

Taste agents as modulators of the feeding behaviour of grazing yaks in alpine meadows



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ARTICLE INFO

Article history:

Received 8 June 2022

Revised 10 December 2022

Accepted 12 December 2022

Available online 19 December 2022

Keywords:

Diet selection

Direct observation

Grazing behaviour

Taste modulators

Qinghai-Tibetan Plateau

ABSTRACT

Feeding behaviour plays a significant role in promoting good animal health and welfare. It is also reflective of the quality and quantity of available feed. In fact, grazing livestock do not select their feed randomly, rather their behaviour is influenced by the texture, taste, and smell of each pasture species. Although taste agents are often used to modify feed intake for captive livestock, the effect on the feeding behaviour of grazing livestock has not yet been extensively evaluated in native grasslands. To address this gap in knowledge, herein, we sprayed three types of taste agents—salty (SA), sweet (SW), and bitter (BT)—on alpine meadows to investigate their effect on the grazing behaviour of yaks (*Bos Grunniens*) on the Qinghai-Tibetan Plateau (QTP). Behavioural observations showed that grazing was concentrated primarily in the morning and afternoon, while ruminating/resting peaked at noon; however, the diurnal behavioural patterns of grazing yaks were not affected by the taste agents. Application of the SA agent significantly increased the yaks' grazing time, bites per minute, bites per step, time per feeding station, and steps per feeding station, while significantly reducing walking time, steps per minute, and number of feeding stations per minute. Meanwhile, application of the SW agent significantly increased the yaks' time per feeding station, however, significantly reduced the steps per minute and number of feeding stations per minute. In contrast, the BT agent significantly increased the yaks' walking time, steps per minute, and number of feeding stations per minute, while significantly reducing grazing time, bites per minute, bites per step, and time per feeding station. Application of the SA agent also significantly increased the intake of favoured, edible, and inedible forage, while the SW agent improved inedible forage intake, however, had a more subtle effect on favoured and edible forage intake. Meanwhile, the BT agent had an inhibitory effect on grazing intake. Hence, the structural equation model suggested that taste agents may directly or indirectly influence grazing behaviour by regulating feeding behaviour. Our findings provide a theoretical basis for using taste agents in grasslands to control the grazing behaviour of livestock and provide a method to promote the stability of grassland communities, while mitigating the degradation of grasslands in the QTP.

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Implications

Animals select plants based on palatability and their feeding behaviour influences how grasslands are grazed, which impacts species composition, dominance, and ecological integrity. In this study, the application of taste agents to influence the grazing behaviour of yaks showed how the selection of plants for feed can be influenced to elicit positive effects in grasslands. Our study considers how to manage the feeding behaviour of grazing animals to enhance their productivity and reduce grassland degradation. This

strategy provides a long-term feasible option to manage grazing livestock for the protection and sustainable utilisation of grasslands.

Introduction

Grasslands are a natural resource that provide food and ecological security in many areas of the world, providing vital ecosystem services (Campos et al., 2016). The provision of these services relies on increasing plant diversity (Fraser et al., 2014), avoidance of foraging matter senescence (Cuchillo Hilario et al., 2017), prevention of grassland degradation (Yang et al., 2019), and promotion of nutrient recycling through faecal deposition (Yang et al., 2020).

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Although grazing is an effective means to utilise natural grassland (Eldridge et al., 2017), poor grazing practices have resulted in a significant decline in grassland biodiversity and multi-functionality, leading to the degradation of approximately 25% of grassland areas worldwide (Bai et al., 2008). This degradation can result from an imbalance between grassland grazing potential and livestock density. Grazing intensity has caused changes in the dominance of various grassland species within plant communities and has affected the ecological and biological characteristics of grasslands (Wang et al., 2007). Therefore, manipulation of livestock grazing intensity plays a critical role in ensuring the sustainable use of grassland resources (Barbero et al., 2015).

One such avenue of manipulation could be grazing behaviour, which directly affects animal productivity, future grazing opportunities, and pasture composition, and productivity (Yang et al., 2021). Feeding behaviour is a core characteristic of grazing behaviour in livestock and the primary cause of grassland reverse succession (degradation) (Wang et al., 2007). That is, while livestock usually graze ad libitum, they selectively choose which plants to eat. Texture, visual perception, taste, and smell are the factors that most strongly influence grazing selection (Villalba et al., 2011). In fact, feeding experience is the most important factor affecting the feeding behaviour of livestock. However, importantly, grazing livestock can acquire feeding experience through learning (Profet, 1991). Livestock continuously assess terrain and vegetation, predicting the characteristics of surrounding resources, and using visual and olfactory cues when selecting grazing areas. This results in the selection of shorter foraging paths to reduce energy consumption and improve feeding efficiency (Howery et al., 2000; Langbein et al., 2008). Moreover, livestock are sensitive to the brightness and colour of pastures (Jacobs et al., 1998; Carroll et al., 2001). Colour responses significantly affect the time sheep will feed on dark green ryegrass, which requires longer feeding times than bright green ryegrass (Bazely and Ensor, 1989). In South Africa's savanna vegetation, goats select thorned plants over non-spinescent plants in all seasons, due to the higher toxin content in the latter (Basha et al., 2012). Accordingly, behavioural research has played an important role in improving grazing management worldwide.

A grassland ecosystem that requires particular attention with regard to grazing-related degradation is the Qinghai-Tibetan Plateau (QTP), commonly referred to as the 'Roof of the World'. The QTP is the highest and most extensive grassland ecosystem in the world (Shang et al., 2014; Yang et al., 2018), covering approximately 130 million hectares (ha), i.e., 44% of China's total grassland (Piao et al., 2012). Reportedly, more than 18 million yaks (*Bos grunniens*) (Fan et al., 2019) and 50 million Tibetan sheep (*Ovis aries*) (Cui et al., 2019) graze this system. Consequently, overgrazing has resulted in the degradation of 38.8% of this grassland system (Sun et al., 2015). Hence, the development of optimised management strategies for grazing is key to protecting natural grasslands from degradation in the QTP (Wang et al., 2016). Indeed, regulating the selective feeding behaviour of grazing livestock has the potential to reduce grassland degradation. Which detailed studies have assessed the use of flavour agents to regulate selective feeding in confined livestock (Burritt et al., 2005; Villalba et al., 2011; Nannig et al., 2018), few have been conducted to determine how best to manage selective feeding in grazing livestock. As such, the aim of the present study was to assess the regulation of selective grazing in yak, by applying salty (SA), sweet (SW), and bitter (BT) taste agents to pastures. Two hypotheses were tested in this study. First, SA and SW treatments will improve the palatability of forage for yaks, leading to increased grazing time, bites per minute, and time at feeding stations when applied. Second, BT agents will reduce the palatability of most forage causing yaks to decrease their grazing time, bites per minute, and time at feeding stations.

Material and methods

Study site

The study site was located in the northeastern region of the QTP (33°03'N; 102°36'E; at an elevation of 3 500 m; Fig. 1). The plateau has a temperate continental cold monsoon climate, with a short spring and autumn season and a relatively cold and long winter. A mean annual temperature of 1.3 °C and mean total rainfall of 758 mm were recorded at the local agrometeorological information station in the year of this study. The vegetation type is typical alpine meadow. The species and palatability (favoured, edible, and inedible) of the forage are listed in Supplementary Table S1. The favoured, edible, and inedible classifications for the forage types were defined according to Wang (2006).

Animals, grazing conditions, and experimental design

The research was conducted from June 23 to September 23. Four blocks were set up randomly in areas used for summer grazing, with gentle terrain and uniform vegetation. Each block was divided into four paddocks, which were sprayed with 0.05 mol/L sodium N-cyclohexylsulfamate (SW), 0.001 mol/L denatonium benzoate anhydrous (BT), 0.17 mol/L sodium chloride (NaCl; SA), or an equal volume of tap water as a control (CK), respectively. Each paddock was also equipped with three 1 m × 1 m × 1 m cages; as the yaks' access was restricted, the areas inside these cages were unaffected by grazing and served as a control to measure the daily mass intake. The daily mass intake was calculated by the difference in forage biomass inside and outside of the cages (Peng et al., 2015). A total of 8 mL m⁻² of each taste agent were sprayed using an agricultural knapsack sprayer. The first spraying took place in late June, and the taste agents were re-sprayed every 7 d thereafter. Grazing was initiated immediately after spraying and proceeded for a period of 7 d.

A total of 20 healthy yak steers (age 3 years; average initial BW, 158.3 ± 3.8 kg [mean ± SD]) were included in the study. Before the start of the study, all test animals were dewormed and introduced into a controlled environment for a 7-d pretest feeding period. After the taste agents had been sprayed, the yaks grazed in the study paddocks at a density of 4.5 yaks ha⁻¹ (Yang et al., 2019; 2021) in individual paddocks from 0700 to 1900. The yaks of each group were rotationally grazed among the four blocks with different taste agent treatment within each block for one week. During the experimental period, all yaks in the study were free to consume water and received no supplementary feeding.

Sampling of plants and analyses of chemical composition

Forage samples were collected after the application of agents and water each week. Five quadrats (0.5 × 0.5 m) were randomly selected in each paddock, and a "W" shape was clipped into the vegetation with scissors, leaving vegetation at a height of 2 cm from the ground. Plant samples from each paddock of each block were mixed, oven dried at 60 °C for 48 h, then ground to less than 1 mm in size and sieved, prior to chemical analysis. The DM, OM, CP, and EE contents of the samples were measured using AOAC methods (AOAC, 2002). The NDF and ADF contents of the samples were measured using the Van Soest method (Van Soest et al., 1991). Samples of aboveground vegetation were collected from 0.5 m × 0.5 m quadrats inside and outside the cages after the yaks had grazed, to measure the daily mass intake of forage that was favoured by, edible to, and inedible to the yaks.

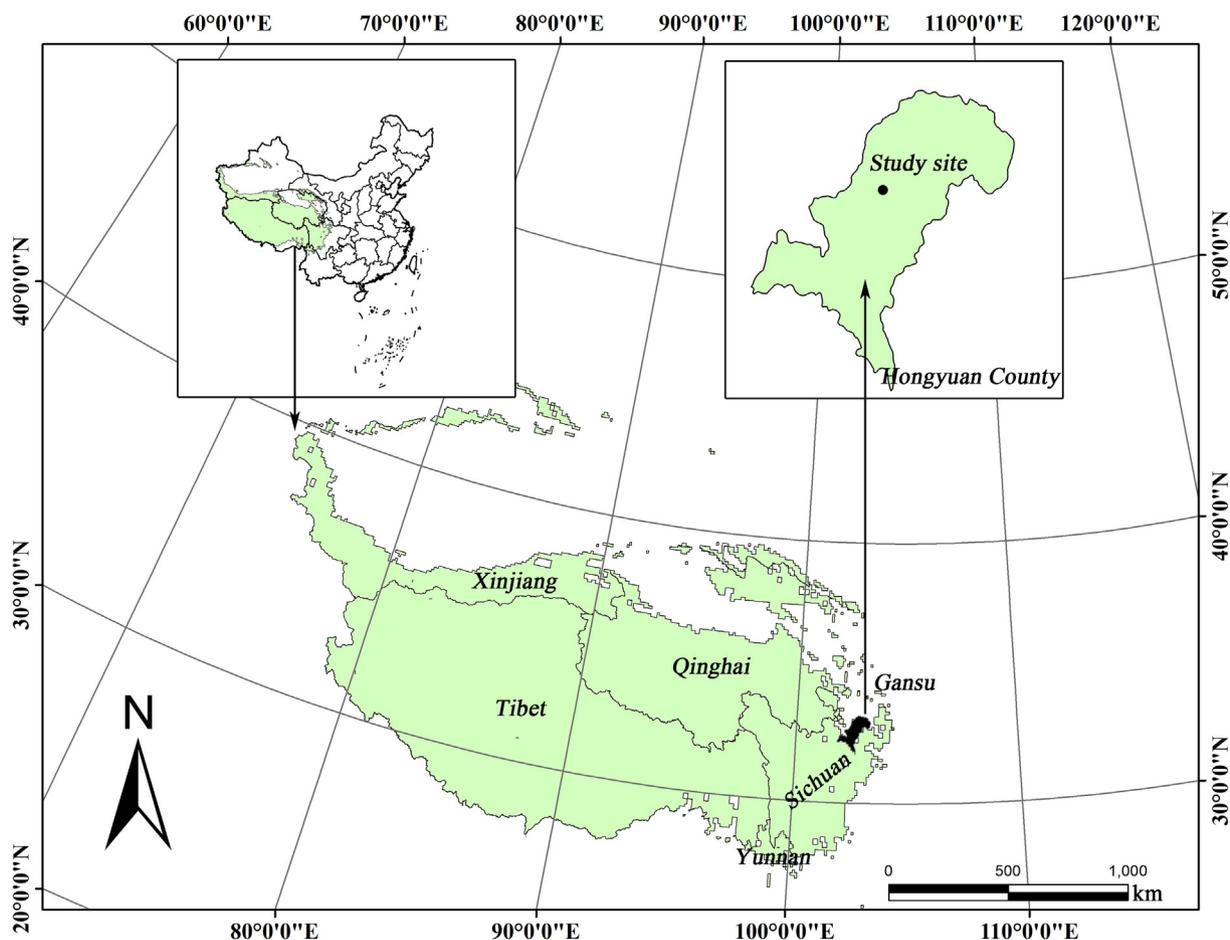


Fig. 1. Study site of yaks' grazing behaviour regulated by taste agents on the Qinghai-Tibetan Plateau.

Behaviour measurements

Three yaks were randomly selected for each treatment as focus animals. The behaviour of the selected animals was observed over the entire experimental period. The primary (i.e., walking, grazing, and ruminating/resting) and secondary (steps per minute, bites per minute, and feeding stations visited per minute) behaviours were recorded for the first five days of each week (observation period). Four trained observers, situated outside the study area, observed all animals with a telescope. During the observation period, each observer randomly selected one of the focus yaks and four yaks in each treatment (one yak per paddock). The other three yaks in each treatment were continuously observed and recorded during the observation period.

The primary behavioural activities of grazing yaks were assessed visually and recorded every 10 min (Arrazola et al., 2020) from 0700 to 1900 h on each observation day. Secondary behavioural activities were assessed visually and recorded as the time required by focus yaks to take either 50 bites, five steps, or visit 10 feeding stations while grazing (Arrazola et al., 2020). A feeding station was defined based on actions such as bites taken by the animals without moving their front hooves (Savian et al., 2020), and designated if at least one bite was taken. The data were then used to calculate mean time bites per minute, steps per minute, bites per step, feeding station per minute, time per feeding station, and steps per feeding station per day.

Statistical analysis

Data for forage nutrient composition, behavioural (primary and secondary) parameters, and DM intake (favoured, edible, and inedible forage) were analysed using the MIXED procedures of SAS (SAS Institute Inc., USA, version 9.2) with repeated measures, as represented by Eq. (1):

$$Y_{ijk} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \gamma_{(i)k} + e_{(ij)k} \quad (1)$$

where Y_{ijk} represents dependent variable of the ijk th forage or yak, μ is overall mean, α_i is fixed effect of the i th taste agent ($i = \text{CK, SW, SA, and BT}$), β_j is the fixed effect of the j th observation period ($j = \text{July, August, and September}$), $(\alpha\beta)_{ij}$ is the fixed interaction of i th different taste agent and j th observation period, $\gamma_{(i)k}$ represents the random effect of the k th paddock within the i th different taste agents, and $e_{(ij)k}$ is the residual error. Analysis of each variable followed the covariance structure (Yang et al., 2021). Results were presented as least squares means for treatment, standard error of the mean, and P -values for the effect of taste agent. Structural equation model analysis (Beaumelle et al., 2016) was conducted using the robust maximum likelihood evaluation method AMOS 26.0, which was assessed based on a non-significant result from the chi-square test ($P > 0.05$).

Results

We first assessed the correlations between the different taste agent treatments and the observation period within the day regarding the forage nutrient composition, behavioural (primary and secondary) parameters, and DM intake (favoured, edible, and inedible forage). There were no significant ($P > 0.05$) correlations between different taste agents and the observation period with any variable. In addition, no differences were observed among the observation periods ($P > 0.05$), thus, only the effect of taste agent treatments was included in subsequent analyses.

Effects of three taste agent types on forage chemical composition

The three types of taste agents had no significant influence on the DM ($P = 0.681$), CP ($P = 0.229$), OM ($P = 0.889$), EE ($P = 0.716$), NDF ($P = 0.523$), or ADF ($P = 0.864$; Table 1) content of forage.

Diurnal patterns of behaviour

The timing of the behavioural patterns of the yaks during the observation period varied greatly between the plots treated with the different taste agents. However, the diurnal grazing behaviour patterns in the pastures were similar (Fig. 2). Grazing activities peaked between 0700 and 0900 h and 1400 and 1800 h. The yaks spent more time resting and sleeping between the two grazing peaks. Peak walking time occurred from 1000 to 1200 h. In the CK group, yaks spent 52–80% of their time grazing (mean 66%),

13–27% walking (mean 20%) and 4–33% ruminating/resting (mean 18.5%). In the BT group, yaks spent 16–41% of their time grazing (mean 28.5%), 39–65% walking (mean 52%), and 5–46% ruminating/resting (mean 25.5%). In the SW group, yaks spent 61–90% of their time grazing (mean 75.5%), 5–16% walking (mean 10.5%), and 4–26% ruminating/resting (mean 15%). In the SA group, yaks spent 47–80% of their time grazing (mean 63.5%), 12–27% walking (mean 19.5%) and 5–33% ruminating/resting (mean 19%).

Effects of three taste agent types on primary behavioural patterns

Although the average ruminating/resting time of grazing yaks was similar in the plots treated with the different taste agents ($P = 0.435$), the taste agents significantly influenced the time spent grazing ($P < 0.001$) and walking ($P < 0.001$; Table 2). Yaks spent more time grazing in the grasslands treated with SA (77.4%) than in the CK plots (66.1%), whereas the time spent walking in the SA treatment was lower than in the CK treatment (9.33% vs 19.1%). Yaks spent less time grazing in grasslands treated with BT (28.9%) than in the CK plots (66.1%), whereas they spent more time walking in the BT treatment plots than in the CK grasslands (54.6% vs 19.1%).

Yaks spent more time grazing during the first and fourth daylight quarters (Q1 and Q4) compared with the second and third daylight quarters (Q2 and Q3) in all plots with different taste agents (66.8 and 66.5% vs 49.6 and 52.7%, respectively; Table 2). The time spent ruminating and resting increased as the day progressed, with averages of 10.7, 21.1, and 23.9% for Q1, Q2, and Q3, respectively, decreasing to 9.29% during Q4. Similarly, the time spent walking

Table 1
Effects of three taste agents on the chemical compositions of forage grazed by yaks in alpine meadows.

Chemical composition	Treatments				SEM	P-value
	CK	BT	SA	SW		
DM (% as fed)	46.8	51.9	47.6	49.3	1.539	0.681
OM (% DM)	85.4	84.9	86.9	85.3	0.894	0.889
CP (% DM)	8.80	9.22	9.07	9.43	0.186	0.229
EE (% DM)	1.55	1.57	1.63	1.62	0.025	0.716
NDF (% DM)	46.2	47.2	45.9	43.9	1.686	0.523
ADF (% DM)	26.2	27.2	28.7	26.4	0.966	0.864

Abbreviations: CK = clean water; BT = bitter agent; SA = salty agent; SW = sweet agent; OM = organic matter; EE = ether extract.

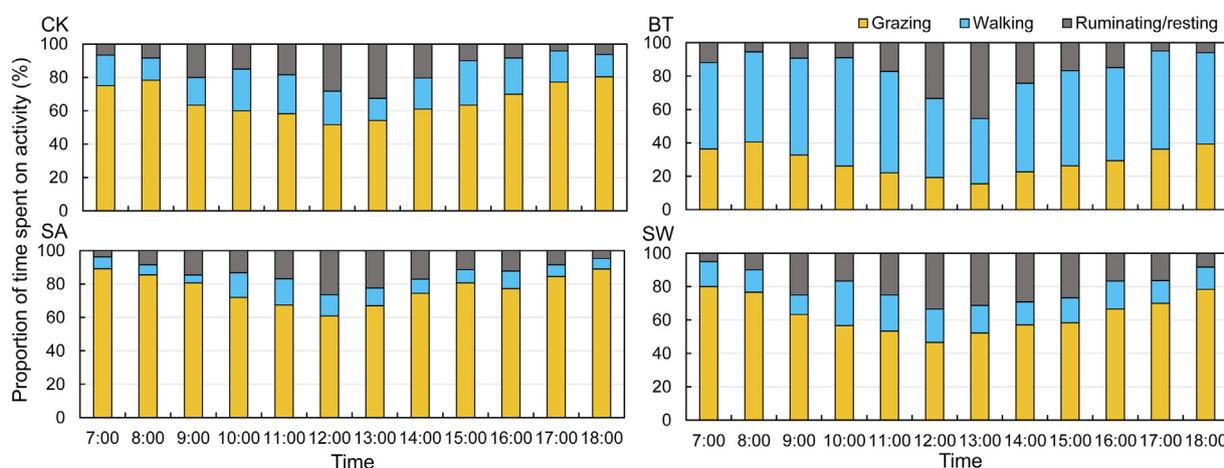


Fig. 2. Time spent grazing, walking, and ruminating/resting by yaks grazing in pastures with the three taste agents. Abbreviations: CK = clean water; BT = bitter agent; SA = salty agent; SW = sweet agent.

Table 2
Effects of three taste agents on the primary behaviour patterns of yaks grazing in alpine meadows.

Behaviour (%) ¹	Daylight quarter ²	Treatments				Mean	SEM	P-value
		CK	BT	SA	SW			
Intaking	Q1	72.2 ^a	36.5 ^b	85.1 ^a	73.3 ^a	66.8	5.933	<0.001
	Q2	56.7 ^b	22.5 ^c	66.8 ^a	52.2 ^b	49.6	5.032	<0.001
	Q3	59.5 ^b	21.5 ^c	74.0 ^a	55.9 ^b	52.7	5.959	<0.001
	Q4	75.8 ^{ab}	34.9 ^c	83.6 ^a	71.7 ^b	66.5	5.727	<0.001
	Mean	66.1 ^b	28.9 ^c	77.4 ^a	63.3 ^b	58.9	2.683	<0.001
Walking	Q1	16.1 ^b	54.6 ^a	5.95 ^c	13.3 ^b	22.5	5.685	<0.001
	Q2	22.8 ^b	57.6 ^a	14.4 ^b	22.8 ^b	29.4	4.981	<0.001
	Q3	19.6 ^b	49.7 ^a	9.06 ^b	15.1 ^b	23.4	4.691	<0.001
	Q4	17.9 ^b	56.4 ^a	7.94 ^c	14.6 ^b	24.2	5.541	<0.001
	Mean	19.1 ^b	54.6 ^a	9.33 ^c	16.5 ^b	24.9	2.163	<0.001
Ruminating/resting	Q1	11.7	8.94	8.95	13.3	10.7	1.293	0.487
	Q2	20.6	19.9	18.9	25.0	21.1	1.973	0.993
	Q3	20.9	28.8	16.9	20.0	23.9	2.967	0.269
	Q4	6.28	8.67	8.44	13.8	9.29	1.295	0.172
	Mean	14.9	16.7	13.3	20.3	16.3	1.735	0.435

Abbreviations: CK = clean water; BT = bitter agent; SA = salty agent; SW = sweet agent.

¹ Values are the proportion of time spent on an activity.

² Q1 = 0700–1000 h; Q2 = 1000–1300 h; Q3 = 1300–1600 h; Q4 = 1600–1900 h.

^{a-c} Values within a row with different superscripts differ significantly at $P < 0.05$.

increased from 22.5% in Q1 to 29.4% in Q2, and then decreased to 23.4 and 24.2% in Q3 and Q4, respectively. The time yaks spent grazing increased significantly in the SA plots compared to CK plots during Q2, Q3, and Q4, whereas that in the BT plots was significantly lower than the CK plots during all daylight quarters. In contrast to grazing patterns, the time yaks spent walking increased significantly in BT plots compared to CK plots in all daylight quarters, whereas the walking time of yaks in the SA treatment plots was significantly lower than in the CK plots during Q1 and Q4.

Effects of three taste agent types on secondary behavioural patterns

The taste agents significantly affected bites per minute ($P < 0.001$), steps per minute ($P = 0.004$), bites per step ($P < 0.001$), number of feeding stations per minute ($P < 0.001$), time at the feeding station ($P < 0.001$), and steps per feeding station ($P = 0.017$, Table 3). Yaks significantly increased bites per minute (75.6 vs 61.2), bites per step (14.1 vs 6.86), time per feeding station (9.49 vs 6.58), and steps per feeding station (2.31 vs 1.74), while significantly decreasing steps per minute (6.33 vs 9.58) and feeding station per minute (2.78 vs 5.54), in the SA treatments compared to the CK treatments. Yaks also significantly increased the time per feeding station in the SW treatments, when compared with CK treatments (7.09 vs 6.58), however, significantly decreased steps per minute (8.42 vs 9.58) and feeding station per minute (5.03 vs 5.54). Yaks significantly increased the steps per minute (14.5 vs 9.58) and feeding station per minute (8.55 vs 5.54) in the BT treat-

ments compared to CK treatments, however, significantly decreased bites per minute (25.7 vs 61.2), bites per step (2.09 vs 6.86), and time per feeding station (3.59 vs 6.58).

Effects of the three taste agent types on DM intake (favoured, edible, inedible, and total forage) of yaks grazing in alpine meadows

The taste agents significantly affected DM intake of favoured forage ($P < 0.001$), edible forage ($P < 0.001$), inedible forage ($P < 0.001$), and total forage ($P < 0.001$, Table 4). Yaks significantly increased DM intake of favoured forage (0.22 vs 0.18), edible forage (1.76 vs 0.89), inedible forage (0.47 vs 0.13), and total forage (2.45 vs 1.20) in SA treatments compared to CK treatments. Similarly, yaks significantly increased inedible forage (0.49 vs 0.13) and total forage (1.61 vs 1.20) in SW treatments compared to the CK treatments. In contrast, yaks significantly decreased favoured forage (0.07 vs 0.18), edible forage (0.23 vs 0.89), and total forage (0.40 vs 1.20) in BT treatments compared to CK treatments.

Relationship among taste agents, feeding behaviour, and grazing behaviour

We estimated the relationship between taste agents, feeding behaviour, and grazing behaviour using a structural equation model analysis (Fig. 3). Our results showed that taste agents either directly or indirectly influence grazing behaviour by regulating feeding behaviour.

Table 3
Effects of three taste agents on the secondary behaviour patterns of yaks grazing in alpine meadows.

Behaviour	Treatments				SEM	P-value
	CK	BT	SA	SW		
Bites per minute	61.2 ^b	25.7 ^c	75.6 ^a	62.1 ^b	3.871	<0.001
Steps per minute	9.58 ^b	14.5 ^a	6.33 ^c	8.42 ^b	0.641	0.004
Bites per step	6.86 ^b	2.09 ^c	14.1 ^a	8.20 ^b	1.034	<0.001
Feeding station per minute	5.54 ^b	8.55 ^a	2.78 ^d	5.03 ^c	0.369	<0.001
Time per feeding station (s)	6.58 ^c	3.59 ^d	9.49 ^a	7.09 ^b	0.380	<0.001
Steps per feeding station	1.74 ^b	1.71 ^b	2.31 ^a	1.68 ^b	0.065	0.017

Abbreviations: CK = clean water; BT = bitter agent; SA = salty agent; SW = sweet agent.

^{a-d} Values within a row with different superscripts differ significantly at $P < 0.05$.

Table 4
Effects of three taste agents on DM intake (favoured, edible, and inedible forage) in yaks grazing in alpine meadows.

DM intake (kg d ⁻¹)	Treatments				SEM	P-value
	CK	BT	SA	SW		
Favoured forage ¹	0.18 ^b	0.07 ^c	0.22 ^a	0.20 ^b	0.019	<0.001
Edible forage ²	0.89 ^b	0.23 ^c	1.76 ^a	0.93 ^b	0.165	<0.001
Inedible forage ³	0.13 ^b	0.09 ^b	0.47 ^a	0.49 ^a	0.056	<0.001
Total forage	1.20 ^c	0.40 ^d	2.45 ^a	1.61 ^b	0.227	<0.001

Abbreviations: CK = clean water; BT = bitter agent; SA = salty agent; SW = sweet agent.

¹⁻³ The species and palatability (favoured, edible, and inedible) of the forage are listed in Table S1. The palatability classification of forage was defined according to Wang (2006).

^{a-d} Values within a row with different superscripts differ significantly at $P < 0.05$.

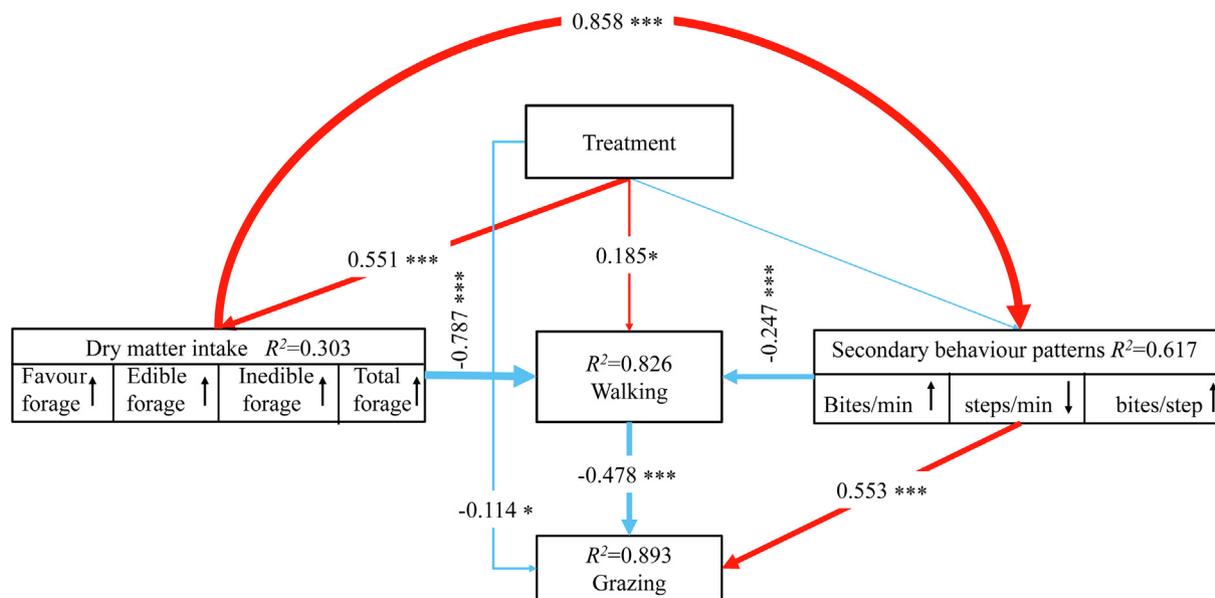


Fig. 3. Structural equation model of the relationship between the taste agents and the DM intake (favoured forage, edible forage, inedible forage, and total forage), primary behaviour patterns (walking time and grazing time), and secondary behaviour patterns (bites/min, steps/min, and bites/step) of grazing yaks. The relative thickness of each arrow represents the strength of the relationship (red: positive relationship, blue: negative relationship). Treatments: bitter agent, salty agent, and sweet agent. *** $P < 0.001$; * $P < 0.05$.

Discussion

Livestock assess forage palatability and develop feeding strategies accordingly (Langbein et al., 2008), favouring pastures with soft texture, deep colour, attractive taste, and high nutritional value (Carroll et al., 2001). Feeding strategies for livestock result from the feeding experience generated through various regulatory pathways, as such, this behaviour is not static and can be manipulated artificially for a positive or negative forage consumption experience. Indeed, this strategy can be applied in grasslands to improve utilisation efficiency, promote sustainable utilisation, and prevent degradation. To this end, our results suggest that (i) SA treatments improve the palatability of forage and enhance grazing levels; (ii) SW treatments enhance the responsiveness of grazing animals to the palatability of forage; and (iii) BT treatments decrease the palatability of pastures and inhibit livestock grazing. These findings have significant value for practical application.

Forage is particularly palatable during the re-green stage, during which time the livestock exhibit a higher forage selectivity. However, as palatable forage suffers from frequent feeding, its competitiveness decreases, causing it to ultimately be replaced by less palatable forage. This disrupts the composition of plant communities and reduces productivity (Hou and Yang, 2006). Meanwhile, livestock reduce their feed intake at the onset of winter when the palatability of grasses decreases, resulting in reduced

livestock productivity (Fan et al., 2020). As such, the application of BT during the re-green stage can inhibit livestock feeding, whereas the application of a weak solution of SA or SW taste agents during pasture withering can improve the palatability of forage. Such management can improve pasture utilisation efficiency.

Selective grazing by livestock is particularly obvious during the vegetative stage. During which, yaks select for palatable forage, rejecting forage with low palatability, causing the structure of grassland communities to change with poisonous or unpalatable plants gradually becoming predominate (Sun et al., 2008; Du et al., 2015). This will cause reverse succession of grassland plant communities, decrease species diversity, and eventually lead to grassland degradation (Hou and Yang, 2006). Meanwhile, regulation of selective grazing in livestock can control the degradation of grassland and maintain the ecological balance. That is, during the vegetative stage, BT treatments can be sprayed on palatable forage to reduce selective grazing, and SA or SW treatments can be sprayed on forage with poor palatability to enhance palatability and achieve a more uniform feeding pattern.

Diurnal patterns of behaviour

The diurnal response pattern to all taste agents was similar. In this study, yaks had two main grazing periods, i.e., a shorter morning (Q1) and an afternoon (Q4) bout. This is typical of ruminants

(Yang et al., 2021). Nutrients and digestibility of forage increased during the day and yaks grazing at dusk maximised nutrient intake (Gibb et al., 1998; Griggs et al., 2005). Further, ghrelin is a hormone that stimulates food intake in ruminants, the concentration of which is highest at dusk and dawn (Roche et al., 2008; Gregorini et al., 2009b). Hence, in our study, yaks increased grazing time in the mornings (Q1) and afternoons (Q4), primarily due to the secretion of hormones and daily changes in the chemical composition of forage. A previous study reported that yaks alter behaviour patterns during the day and typically begin ruminating at noon and night after the rumen reaches a certain fullness (Ding et al., 2007; 2008). Moreover, Cuchillo Hilario et al. (2017) observed a 6–8 h rumination peak in cattle and sheep between grazing events, possibly to ensure sufficient fibre degradation rates to decrease satiation. Meanwhile, Ding et al. (2007 and 2008), Liu et al. (2019), and Yang et al. (2021) reported that yaks enter a rumination/rest peak around 1200–1400, after a grazing peak, which is consistent with our results. Aublet et al. (2009) reported that the alpine ibex in high-altitude areas rarely eats at noon due to the high summer temperatures and solar radiation, which is conducive to ruminating and resting. Similarly, the moose stops foraging at noon to escape the summer heat (Van Beest et al., 2012). However, in our study, the yak did not decrease grazing at noon in summer, suggesting that future studies could evaluate yaks grazing at noon to provide a species-specific comparison.

Effect of taste agents on primary and secondary behavioural patterns in grassland grazing

The results of this study are consistent with our hypothesis that the number of bites per minute and time spent at each feeding station will increase when SA and SW treatments are used in grasslands, and decrease when BT taste agents are applied. According to foraging theory (Charnov, 1976), the greater the available biomass at a feeding station, the longer the time spent there. However, the available biomass of feeding stations in our study did not differ significantly nor did the time at each feeding station. Meanwhile, when SA and SW treatments were applied to pastures, animals spent more time at each feeding station, and less time when BT treatments were applied. Hence, taste agents may directly influence grazing behaviour. Similarly, Guda (2018) and McMeniman et al. (2006) showed that SA and SW treatments, respectively, improve forage palatability, while Yan et al. (2019) demonstrated that BT treatments have the opposite effect. Ruyle and Dwyer (1985) also reported that sheep spend more time at feeding stations with more palatable forage and vice versa. Our study supports these observations and further found that taste agents may influence grazing behaviour indirectly by regulating livestock feeding behaviour (feed intake). Additionally, Gregorini et al. (2009a) revealed that as forage availability increases, the requirement to move to find forage is significantly reduced, thus, increasing grazing efficiency. We postulate that spraying SA and SW taste agents on grasslands can increase the utilisation of existing forage and enable yaks to achieve the same forage intake in a shorter period, thereby enhancing the efficiency of grazing per unit area.

The energy consumption of yaks increased when BT treatments were applied as walking time, steps per minute, and feeding station per minute all increased. However, spraying SA treatments on grassland had the opposite effect. Yang et al. (2021) reported that walking time and steps per minute increase with an increase in shrub coverage, as does the energy consumption of the yak. Moreover, Fierro and Bryant (1990) and Lachica and Aguilera (2005) reported that walking accounts for 45% of energy consumption in sheep muscles per day. Indeed, grazing sheep have higher energy requirements than captive sheep, due to the increased mus-

cle strength required for walking and eating. Hence, spraying BT treatments on an alpine meadow increases walking and feeding behaviours and the energy consumption of grazing yaks, thus, greatly reducing the amount of metabolic energy available for growth and production (Yang et al., 2021). However, spraying SA treatments have the opposite effect.

Effects of applying taste agents to grazing grassland on feed mass intake

Feeding activity is a core feature of grassland grazing systems (Wall et al., 2018). Selective feeding by livestock involves selecting favourable water sources, topography, and soil, as well as plant species, quality, and palatability (Pfeiffer et al., 2019). The feed intake of grazing livestock is representative of preference levels for specific forage and aboveground biomass (Michez et al., 2019). Hitherto, most research on the regulation of grazing livestock has focused on the effects of grazing intensity (Winck et al., 2019), while few have evaluated the feeding behaviour of grazing livestock after spraying taste agents on grasslands. Our results indicate that SA treatments stimulate appetite and significantly affect the intake levels of favoured, edible, and inedible forage (Arieli et al., 1989). Related research shows that SA treatments can enhance the appetite of sheep and increase feed intake (Thomas et al., 2007). In fact, SA agents play an important role in the normal physiological metabolism of livestock. That is, grazing livestock select for forage with salt to regulate osmotic pressure stability, blood pressure stability, water balance, acid-base balance, normal excitability of nerves, and muscles (Guda, 2018). Hence, future research should focus on the upper bound of agent concentration as SW treatments increased the intake of inedible forage, however, had a subtle effect on favoured and edible forage. Furthermore, Villalba et al. (2014) demonstrated that SW treatments can increase the feed intake of livestock. This is inconsistent with the results of our study and may be due to the use of different substances in the sweeteners. More specifically, high-energy sucrose was used as a sweetener by Villalba et al. (2014), whereas cyclamate, which does not contain energy, was used in our study. This indicates that sweetness did not induce feeding, but rather livestock selectively consume for energy (Burrill et al., 2005). In contrast, BT treatments inhibit grazing intake. Livestock tend to avoid bitter foods as bitterness often indicates the presence of toxins (Yeheyis et al., 2012). In fact, spraying with BT resulted in the lowest intake mass, which may differ among different ruminants (Van Soest, 1994).

Currently, the feeding behaviour of grazing livestock appears to be determined primarily via the distribution and nutritional status of grassland plants, as well as the feeding experience of grazing livestock (Cuchillo Hilario et al., 2017; Yang et al., 2020). In general, the feeding behaviour of grazing livestock on the QTP is relatively unrestricted with no manipulation. However, this does not promote the efficient use of grasslands and future grazing systems should design strategies to artificially control the feeding of grazing livestock. Currently, unmanned aerial vehicles (UAVs) have been extensively employed in sowing, spraying fertiliser, and pesticide (Kim et al., 2019). Hence, UAVs can also be applied, as part of the grazing management system of the QTP, to spray taste agents to control the grazing behaviour of livestock, thereby balancing the feed intake of livestock, and significantly promoting the healthy development and efficient utilisation of grasslands.

Conclusion

Structural equation models suggest that taste agents may directly or indirectly influence grazing behaviour by regulating

feeding behaviour. Although the effects of SA, SW and BT agents on different forage vary, in general, the SA taste agent can improve the palatability of forage and increase intake by grazing yaks. Moreover, while the effect of the SW agent is not as obvious, grazing yaks can be more responsive to certain forage, and SW treatments can improve the palatability of inedible forage. Meanwhile, BT agents reduce the palatability of most forage and can inhibit live-stock feeding. Our study provides novel evidence that applying taste agents to grasslands regulates the selective intake of grazing livestock. In future, the grazing management system of the QTP should seek to employ UAVs to spray various taste agents in a large area to control the feeding and grazing behaviour of grazing livestock, thus, providing a feasible strategy for the protection and sustainable utilisation of grasslands.

Supplementary material

Supplementary material to this article can be found online at <https://doi.org/10.1016/j.animal.2022.100703>.

Ethics approval

The study, and all animal procedures therein, was approved by the ethics committee of Lanzhou University (Nos. 2010-1 and 2010-2).

Data and model availability statement

None of the data were deposited in an official repository. Data are confidential but available to reviewers upon request.

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Declaration of interest

The authors declare no competing financial interest.

Acknowledgements

We would like to extend our sincere gratitude to Shulin Wang for their assistance in data analysis. We would also like to thank Editage (www.editage.com) for English language editing.

Financial support statement

This study was funded by the National Key Research and Development Program of China, Grant/Award Number: 2021YFD1300504, the National Natural Science Foundation of

China, Grant/Award Number: U21A20242, the Program of National Science and Technology Assistance, Grant/Award Number: KY202002011, the Program for Innovative Research Team of Ministry of Education, Grant/Award Number: IRT17R50, and the Fundamental Research Funds for the Central Universities (Izujbky-2021-it01).

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