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Small mammalian herbivores at moderate densities facilitate 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 **convincing**, supported by a manipulative field experiment and appropriate measurements of intermediary ecological processes. The work will be of interest to ecologists, conservation biologists, and rangeland managers, particularly those studying grassland herbivore interactions and livestock management.

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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. Although large herbivores can significantly affect the smaller ones, the reversal effect is largely unknown. 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 the presence of pikas facilitates weight gains of yaks (*Bos grunniens*) by improving vegetation composition at a moderate density level. Compared to the pika-present treatment, pika removal dramatically increased cover of the poisonous *Stellera* forbs by two-fold, reducing the abundance and protein content of palatable grasses and sedges, yak foraging efficiency, and yak weight gain by up to 42%. Notably, we found a humped relationship between yak weight gains and pika burrow densities in the pika-present plots; the facilitative effect of pikas on yaks was highest at about 200 burrows/ha, but shifted to a competitive effect at pika densities exceeding 400 burrows/ha. These results provide the first empirical evidence that maintaining a moderate density of small mammalian herbivores can benefit growth performance of livestock by improving vegetation composition. Our study highlights the significance of moderate populations of ecosystem-engineering small mammals in sustaining pastoral productivity in rangelands.

Introduction

Both large and small mammalian herbivores are key consumers in grasslands worldwide, exerting profound impacts on ecosystem structure and functions (Dickman, 1999; Keesing, 2000; Davidson et al., 2012; Ripple et al., 2015; Pringle et al., 2023; Barbero-Palacios et al., 2024; Lundgren et al., 2024). They have co-evolved with grasslands and with each other over millions of years, but how these mammals co-exist remains poorly understood (Smith and Foggin, 1999; Detling, 2006; Davidson et al., 2010; Li et al., 2019; Speakman et al., 2021). 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 (Arsenault and Owen-Smith, 2002; Odadi et al., 2011; Augustine and Springer, 2013; Barrio et al., 2013; Zhong et al., 2014; Harris et al., 2015; Anderson et al., 2024). 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 (Keesing, 1998; Smit et al., 2001; Bakker et al., 2009; Munoz et al, 2009; Badingqiuying et al., 2018; Wang et al., 2019; Trepel et al., 2024), whereas the potential for reverse effects have received little attention (Detling 2006; Wang et al., 2020; Augustine and Derner, 2021; Augustine et al., 2024).

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 (Jones et al., 1994; Smith and Foggin, 1999; Zhang et al., 2003; Davidson et al., 2012; Augustine et al., 2023). Through their feeding, clipping, and burrowing activities they profoundly alter vegetation and soil properties, with potential cascading effects on co-occurring large herbivores (Detling, 2006; Davidson et al., 2012; Wang et al., 2020; Augustine and Derner, 2021; Augustine et al., 2024). 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 (Zhang and Wang, 1998; Dickman, 1999; Singleton et al., 2010; Singleton et al., 1999). However, it remains unclear whether the competitive effects of outbreaks of small mammalian herbivores on livestock diminish or even shift to facilitation when the smaller species are at lower, non-outbreak levels as predicted by the ecological nonmonotonicity theory (Zhang et al., 2015). Livestock grazing currently uses ~77% of global agricultural land, and sustains billions of people worldwide (Maestre et al., 2022). 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 (Long et al., 2008). These herds are vital to pastoral livelihoods and key ecosystem functions across the region' s 2.5 million km² expanse (Dong et al., 2020). 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 (Fan et al., 1998, 1999; Smith and Foggin, 1999; Delibes-Mateos et al., 2011). 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 (Fan et al., 1998, 1999; Zhang et al., 1999). 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 (Pan et al., 2019; Li et al., 2023), whereas pikas prefer to clip and feed on the leaves of dicotyledonous plants (Jiang and Xia 1985; Liu et al., 2008). Thus, whether plateau pikas and yaks compete for pasture largely may depend on their diets and population densities.

In line with global trends in weed invasions in rangelands (DiTomaso, 2000), intensive livestock grazing and other human disturbances have facilitated grassland degradation on the Qinghai-Tibet Plateau, creating opportunities for the proliferation of toxic weeds (Lu et al., 2012). Among these, the *Stellera chamaejasmehas* become a predominant species, now covering approximately 20 million hectares, as it outcompetes palatable grasses and sedges while thriving under grazing pressure (Li and Zhao, 2025). The expansion of this poisonous plant species on the Qinghai-Tibetan Plateau poses a dual threat to livestock, either by causing direct toxicity (Keeler et al., 2013) or by reducing forage availability through competition with palatable species for light and soil nutrients (Lu et al., 2012; Li and Zhao, 2025). However, plateau pikas may indirectly benefit yak foraging by selectively clipping large plants (Liu et al., 2019; Zhang et al., 2020), especially those poisonous forbs such as *S. chamaejasme* (Fan et al., 1998) (Fig. 1)—a behavior that reduces predation risk (Dickman, 2022; Zhong et al., 2022) 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 consumed greater proportions of grasses and sedges (Fig. 2A,B, Table S1, S2), supporting findings of previous studies (Jiang and Xia, 1985; Fan et al., 1998; Liu et al., 2008; Pan et al., 2019; Li et al., 2023). 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, Table S3) and with yak foraging activity, as indicated by dung density (R^2 = 0.43, P < 0.001; Fig. 2D, Table S4).

In the manipulative field experiment, pika removal led to a 90% reduction in the number of active burrows per hectare, with 182.9 ± 24.5 burrows/ha in pika-present plots compared to 19.0 ± 1.6 burrows/ha in the pika-absent plots (Fig. 3A, Table S5). In the presence of *Stellera*, pika absence reduced daily weight gains of yaks by 42% compared to those in the pika-present treatment, but such effects disappeared once *Stellera* was removed (Fig. 3B, Table S5, S6). Notably, yak weight gains exhibited a hump-shaped relationship with pika densities, with the

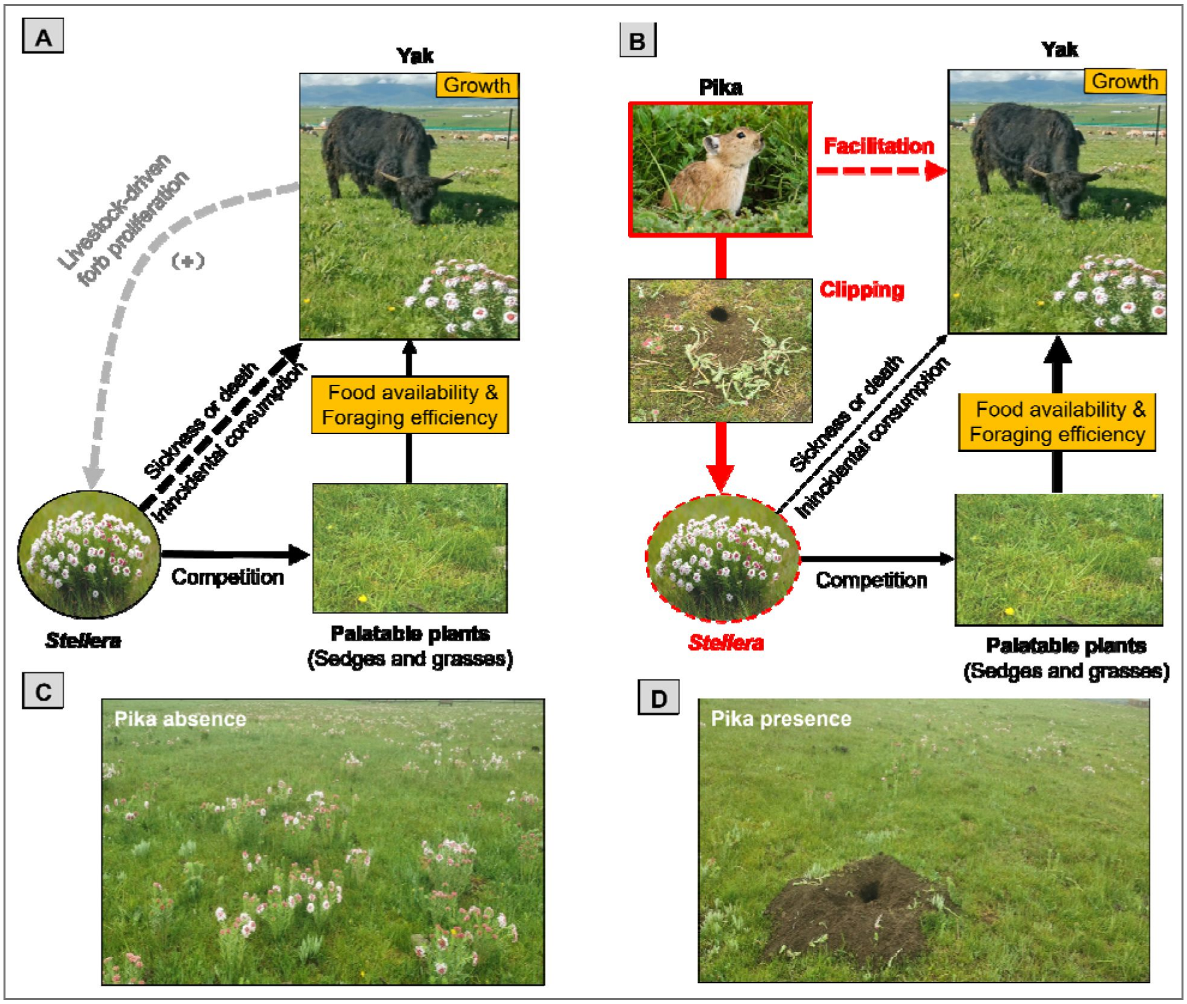

Figure 1. **Conceptual diagram of the hypothesized facilitative effects of pikas (*Ochotona curzoniae*) on yak (*Bos grunniens*) growth performance on the Qinghai-Tibetan Plateau.**

(**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).

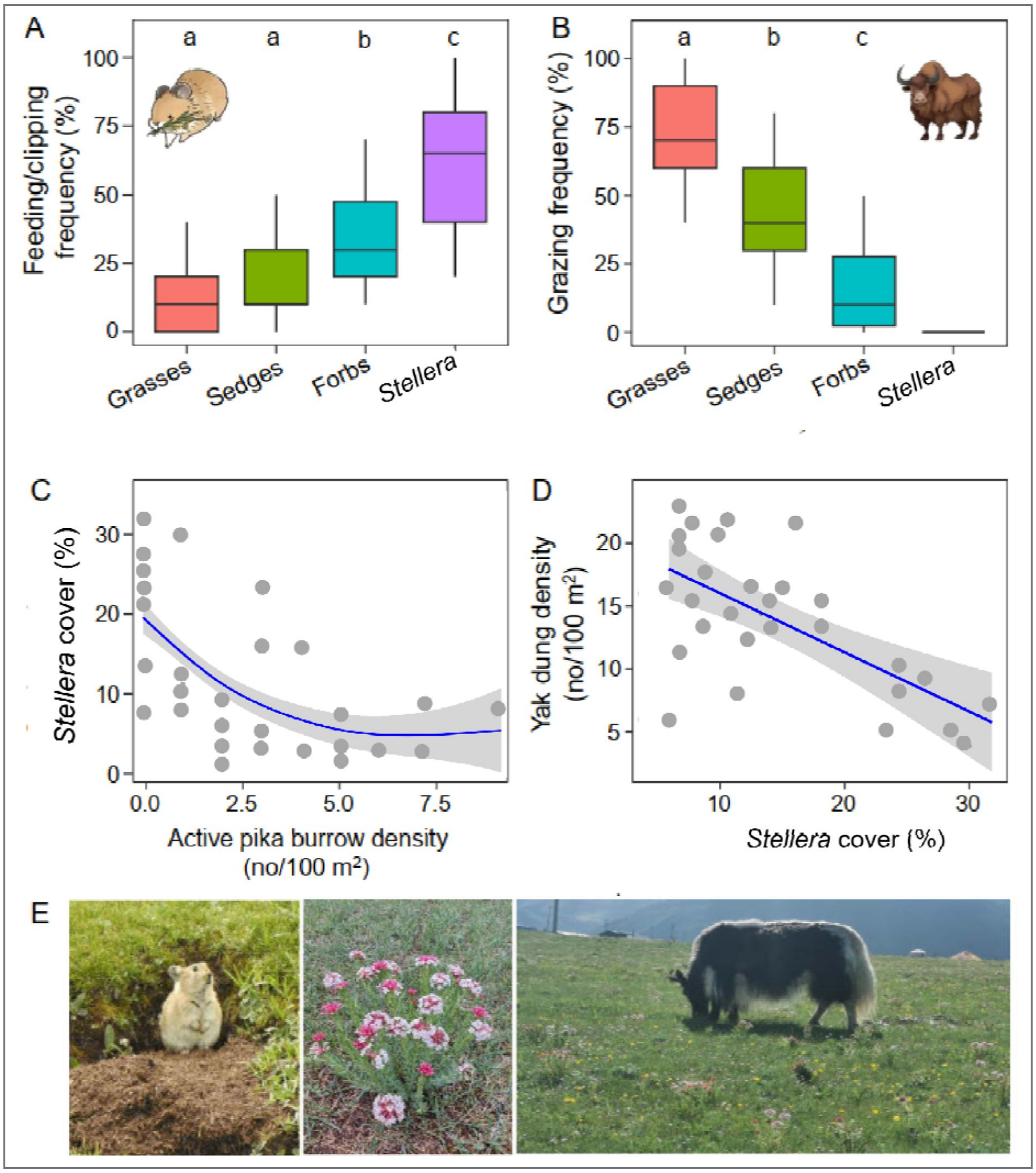

Figure 2. **Diet selection of pikas and yaks and their potential interactions mediated by poisonous plants based on field surveys in July 2021.**

(**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).

highest growth at about 200 active burrows/ha, after which, yak growth decreased linearly as pika density increased (R^2 = 0.75, P < 0.001; Fig. 3C, Table S7). Weight gain was ~ 0.3 kg/yak/day at zero pika density, peaked at ~0.4 kg/yak/day around 200 burrows/ha, and fell below the baseline when pika density exceeded 400 burrows/ha. These data indicate that pikas facilitated yak weight gains by up to 30% across 0-400 burrows/ha, with maximum benefit at ~ 200 burrows/ha, whereas higher pika densities (> 400 burrows/ha) suppressed yak weight gains. The pika-yak facilitation peak and the facilitation-competition transition therefore occur at approximately 200 and 400 burrows/ha of pika density levels, respectively.

In the presence of *Stellera*, pika removal increased the cover abundance of this forb by two-fold (Fig. 3D, Table S5, S6), which led to decreases of 50% and 15% in cover abundances of co-occurring grasses and sedges, respectively (Fig. 3E,F, Table S5, S6). These shifts in vegetation composition also reduced the nutritional value of the major available forage for yaks, with decreases of 14% in crude protein (CP) content and 6% in acid detergent fiber (ADF) content in the pika-absent treatment compared with the pika-present treatment (Fig. 3G,H, Table S8, S9).

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). These results suggest that, in the presence of *Stellera*, pikas facilitate yak growth by suppressing poisonous plants, increasing both the availability and quality of palatable food plants 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 (Odadi et al., 2009). In the presence of *Stellera*, sedge bite rate and sedge bites per step of yaks significantly decreased by 32% and 46%, respectively (Fig. 4A,C, Table S10, S11), and grass bite rate and grass bites per step decreased similarly by 29% and 43% (Fig. 4B,D, Table S10, S11), in the pika-absent treatment compared to pika-present treatment. These decreases in yak foraging efficiency in the absence of pikas can be attributed to the increases in cover of the poisonous *Stellera* (Fig. 3D), which often act as a grazing deterrent and reduce access by yaks to palatable food items. Pikas and *Stellera* had no interactive effects on yaks' foraging efficiency on forbs (Fig. S2, Table S10).

Discussion

By combining field surveys and manipulative experiments, we have demonstrated that pikas—when occurring at moderate densities—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 reconcile debates on the effects of pikas on yak production through changing vegetation properties. These observations provide new insights into how small and large mamamlian herbivores co-exist in a complex way in nature.

Ecosystem engineering is a key mechanism driving interspecific facilitation (Jones et al., 1994; Bruno et al., 2003; Machicote et al., 2004). Engineering activities of one herbivore species can indirectly benefit another by either increasing access to food resources or ameliorating abiotic conditions in particular habitats (Arsenault and Owen-Smith, 2002; Odadi et al., 2011; Zhong et al., 2014; Pan et al., 2019). 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-I). We speculate that these improvements in food availability and nutrition for yaks may be due to the release of grasses and sedges from competition with the poisonous forbs for limiting above- and below-ground resources (Lu et al., 2012; Li and Zhao, 2025). 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 (Lu et al., 2012; Li and Zhao, 2025), which can cause biochemical or physiological stresses in yaks that lead to sickness or even death (Keeler et al., 2013).

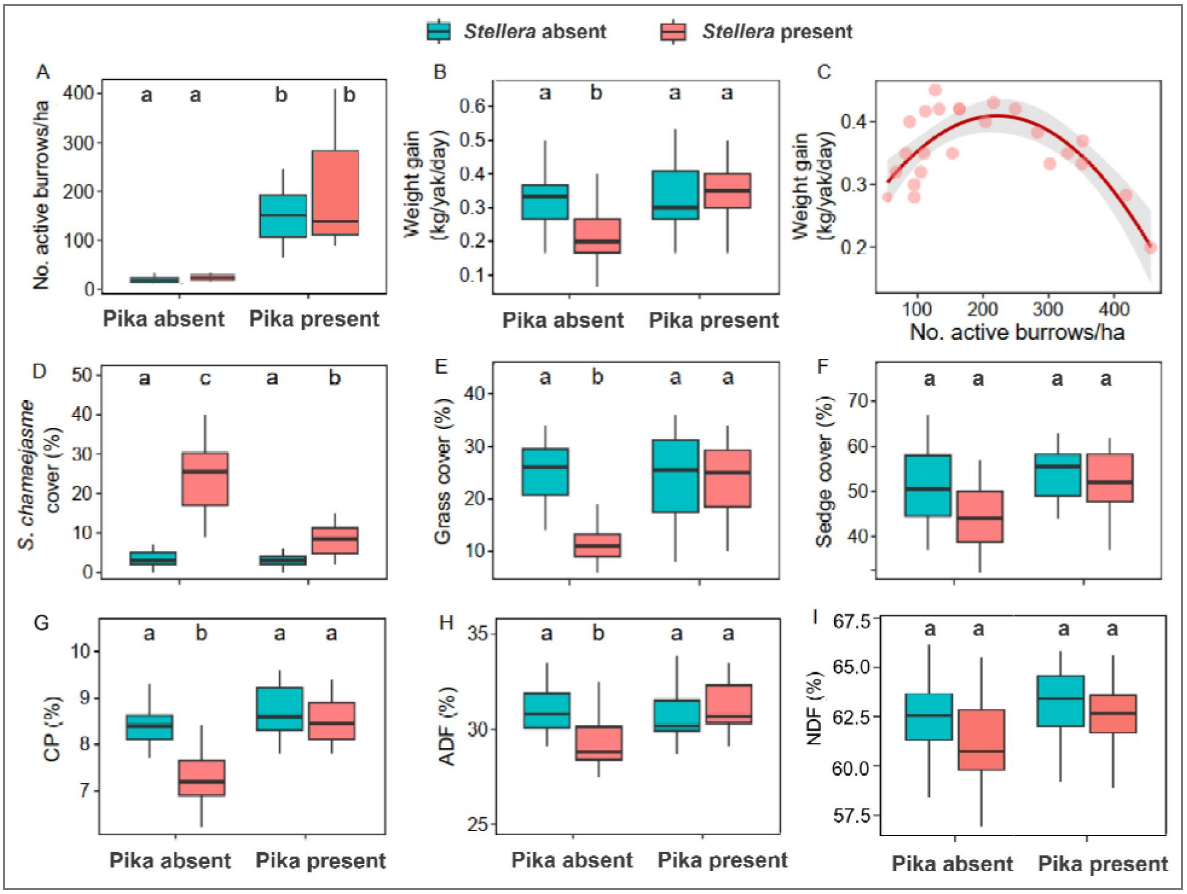

Figure 3. Combined effects of two-year (2022–2023) pika and *Stellera* removal treatments on yak growth, forage quantity, and quality in the field manipulative experiment.

(**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 fiber (ADF) content, and (**I**) neutral detergent fiber (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 S5). Error bars indicate ± SE.

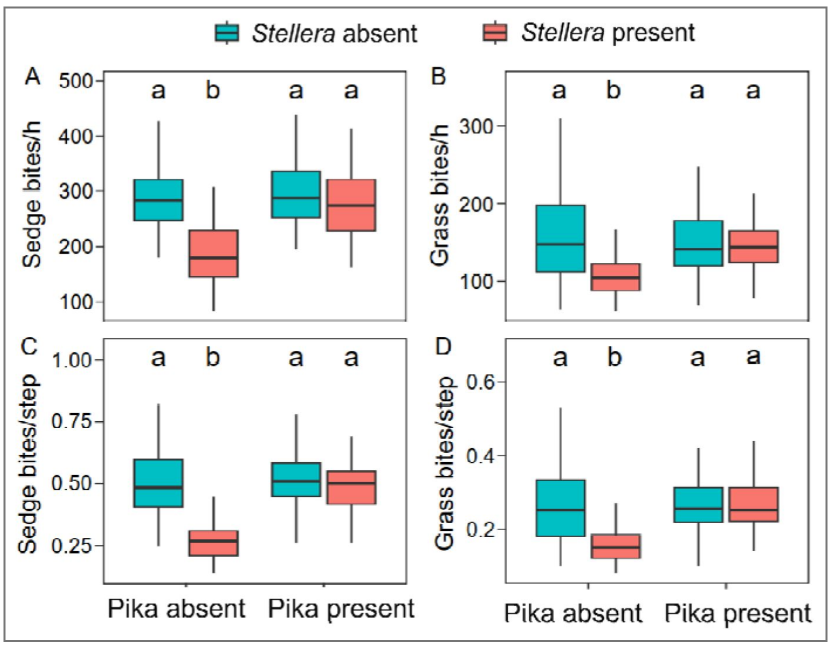

Figure 4. **Combined effects of two-year (2022–2023) pika and *Stellera* removal treatments on yak foraging efficiency in the field manipulative experiment.**

(**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 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 (O'Meilia et al., 1982; Detling 2006; Augustine and Derner, 2021; Augustine et al., 2024). 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 (Retzer, 2007). 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.

Our results reveal the importance of wild small herbivores in counteracting livestock grazing-induced vegetation imbalance in rangelands. The coexistence of a diverse of herivore species with different diet selections and size classes can lead to an "compensatory effect" on grass and forb biomass that helps to maintain a balance and diverse plant community (Ritchie and Olff, 1999), 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 (Lu et al., 2012; Li and Zhao, 2025). 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) (Lu et al., 2012; Li et al., 2023; Li and Zhao, 2025). 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 (Davidson et al., 2010, 2012; Goheen et al., 2010; Clark et al., 2012; Zhong et al., 2014).

Because of the natural variations in pika density in the pika-present treatment, we were able to obtain a hump-shaped relationship between yak weight gains and pika burrow densities in these plots. Compared with the absence of pikas, the facilitative effect reached its maximum at approximately 200 burrows/ha but became competitive at densities exceeding 400 burrows/ha (Fig. 3C). This result reveals that pika density modulates the net outcome for yak weight gain, with a facilitation peak at ~200 burrows/ha and a competition onset above 400 burrows/ha. Our findings offer empirical evidence for the non-monotonicity theory, under which the competition-facilitation balance varies with population density: facilitation dominates at low densities, competition at high densities, and these density-dependent shifts may underpin community stability and productivity (Zhang, 2003; Zhang et al., 2015). The theory further holds that the facilitation threshold, not the competition-facilitation transition, is the critical factor governing the stability of interacting species or communities (Zhang et al., 2015).

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 reconcile the debate that small mammalian herbivores act as rangeland pests in outbreaking years and as beneficial ecological engineers in non-outbreaking years (Fan et al., 1998, 1999; Zhang and Wang, 1998; Singleton et al., 1999, 2010; Smith and Foggin, 1999; Delibes-Mateos et al., 2011). Our study demonstrates that small mammalian herbivores enhance pastoral systems at moderate densities but impair them at high densities. Thus, at burrow densities below 400 burrows/ha, no pika population management is required in the study region.

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 the documented facilitation of yaks by pikas prompts herders to increase yak densities, could the resulting rise in livestock herbivory push pika populations beyond the levels observed here, potentially toward the threshold where facilitation gives way 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 applies to the other principal livestock species in the area, such as domestic sheep and goats.

Current rangeland management practices often rely heavily on rodenticides and other toxic compounds, leading to widespread small-mammal eradication (Fan et al., 1998, 1999; Zhang and Wang, 1998; Singleton et al., 1999, 2010). Our findings show that coexistence when small herbivorous mammals at low to moderate densities can enhance livestock growth performance. 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 from pest eradication toward ecologically based management (Singleton et al., 1999) that regulates herbivore populations through ecosystem processes and habitat management. Such an approach embraces the full spectrum of herbivores—from rodents to megafauna to livestock—as contributors to multifunctional landscapes in the Anthropocene (cf. Svenning et al., 2024).

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 (37°48' N, 101°56' 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 (Lu et al., 2012; Li and Zhao, 2025).

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 (Qu et al., 2013). When populations outbreak, pika population densities can reach over 500-1000 active burrows per hectare (Fan et al., 1998,1999; Zhang et al., 1999). 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 (Qu et al., 2013). 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 (Smith et al., 2019). By selectively feeding on and clipping large dicotyledonous plants such as forbs (Jiang and Xia, 1985; Liu et al., 2008), 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 (Pan et al., 2019; Li et al., 2023). Notably, pikas often clip (although do not eat) the poisonous *S. chamaejasmehas* because its relatively large size hinders predator detection (Fan et al., 1998). This species of pika prefer habitats where vegetation height is low than where it is higher. 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.

Tibetan yak (*Bos grunniens*) is the major ruminant species on the Tibetan rangelands due to the species' excellent adaptability and production performance (Long et al., 2008). 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 (Dong et al., 2020). 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. Before cage installation, we carefully checked the plants within each plot and removed those that had been previously grazed or damaged by herbivores. 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% (Clark et al., 2012). To document yak diet composition, 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 facilitation of pikas on yaks mediated by the poisonous *Stellera* forbs under unmanipulated field conditions 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 intensities (i.e., 0.5-1.5 animal units/ha), with varying abundance of pikas and the poisonous *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 (Eldridge et al., 2025).

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 with similar plant community composition and pika densities in the study site (Table S12). 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 ± 7.8 kg 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 (Dong et al., 2003). 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. For the no-pika treatment, pikas were trapped once every two weeks using 30 live traps (25 cm high × 25 cm wide × 40 cm long) within each plot 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 behavior of pikas, we clipped only those *Stellera* forbs exceeding 20 cm in height. This threshold was chosen based on previous observations that pikas preferentially target large forbs of this size (Liu et al., 2009). 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 (Odadi et al., 2009).

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, 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.

We analysed forage samples for crude protein (CP), acid detergent fiber (ADF), and neutral detergent fiber (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).

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. There were two models that used the tweedie family (forb and sedge bite rate). We chose to use tweedie because a normal gaussian family model fitted the results poorly. 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* (Brooks et al., 2017) and *mgcv* (Wood, 2017), with *DHARMa* (Hartig, 2022) used for model diagnostics. Data management relied on the *tidyverse* (Wickham et al., 2019) suite of packages. A summary of all statistical models used in the study is available in Table S13. A complete record of package versions is available in the renv.lock file in the repository Zenodo: *https://doi.org/10.5281/zenodo.18290921*.

Supplementary Materials

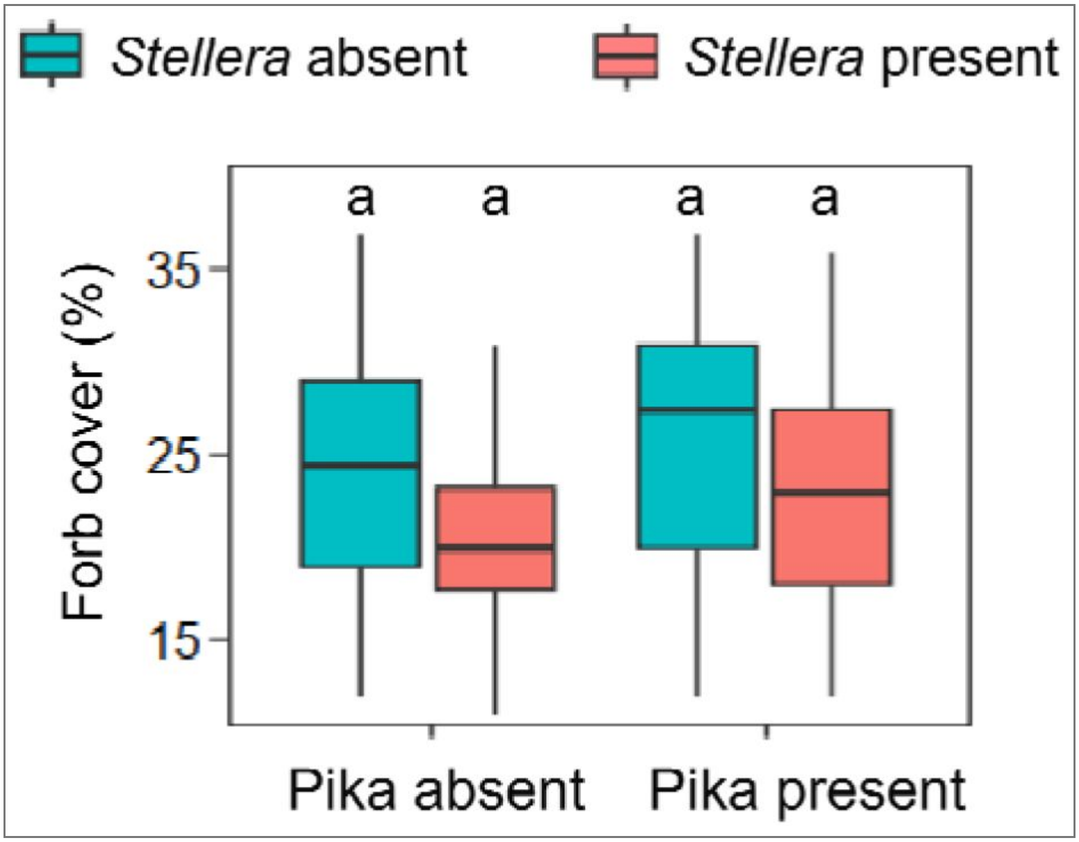

Figure S1. **Combined effects of two-year (2022–2023) pika and *Stellera* removal on forb cover in the field manipulative experiment.** The average values of each variable in the two years were used for statistical analysis, providing a single data point for each variable in each 150 × 150 m plot. Error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

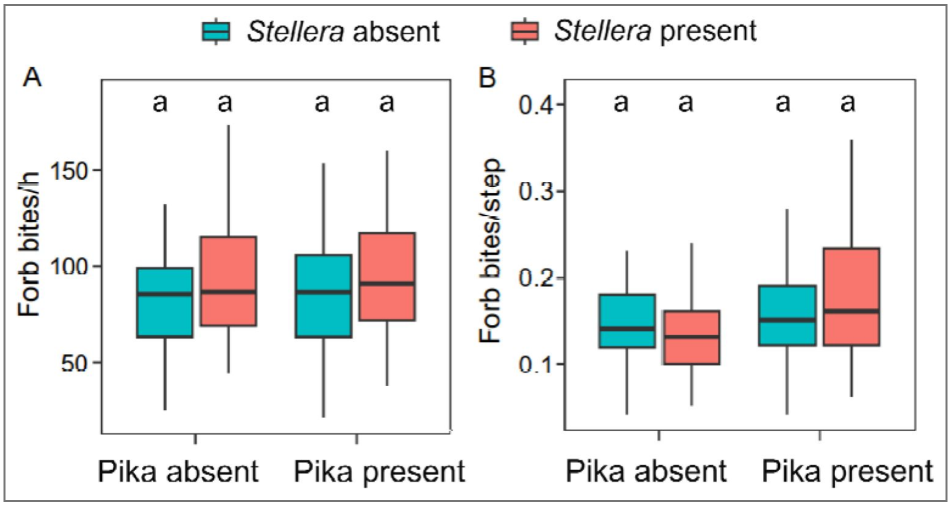

Table S1. **Model summary for diet and clipping selections of pikas and yaks in the field surveys in July 2021.**

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	*Stellera*	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

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

Contrast	Estimate	SE	df	*t* ratio	*P*
Pika feeding/clipping					
Forbs–Grasses	21.67	4.39	113.00	4.94	**<0.001**
Forbs–*Stellera*	-23.67	4.39	113.00	-5.39	**<0.001**
Forbs–Sedges	18.67	4.39	113.00	4.25	**<0.001**
Grasses–*Stellera*	-45.33	4.39	113.00	-10.33	**<0.001**
Grasses–Sedges	-3.00	4.39	113.00	-0.68	0.90
Stellera–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 S3. Model summary for *Stellera* cover regressed on active pika burrow density.

Estimates are from a generalized additive mixed model (Gaussian family) with plot as a random effect (n = 30 plots). density

Term	Estimate	SE	Statistic	*P*	edf	ref.df
Intercept	13.33	1.21	10.99	< **0.00**	NA	NA
Active pika burrow density	NA	NA	13.17	< **0.00**	2.10	7.00
Plot	NA	NA	1.17	0.06	15.12	29.00

Table S4. Model summary for yak dung density regressed on *Stellera* cover.

Estimates are from a linear regression model (n = 30 plots).

Term	Estimate	SE	Statistic	*P*
Intercept	19.07	1.41	13.50	< **0.00**
Stellera cover	–0.42	0.09	–4.62	< **0.00**

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	*Stellera*	−2.42	22.01	−0.11	0.91
Fixed	Pika × *Stellera*	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	*Stellera*	−0.11	0.01	−7.70	**<0.001**
Fixed	Pika × *Stellera*	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
		***Stellera* cover**			
Fixed	(Intercept)	−3.44	0.26	−13.39	**<0.001**
Ffixed	Pika	−0.11	0.22	−0.49	0.62
Fixed	*Stellera*	2.25	0.17	12.91	**<0.001**
Fixed	Pika × *Stellera*	−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 S5. **Model summary for interactive effects of pikas and *Stellera* on pika burrow density, yak weight gain, *Stellera* cover, grass cover, sedge cover, and forb cover in the field manipulative experiment in 2022-2023.**

Fixed	*Stellera*	−0.88	0.11	−7.76	**<0.001**
Fixed	Pika × *Stellera*	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	*Stellera*	−0.27	0.08	−3.51	**<0.001**
Fixed	Pika × *Stellera*	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	*Stellera*	−0.22	0.10	−2.21	**0.03**
Fixed	Pika × *Stellera*	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 S5. (continued)

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

Table S6. **Model contrasts for yak weight gain, *Stellera* cover, and grass cover in the field manipulative experiment in 2022-2023.**

Table S6. (continued)

Pika + *Stellera*					
Pika + No *Stellera*– No pika + *Stellera*	NA	0.25	Inf	NA	**<0.001**
Pika + No *Stellera*– Pika + *Stellera*	NA	0.10	Inf	NA	1.00
No pika + *Stellera*– Pika + *Stellera*	NA	0.05	Inf	NA	**<0.001**

Table S7. Model summary for yak weight gain regressed on active burrow count in plots with both pika presence and *Stellera* presence.

Estimates are from a generalized additive mixed model (Gaussian family) with a non-linear smooth for active burrows, block, year, and month as random effects (n = 24 observations from the pika + *Stellera* treatment).

Term	edf	ref.df	statistic	*P*
Active burrows	2.27	14.00	4.74	**<0.001**
Block	1.72	3.00	1.44	0.09
Year	0.23	1.00	0.31	0.25
Month	1.57	2.00	5.24	**0.01**

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	*Stellera*	−0.15	0.02	−8.72	**<0.001**
Fixed	Pika × *Stellera*	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	*Stellera*	−0.06	0.02	−3.14	**<0.001**
Fixed	Pika × *Stellera*	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	*Stellera*	−0.05	0.02	−2.03	**0.04**
Fixed	Pika × *Stellera*	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

Table S8. Model summary for interactive effects of pikas and *Stellera* on crude protein (CP) %, acid detergent fiber (ADF) %, and neutral detergent fiber (NDF) % of total forage in the field manipulative experiment in 2022-2023.

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

Table S9. **Model contrasts for crude protein (CP) % and acid detergent fiber (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	*Stellera*	−45.34	8.61	−5.27	**<0.001**
Fixed	Pika × *Stellera*	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	*Stellera*	−0.42	0.05	−8.71	**<0.001**
Fixed	Pika × *Stellera*	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	*Stellera*	0.13	0.07	1.90	0.06
Fixed	Pika × *Stellera*	−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	*Stellera*	−0.60	0.10	−6.28	**<0.001**

Table S10. **Model summary for interactive effects of pikas and *Stellera* 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 × *Stellera*	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	*Stellera*	−0.95	0.12	−7.61	**<0.001**
Fixed	Pika × *Stellera*	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	*Stellera*	−0.05	0.09	−0.49	0.63
Fixed	Pika × *Stellera*	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 S10. (continued)

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

Table S11. 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 S11. (continued)

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

Table S12. 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 presence/absence and *Stellera* presence/absence treatments.

	Pika		*Stellera*		Pika ×*Stellera*	
	F^*	P	F^*	P	F^*	P
Stellera 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.

Statistical Models Summary					
Response Variable	Model Type	Distribution/ Family	Interaction Terms	Random Effects	Sample Size
Diet selection					
Pika feeding frequency	GLMM	Gaussian		Plot, month	n = 10 plots
Yak grazing frequency	GLMM	Gaussian		Transect, month,	n = 10 transects
Stellera cover	GAM	Gaussian		plot	n = 30 plots
Yak dung density	LM	Gaussian			n = 30 plots
Yak performance					
Yak weight gain	GLMM	Gaussian	Pika × *Stellera*	Block, year, month	n = 16 plots, 2 years
Yak weight gain (vs burrow density)	GAM	Gaussian		Block, year, month	n = 16 plots
Plant cover					
Grasses	GLMM	Beta	Pika × *Stellera*	Block, year, month	n = 16 plots, 2 years
Sedges	GLMM	Beta	Pika × *Stellera*	Block, year, month	n = 16 plots, 2 years
Forbs	GLMM	Beta	Pika × *Stellera*	Block, year, month	n = 16 plots, 2 years
Stellera	GLMM	Beta	Pika × *Stellera*	Block, year, month	n = 16 plots, 2 years
Active burrow density	GLMM	Gaussian	Pika × *Stellera*	Block, month	n = 16 plots, 2 years
Forage quality					
Crude protein (%)	GLMM	Beta	Pika × *Stellera*	Block, year, month	n = 16 plots, 2 years
Acid detergent fiber (%)	GLMM	Beta	Pika × *Stellera*	Block, year, month	n = 16 plots, 2 years

Table S13. Summary of all statistical models used in the study, including response variables, model type, distribution family (with Tweedie power parameter where applicable), interaction terms, random effects structure, and sample sizes.

All field experiments (2022-2023) used a 2 × 2 factorial design with pika presence/absence and *Stellera* presence/absence treatments. GLMM = Generalized Linear Mixed Model; GAM = Generalized Additive Mixed Model; LM = Linear Model. For Tweedie distributions, p indicates the power parameter.

Neutral detergent fiber (%)	GLMM	Beta	Pika × *Stellera*	Block, year, month	n = 16 plots, 2 years
Foraging efficiency					
Sedge bite rate	GLMM	Tweedie ($p = 0.04$)	Pika × *Stellera*	Block, year, month	n = 16 plots, 2 years
Grass bite rate	GLMM	Gaussian	Pika × *Stellera*	Block, year, month	n = 16 plots, 2 years
Forb bite rate	GLMM	Tweedie ($p = 0.07$)	Pika × *Stellera*	Block, year, month	n = 16 plots, 2 years
Sedge bites/step	GLMM	Beta	Pika × *Stellera*	Block, month	n = 16 plots
Grass bites/step	GLMM	Beta	Pika × *Stellera*	Block, month	n = 16 plots
Forb bites/step	GLMM	Beta	Pika × *Stellera*	Block, month	n = 16 plots

Table S13. (continued)

Data availability

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

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Zhiwei Zhong, Conceptualization, Investigation, Visualization, Methodology, Funding acquisition, Writing-original draft, Writing-review and editing; Bingbo Ni, Data curation, Investigation; Douglas Lawton, Software, Formal analysis, Writing-original draft, Writing-review and editing; Xiaofei Li, Data curation, Investigation, Funding acquisition; Xiaona Zheng, Data curation, Investigation; Huakun Zhou, Writing-review and editing; Junhu Su, Writing-review and editing; Wenjin Li, Writing-review and editing; Fujiang Hou, Writing-review and editing; Zhenggang Guo, Writing-review and editing; Quanmin Dong, Writing-review and editing; Shikui Dong, Writing-review and editing; Christopher R. Dickman, Writing-review and editing; Jens-Christian Svenning,

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71. **Zhang Z** (2003) Mutualism or cooperation among competitors promotes coexistence and competitive ability. *Ecological Modelling* **164**:271-282 https://doi.org/10.1016/S0304-3800(03)00069-3
72. **Zhang Z,** Yan C, Krebs C J, Stenseth NC (2015) Ecological non-monotonicity and its effects on complexity and stability of populations, communities and ecosystems. *Ecological Modelling* **312**:374-384 https://doi.org/10.1016/j.ecolmodel.2015.06.004
73. **Zhang Z,** Wang Z (1998) *Ecology and Management of Rodent Pests in Agriculture* Beijing, China: Ocean Press.
74. **Zhang Z,** Zhong W, Fan N, Singleton GR, Hinds LA, Leirs H, Zhang Z (1999) *Ecologically-based Rodent Management* Canberra, Australia: Australian Centre for International Agricultural Research. pp. 113-133
75. **Zhong Z,** Li G, Sanders D, Wang D, Holt RD, Zhang Z (2022) A rodent herbivore reduces its predation risk through ecosystem engineering. *Current Biology* **32**:1869-1874 https://doi.org/10.1016/j.cub.2022.02.074 | PubMed
76. **Zhong Z,** Wang D, Zhu H, Wang L, Feng C, Wang Z (2014) Positive interactions between large herbivores and grasshoppers, and their consequences for grassland plant diversity. *Ecology* **95**:1055-1064 https://doi.org/10.1890/13-1079.1 | PubMed

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 2 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.

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 on 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?

https://doi.org/10.7554/eLife.111340.2.sa2

Reviewer #2 (Public review):

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 use of shared resources.

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 of demonstrating the potential conservation impacts of their research.

https://doi.org/10.7554/eLife.111340.2.sa1

Author response:

The following is the authors’ response to the original reviews.

> ***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 provide point-by-point responses to the comments from the two peer reviewers, and we hope these revisions are satisfied by you and the reviewers.

> ***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.*

Thank you for this suggestion. We have acknowledged this limitation in the Discussion by adding the paragraph below (see the Third point):

"Despite of these, several questions 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 the documented facilitation of yak nutrition by pikas prompts herders to increase yak densities, could the resulting rise in livestock herbivory push pika populations beyond the levels observed here, potentially toward the threshold where facilitation gives way to competition? Third, our study site is located at approximately 3,200 m elevation, 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."

See these revisions in Line 272-286 in the Discussion section.

> *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*

Thank you for this suggestion. We have added more details about the study site, particularly regarding wild ungulates, in the Methods section. Specifically, we have included the sentence of "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."

See these revisions in Line 333-335 in the Methods 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).*

Thank you for the suggestion. We have acknowledged this limitation in the Discussion, by adding a paragraph as: "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."

See these revisions in Line 284-286 in the Discussion section.

> *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?*

Thank you for your suggestion. We have acknowledged this limitation in the Discussion, by adding the paragraph as "Second, if the documented facilitation of yaks by pikas prompts herders to increase yak densities, could the resulting rise in livestock herbivory push pika populations beyond the levels observed here, potentially toward the threshold where facilitation gives way to competition (Yang et al., 2026)?"

See these revisions in Line 276-279 in the Discussion section.

> ***Reviewer #1 (Recommendations for the authors):***
>
> *Although no doubt a bit sensitive, it would have been better to reveal a bit more about how pikas were removed.*

We have provided more details about how pikas were removed in the no-pika treatment, by adding "For the no-pika treatment, pikas were trapped once every two weeks using 30 live traps (25 cm high × 25 cm wide × 40 cm long) within each plot and relocated elsewhere in the study site." in the Methods section. We didn't recorded how many pikas were removed from the corresponding plots, so no data were available for this point.

See these revisions in Line 411-413 in the Methods section.

> *The authors also missed a few relevant papers worth citing, including Badingqiuying, R. B. Harris, and A. T. Smith. 2018. Summer habitat use of plateau pikas (Ochotona curzoniae) in response to winter livestock grazing in the alpine steppe Qinghai-Tibetan Plateau. Arctic, Antarctic, and Alpine Research 50 (1): e1447190*

We have cited this key paper in Line 75 in the Introduction section.

> ***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 Stress Gradient Hypothesis (SGH). Thus, we deleted the description on SGH. However, the finding of a humped relation between yak weight gains and pika burrow densities (Figure 3C) is very important which provides evidence that moderate densities of pikas has the best beneficial effects on yak growth. We added a separate paragraph in discussion to have a clear discussion.

We have made the major revisions below to address these concerns.

(1) We have revised the title into "Small mammalian herbivores at moderate densities facilitate livestock growth by improving vegetation composition in grasslands ".

(2) We have deleted all the statements about facilitation and competition predicted by the SGH in the Abstract (Line 56-59), Introduction (Line 88-91), Discussion (Line 231-233, the whole paragraph about SGH was removed here), and the References sections.

(3) We added a paragraph in discussion (Line 248-259) to have a clear discussion on the humped relation between yak weight gains and pika burrow densities as "Because of the natural variations in pika density in the pika-present treatment, we were able to obtain a hump-shaped relationship between yak weight gains and pika burrow densities in these plots. Compared with the absence of pikas, the facilitative effect reached its maximum at approximately 200 burrows/ha but became competitive at densities exceeding 400 burrows/ha (Figure 3C). This result reveals that pika density modulates the net outcome for yak weight gain, with a facilitation peak at ~200 burrows/ha and a competition onset above 400 burrows/ha. Our findings offer empirical evidence for the non-monotonicity theory, under which the competition-facilitation balance varies with population density: facilitation dominates at low densities, competition at high densities, and these density-dependent shifts may underpin community stability and productivity (Zhang, 2003; Zhang et al., 2015). The theory further holds that the facilitation threshold, not the competition-facilitation transition, is the critical factor governing the stability of interacting species or communities (Zhang et al., 2015)."

> *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 places where we discussed non-significant interactions: Line 175–177 "Pikas and *Stellera* had no interactive effects on abundance of sedges, forbs, and neutral detergent fiber (NDF) of total forage for yaks (Figure 3F, I and Appendix 1—figure 1, table 5,8)." and Line 190–192 "Pikas and *Stellera* had no interactive effects on yaks' foraging efficiency on forbs (Appendix 1—figure 2, table 10).".

We have cross-checked both the Results section and the Figures sections mentioned above, and confirmed that they are consistent now.

> *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.*

Thank you for the suggestion. Now we have added the Appendix 1—table 3 and Appendix 1—table 7 for the model results of generalized additive models (GAMs) for Figure 2C and Figure 3C that plotted with smoothed lines in Appendix 1.

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

We have provided the Appendix 1—table 13 to summarize all statistical models used in the study, including the distributions used and the sample sizes in the Appendix 1.

We have also added a sentence of "A summary of all statistical models used in the study is available in Appendix 1 table 13." in Line 475-476 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 have revised 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 have revised 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* (Figure 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."

See these revisions in Line 439-447 in the Methods section.

> ***Reviewer #2 (Recommendations for the authors):***
>
> *(1) Introduction*
>
> *Line 53 - I wouldn't describe small mammals like rodents as keystone species. They can have strong impacts on ecosystems, but not disproportionate relative to population size, which is a key part of that definition. It may be true when you talk specifically about pikas later on, but not small mammals as a general category.*

We have replaced this term with "consumers" here, see Line 63.

> *Lines 58-61 - Good hook*

Thank you for this positive comment.

> *Lines 69-74 - I don't think the stress gradient hypothesis is the right pitch for this work. The SGH posits that facilitation increases with abiotic stress, but no abiotic stressors were measured in this study. Population density interacts with abiotic factors in the SGH, but population density in and of itself is not an abiotic stressor. The papers you cite here all look at the interaction between population density and abiotic stressors (e.g., water availability). So these lines set me up to expect a stress gradient in your experiment that didn't exist, then left me confused later on. It would be better to highlight the strength of your work (lines 70-76 pose interesting questions and predictions) rather than trying to make it fit within the SGH.*

Thank you for pointing out this problem. We have deleted the statements about SGH here.

See these revisions in Line 88-91 in the Introduction section.

> *(2) Materials and Methods*
>
> *Lines 498-509 - Did you verify beforehand that no plants within the enclosures had been grazed on? How did you know that the consumption or clipping was specifically from those pikas?*

We have clarified here by adding “Before cage installation, we carefully checked the plants within each plot and removed those that had been previously grazed or damaged by herbivores.” in the Methods section. In this case, we made it sure that the consumption or clipping was specifically from those pikas with the cages.

See the revisions in Line 349-350 in the Methods section.

> *Lines 509-512 - I would be careful calling this preference. It's really just a record of what they consumed along paths they were walking, which could be about accessibility and convenience as much as preference.*

We have replaced “diet preferences” with “diet composition” here, see Line 359 in the Methods section.

> *Line 514 - Clarify the specific question or hypothesis you're testing with this field survey, beyond just generally testing associations.*

We have modified the sentences here as “In July 2021, we investigated the potential facilitation of pikas on yaks mediated by the poisonous *Stellera* forbs under unmanipulated field conditions in the study site.”.

See Line 365-366 in the Methods section.

> *Lines 532-534 - The intro for this paper sets it up to be about density-dependent movement from competition to facilitation, but the experiment here is set up to compare pika presence/absence. The framing of the paper needs to be adjusted to better align with this experimental design.*

The same issue as mentioned above. We agree that our work had explored only the facilitative effects of pikas on yaks, rather than the balance between competition and facilitation as predicted by the Stress Gradient Hypothesis (SGH). However, the finding of a humped relation between yak weight gains and pika burrow densities (Figure 3C) is very important which provides evidence that moderate density of pika has the best benefical effect on yak. We added an separate paragraph in discussion to have a clear discussion about this point in the Discussion section.

We have made the major revisions below to address this concern.

(1) We have revised the title as “Small mammalian herbivores at moderate densities facilitate livestock growth by improving vegetation composition in grasslands”.

(2) We have deleted the statements about facilitation and competition and the SGH in the Abstract (Line 56-59), Introduction (Line 88-91), Discussion (Line 231-233, the whole paragraph about SGH was removed here), and the References sections.

(3) We kept the discussion on the humped relation between yak weight gains and pika burrow densities (Figure 3C). We added an separate paragraph in discussion to have a clear discussion about this point. For details, see Line 248-259 in the Discussion section.

> *Lines 566-569 - Why did you need to simulate pika clipping when you already had pika presence/absence treatments?*

We conducted *Stellera* removal treatment by simulating poisonous plant clipping behaviors of pikas because we want to confirm that the shifts in abundance of this dominant poisonous plant species is the key mechanism in driving pika-yak facilitation in our system. If we simply looked the differences in yak weight gain in the pika presence/absence treatments, it should be difficult to secure the underlying mechanism. In addition to the reduction in abundance of the poisonous *Stellera*, pikas may cause a variety of shifts vegetation properties including plant productivity and diversity, and soil disturbances that can exert direct and indirect effects on yak foraging activities, and thus their weight gains.

> *Lines 566-569 - Is there another citation you can give showing that Stellera forbs taller than 20cm are both preferred by pikas and exert greater impacts on plant/animal communities? Those are big assumptions that need to be better supported or explained. If there was a logistical reason that you didn't remove all of the smaller forbs, that needs to be laid out as well.*

We have added one new citation here to support this method here. We have revised this section as "To simulate the clipping behavior of pikas, we clipped only those *Stellera* forbs exceeding 20 cm in height. This threshold was chosen based on previous observations that pikas preferentially target large forbs of this size (Liu et al., 2009)."

Liu W, Zhang Y, Wang X, Zhao JZ, Xu QM, Zhou L. 2009. The relationship of the harvesting behavior of plateau pikas with the plant community (In Chinese). Acta Theriologica Sinica 29:40-49.

Also, we have deleted the sentence of "and can exert significant impacts on the plant community and on yak grazing behaviors (Z.Z., field observations)" mentioned above, because these patterns were observed only by the authors in the field and lack supporting data.

See these revisions in Line 419-422 in the Methods section.

> *Line 587 - sample size per treatment? Was it consistently one species that you measured, and if so, which one? If you collected different species or a mix of species across treatments, then you can't really compare the nutrient values because you haven't accounted for interspecific variation.*

We have revised 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 have revised 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."

See these revisions in Line 439-447 in the Methods section.

> *Lines 603-613 - Please provide the dependent variables in each model, as well as any interaction terms, in addition to the random effects. Please also state explicitly what you were trying to test with each of these models.*

There are two models that use the tweedie family (forb and sedge bite rate). Indeed, we need to include the tweedie power parameter to help understand the mixture of the three families. We have included the p-value (power) in the Appendix 1—table 13 in the Appendix 1. We chose to use tweedie because a normal gaussian family model fitted the results poorly.

We have added the Appendix 1—table 13 in the Appendix 1, which provides the summary of all statistical models used in the study, including response variables, model type, distribution family (with Tweedie power parameter where applicable), interaction terms, random effects structure, and sample sizes.

Also, we have added a sentence of "A summary of all statistical models used in the study is available in Appendix 1—table 13." in Line 475-476 in the Statistical analyses section to indicate this information.

> *Lines 613-614 - Tweedie is a category of distributions that includes quite a few different options, including Gaussian, Poisson, and Gamma distributions, some of which are normal and some of which are not. So, justifying the use of Tweedie distributions in your model structure doesn't really make sense, and it doesn't really tell me which distribution each model pulled from. Please clarify specifically which distributions you used for each model and why.*

We have now added the reason why we used Tweedie distributions by adding the sentence of "There were two models that used the tweedie family (forb and sedge bite rate). We chose to use tweedie because a normal gaussian family model fitted the results poorly" in Line 468-470 in the Statistical analyses section.

We have also included the p-value (power) for forb and sedge bite rate in the Appendix 1—table 13 in the Appendix 1.

> *Lines 615-618 - Provide citations for R packages described in the text.*

We have provided all the related citations for all R packages described in the text, as listed below.

glmmTMB: Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M., & Bolker, B. M. (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal, 9(2), 378–400. *https://doi.org/10.32614/RJ-2017-066*

mgcv: Wood, S.N. (2017). Generalized Additive Models: An Introduction with R (2nd edition). CRC Press. AND Wood, S.N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society: Series B (Statistical Methodology), 73(1), 3–36. *https://doi.org/10.1111/j.1467-9868.2010.00749.x*

DHARMa: Hartig, F. (2022). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.6. *https://CRAN.R-project.org/package=DHARMa*

tidyverse: Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T.L., Miller, E., Bache, S.M.,

Müller, K., Ooms, J., Robinson, D., Seidel, D.P., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., & Yutani, H. (2019). Welcome to the tidyverse. Journal of Open Source Software, 4(43), 1686. *https://doi.org/10.21105/joss.01686*

See these revisions in Line 472-475 in the Statistical Analyses section.

> *(3) Results*
>
> *Line 127 - Somewhere in the intro or methods, describe what clipping is and why the pikas do it.*

We have provided more details about the clipping behaviors of pikas by adding "Notably, pikas often clip (although do not eat) the wolf poison *S. chamaejasmehas* because its relatively large size hinders predator detection (Fan et al., 1998)." in Line 330-332 in the Methods section.

> *Line 128 - Change from "preferred" to "consumed greater proportions of"*

See the correction in Line 146 in the Results section.

> *Line 136 - You measured yak weight once a month, so give the result in monthly weight gain rather than daily.*

Here we preferred to keep the unit of daily weight gains (converted from monthly ones), as this is the standard presentation for livestock growth performance, also see Fig. 1 in Odadi et al., 2011 Science's paper.

W. O. Odadi, M. K. Karachi, S. A. Abdulrazak, T. P. Young, Science 333, 1753–1755 (2011).

> *Lines 138-140 - The linear models, as you described them in the methods (lines 603-620), don't test for hump-shaped relationships. Please update the methods to explain how you tested the density relationship and how you got this interpretation.*

The description for Figure 3C here showed estimates from a GAM (family: gaussian), and we did not use a linear model in this figure.

We have now added a new model summary Appendix 1—table 7 for this Figure 3C in the Appendix 1.

> *Line 145 - I don't think you can claim that the total available forage was more nutritious for yaks, as you picked plants that yaks happened to be chewing along a grazing path. You would need to take samples from a consistent set of plant species at random locations to make this claim.*

Sorry for this confusion. We modified "the total available forage" as "the major available forage" here (see Line 172) because we collected the same forage plant species and analyzed their nutrients.

The same as mentioned above, to clarify the sampling methods, we have also revised this point in the Methods section to provide more detail on how forage samples were collected and their quality were analyzed. See these revisions in Line 439-447 in the Methods section.

> *(4) Discussion*
>
> *Line 166 - Need to address inconsistency in how you talk about pika density. Here you talk about the impacts of pikas at moderate densities, which I think is a fair claim. Elsewhere, you talk about density-dependence, which I don't think you really measured, given that all your sampling was either in the absence of pikas or within a narrow window of densities that can all be categorized as moderate.*

Done! As mentioned above, we have removed the term of “density-dependence” in the whole manuscript, but keep the term of “moderate density” in the Abstract (Line 56-59), Introduction (Line 88-91), Discussion (Line 231-233, the whole paragraph was removed here), and the References section.

> *Line 176-178 - This is a really cool finding.*

Thank you for this positive comment.

> *Lines 179-181 - You didn't test competition between plant species, and you didn't measure light, soil moisture, or soil nutrients. So you can suggest competition as a potential mechanism, but you can't say definitively that's what is happening.*

We now have lowered our tone here as “We speculate that these improvements in food availability and nutrition for yaks may be due to the release of grasses and sedges from competition with the forbs for limiting above- and below-ground resources”.

See the revision in Line 208-211 in the Discussion section.

> *Lines 184-186 - You did a good job of it here, suggesting a likely potential mechanism at play without claiming it is for sure happening when it hasn't been measured.*

Thank you for this positive comment!

> *Lines 188-199 - Strong paragraph. The impacts of large herbivores on smaller animals are well-studied, but reciprocal impacts are often overlooked.*

Thank you for this positive comment!

> *Lines 201-205 - You didn't test the stress gradient hypothesis because there was no abiotic gradient. You also did not take any measurements during outbreaks, so you cannot claim to have compared low-moderate to outbreak pika densities. I think the paper would be much stronger if you removed the stress gradient hypothesis and instead focused more on the literature around facilitation between mammals of different body sizes, as you do in lines 205-209.*

We agreed that our work didn’t specifically design to test the stress gradient hypothesis (SGH) between pikas and yaks, so we have deleted this paragraph here, see Line 231-233 in the Discussion section.

> *Line 209-215 - Again, you didn't test a competition-facilitation balance because you never tested or demonstrated competition. One of the main strengths of this paper is demonstrating facilitation, so build on that strength rather than referencing things you didn't measure.*

The same as mentioned above, we have deleted this paragraph here, see Line 231-233 in the Discussion section.

> *Lines 218-222 - Not an accurate description of the relationship between herbivore diet and body size. Larger herbivores typically tolerate lower-quality plants in order to consume sufficient calories, but plenty of them do this via mixed feeding. Grazing in large herbivores and livestock is usually due to specifics of the digestive tract (e.g., hindgut fermentation) rather than specifically about body size.*

We have deleted this description of the relationship between herbivore diet and body size here. Instead, we have modified this statement as “The coexistence of a diverse of herbivore species with different diet selections and size classes can lead to an “compensatory effect” on grass and forb biomass that helps to maintain a balance and diverse plant community" in the Discussion section.

See these revisions in Line 234-237 in the Discussion section.

> *Lines 245-251 - Paragraph addresses an important point. Lines 247-249, though, overstate what you measured. There's no measurement of livestock production or biodiversity in the study.*

We have replaced the term of "livestock production and biodiversity" with "livestock growth performance" here. See Line 288-298 in the Discussion section.

> *(5) Figures*
>
> *Figure 2C-D - This applies to all figures, but you need to plot the best-fit line generated from your model instead of using geom_smooth, which is what these lines look like. You can do this using functions like predict or ggpredict. Using these smoothed lines implied non-linear relationships that you didn't actually test for.*

We have redrawn Figures 2C and 2D to use model estimates directly and have included the related model summaries as Appendix 1—table 3 and table 4 in the Appendix 1.

> *Figure 3B - This figure doesn't show yak weight gain in the presence of pikas. Instead, it shows weight loss when pikas are absent. It's a subtle difference, but very important for interpretation. Yak can maintain weight just fine without pikas as long as Stellera are absent, too. Your results consistently show no Pika x Stellera interactions, but that doesn't match your significance values here. Need to double-check and explain that.*

We have revised the descriptions for Figure 3 and 4 in the Results section, by emphasizing that the absence of pikas REDUCED weight gains of yaks, INCREASED toxic plant abundance, and REDUCED the quantity and quality of palatable grasses and sedges. We have revised these sections as below:

Abstract (see Line 51-53)

"Compared to the pika-present treatment, pika removal dramatically increased cover of the poisonous Stellera forbs by two-fold, reducing the abundance and protein content of palatable grasses and sedges, yak foraging efficiency, and yak weight gain by up to 42%."

Results (see Line 153-167, Line 169-175, Line 184-192)

Also, we did find significant Pika x *Stellera* interactions for yak weight gains, we have provided these details in the Appendix 1—table 5 and table 6 in the Appendix 1.

> *(6) Recommendations*
>
> *Lines 245-257 - Would recommend combining the last two paragraphs into one.*

We have combined the last two paragraphs, see Line 288-298 in the Discussion section.

> *Line 530 - Can you replace large with a more precise measure of area?*

We are unable to provide a more precise measure of area here, so we have deleted the description of "in a large area", but we have also added the note of "in the study site" by the end of the sentence to better describe the location of the plots.

See the revision in Line 413 in the Methods section.

> *Line 541 - Does this mean +/- 7.8 standard deviations? If so, how big is that range in kg?*

Here should be “115±7.8 kg”, we have done this correction in Line 392 in the Methods section.

> *Figure 3 - Would be helpful to use "Stellera/pika present" and "Stellera/pika absent" rather than saying "No Stellera/pika" since you also use the No. abbreviation for numbers a lot in this figure.*

We have revised all the related Figures for this issue in Figure 3, 4, and Appendix 1—figure 1,2.

> *Figure 3F and I - Show letters for significance on these two plots as well, even if it is just a row of a's.*

We have redrawn Figure 3F,I to address this issue.

> *Figure S1 - Applies to all boxplots. Be consistent about showing significance, even if it is a row of a's indicating no difference between treatments.*

We have re-drawn Appendix 1—figure 1,2 to address this issue.

> *Table S1 - Something happened with the line numbers, so they are in the table instead of on the left side.*

We have fixed this problem for Appendix 1—table 1 in the Appendix 1.

> *Table S1 - Applies to all tables. Include the type of model that you ran (including distribution if not Gaussian) in the table legend.*

We have provided an summary of all statistical models used in the study in Appendix 1—table 13 in the Appendix 1.

Also, we have added a sentence of “A summary of all statistical models used in the study is available in Appendix 1—table 13.” in Line 475-476 in the Statistical analyses section to indicate this information.

> *Table S9 - This legend has a good description, including the type of model you used and what you were testing. Apply this more detailed legend to the rest of the tables.*

Again! We have provided an summary of all statistical models used in the study in Appendix 1—table 13 in the Appendix 1.

Also, we have added a sentence of “A summary of all statistical models used in the study is available in Appendix 1—table 13.” in Line 475-476 in the Statistical analyses section to indicate this information.

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