of wild ungulates, so it is unclear what, if any, role they may have played in this system. At least one study in Qinghai Province, albeit at a slightly higher elevation, showed that not only pikas, but also Tibetan gazelles (Procapra picticaudata), which were commonly observed on grazed pastures, grazed more frequently on some dicots avoided by domestic sheep than did the livestock themselves (Harris et al. 2015). Citation:*
>
> *Harris RB, Wang, WY, Badinqiuying , Smith AT, Bedunah DJ (2015) Herbivory and Competition of Tibetan Steppe Vegetation in Winter Pasture: Effects of Livestock Exclosure and Plateau Pika Reduction. PLoS ONE 10(7): e0132897.*
>
> *doi:10.1371/journal.pone.0132897*

Agree! We will add more details about the study site, particularly regarding wild ungulates, in the Methods section. Specifically, we will include the following sentence: “Wild ungulates, such as Tibetan gazelles (*Procapra picticaudata*) (Harris et al., 2015), and other small mammals such as rabbits and zokors, occur rarely in the area.” This key reference will also be cited in this section.

> *It would also be instructive to learn if similar facilitation as observed here applied to the other principal livestock species in the area, domestic sheep (which are often herded together with smaller numbers of domestic goats).*

Agree! The same as mentioned above. We will acknowledge this limitation in the Discussion, by adding the paragraph below (see the Final point):

“Despite of these, several questions remain deserve further investigation. First, our study examined pika–yak interactions only during the summer period, when food resources are most abundant. Whether such facilitative effects weaken or even shift toward competition under more stressful conditions—for example, when forage becomes limited during autumn or winter—remains to be tested. Second, if pika facilitation of yak nutrition at the densities documented results in herders increasing yak density, might the increased herbivory from the domestic animals provide the conditions for the pika population to increase beyond the densities observed here, and thus toward the levels where facilitation yields to competition (Yang et al., 2026)? Third, our study site located at approximately 3,200 m elevation, was relatively low by Qinghai-Tibetan Plateau standards. *Stellera* becomes less common at elevations > 4,000 m, where a majority of livestock grazing occurs. It would be instructive to learn, through follow-up studies, whether similar facilitation occurs where unpalatable (and mildly poisonous) species in such genera as *Astragalus*, *Oxytropis*, and *Thermopsis* replace *Stellera* as the problematic plants for pastoralists (Lu et al., 2012; Li and Zhao, 2025). Finally, it is unclear whether similar facilitation as observed here applied to the other principal livestock species in the area, such as domestic sheep and goats.”

> *Finally, as suggested by this study, the interactions between all components of the system are complex and interactive. If pika facilitation of yak nutrition at the densities documented results in herders increasing yak density, might the increased herbivory from the domestic animals provide the conditions for the pika population to increase beyond the densities observed here, and thus toward the levels where facilitation yields to competition?*

Agree! The same as mentioned above. We will acknowledge this limitation in the Discussion, by adding the paragraph below (see the Second point):

“Despite of these, several questions remain deserve further investigation. First, our study examined pika–yak interactions only during the summer period, when food resources are most abundant. Whether such facilitative effects weaken or even shift toward competition under more stressful conditions—for example, when forage becomes limited during autumn or winter—remains to be tested. Second, if pika facilitation of yak nutrition at the densities documented results in herders increasing yak density, might the increased herbivory from the domestic animals provide the conditions for the pika population to increase beyond the densities observed here, and thus toward the levels where facilitation yields to competition (Yang et al., 2026)? Third, our study site located at approximately 3,200 m elevation, was relatively low by Qinghai-Tibetan Plateau standards. *Stellera* becomes less common at elevations > 4,000 m, where a majority of livestock grazing occurs. It would be instructive to learn, through follow-up studies, whether similar facilitation occurs where unpalatable (and mildly poisonous) species in such genera as *Astragalus*, *Oxytropis*, and *Thermopsis* replace *Stellera* as the problematic plants for pastoralists (Lu et al., 2012; Li and Zhao, 2025). Finally, it is unclear whether similar facilitation as observed here applied to the other principal livestock species in the area, such as domestic sheep and goats.”

> ***Reviewer #2 (Public review):***

> *Summary:*
>
> *This study uses a combination of field sampling and manipulative experiments to test for facilitative impacts of pikas on yaks via suppression of a poisonous forb. The authors found that, when Stellera forbs were present, yak weight increases over the growing season were greater in the presence of pikas compared to in their absence. This occurred because, although pikas do not consume Stellera, they clip it and use it in nest/burrow construction, thereby decreasing its relative abundance in the plant community. Thus, overall, the study contributes to our understanding of how herbivores of different size classes indirectly affect each other via the use of shared resources.*
>
> *Strengths:*
>
> *It is well known that large herbivores on grasslands impact smaller animals, but the reciprocal interaction is rarely tested. Thus, this study asks a valuable question, and the experiment is well-designed to test it. The authors also do a good job of demonstrating the potential conservation impacts of their research.*

We appreciate these positive comments on our work.

> *Weaknesses:*
>
> *What the authors tested is really cool, but their claims go far beyond what they can say based on their experimental design. For example, the authors claim to show that pika impacts on yaks display density-dependent transitions from competition to facilitation. However, their experiment only looked at the presence (at moderate densities) and absence of pikas, and they only tested for facilitation, not competition. The paper would also benefit from changes to the framing in the introduction and discussion. For example, the authors pitch the work as a test of the stress-gradient hypothesis. However, there is no abiotic stress gradient in the study, which is an essential component of the SGH. They also pitch the work in terms of density dependence, but there is no significant variation in population densities beyond the presence-absence binary. The paper would be stronger if they focused their framing around the literature on facilitative interactions across mammals of different size classes, especially indirect facilitation via use of shared resources, which is what this paper is really about.*

We agree that our work had explored only the facilitative effects of pikas on yaks, rather than the density-dependent balance between competition and facilitation, and the Stress Gradient Hypothesis (SGH).

We plan to make the major revisions below to address this important concern.

(1) We will revise the title as “Moderate density of small mammalian herbivores facilitates livestock growth in grasslands ”.

(2) We will delete all the statements about density-dependent transition of facilitation and competition and the SGH in the Abstract, Introduction, Discussion, and the References sections.

> *Finally, the paper has significant weaknesses in the experimental and statistical methodology. Most importantly, there are inconsistencies in what is visualized in the figures compared to the model results. For example, the results section in several places notes a lack of significant interaction terms in the model but shows interactions in the p-values on the figures.*

In the Results section, there are only two locations where we discussed non-significant interactions: Line 148–149 “Pikas and *Stellera* had no interactive effects on abundance of sedges, forbs, and neutral detergent fiber (NDF) of total forage for yaks (Fig. 3F,I, fig. S1, table S3,5).” and Line 161–162 “Pikas and *Stellera* had no interactive effects on yaks’ foraging efficiency on forbs (fig. S2, table S7).”.

We have cross-checked both the manuscript as submitted and the website, and in every instance we are consistent in not reporting interactions as non-significant when the model output shows significance.

We will confirm these details in the revised version as “Pikas and Stellera had no interactive effects on abundance of sedges, forbs, and neutral detergent fiber (NDF) of total forage for yaks (Fig. 3F,I, Fig. S1, Table S5, S8). ”; and “Pikas and Stellera had no interactive effects on yaks’ foraging efficiency on forbs (Fig. S2, Table S10).” in the Results section.

> *The authors also plot smoothed lines rather than their model results and then draw interpretations from those lines that cannot be tested in the models that they used.*

Agree! There are only two figures in which we used generalized additive models (GAMs) to plot smoothed lines: Figure 2C and Figure 3C.

For Figure 2C, the supplementary table for the GAMM associated with the smoothed line was not originally included, but we will add it as Table S4 in the revised version. For Figure 3C, we explicitly fit a GAMM corresponding to the plotted line, and the model results will be reported in the Table S7 in the revised version.

> *There are also missing details that are important for model interpretation, including the distributions used and the sample sizes.*

Agree! We will provide the Table S13 to summarize all statistical models used in the study, including the distributions used and the sample sizes in the Supplementary Materials. We will also add a sentence of “A summary of all statistical models used in the study is available in table S13.” in the Statistical analyses section to indicate this information.

> *Another major concern with experimental design is in the forage nutrient analyses. The authors picked plants along a grazing trail, then measured nutrient content without standardizing based on plant species, so any differences across treatments could be because of what they happened to grab rather than overall forage quality.*

We will revise this section to provide more details on how forage samples were collected and their quality were analyzed. Specifically, five forage samples were collected per grazing plot, focusing on the two dominant plant species —one sedge and one grass—that were most frequently grazed by yaks. To ensure comparability across plots and treatments, we mixed the two species at equal dry mass (5 g). We will revise this section as below.

“To assess forage quality, five forage samples were collected from each grazing plot to quantify their nutritive values. To obtain samples that reflect the forage actually consumed by yaks, we tracked the animals along their grazing paths and collected the plant tissues of the two most frequently consumed species: the dominant sedge *Kobresia humilis* and the dominant grass *Elymus nutans* (Fig. 2B; Pan et al., 2019). The collected tissues of each species were dried in a forced-air oven at 60 °C for 48 h, then ground through a 1-mm mesh. Subsequently, 5 g of each dried and ground species were combined in a 1:1 dry mass ratio, and the resulting mixture was stored in plastic bags for subsequent analyses.”

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