Pika-Yak Interaction: Plant Cover

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1 Methods

1.1 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. Posthoc comparisons were conducted only when the pika × S. chamaejasme interaction term was significant. For the 2021 field surveys, we fit generalized linear mixed models with plot and month as random effects. We then used generalized additive mixed models for S. chamaejasme cover and active pika burrow density, with plot as a random effect, and linear regression models for dung density and S. chamaejasme cover. For the field manipulation experiments in 2022 and 2023, we constructed generalized linear mixed models with the dependent variables (e.g., grass bites per step, sedge total bites, weight gain) regressed against the interactive effect of pika and S. chamaejasme treatments, while including block, year, and month as random effects to capture the hierarchical structure of the data. Models assumed gaussian, beta (for proportions), or tweedie (for non-normal data) distributions, selected based on data type and model fit. A significance threshold of $P = 0.05$ was applied, with TukeyHSD or Sidak posthoc tests used where appropriate. All data management, modeling, and visualization were carried out in R, with dependencies managed using *renv*. The main modeling packages were *glmmTMB* and *mgcv*, with *DHARMa* used for model diagnostics. Data management relied on the *tidyverse* suite of packages. A complete record of package versions is available in the renv.lock file in the repository: https://github.com/ddlawton/pika_yak_interactions.

2 Results and Discussion

First, we carried out a set of field observational experiments to investigate diet selection by pika and yak, as well as the associations among pika abundance, S. chamaejasme abundance, and yak activity under natural field conditions. Consistent with previous studies[5,11,24–25], we found that pika and yak have distinct diet preferences: yaks preferred grasses and sedges, while pika preferred the poisonous S. chamaejasme (Figure **??** A,B, Supplementary Table **??**, Supplementary Table **??**). We also found that S. chamaejasme abundance was negatively associated with active pika burrow abundance (Figure **??** C) and with yak foraging activity, as indicated by dung density (Figure **??** D).

Building on these results, we conducted an in-situ manipulative field experiment using fenced enclosures to test the interactive effects of pika and S. chamaejasme on yak weight gain, foraging quantity and quality, and grazing behavior. For weight gain, yaks gained less in poison-plant plots than in non-poison plots, and there was a significant interaction between pika and S. chamaejasme treatments (Supplementary Table **??**). When pika were present, yaks showed higher weight gain (Supplementary Table **??**). This effect was driven by pika feeding on S. chamaejasme (Figure **??** B, Supplementary Table **??**, Supplementary Table **??**), which increased grass cover (Figure **??** C, Supplementary Table **??**, Supplementary Table **??**) compared to plots with S. chamaejasme but no pika.

Food quantity and quality are key drivers of individual performance and population dynamics in large herbivores[30–32]. In the presence of *S. chamaejasme* forbs, pika doubled the cover of yak's most preferred grasses (Figure **??** C, Supplementary Table **??**, Supplementary Table **??**) and increased the crude protein content of total forage by approximately 16% (Figure **??** D, Supplementary Table **??**, Supplementary Table **??**), suggesting that pika facilitate yak by enhancing both the quantity and quality of forage. Acid detergent fibre (6%) was higher in pika plots, while ether extract also differed significantly between treatments (Figure **??** E,F, Supplementary Table **??**, Supplementary Table **??**). These increases in grass abundance and forage quality were likely driven by the decline in poisonous plants induced by pika (Figure **??** B), which reduced interspecific competition for shared resources (e.g., light, soil moisture, nutrients) and allowed grasses to expand[27–28]. In the absence of S. chamaejasme forbs, however, the positive effects of pika on food resources and yak weight gain disappeared (Figure **??** A,C,D). Pika and poisonous plants influenced sedge cover in a similar way as grass cover (Supplementary Figure **??** A), while interactions with forb cover were more complex (Supplementary Figure **??** B). There was no impact of pika or poisonous plants on neutral detergent fibre (Supplementary Figure **??** C).

Pika-yak facilitation was also linked to improved foraging efficiency in yak when grazing alongside pika. Optimal foraging theory predicts that animals minimize energy costs to exploit high-quality food items and maximize intake of digestible nutrients, thereby improving performance[33]. In ruminants, bite rate, step rate, and bites per step are key predictors of foraging efficiency[34] and, ultimately, animal performance[35]. In the presence of *S. chamaejasme* forbs, yak total, sedge, and grass bite rates increased by roughly 35% (Figure **??** A), 48%