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Livestock grazing impacts on plateau pika (*Ochotona curzoniae*) vary by species identity

Xincheng Li[a], Zhongnan Wang[a], Deli Wang[a,*], Ling Wang[a], Duofeng Pan[a,b], Jie Li[a], Kejia De[c], Timothy R. Seastedt[d]

[a] *Institute of Grassland Science/School of Environment, and Key Laboratory of Vegetation Ecology/Key Laboratory for Wetland Ecology and Vegetation Restoration, Northeast Normal University, Changchun, Jilin 130024, China;*

[b] *Institute of Forage and Grassland Sciences, Heilongjiang Academy of Agricultural Sciences, Harbin, Heilongjiang 150086, China*

[c] *Qinghai Academy of Animal Science and Veterinary Medicine, Qinghai University, Xining 810016, China*

[d] *Department of Ecology and Evolutionary Biology, Institute of Arctic and Alpine Research, University of Colorado, Boulder, Colorado 80309, USA*

*Corresponding author. E-mail address: wangd@nenu.edu.cn (D. Wang)

Abstract

Livestock and small burrowing mammals are potential ecosystem engineers and major drivers of ecosystem processes. Small mammals, often considered competitors with livestock, have been reported to increase in recent years and have been identified for their negative impacts on ecosystem services such as plant production and soil carbon sequestration. However, these increases and impacts by small mammals have rarely been studied with respect to how they may be influenced by livestock grazing. Here we experimentally manipulated large enclosures on the alpine grassland of Qinghai-Tibetan plateau, each with different livestock assemblages: yak (*Bos grunniens*), Tibetan sheep (*Ovis aries*), mixed populations of yak and sheep, and a control plot containing no livestock to study the potential impacts of livestock on the dominant small mammalian herbivore in the region, the plateau pikas (*Ochotona curzoniae*). We found that during the period of peak vegetative growth all pika populations in livestock experimental plots increased compared with those in the control plots. Additionally, pika populations and active pika burrow density increased more in experimental plots containing yaks compared with the sheep-only experimental plots. These results provide evidence that livestock grazing can increase the risk of pika outbreaks, which has led to this species being classified as a pest and subject to widespread control measures. We suggest explicitly incorporating livestock species identity in addition to grazing intensity and duration into management considerations to ensure maintenance of native biodiversity and long-term sustainability on the alpine grasslands of the Qinghai-Tibetan plateau.

Keywords

Alpine meadow, Grassland management, Indirect effect, Large herbivore, Sanjiangyuan,

Source of the Three Rivers

1. Introduction

Grasslands worldwide are fundamentally shaped by a group of social, semi-fossorial, herbivorous small mammals, where they play keystone roles having both trophic and ecosystem engineering effects on communities (Smith and Foggin, 1999; Zhang et al., 2003; Davidson et al., 2010; Davidson et al., 2012). However, over the past decades, some of the species (e.g. European rabbits *Oryctolagus cuniculus*, American prairie dogs *Cynomys* spp., and burrowing Asian pikas *Ochotona* spp.) have been reported to exhibit dramatic increases in population density which has led to their being perceived as pests because of their putative negative impacts on grassland conditions, production and risk of diseases (Kang et al., 2007; Delibes-Mateos et al., 2011). Hence, small mammals are commonly facing persecution such as extensive, ongoing poisoning campaigns targeted toward their control or eradication (Delibes-Mateos et al., 2011). Nonetheless, the decline of small mammals may result in losses in ecosystem services, such as providing nesting burrow habitats for other animals (Smith and Foggin, 1999; Arthur et al., 2008; Smith et al., 2018), serving as prey for predators (Badingqiuying et al., 2016), burrowing to enrich topsoil nutrients and infiltration of rainfall (Wilson and Smith, 2015; Ma et al., 2018), as well as maintaining vegetation heterogeneity (c.f. Davidson and Lightfoot, 2008; Root-Bernstein and Ebensperger, 2013; Smith et al., 2018). The relationship between small mammals and livestock grazing is increasingly of concern in managed grasslands that are co-occupied by livestock and small mammals. An important management question becomes: to what extent does grazing by livestock impact populations of small mammals?

Livestock normally generate indirect effects on small mammals by altering plant community composition, vegetation structure (Milchunas and Lauenroth, 1993; Olff and Ritchie, 1998), and soil properties (Greenwood and McKenzie, 2001), that provide food resources and habitat structures for the small mammals (Foster et al., 2014; van Klink et al., 2015; Su et al., 2016; Fig. 1). Resource changes can alter small mammals' behavioral or physiological traits and their fitness, ultimately leading to abundance changes (Batzli, 1992). For instance, a case study from Inner Mongolia grasslands indicated that successive sheep grazing caused reduction of food quantity (i.e., less biomass and cover of preferred plants) and deterioration of food quality (i.e., more tannin and total phenol content) for voles, and thus reduced their abundance (Li et al., 2016a). In contrast, some studies have revealed that livestock could enhance survival of rabbits or pikas by creating their preferred habitats (i.e. reduced vegetation height and cover; Wangdwei et al., 2013; Yin et al., 2017). Despite limited experimental evidence, livestock trampling and wallowing have also been hypothesized to negatively affect the suitability of burrow systems for small mammals (Torre et al., 2007). Overall, the vegetation changes induced by livestock foraging and destructive impacts can alter habitat structure, to the benefit or detriment of small mammals; While competition may arise where livestock reduces shared food resources for small mammals, a feeding facilitation might otherwise arise when grazing stimulates plant regrowth or makes more grass accessible to small mammals.

In practice, most grasslands, especially those occupied by nomadic pastoralists, are grazed by livestock assemblages containing various species with different body-size. Livestock with diverse species identity would selectively feed on plants differing in quantity and quality due to their nutritional requirements (Liu et al., 2015). Small or medium-sized herbivores (e.g. small mammals or sheep) are assumed to desire high-quality food resources, while larger ones (e.g. cattle or yak) primarily forage to maximize their food intake and could cope with plants of lower-quality (Codron et al., 2007). Livestock also have distinctive trampling effects over their foraging areas and compaction intensity for their different body masses and hoof areas (Cumming and Cumming, 2003). Therefore, livestock could generate impacts on plant resource abundance and distribution, vegetation structure and soil conditions for small mammals. Moreover, when multiple species of herbivores graze, the interactions between them can be facilitative or competitive, thereby assemblages could result in additive or compensatory effects on grassland quality (Arsenault and Owen-Smith, 2002). In particular, diet overlap of multiple herbivores may result in overutilization some species of plants and underutilization of others, while diet partitioning could lead to an even usage across all plant species. For example, in eastern Eurasian steppe, mixed grazing by cattle and sheep increased plant diversity and spatial heterogeneity of soil available N compared with single species grazing sites (Liu et al., 2015; Liu et al., 2016; Liu et al., 2018a). Currently, studies exploring the effects of different species identity and assemblages of livestock generally focus on plant composition (Albon et al., 2007; van der Plas et al., 2016), plant diversity (Bakker et al., 2006; Liu et al., 2015), litter decomposition (Wang et al., 2018), and soil nutrient (Chang et al., 2018), as well as arthropod abundance and diversity (Zhu et al., 2012; Zhu et al., 2015). Few studies have documented the cascading effects of livestock species and their assemblages on small mammals.

The impacts of large herbivores on small mammals have been found to be either positive or negative in studies across the African savanna, North American prairie and Eurasian steppe (Bakker et al., 2009; Hagenah et al., 2009; Davidson et al., 2010), but how various livestock assemblages affect small mammals remains controversial in the Qinghai-Tibetan Plateau (QTP) ecosystems. Tibetan grasslands are the world's highest and most expansive, but this region is also sensitive and contains fragile alpine grazing ecosystems (Suttie et al., 2005). Most important, the QTP provides important animal production and ecosystem services for human livelihoods (Harris, 2010). These rangelands, particularly the alpine meadows, have suffered from serious degradation for several decades due to human activities as well as climate warming and permafrost melting, leading to declines in primary production, soil carbon, and nutrient stocks (Harris, 2010; Xu et al., 2016; Liu et al., 2018b). In particular, overstocking of livestock such as yak and Tibetan sheep is considered one of the most serious human disturbances (Harris, 2010). Meanwhile, the outbreaks of "rodents" (specifically the plateau pika; *Ochotona curzoniae*) are also blamed for creating "black beach" habitats (highly eroded areas; Wang et al., 2016). At present, there is an increasing recognition that population dynamics of small mammals are highly correlated with livestock grazing (Kang et al., 2007). Some studies assume pikas at high population densities have a competitive relationship with livestock for plant food resources, while others suggest that vertebrate grazing decreases plant height and cover thereby leading to increased densities of pika (Roger et al., 2007; Delibes-Mateos et al., 2011; Badingqiuying et al., 2018). There exists a lack of experimental evidence to demonstrate cause and effect relationships between livestock grazing and pika abundance, and such information is needed to manage small mammal outbreaks and inform livestock management.

In this study, we performed a replicated large-scale enclosure experiment with different livestock assemblages (yak *Bos grunniens*, Tibetan sheep *Ovis aries*, mixed populations of yak and sheep, and a control with no livestock grazing) to examine the effects of grazing on plateau pikas. We focused on grazing effects on vegetation and soil condition. We asked (1) How did livestock grazing effect abundance of plateau pikas and (2) how did these effects differ among livestock species and their assemblages? We hypothesize that, (1) suitable habitat quality induced by livestock grazing may facilitate pika abundance and (2) due to their distinct body sizes and diet preferences, yak, sheep and their mixed herds may pose different effects on plant composition and food resources that affect the pikas.

2. Materials and methods

2.1. Study system

This study was conducted at a grassland (33.33°N 97.42°E; 4260 m above sea level) near the "Zhenqin Alpine Meadow Ecosystem Research Station" established by Qinghai University in Chengduo County, Qinghai Province. The site is a typical alpine meadow in the central QTP and Sanjiangyuan Area (known as "Source of Three Rivers" including the Yellow, the Yangtze, and the Mekong). The study site has cold winters and warm summers (temperature ranging from -25.6°C to 15.0°C for monthly mean of daily minimum and maximum temperature respectively). The annual precipitation was 482.0–652.0 mm, with about 75% occurring during the growing season (May–September, when mean daily temperature was above 0°C, Fig. A1; meteorological data from previous 10 years of 2005–2014; Yushu weather station, available online http://data.cma.cn). The grassland is dominated by the sedge *Kobresia pygmaea.* Subdominant species include grasses such as *Stipa capillata*, *Elymus nutans*, and companion species of forbs (e.g. *Gentiana straminea*, *Saussurea pulchra*, *Potentilla discolor* and *Oxytropis deflexa*). Though not heavily impacted by pastoralists' grazing management, biomass of grasses was historically low here (personal communication with the landowner). The soil type is alpine meadow soil, which is classified as mat cryo-sod soil based on the Chinese national soil classification system (Gong, 2001). It is characterized by high organic content, and a thin soil layer, which has average thickness of 0.65 m (Kato et al., 2004).

This grassland has been managed by pastoralism of domesticated yaks and Tibetan sheep for years, and the grazing intensity is mainly controlled by pastoral practice. The plateau pika (body weight *c*. 150 g) is the most dominant and abundant small burrowing mammal in this area. The pika population exhibits seasonal fluctuations and interannual variability. Pikas live in social groups and have a breeding season during the warm summer. They reproduce two or three times a year and have an average lifespan about 123-246 days. (Qu et al., 2013).

2.2 Experimental design and grazing treatments

We used a block design with three replicate blocks in the study area. Within each block, four enclosures (plots) were established with woven-wire fences (1.5 m high; 10 cm mesh size) for different grazing treatment, including no grazing (Control), yak grazing (Yak), Tibetan sheep grazing (Sheep), mixed grazing by yak and sheep (Mixed). Specific treatments were selected to maximize within-treatment landscape heterogeneity within blocks (Fig. A2).

A moderate grazing intensity with approximate 50% of aboveground plant biomass removal during the growing season (June–August) was designed in all grazing treatments at a stocking rate of about 6.17 sheep ha^{-1}.. This was achieved by using 9 yak (*c.* 350 kg) and 45 Tibetan sheep (*c.* 50 kg) in each single grazing treatment respectively, while the mixed grazing treatment was comprised of 9 yak and 45 Tibetan sheep on plots twice the area of those with single species. All livestock were mature and about 3–6 years age. Plot size was 100×200 m on controls and single species plots and 200×200 m on mixed grazing plots. Grazing occurred from early June to late August (i.e., 3 month each year). Grazing treatments were conducted in a rotational stocking management, so that each plot was grazed 6 days in total and with a 2-week interval between each time. Grazing was not conducted on days experiencing substantial rainfall. The design was based on local habitat productivity and method of rangeland carrying capacity calculation published by agriculture industry standard NY/T 635-2015 (Ministry of Agriculture of the People's Republic of China).

We used large-scale plots because natural grazing impacts by livestock are better mimicked in large enclosures, and allowed for a better estimate pika population response to grazing. Family-occupied home range size of pikas is reported to be about 106–178 m^2 (Qu et al., 2018) or even larger at our site.

2.3. Pika population survey

We conducted transect counts of plateau pika (as a proxy for population density of pikas) in each plot during the warmest season when they had completed reproduction and had thus reached the peak population size (late July to August; Fig. A1). We walked transects to count pikas at a spatial scale representative of the core plot areas (Roger et al. 2007). Surveys were conducted between 09:00 and 11:30 on each sunny day when most pikas were active and easily observed. Three observers walked in separate lines and counted all pikas within sight to cover a total of 60-m wide and 100-m long belt transects (2 × 60 × 100 m in mixed grazing plots by walking two transects). Pikas would run into adjacent burrows when humans walked close by, and we could catch sight of pikas easily due to the low vegetation height in our study areas. To account for observer bias, each plot was counted on 2–3 mornings. We used mean values of the replicated counts. An index of pika abundance was then calculated and transformed to counts of pikas per hectare. In addition, to ensure that there was no significant differences prior to our grazing treatments, we also surveyed pika population in May 2015 using the same protocols (Fig. A4).

As a second index of pika abundance, we counted pika burrow entrances in three 20 × 20 m subplots spaced over 10 m apart in the pika counts survey areas within each plot. Active burrows (hole entrances characterized by clear openings, fresh soil or pika feces) and other burrows (including inactive burrow entrances with undisturbed material such as invaded plant species or spider webs, and burrows with no openings) were counted separately (Fig. A3). Total burrows were calculated as the sum of active burrows and other burrows. Density of burrows was calculated and transformed to number of burrows per hectare.

2.4. Vegetation measurement and soil sampling

We sampled vegetation in late August. We evaluated changes in pika food resources by estimating plant biomass and species richness. The biomass (grams per 1/4 square meter) and richness (the number of plant species found within each quadrat) were measured in 12–18 quadrats (0.5×0.5 m; number varied according to the plot size of treatments). These were sampled from quadrats equally spaced in three lines in the center core of each treatment plot. Aboveground plant materials were clipped at ground level, separated by species group (grasses, sedges, legumes and other forbs), stored temporarily in paper envelopes, and then dried in an oven at 80°C to a constant mass.

We measured vegetation cover and plant height to evaluate habitat characteristics of plateau pikas. Vegetation cover was visually estimated as total species' aerial cover in each quadrat surveyed as described previously. Vegetation height was measured as community-weighted mean plant height (Niu et al., 2016). First, plant height was measured on three haphazardly chosen stems for each species in a quadrat. In the meantime, each quadrat was divided into 25 sub-quadrats using plastic lines and species frequency was measured as occurrence times of 25 sub-quadrats. Vegetation height was then calculated as a species frequency weighted mean value of plant height in each quadrat.

Soil bulk density and water content were measured to estimate soil physical properties. We sampled the soil for 6 replicates in a line within the core space of each plot. In order to prevent effects of pikas burrows on measurements, we sampled soil away from plateau pika entrance burrows. All soil samples were weighed before and after oven drying at 105°C to a constant weight. Soil bulk density was measured at the upper soil layer (0–10 cm) by the core sampling method with a stainless-steel ring and determined by the dry matter in the soil that occupies a core of 100 cm^3 volume. The soil water content was estimated by the mass of water per mass of dry soil using the same sample as described previously.

2.5. Livestock foraging behavior measurement

To evaluate livestock diet choices, we measured the relative grazing frequency of different plant species groups (grasses, sedges, legumes, and other forbs) fed on by livestock in July. In each grazing plot, we choose 4 individuals of healthy livestock and recorded about

20 bites of foraging for each one. To minimize human disturbance, we followed livestock at a distance. Each bite of plant was scored for visual evidence of plant shoot removal by livestock. When a plant was removed, we assigned that bite a value of one for the belonging species group. Values assigned for each species group were summed per livestock type and divided by total bites of plants to obtain a relative grazing frequency of species groups ranging from 0%–100%, similar to procedures of Clark et al. (2012) and Zhong et al. (2014). We also evaluated bite frequency of the livestock. We choose one animal per species in each grazing plot, observed at a distance, and counted the bite number during their foraging peak period (9:00–12:00 and 15:00–18:00) with a 10 min interval (total 3 h per day). Livestock bite frequency was calculated as number of bites per hour.

2.6. Statistical analyses

We used linear mixed effect models (LMMs) with grazing treatment treated as a fixed effect and block as a random effect to assess the impacts of grazing on pika abundance index, vegetation height, soil bulk density, soil water content, above-ground plant biomass, legumes biomass within each year (2015 and 2016 separately). Active burrow density, total burrows density, vegetation cover and plant species richness were analyzed with generalized linear mixed effect models (GLMMs) including treatment as a fixed factor and block as a random factor assuming Poisson or log-linked Gaussian error structure based on the distribution pattern of each variable. For 2 year grouped data, we used the same models but additionally with factor year as a repeated covariance structure in which year and block were treated as crossed random effects in the model. Analyses were performed with software R version 3.4.3 (R Core Team, 2017). LMMs and GLMMs were achieved using the function *lmer* and *glmer* respectively from the package *lme4*. Tukey tests for between treatment comparisons within each year were performed with the function *glht* from the *multcomp*. We quantitatively tested the compositional similarity of plant communities using the *adonis* function of the *vegan* package, which conducts permutational MANOVA using Bray–Curtis distance matrices; we specified models with treatment nested within block as factors, and with 100,000 permutations per test. One-way ANOVA was used to test the differences of bite frequency between single grazing and mixed grazing treatments within each livestock species identity.

We used partial least squares regression (PLSR; Carrascal et al., 2009; Yang et al., 2017) to identify the relationships between vegetation height, legume biomass, total plant biomass, soil bulk density with pika abundance index respectively after conditionally accounting for the other environmental factors including vegetation cover, total burrow density. We used the function *plsreg1* in the package *plsdepot* with 2 components chosen to implement PLSR and extracted residuals from model results to plot scatterplots.

3. Results

3.1. Background of study area

During the experimental period in 2015–2016, the seasonal temperature and precipitation displayed a similar pattern, but with lower annual precipitation than the previous 10-year average (488.7 mm in 2015 and 434.0 mm in 2016 vs. 584.1 mm; Fig. A1). Climate in 2016 was hotter and drier (average temperature 5.7°C, and total precipitation 325.2 mm during the growing seasons from May to September) than in 2015 and 2005–2014 (correspondingly 4.7°C, 404.2 mm; 5.2°C, 487.7 mm). Pre-grazing pika abundance indices ranged from 14 to 27/ha across treatments and were not significantly different (Fig. A4).

3.2. Effects of livestock on pika population

Abundance of plateau pika was increased in grazing plots compared with the control during the peak period of vegetation in 2015 and 2016 (Fig. 2; Table 1). The abundance index increased by 95%, 89%, and 143% respectively in sheep grazing, yak grazing and mixed grazing plots than controls in 2015, and correspondingly 33%, 48%, 94% of those than controls in 2016. Notably, the abundance index was higher in mixed grazing plots compared to that in both single species sheep or yak plots (Fig. 2a). The density of active burrow entrances in 2016 was also higher in grazed plots containing yaks versus controls in 2016; burrow density was 35% and 37% higher in yak and mixed grazing plots respectively than the control (Fig. 2b; Table 1).

3.3. Effects of livestock on pika habitat structure

Vegetation height was significantly affected by livestock grazing both in 2015 and 2016 (Table 1), in which height was reduced by 24%, 22% and 23% separately in sheep grazing, yak grazing and mixed grazing plots compared to control plots in 2015, and correspondingly by 15%, 20% and 15% of these plots in 2016 (Fig. 3a). No significant difference was detected among different grazing treatments. There was no significant difference of grazing effect on vegetation cover at the plot scale each year (Table 1).

Soil bulk density was significantly increased in yak and mixed grazing plots relative to controls in both years, while sheep grazing had no effect (Fig. 3d). Among grazing plots, soil bulk density increased significantly in mixed grazing (in 2015 and 2016) and yak grazing plots (in 2015) compared with sheep grazing plots. In contrast, soil water content was only significantly decreased by livestock grazing in 2015, in which mixed grazing decreased water content more than that in both sheep grazing and control plots (Fig. 3e). We did not find any significant difference of grazing effect on density of total burrows in the 2 years (Table 1).

3.4. Effects of livestock on pika food resources

Grazing significantly reduced above-ground total plant biomass (Table 1), within which biomass was reduced by 31%, 31% and 24% respectively in sheep, yak and mixed grazing plots compared with controls in 2015, while no significant difference was found among grazing plots (Fig. 3b). In 2016, only yak grazing significantly lowered plant biomass by 30% compared to the control. In contrast, the percentage of legume biomass was considerably increased by livestock grazing (Table 1), in which mixed and yak grazing raised this value to about 54% and 90% respectively compared with the control in 2015, and correspondingly 58% and 115% of these plots in 2016 (Fig. 3c). There were no significant differences in plant species richness across the treatments (Table 1), but plant community composition was significantly different between yak grazing and sheep grazing plots (perMANOVA test, F = 5.28, $P < 0.001$).

3.5. Relationships of pika population with habitat structure, and food resources

Decreased vegetation height was negatively correlated with the index of pika abundance in PLSR analysis when accounting for the effects of other factors including vegetation cover, total burrow density, soil bulk density and total plant biomass ($r^2 = 0.3$, $P = 0.005$, Fig. 4a). Contrarily, biomass of legumes was positively correlated with the index of pika abundance in PLSR analysis when accounting for the effects of other factors including vegetation height, vegetation cover, total burrow density, soil bulk density and total plant biomass ($r^2 = 0.25$, P

= 0.012, Fig. 4b). No significant difference was found among total plant biomass, soil bulk density and our index of pika abundance (Fig. 4c-d).

3.6. livestock foraging habits

Livestock appeared to exhibit selectivity in grazing plant species groups. The average relative grazing frequencies of sheep on forbs, sedges, grasses and legumes were 73%, 13%, 7%, and 11% respectively, while those of yak were 54%, 33%, 9%, and 8% (Fig. 5a). Mixed grazing did not considerably alter diet choices of yak or sheep based on their relative grazing frequency of species groups, but significantly increased sheep bite frequency by about 19% more than in single species grazing plots (Fig. 5b).

4. Discussion

We asked whether livestock grazing could lead to increases in the abundance of a small mammal. By manipulating grazing enclosures with different livestock assemblages, we provided evidence that livestock grazing led to environmental changes that in turn led to an increase in the population size of plateau pikas. We also found that the magnitude of those effects differed among livestock assemblages by species.

In our study livestock grazing reduced the vegetation height and this effect concurrently increased the index of pika abundance, as the peak population of pikas in autumn was negatively correlated with vegetation height (Fig. 4a). Plateau pikas are often considered favoring open habitat reflected by low vegetation height or sparse coverage (Bian et al., 1999; Smith and Foggin, 1999). In such habitat, it is adaptive for pikas to be on guard against predation and escape into surrounding burrows, thereby diminishing their predation losses (Wangdwei et al., 2013; Badingqiuying et al., 2018). Due to reduced predation risk, pikas are also recorded having low levels of physiological stress which could decrease natural mortality and/or increase reproductive success (Yin et al., 2017).

In our experiment, vertebrate grazing significantly decreased the vegetation height, but did not affect the vegetation cover (Fig. 3a; Table 1). The height reduction was mostly caused by livestock foraging on grasses like *E. nutans* and *S. capillata* which were dominant in the vegetation structure. Meanwhile, reduction of these grasses led to increased colonization of competitive forbs which in turn maintained the vegetation cover. Therefore pika abundance was enhanced by increasing perception of ability to perceive predators, and/or an increase in fecundity in the open habitat. (Arsenault and Owen-Smith, 2002)Small mammals such as field voles in wet meadows (Schmidt et al., 2005), mice in deciduous forest (Smit et al., 2001), rabbits and voles in floodplain grassland (Bakker et al., 2009) all showed changes in abundance in response to ungulate grazing-induced vegetation structure alteration. Our results support the habitat facilitation hypothesis that habitat structure altered by grazing can benefit other species (Arsenault and Owen-Smith, 2002), and confirm that large herbivores are strong habitat constructors via ecosystem engineering effects (Jones et al., 1997; Zhong et al., 2017).

A food competition relationship has often been proposed between small mammals and livestock for some degrees of diet overlap, although competition between herbivores is usually dependent on contextual factors such as the temporal and spatial extent of animal activities and habitat productivity (Arsenault and Owen-Smith, 2002; Odadi et al., 2011; Augustine and Springer, 2013). In our experiment, pika populations were not correlated to the total biomass of aboveground plants (Fig. 4c) which was reduced under livestock grazing

(Fig. 3b), indicating food resources were unlikely to be a limiting factor for pikas. Previous studies reveal that livestock and pikas have different diet preferences (Jiang and Xia, 1987; Harris et al., 2015), and pikas are capable of varying the diets with habitats (Liu et al., 2008). Notably, some species of legumes (such as *Oxytropis* and *Astragalus spp.* in our site) are reported to be poison for livestock (Stegelmeier et al., 1999; Cook et al., 2009) but are highly preferred by plateau pikas across different habitats and seasons (Jiang and Xia, 1985; Liu et al., 2008; Li et al., 2016b). We found the proportion of legumes was increased after grazing by livestock (Fig. 3c) due to their selective foraging on graminoids (grasses and sedges) and other forbs (Fig. 5a), and pika populations were higher in situations when there was a greater biomass of legumes (Fig. 4b). The more accessibility of legumes and their high nitrogen and phosphorus, which constitute a high food proportion and grazing frequency for pikas, may be beneficial and critical to the nutrient uptake of plateau pikas (Wang et al., 1992), hence potentially increasing their survival or reproduction. Therefore, our findings are also consistent with the feeding facilitation hypothesis that livestock grazing could increase nutritional legume resource access for plateau pikas (Arsenault and Owen-Smith, 2002).

We found that livestock species identity plays an important role in the grazing effects on plateau pikas. We anticipated that livestock assemblages with large grazers (i.e. yak) would increase the abundance of plateau pikas, while the impacts from medium-sized grazers (i.e. sheep) may be conditional due to their close niche overlaps and competition may arise when habitat altered (Jiang and Xia, 1987). In our experiment, yak grazing and mixed grazing both increased the abundance index and active burrow density of pikas, while sheep grazing increased the abundance index but not the burrow density in two consecutive years (Fig. 2).

This difference was related to several factors. First, there are inconsistent dynamics between active burrow and pika populations due to the existence of a temporal lag in burrow density change during shifts in pika populations (Badingqiuying et al., 2018). Second, pikas could also have a different burrow-in-use ratio when their population is changing (Zhang et al., 2018). Thus, the active burrow density may not as accurately reflect the current pika population. Third, due to selective grazing and different trampling effects, we found plant community composition and soil condition in plots differed among grazing treatments (Table 1). Although there was no difference between yak grazing and sheep grazing in pika abundance, mixed grazing increased both pika abundance and active burrow density more than sheep grazing alone. Unlike yak, sheep prefer high quality plants, which increased their diet overlap with pikas for forbs (Fig. 5a). We also found that in mixed grazing, sheep bite frequency were influenced by the presence of yaks (Fig. 5b), thus mixed grazing may have an additive effect on the decline of dominant graminoid and forb due to selective foraging and interspecific interactions (Liu et al., 2015; Chang et al., 2018; Liu et al., 2018a). Under these conditions, sheep were facilitated by yak grazing by reducing graminoid cover and increasing access to their preferred forbs, while yak may also be facilitated by sheep grazing via reducing other forbs. This would then make it easier to avoid legumes. The fact that the pika abundance index did not differ significantly between yak grazing and sheep grazing may be because the habitat and food resources of pikas had not dramatically changed. Thus, we confirmed that livestock grazing with assemblages of large grazers could lead to a rise in the population of native keystone species, the pika, by modifying plant community structure and nutritional characteristics.

5. Conclusion

Our study confirmed the positive effects of livestock grazing on population levels of plateau pikas, and found that varying livestock species identities have different effects on the growth of the pika population. Livestock herds with large grazers such as yak would have larger effects causing a higher increase of pikas compared with areas grazed by the smaller sheep. We believe that reducing the height of vegetation is an important factor determining the population size of plateau pikas.

Excessive levels of plateau pika populations are often identified as one of the main factors of grassland degradation (Harris, 2010). At present, the prevention and control methods of the pika population include poisoning, prohibition of livestock grazing with enclosures, and grass planting to protect vegetation (Wang et al., 2016; Xu et al., 2016), all of which is expensive and time consuming. Hence, one of the important goals of livestock grazing management is to concurrently prevent and control the population of plateau pikas and avoid their outbreaks. Clearly, vertebrate grazing intensity must be controlled to avoid vegetation decline (Herrero-Jáuregui and Oesterheld, 2018). Meanwhile, changes in vegetation composition caused by selective foraging of livestock will also change the food resources of the pika. In our study, the mixed grazing of yak and sheep increased the food resources of pikas, which is not conducive to the prevention of plateau pika population control. However, because of the wide range of diets in pikas and the increased adaptability to seasonal and environmental changes, more long-term research is needed in the understanding of the relationships between livestock, livestock composition, and pikas on food resources.

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Table 1. Mixed model results for effects of grazing (control, sheep, yak, mixed grazing) on plateau pika, plant and soil properties. (see text for statistical tests.) Shown are F-value and P-value (in parenthesis). An asterisk (*) indicates significant differences (* $P < 0.05$; ** $P < 0.1$; *** $P < 0.001$).

Variables	2 years pooled	2015	2016
	Df = 3, 20	Df = 3, 8	Df = 3, 8
Pika abundance index	45.52 (< 0.001) ***	35.42 (< 0.001) ***	23.36 (< 0.001) ***
Active burrow density	154.97 (< 0.001) ***	0.50 (0.691)	122.34 (< 0.001) ***
Vegetation height	16.76 (< 0.001) ***	8.84 (0.006) **	17.02 (0.001) ***
Vegetation cover	1.78 (0.183)	0.38 (0.769)	1.81 (0.224)
Total burrow density	0.19 (0.90)	0.04 (0.987)	0.57 (0.648)
Total plant biomass	10.59 (< 0.001) ***	54.93 (< 0.001) ***	7.28 (0.028) *
Legumes biomass	13.72 (< 0.001) ***	4.00 (0.052)	12.12 (0.002) **
Plant species richness	1.23 (0.325)	1.98 (0.196)	1.87 (0.212)
Soil bulk density	11.56 (< 0.001) ***	10.24 (0.004) **	6.16 (0.018) *
Soil water content	2.56 (0.084)	4.86 (0.033) *	0.79 (0.531)

Figure legends

Fig. 1. conceptual framework of the mechanistic pathways of livestock assemblage impact on small mammals. The first column of boxes displays livestock assemblages. The second column represents grassland conditions modified by livestock; The third column represents the habitat quality of small mammals.

Fig. 2. Effects of grazing (control, sheep, yak, mixed grazing) on plateau pikas: (a) index of pika abundance during peak period in 2 years; (b) active burrow density. Different small letters above the bars indicate significant differences among treatments within each year ($P < 0.05$). Error bars represent ±1 SE.

Fig. 3. Effects of grazing (control, sheep, yak, mixed grazing) on plateau pika habitat quality at peak standing crop in August within each year: (a) vegetation height, (b) above-ground total plant biomass, (c) proportion of legumes in total plant biomass. (d) soil bulk density, (e) soil water content. Different small letters above the bars indicate significant differences among treatments within each year ($P < 0.05$). Error bars represent ±1 SE.

Fig. 4. The internal relationships between habitat quality characteristics and pika abundance index when accounting for the effects of other vegetation and soil factors based on partial least square regression (see text for statistical tests). (a) Relationship between vegetation height and pika abundance; (b) Relationship between legumes biomass and pika abundance; (c) Relationship between above-ground total plant biomass and pika abundance; (d) Relationship between soil bulk density and pika abundance. The solid red lines indicate statistical significance for the relationships. The dashed lines indicate no statistical significance for the relationships. The shaded areas show the 95% confidence interval of the

fit.

Fig. 5. Livestock foraging habits between different livestock assemblages (single vs. mixed grazing). (a) Relative livestock grazing frequency of plant species groups (forbs, sedges, grasses and legumes). (b) Bite frequency. Different small letters above the bars indicate significant differences among treatments (single vs. mixed grazing; $P < 0.05$). Error bars represent ±1 SE.

Fig. 1

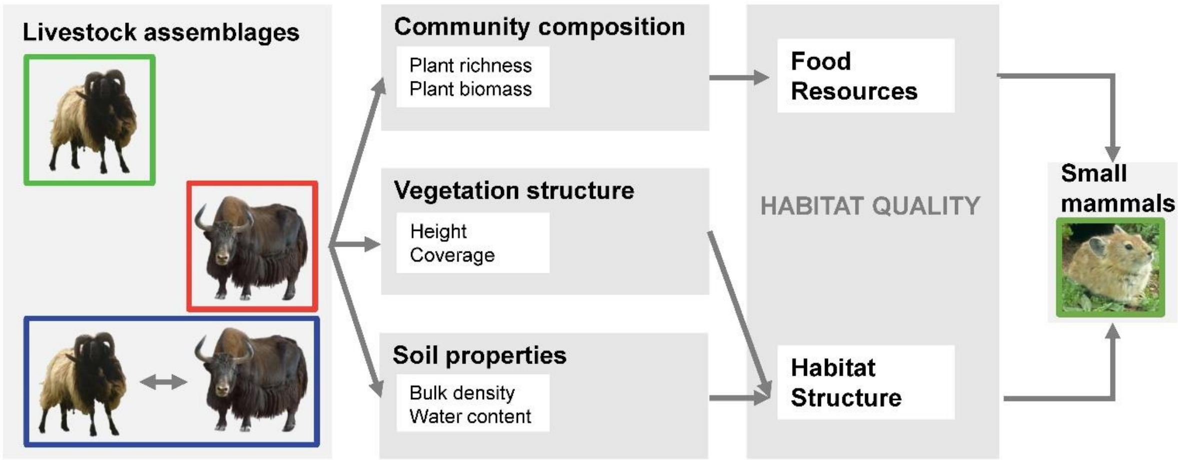

Livestock assemblages
Community composition
Plant richness
Plant biomass
Vegetation structure
Height
Coverage
Soil properties
Bulk density
Water content
Food Resources
HABITAT QUALITY
Habitat Structure
Small mammals

Fig. 2

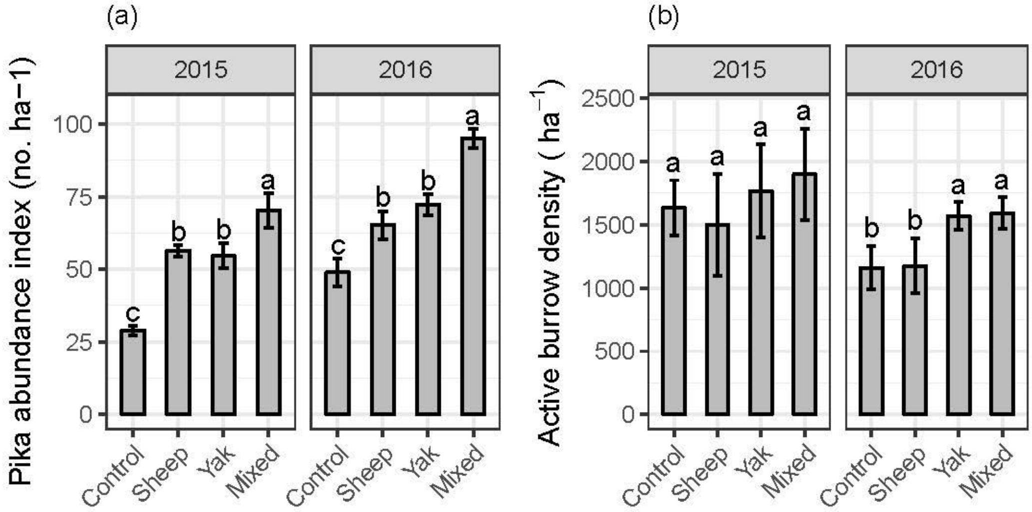

(a)
(b)
2015
2016
Pika abundance index (no. ha−1)
Active burrow density (ha−1)
Control
Sheep
Yak
Mixed

Fig. 3

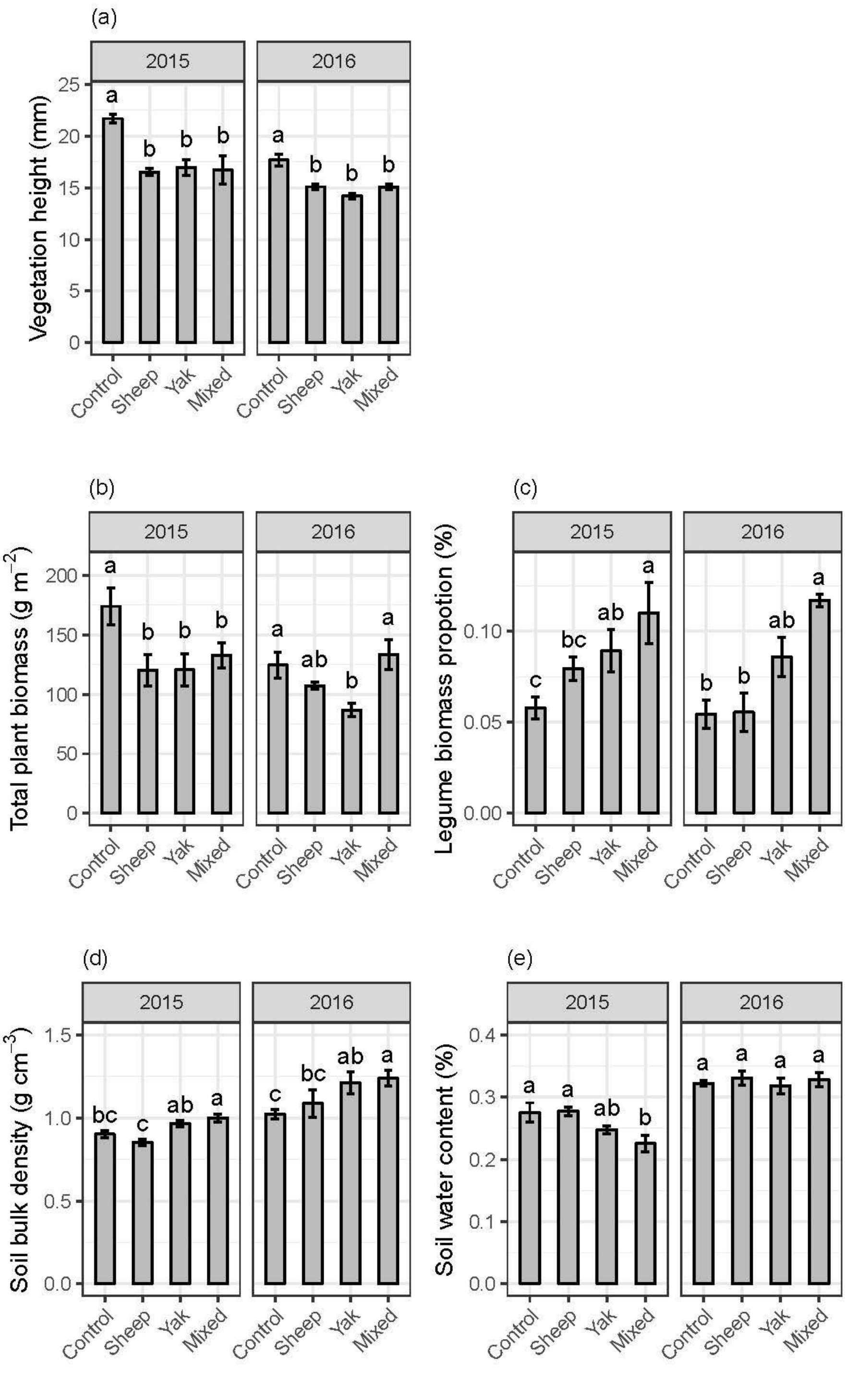
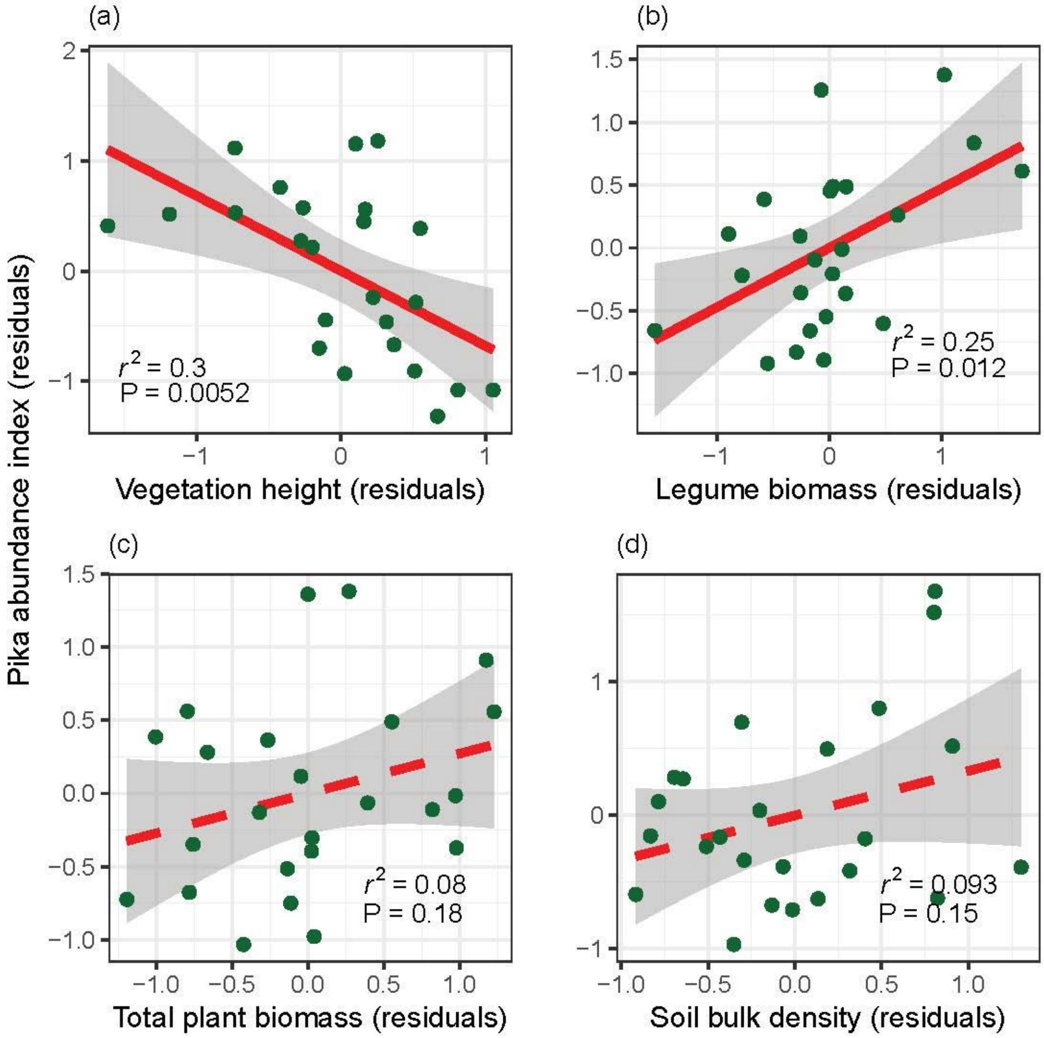
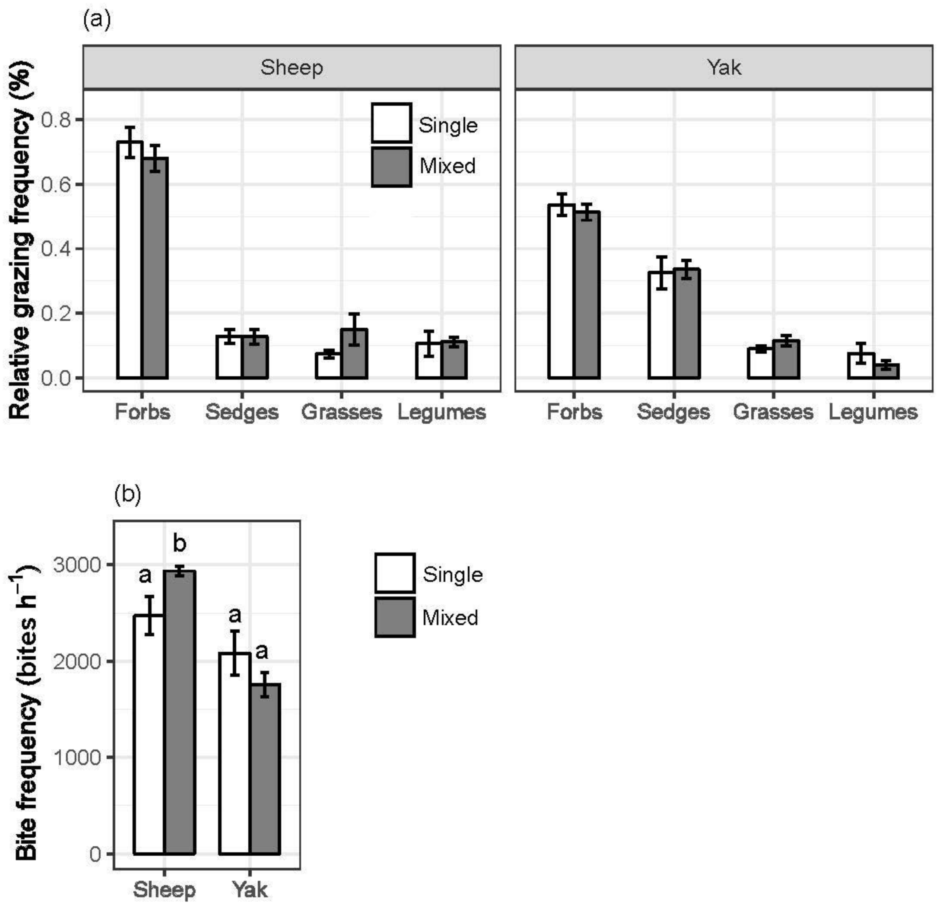

(a)
2015
2016
Vegetation height (mm)
(b)
Total plant biomass (g m−2)
(c)
Legume biomass propotion (%)
(d)
Soil bulk density (g cm−3)
(e)
Soil water content (%)
Control
Sheep
Yak
Mixed

Fig. 4



(a)
(b)
(c)
(d)
Pika abundance index (residuals)
r^2 = 0.3
P = 0.0052
r^2 = 0.25
P = 0.012
r^2 = 0.08
P = 0.18
r^2 = 0.093
P = 0.15
Vegetation height (residuals)
Legume biomass (residuals)
Total plant biomass (residuals)
Soil bulk density (residuals)

Fig. 5


(a)
Sheep
Yak
Relative grazing frequency (%)
0.0
0.2
0.4
0.6
0.8
Single
Mixed
Forbs
Sedges
Grasses
Legumes
Forbs
Sedges
Grasses
Legumes
(b)
Bite frequency (bites h⁻¹)
0
1000
2000
3000
a
b
a
a
Single
Mixed
Sheep
Yak

Appendix

Fig. A1. Monthly precipitation (bars) and mean temperatures (lines) in 2015, 2016 and average of 10 years (2005–14) in experiment site.

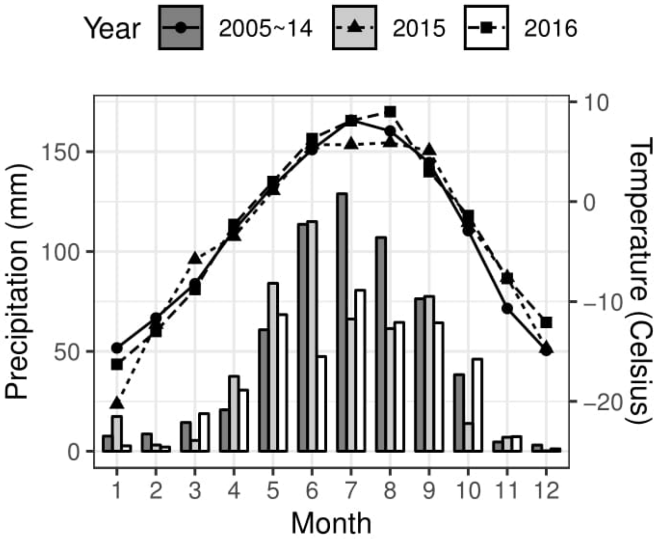


Fig. A2. Experiment location and block arrangement and experimental layout. The study area is located at Zhenqin village, east of Sanjiangyuan Area, central of Qinghai-Tibet Plateau. There were three blocks, each block was divided into four plots for treatments. The plots were assigned to four treatments: yak, Tibetan sheep, mixed by yak and sheep, and control (no grazing).

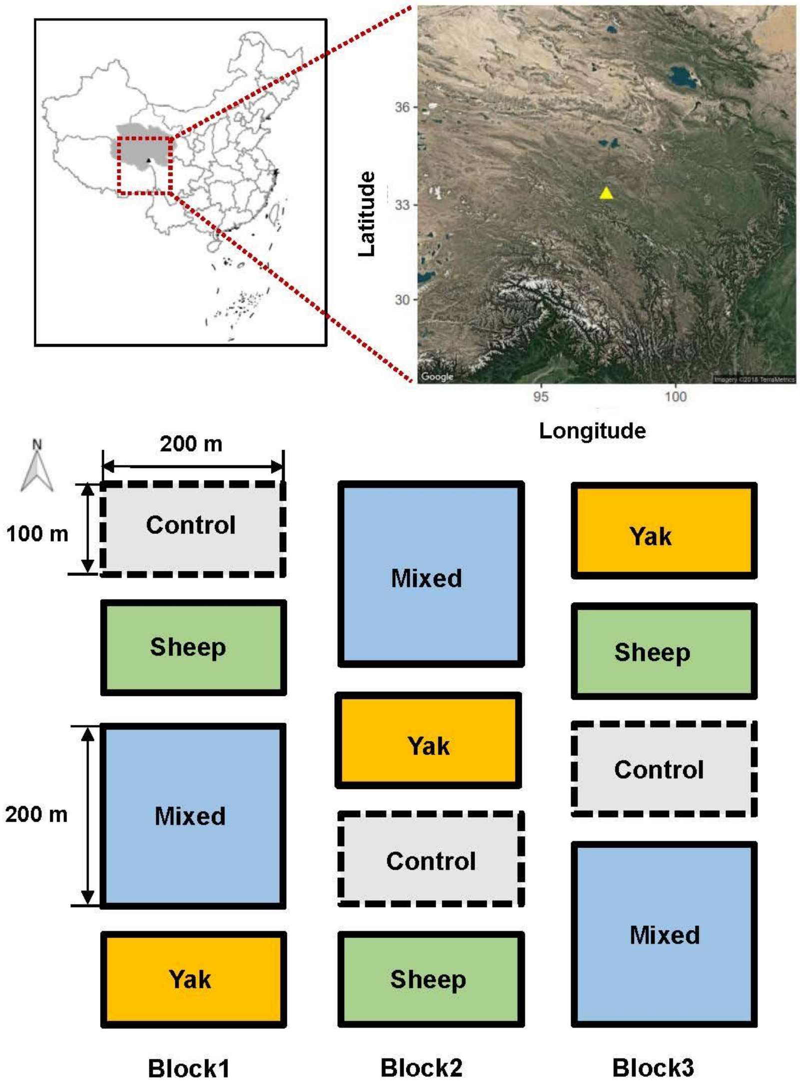


Fig. A3. Illustrations showing a standing plateau pika (*Ochotona curzoniae*) (left picture) and two types of burrows: active burrow (middle picture), dead burrow (right picture).

Fig. A4. Pre-grazing pika abundance index in 2015 spring among grazing treatments. Different small letters above the bars indicate significant differences among treatments ($P < 0.05$). Error bars represent ±1 SE.