Grazing-Induced Cattle Behaviour Modulate the Secondary Production in a Eurasian Steppe Ecosystem

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Grazing-induced cattle behaviour modulates the secondary production in a Eurasian steppe ecosystem

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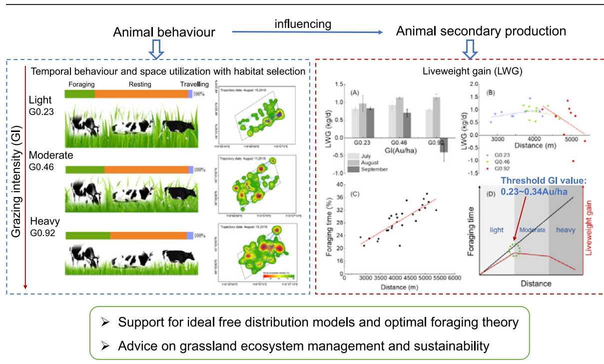
HIGHLIGHTS

- Thresholding the behaviour of cattle for velocity using classification methods
- Quantifying the spatial and temporal behaviour of grazing cattle
- Assessing the relationship between cattle behaviour and vegetation features
- Combining animal behaviour with secondary productivity validates the basic theory

GRAPHICAL ABSTRACT



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ABSTRACT

Livestock-grassland interactions are among the most important relationships in grazed grassland ecosystems, where herbivores play a crucial role in plant community and ecosystem functions. However, previous studies primarily have focused on the responses of grasslands to grazing, with few focussing on the effects of livestock behaviour that in turn would influence livestock intake and primary and secondary productivity. Through a 2-year grazing intensity experiment with cattle in Eurasian steppe ecosystem, global positioning system (GPS) collars were used to monitor animal movements, where animal locations were recorded at 10-min intervals during the growing season. We used a random forest model and the K-means method to classify animal behaviour and quantified the spatiotemporal movements of the animals. Grazing intensity appeared to be the predominant driver for cattle behaviour. Foraging time, distance

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travelled, and utilization area ratio (UAR) all increased with grazing intensity. The distance travelled was positively correlated with foraging time, yielding a decreased daily liveweight gain (LWG) except at light grazing. Cattle UAR showed a seasonal pattern and reached the maximum value in August. In addition, the canopy height, above-ground biomass, carbon content, crude protein, and energy content of plants all affected cattle behaviour. Grazing intensity and the resulting change in above-ground biomass and forage quality jointly determined the spatiotemporal characteristics of livestock behaviour. Increased grazing intensity limited forage resources and promoted intraspecific competition of livestock, which induced longer travelling distance and foraging time, and more even spatial distribution when seeking habitat, which ultimately led to a reduction in LWG. In contrast, under light grazing where there were sufficient forage resources, livestock exhibited higher LWG with less foraging time, shorter travelling distance, and more specialized habitat occupation. These findings support the Optimal Foraging Theory and the Ideal Free Distribution model, which may have important implications for grassland ecosystem management and sustainability.

1. Introduction

Grassland ecosystems consist of plants, animals, soil, and the environmental components. Their management includes climate, herders, society, and ecosystems through adaptive mechanisms to cope with livestock grazing (Diaz et al., 2007; Tietjen and Jeltsch, 2007). For many grasslands, grazing has been an important land use utilization practice for thousands of years (Xin et al., 2020; Chen et al., 2022). Despite its importance, there is no consensus on how grazing affects livestock behaviour and therefore livestock production. In these ecosystems livestock influence species composition, community diversity, plant dynamics, grassland ecosystem evolution and services (McNaughton, 1985; Collins et al., 1998; Maestre et al., 2022). It has been hypothesised that there is mutual feedback in plant-animal interactions through strengthening the connections between livestock and grasslands (Lima and Zollner, 1996).

Animal behaviour is partially the result of the interactions between animals and their living ecological environments. Grazing animals have greater energy consumption compared to other domesticated animals in confined spaces, mediated through several major behaviours such as travelling movement, browsing, and breeding (Arnold and Dudzinski, 1979; Animut et al., 2005). Livestock behaviour, a fundamental characteristic of grazing ecosystems, is a major process in the transition from biological productivity to secondary productivity (Nathan et al., 2008), So does livestock behaviour have an impact on production and other on ecosystem functions and services? The premise that grazing animals tend to gain maximum benefits at minimum costs during the foraging period is known as the optimal foraging theory (Perry and Pianka, 1997). Unfortunately, most previous studies on livestock behaviour have focused on browsing activities, such as foraging frequency, grazing time, forage intake, dietary selection, and plant palatability (Laca et al., 1994; Prache, 1997; Wang et al., 2010). Spatiotemporal behaviour of livestock has rarely been studied because of the limitation of data that makes it difficult to obtain long-term, high frequency, and longitudinal data, especially in the Eurasian steppe. Rivero et al. (2021) synthesized 283 articles about grazing cattle activity published between 2000 and 2020 and found that only 24 % and 5 %–6 % of the studies were carried out in the Europe and Asia, respectively.

In the past two decades, advances in tracking technology have led to an exponential increase in animal location data. Light and durable GPS devices can be widely used in research on grassland-animal interactions for monitoring animal activity, tracking routes, planning pasture utilization and virtual fencing, to the extent that livestock behaviour can be investigated on a spatiotemporal scale, providing the foundation for the development of "smart pastures" (Schlecht et al., 2004; Li et al., 2021; Tzanidakis et al., 2023). For instance, Turner et al. (2000) studied the movement trajectory and spatial distribution of grazing beef cattle using GPS collars and showed that water resources, temperature, and individual interactions affected movement behaviour. Thomas et al. (2011) also used GPS collars to study cattle grazing activity, including animal travelling distance and spatial distribution, and assessed cattle adaptive ability from one pasture to a new environment. Some studies have found that speed of movement rather than distance was a key indicator of livestock behaviour (Ungar et al., 2005; Perez et al., 2017). To be more specific, Anderson et al. (2012) measured movement speed of cows at 1-min intervals and proposed the following velocity thresholds: resting (standing), 0–0.06 m/s; critical foraging and walking points, 0.50 m/s; and the maximum travelling speed, 1 m/s. Nevertheless, it is undeniable that the speed thresholds corresponding to each behaviour of livestock vary by environmental condition (Moritz et al., 2010; Sarova et al., 2010). Investigating livestock movement can also be used to monitor animal welfare issues such as the health and fitness of livestock, as well as habitat selection which is closely related to the spatial pattern of habitat occupation and resource utilization strategy (Signer et al., 2019; Rivero et al., 2021). Maestre et al. (2022) also used the size and density of livestock tracks as measure of historic grazing. In addition to these studies on the behaviour of grazing livestock, there is also research focused on wild animals, especially long-distance migration of birds and large mammals, and animal-vectored seed dispersal (Kleyheeg et al., 2017; Teitelbaum and Mueller, 2019; Nield et al., 2020). Presently, it is essential to emphasise that the underlying mechanisms for animal behaviour modulates the secondary production have not been thoroughly explored.

In practice, it is difficult to determine how natural resources affect animal behaviour in complex environments (Giuggioli and Bartumeus, 2010). Overall, behaviour of grazing livestock can be influenced by population density, habitat conditions, vegetation distribution, livestock breeds, and animals' rhythmic features. Increased densities of grazing animals may not only change the plant community structure but also increase interspecific competition and alter animal behaviour. Schoenbaum et al. (2017) found that cattle at high stocking rates spent more time grazing compared with cattle at lower population densities. Venter et al. (2019) reported that grazing intensities did not change the time engaged in different animal behaviours, such as foraging, resting, and walking; however, habitat conditions including slope, terrain roughness, and water source locations had a distinct impact on spatial distribution of livestock and pasture utilization (Rivero et al., 2021). The Ideal Free Distribution model, which assumes that animals tend to move and occupy ideal places to maximize fitness, can be applied to explain habitat selection or utilization distribution (Morris, 2006; Owen-Smith et al., 2010; Bonar et al., 2020). When population density is low, all individuals will select the habitat with the highest environmental quality; however, as animal population density increases, the fitness of individuals in the habitat decreases. As a result, some individuals will turn to using lower quality habitat in order to enhance their own fitness (Fig. S1). Furthermore, Putfarken et al. (2008) found that cattle and sheep have different grazing habits and are therefore spatially complementary in the same region. The spatial distributions of resource and species composition of vegetation can strongly affect livestock grazing, because grazing animals usually avoid interactions with poisonous, prickly, or low-protein plants (Venter et al., 2019; Rivero et al., 2021). Some research has reported on the temporal patterns of grazing livestock, such as a higher frequency of foraging activity in the early morning and late afternoon (Schoenbaum et al., 2017). Ge (2008) suggested that the temporal pattern of grazing activity is determined mainly by species and breed of livestock, coupled with regional climate.

Meadow steppe is the most productive grassland type of Eurasian steppe, with rich plant species and relatively high vegetation productivity. Previous studies have indicated that grazing has a significant impact on community structure, plants, and livestock productivity; yet few have investigated whether the behavioural responses of livestock under different grazing pressures have an impact on livestock production, for which we hypothesize a mechanism to explain the animal-vegetation interactions (Seman et al., 1991; Milchunas and Lauenroth, 1993; Buttolph and Coppock, 2004; Zhang et al., 2022). In this study, we explore the effects of grazing intensity on cattle behaviour on the Hulunbuir meadow steppe in China. Our study objectives are to: (1) characterize grazing cattle behaviour based on GPS-tracked movement and field observations of the cattle, (2) investigate spatiotemporal characteristics of cattle behaviour under different grazing intensities, and (3) identify the principal factors that influence behaviours of grazing cattle and cattle productivity performance and simultaneously explore its implications for grazing practice.

2. Materials and methods

2.1. Study site and experimental design

This study is based on a manipulative experiment at the Hulunbuir Grassland Ecosystem Observation and Research Station (49°32′–49°34′ N, 119°94′–119°96′ E, 670–677 m a.s.l.) in Inner Mongolia, China. The region is characterized by a temperate semi-arid inland climate with a mean annual temperature of −3 to 1 °C and a mean annual precipitation of 350–400 mm (80 % of which falls during July–September). The soil is a chernozem type (or Mollisols in the US soil taxonomy); the steppe vegetation is dominated by *Leymus chinensis*, *Stipa baicalensis*, *Carex pediformis*, *Galium verum*, and *Bupleurum scorzonerifolium* (Yan et al., 2018).

The research site was located on relatively flat terrain. Regional average stocking rate was 0.46 animal units per hectare (0.46 cow Au/ha, where 1 Au = 500 kg adult cattle). Three grazing intensities were applied to a total of 9 plots (5 ha each): 0.23 (light grazing), 0.46 (moderate grazing), and 0.92 (heavy grazing) cow Au/ha. Each grazing intensity was replicated three times. There were two, four, and eight adult cattle, respectively, for the three grazing treatments, with live weights of 250–300 kg cattle on each plot. Wire fences were established in the experimental plot without herders, and there was no supplementary feeding throughout the free grazing season (June–September) each year in 2017 and 2018 (Fig. 1).

2.2. Vegetation sampling

Plant community surveys were conducted on five randomly selected 1 m × 1 m quadrats per plot at the beginning of each month from July through September 2018. The height and number of individual stems (tillers) of each plant species was recorded (Table S1). The aboveground component of each species was cut, collected, and dried to constant weight at 65 °C for 48 h; the sum of the dry weights of individual species in the quadrats was termed as aboveground biomass (AGB). Plant samples of approximately 2.5 kg were collected randomly in each plot to mimic cattle foraging ingestion, kept at −20 °C, freeze-dried and ground to pass through a 1 mm sieve for measurement of nutrient concentrations. The C and N concentrations were determined using an Elemental Analyzer (Vario EL *III*; Elementar Analysen systeme GmbH, Langenselbold, Germany). Crude protein (CP) was calculated by N × 6.25 (Van Soest and Robertson, 1985). Neutral detergent fibre (NDF) and acid detergent fibre (ADF) contents were measured with an ANKOM 200 Automatic Fibre Analyzer (Van Soest et al., 1991) with the ash content determined using muffle furnace combustion at 550 °C for 6 h. Gross energy (GE) was determined using a MTZW-A4 high-precision dual-purpose automatic oxygen bomb calorimeter (Shanghai Mitong, Shanghai, China).

2.3. The grazing cattle

The cattle weight was recorded at the start of the experiment and then every month to calculate averaged daily liveweight gain (LWG). Two cattle in each plot were selected and equipped with portable GPS electronic collars (ZM-YDM-01, Inner Mongolia, China) around their necks to monitor their movement. The collars had a positioning accuracy of 5–10 m, package size of 65 × 50 × 17 mm (length × width × height), weighed approximately 500 g, and had a battery capacity of 1000 mA for one month. The positions of the cattle were recorded at 10-min intervals throughout July, August, and September. To examine the accuracy of the GPS collar recording system, two collared cattle in each plot were manually observed from 06:00 to 18:00 on two consecutive days in early July, August, and September, as well as their behaviours, including foraging, resting, and travelling.

Previous studies suggested that the movement behaviours of animals could be classified into three mutually exclusive primary activities, namely resting (lying, ruminating, and socialising), foraging (browsing, standing, and drinking), and travelling (Schlecht et al., 2004; Kilgour et al., 2012; Augustine and Derner, 2013; Manning et al., 2017). In this study, the movement behaviours were defined according to cattle's moving speed, with M0 representing resting ($0 \leq V < V_1$), M1 foraging ($V_1 \leq V < V_2$), and M2 travelling ($V_2 \leq V \leq V_3$). Here V was the averaged movement speed of cattle; V_1, V_2, and V_3 were determined through a combination of the manually observed and GPS recorded cattle movement data (Fig. 2).

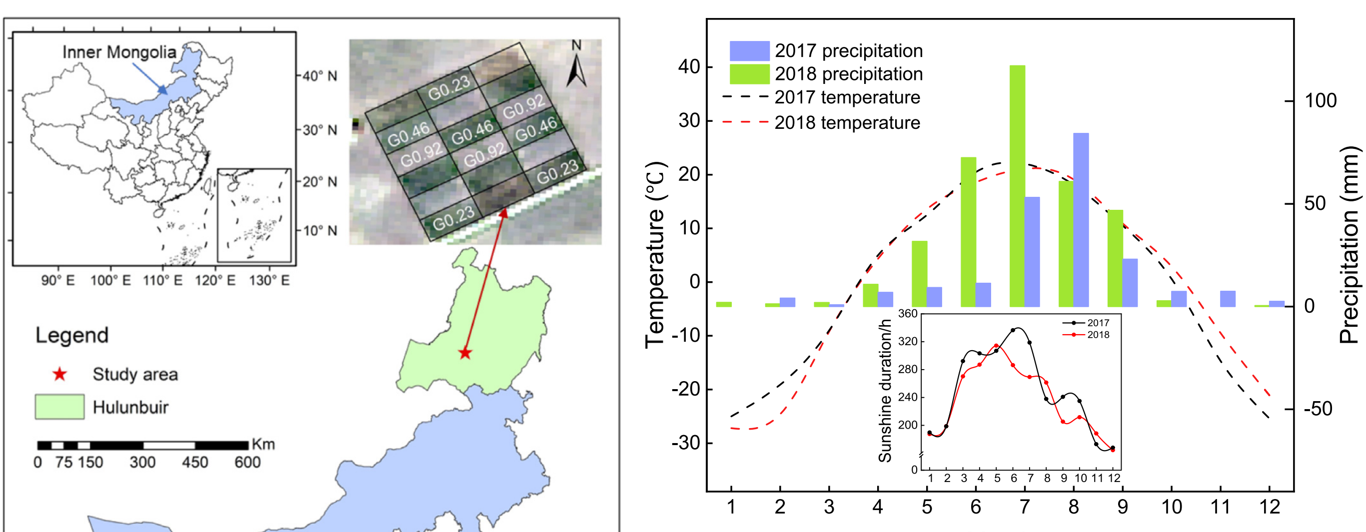

Fig. 1. Study area (left) and the climate in 2017 and 2018 (temperature, precipitation, and sunshine duration) (right).

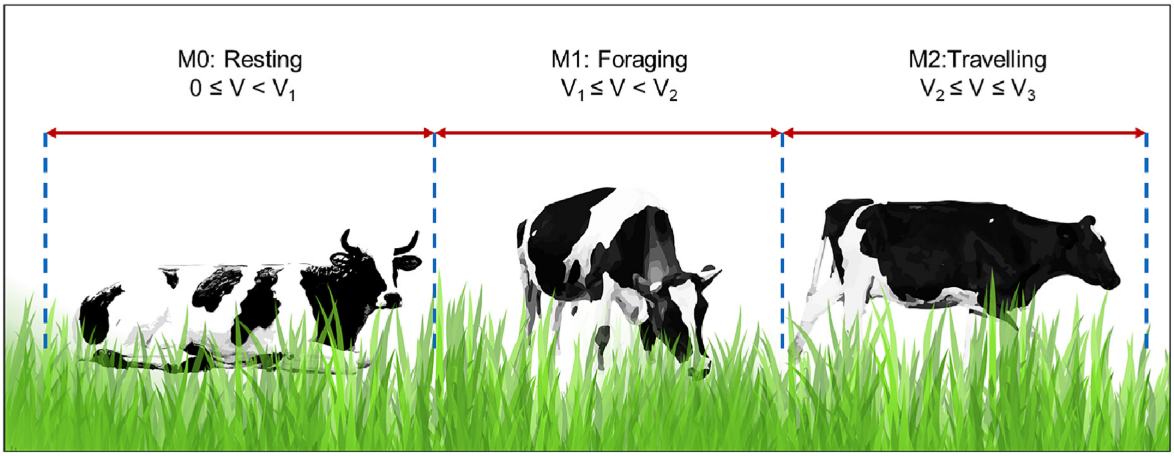

Fig. 2. Schematic diagram of livestock movement behaviours.

2.4. Statistical analysis

Plant diversity indices of community were calculated as:

$$\text{Margalef richness } \left(\text{Ma} = {}^{(S-1)}\!/_{lnN}\right) \tag{1}$$

$$\text{Shannon} - \text{Wiener diversity } \left(\text{H} = -\Sigma_{i=1}^{S} Pi\ lnPi\right) \tag{2}$$

$$\text{Simpson diversity } \left(\text{D} = 1 - \Sigma_{i=1}^{S} Pi^2\right) \tag{3}$$

$$\text{Evenness } \left(\text{E} = {}^{H}\!/_{lnS}\right) \tag{4}$$

where S is the number of species in the quadrat, N is the total number of individuals per species, and Pi is the proportion of the species i within the total number of individuals.

As GPS signals often were unstable under extreme field conditions, there were data gaps (Frair et al., 2004). In this study, cattle trajectory data were selected with a number of data entries ≥130 (144 × 90 %). The GPS data were converted from the geographic coordinate system WGS 1984 to the projected coordinate system WGS 1984 UTM Zone 51N using the ArcGIS 10.6 (ESRI, Redlands, CA, USA). Cattle movement was calculated as:

$$D = \sqrt{(\text{x1} - \text{x2})^2 + (\text{y1} - \text{y2})^2} \tag{5}$$

$$V = \Delta\text{D}/\Delta\text{t} \tag{6}$$

where D is the distance and V is the velocity of the animal, (x_1, y_1) and (x_2, y_2) are the projection coordinates of two adjacent positions recorded by GPS, and Δt is the time interval between the two positions.

Home range analysis was used to quantify the spatial utilization distributions of cattle and the areas of grazing. The utilization area ratio (UAR) for each plot was calculated daily using the home range tools (HRT) in ArcGIS v. 10.6 (Hooge et al., 2001) based on the range of area occupied by cattle with a 95 % probability from observed GPS points distribution (Kraft et al., 2023).

The utilization distribution density function (f_h) of the area was calculated as:

$$f_h(x) = \frac{1}{nh^2}\Sigma_{i=1}^{n} k\left(\frac{x - X_i}{h}\right) \tag{7}$$

where n is the total number of GPS points, x is the point of evaluation, X_i is a random sample of independent points from an unknown utilization distribution, k is a unimodal symmetrical bivariate probability density function, and h is the set bandwidth or variance of the selected kernel function. The bandwidth was determined by least-squares cross validation.

An unsupervised classification method (i.e., k-means clustering analysis) was used to classify behaviour data and define the speed thresholds corresponding to each movement behaviour, with the GPS velocities corresponding to field-observed cattle behaviour serving as the verification data (Figs. S1, S2). The random forest algorithm method of Valletta et al. (2017) was used to classify cattle behaviour using the predicted metrics and field-observed behaviour data. The random forest model was assessed by a tenfold cross-validation to separate the data into a training and testing dataset that had 91 % accuracy and a kappa coefficient of 85 %. We compared the classified results of both k-means and random forest methods with a similarity of 87 %, further indicating that the k-means results can be used as a basis for behavioural classification in our study. We then performed statistical analysis of the GPS data for August 2017 based on the speed thresholds for each movement behaviour of cattle and divided all the data into two sets: (1) monthly data to compare the effect of month and grazing intensity on cattle movement and (2) annual (2017 and 2018) data to compare the effect of year and grazing intensity on cattle movement from precipitation and AGB.

Two-way ANOVA (SPSS Statistics v. 23, IBM Corp., Armonk, NY, USA) was used to examine the differences in cattle spatiotemporal behaviours for grazing intensity and grazing months; Duncan's multiple range test was used to determine significance at a 95 % confidence interval. Pearson's correlation was applied to analyse the relationships between cattle behaviour and vegetation quality (i.e., DM, OM, C, ADF, NDF, CP, GE) and quantity (i.e., AGB, height, density, species diversity) (Table S2). Mantel tests using the Spearman method with 1000 permutations were also used to determine the associations between cattle spatiotemporal patterns and vegetation characteristics in R “ggcor” package.

3. Results

3.1. Cattle behaviour and movement

We found variations in grazing behaviour (Fig. 3A) had definite rhythmic patterns. Cattle under the three grazing intensities had the same activity rhythm, with most of the movement activity occurring during 4:00–9:00 h and 16:00–22:00 h. In July 2018 movement activity of cattle commenced after 4:00 h and peaked between 6:00 and 20:00 h; in August the start and end of movement activity delayed by approximately 1 h, starting at ~5:00 and ending at ~21:00; and in September cattle started moving at ~6:00 h and ended at ~20:00 h. In August 2017 movement activity started ~30 min earlier than in August 2018. The average velocity of cattle movement increased gradually from 22:00 h and 4:00 h from July until September, with an average of 37.09 m/h in July, 54.30 m/h in August, and 72.58 m/h in September. During the peak period of movement activity (4:00–9:00 h and 16:00–22:00 h), the average velocity was 284.37 m/h (Fig. 3B). Although the sunrise and sunset times changed in

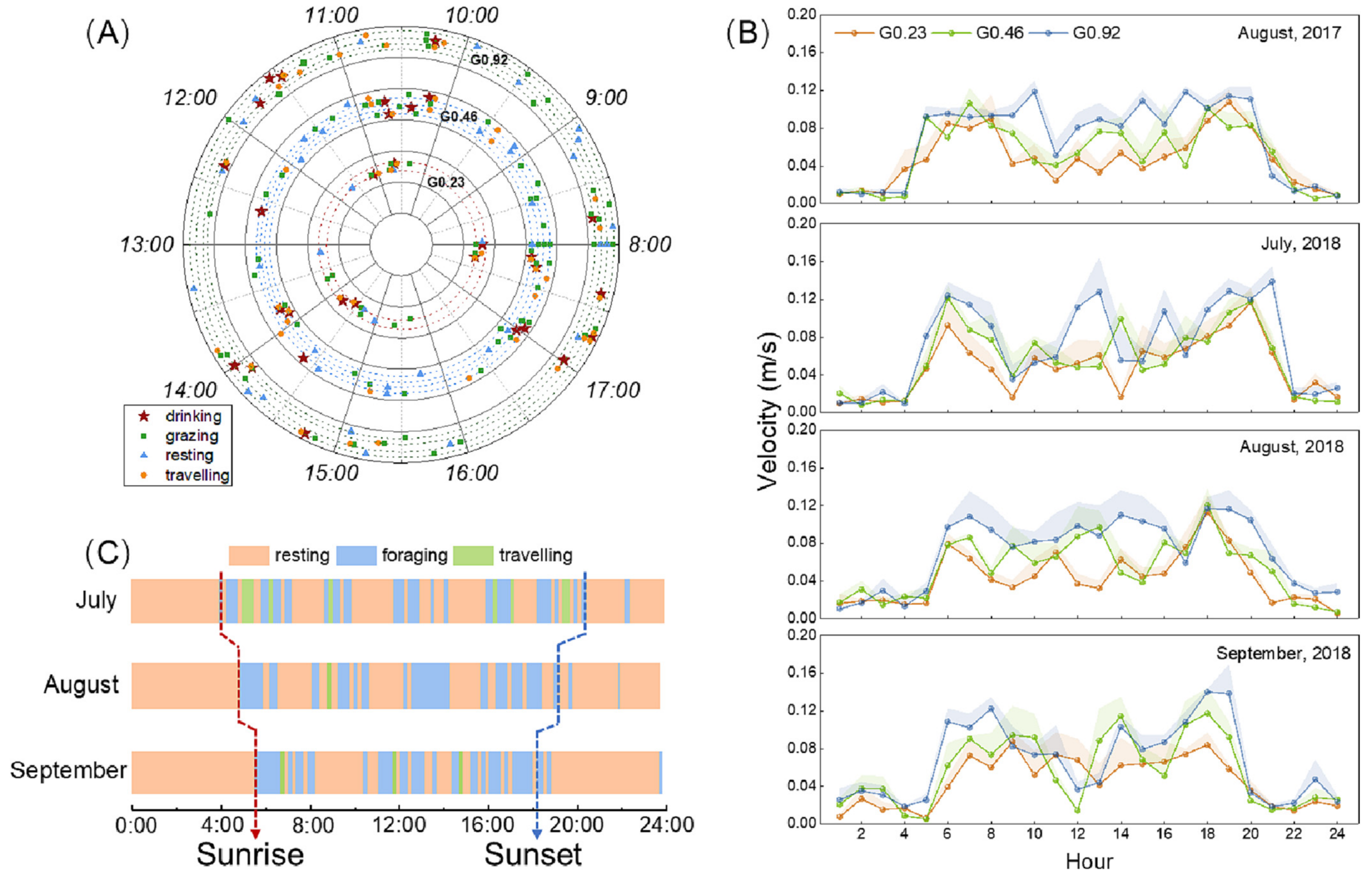

Fig. 3. Cattle behaviours during the daytime (A). The circle represents grazing intensity, and the number of dashed lines within the circle represents the number of individual cattle, which is based on individual behaviour corresponding to the actual time of observation of the manual tracks in the same period. Average moving velocity (B) under three grazing intensities; shaded regions show the standard errors (SE). Daily dynamics of cattle behaviour for July, August, and September (C); cattle behaviour under three grazing intensities differed significantly (monthly trends are shown).

July, August, and September (i.e., daylight hours became gradually shorter), cattle's resting time decreased during the daytime and increased at night, resulting in no significant change in the total daily resting time (Fig. 3C). These findings illustrate the behavioural characteristics of livestock by month and grazing pressure.

3.2. Temporal behaviour

Using the speed thresholds for establishing behavioural categories, we determined the percentage of each of movement behaviour during daytime and found that grazing intensity (GI) significantly influenced resting and foraging times ($P < 0.05$) and differences between 2017 and 2018 ($P < 0.05$) (Fig. S4, Table 1). As GI increased, the resting time decreased gradually, while the foraging time increased gradually. The GI alone explained 78 %, 78 %, and 45 % of the variances in cattle resting, foraging, and travelling times, respectively, which was greater than those of month and the interaction between GI and month. Comparing 2017 with 2018, GI alone explained 77 % and 83 % of the variances in cattle resting and foraging times, respectively, and the effect was greater than the difference in year (Fig. S4, Table 1).

3.3. Spatial behaviour

The spatial pattern of cattle behaviour was quantified with movement trajectory and livestock habitat occupation. The cattle trajectory complexity, travel distance, and UAR increased with increasing grazing intensity; the travel distance of heavy grazing (G0.92) was the farthest at 4892 m/d, and it also had the greatest UAR at 69.62 % per day ($P < 0.01$). Grazing

Table 1
Significance of grazing intensity (GI), month, and year on the proportions of times allocated to each of behavioural category.

	Factor	df	Resting			Foraging			Travelling		
			R^2	F-ratio	*P*-value	R^2	F-ratio	*P*-value	R^2	F-ratio	*P*-value
Data set 1	GI	2	0.78	32.10	<0.01**	0.78	31.56	<0.01**	0.45	7.47	<0.01**
	Month	2	0.06	0.57	0.58	0.04	0.32	0.73	0.16	1.72	0.21
	GI*Month	4	0.17	0.94	0.47	0.16	0.85	0.52	0.11	0.55	0.71
	Corrected model	8	0.79	8.64	<0.01**	0.79	8.39	<0.01**	0.53	2.57	0.05
Data set 2	GI	2	0.77	19.76	<0.01**	0.83	28.96	<0.01**	0.21	1.58	0.25
	Year	1	0.30	5.11	0.04*	0.47	10.79	<0.01**	0.01	0.11	0.75
	GI*Year	2	0.28	2.37	0.14	0.43	4.53	0.03*	0.01	0.06	0.94
	Corrected model	5	0.80	9.87	< 0.01**	0.87	15.56	<0.01**	0.22	0.68	0.65

Data set 1: Grazing intensity (GI) in July, August, and September (month) in 2018. Data set 2: GI in August 2017 and 2018 (year). The differences were analysed using a two-way ANOVA with Duncan post hoc test. *: $P \leq 0.05$, **: $P \leq 0.01$, the same as below.

intensity explained 80 % of the variance in cattle distances in 2018. The distance travelled and UAR were both greater in 2017 than those in 2018, but not significantly so ($P > 0.05$). The UAR differed by month ($P < 0.05$) and was greatest in August (average 67.25 %). Grazing intensity and month explained 49 % and 36 % of the variance in UAR, respectively (Figs. 4, 5).

Habitat selection is an important feature of livestock behaviour. Fig. 5 showed the spatial distribution of cattle at different grazing intensities, characterizing the habitat selection preferences and resource utilization characteristics of cattle at different population densities. In general, livestock habitat selection is relevant to the spatial distribution of resources, the nature of livestock, and acquired habitat preference. The red coloured areas in Fig. 5 indicated the frequently occupied habitats in the plot, which were generally near the gates, fences, and water sources, representing a fixed behaviour pattern derived from animal instincts. In addition, the habitat occupation of individual cattle increased with grazing intensity, supporting the Ideal Free Distribution model premise that animals tend to occupy more habitats at higher population sizes in order to maximize their fitness to obtain richer resources.

3.4. Interactions among cattle behaviour, vegetation, and animal production

The Mantel test showed a strong relationship between cattle behaviour and plant characteristics (Fig. 6). Cattle foraging time and travel distance were inversely related to the aboveground biomass and plant height ($P < 0.05$), and plant height explained 51 % of the variance in cattle movement distance and 50 % of the foraging time proportion (Table S2). Plant species diversity and complexity of grassland vegetation also influenced livestock foraging time but was less correlated with livestock behaviours compared to vegetation canopy and the nutrient indicators. The C, CP, and GE contents of vegetation also affected the cattle foraging time, which respectively explained 15 %, 35 %, and 34 % of the variances in cattle foraging time (Fig. 6, Table S2). Cattle travel distance was significantly correlated with the Margalef index, ADF and C contents, and the UAR was closely related to GE content (Fig. 6).

Livestock production appeared to be jointly determined by vegetation features and cattle behaviour. The average daily liveweight gains for all cattle throughout the growing season was 0.77 ± 0.18 kg/d. However, livestock weight gain decreased in the later growing season when the forage resource diminished (Fig. 7A). We found that the relationships between livestock weight gain and vegetation features were weaker (i.e., explained a smaller fraction of the variability) than the relationships between livestock weight gain and animal behaviours such as livestock foraging time, distance and UAR, with R values of −0.26, −0.33 and −0.06, respectively ($P > 0.05$). There were different trends in livestock movement distance and weight gain at different grazing intensities, with livestock weight gain declining with increasing movement distance under moderate and heavy grazing (Fig. 7B). Additionally, our results suggested that the cattle travel distance was strongly positively correlated with the cattle foraging time ($R^2 = 0.68$; $P < 0.01$) (Fig. 7C). Therefore, the combination of livestock foraging time, movement distance, liveweight gain, and grazing intensity clearly indicated that light grazing could increase livestock production with minimal distance and foraging time (Fig. 7D).

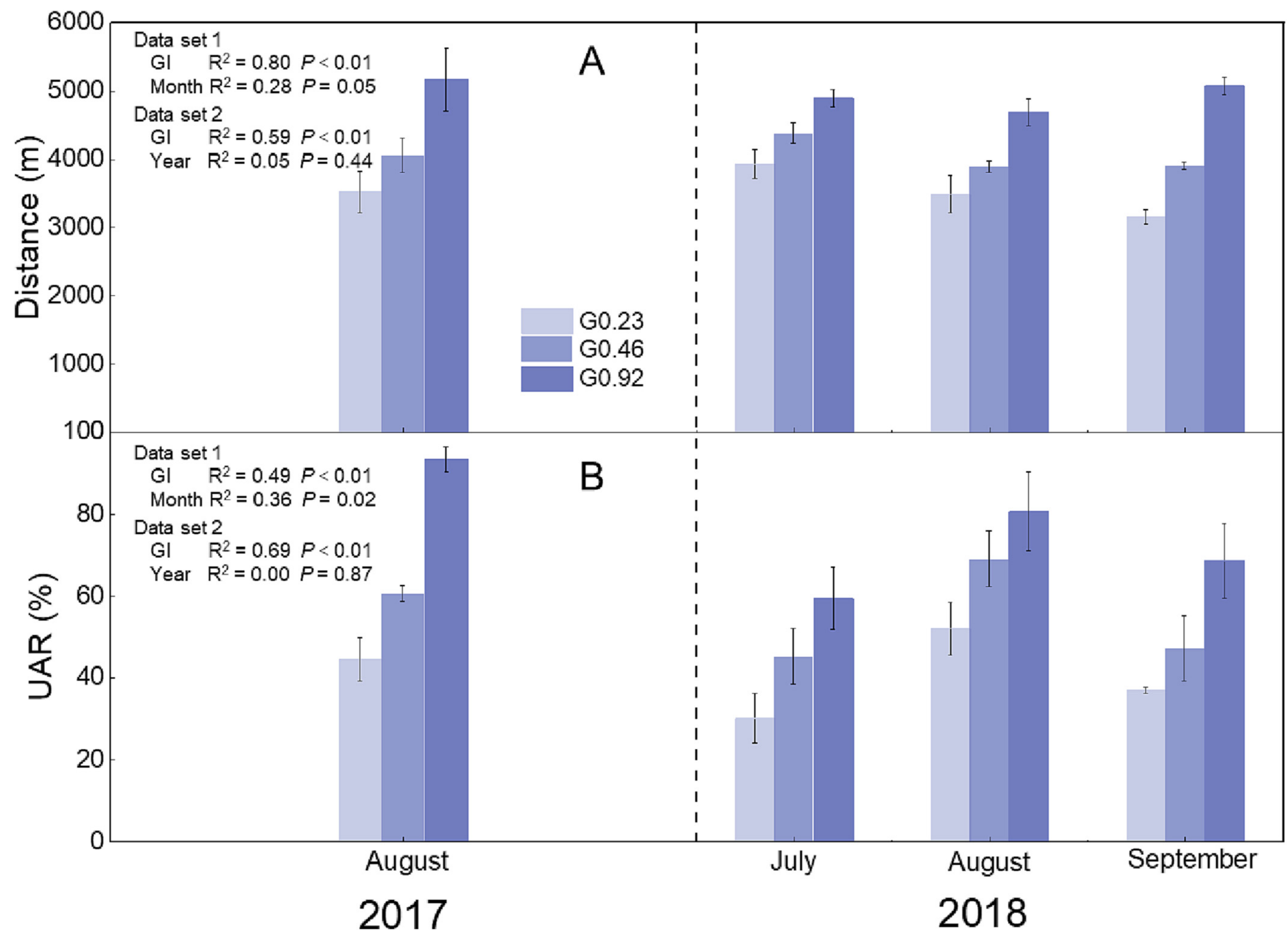

Fig. 4. Travel distances and utilization area ratio (UAR). Two-way ANOVA of the effects of grazing intensity (GI) and month, and GI and year on the spatial behaviour of cattle. Data set 1 represents GI and month for 2018; data set 2 represents GI and year for August 2017 and 2018.

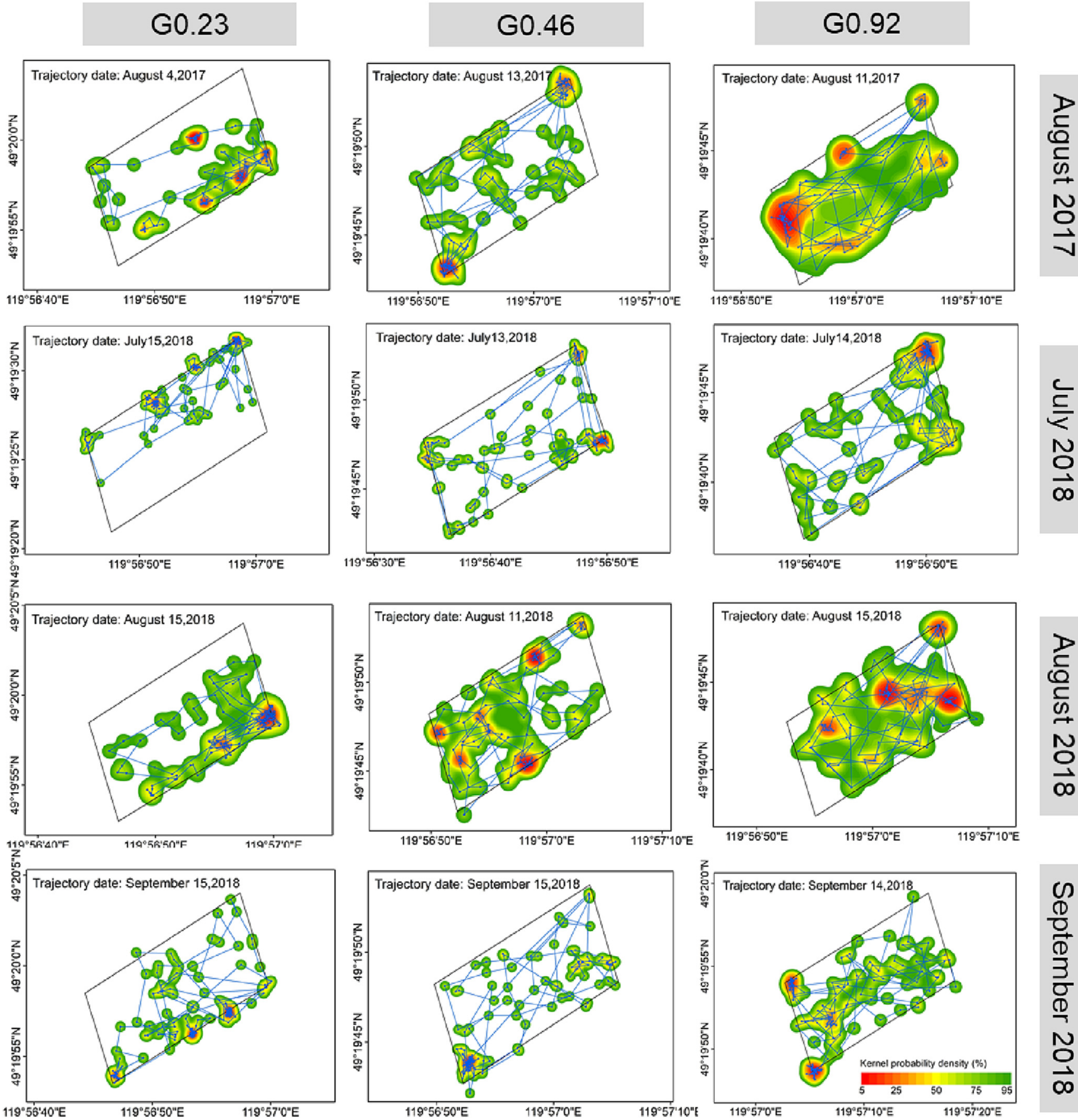

Fig. 5. Spatial characteristics of cattle under different grazing intensities. The black border represents the plot boundary, the blue dot represents the locations and the blue line indicates the cattle trajectory. Kernel probability density estimator (%) increases with colour depth. The red colour areas show where cattle most frequently occupied.

4. Discussion

4.1. Responses of cattle to grazing intensity

We found clear temporal rhythms of livestock behaviour that depend on animal nature, while foraging behaviour, movement behaviour and habitat selection were more influenced by the environment, especially grazing intensity. Previous studies have shown that grazing livestock forage mainly around sunrise and sunset, foraging for an average of 36 %–63 % of the day, and diurnal (06:00–18:00 h) cattle foraging accounts for 51 % of the total daily grazing time, about 6.1 h of the day (Kilgour et al., 2012). Hou et al. (2021) showed that cattle spend 53 % of the daytime foraging. In this study, we found that grazing cattle spent more time resting than foraging, with the resting time decreased with grazing intensity, and the total resting time within a day in different months did not change significantly. Cattle altered their resting time according to changes in sunrise and sunset times over the season, and they spent more time resting at night when the day length became shorter (Fig. 3C). These results broaden and validate previous findings that animal activity is delayed in the morning and advances towards the end of the night as the solar elevation angle changes with season (Payne et al., 1951; Dudziński and Arnold, 1979; Sprinkle et al., 2020). Importantly, we found that cattle foraging times were significantly longer at moderate (G0.46) and heavy (G0.92) intensity in 2017 than in 2018, possibly because of lowed precipitation and AGB in 2017.

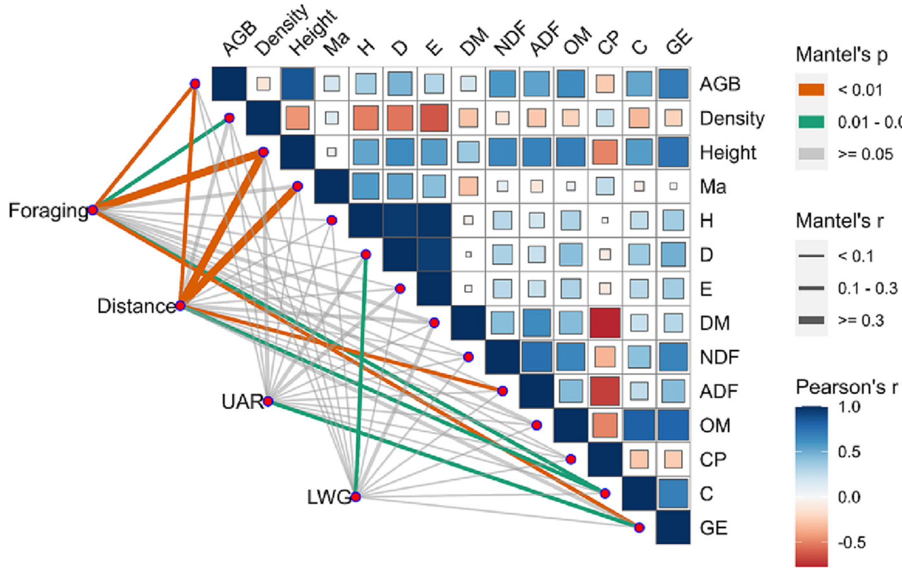

Fig. 6. The correlation matrix of cattle and vegetation characters (Mantel test results). ADF, acid detergent fibre; AGB, aboveground biomass; C, carbon content; CP, crude protein content; D, Simpson diversity; DM, dry matter content; E, evenness; GE, gross energy content; H, Shannon-Wiener diversity; LWG, liveweight gain of cattle; Ma, Margalef richness; NDF, neutral detergent fibre; OM, organic matter; UAR, utilization area ratio.

Spatial patterns of cattle behaviour, such as trajectory and utilization distribution, varied with grazing intensity in this study. Cattle moved 3526, 4051, and 4892 m/d, respectively, for light, moderate and heavy grazing in 2018. Several observational studies reported strong relationships between the movement distance and plot size, such as a similar daily movement distance of 3093 m within a 5-ha area with the grazing cattle using 75.8 % of a paddock of 261 ha (Kilgour et al., 2012; McGavin et al., 2018). Other factors, such as intraspecific competition, can also affect grazing livestock trajectory. In our study, animals under heavy grazing had the greatest travel distance and UAR, with the travel distance shortest in August, when the grassland reached maximum growth and available biomass adequate to meet animals' requirements for nutrients (i.e., less need for cattle to browse a larger area). In sum, it seems that the spatial distribution of cattle under different grazing pressure supports the Ideal Free Distribution model and animal welfare, i.e., cattle tend to occupy more habitat to enhance their fitness as population density increases.

We also found that heavy grazing increased cattle travel distance and foraging time (Figs. 5, S4), while body weight depended on the

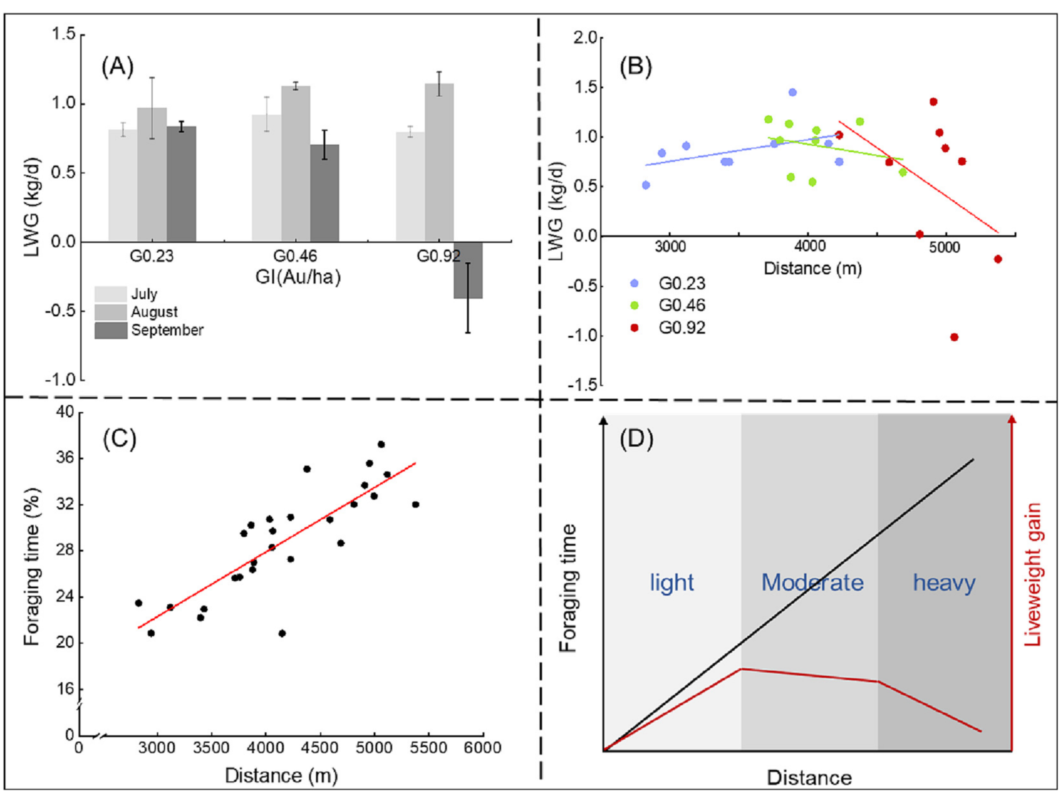

Fig. 7. Changes in liveweight gain (LWG) with grazing intensity for July, August, and September (A), cattle travel distance with LWG (B) and with foraging time (R^2 = 0.68; P<0.01) (C), and foraging time with grazing intensity (D).

aboveground biomass that varied from month to month ($R^2 = 0.22$, $P < 0.05$). It has been suggested that an increase in grazing intensity would enhance intraspecific competition when aboveground biomass is limited, causing cattle to spend more time foraging or moving longer distances for food. Interestingly, such increased travel and foraging time does not seem to be sufficient to maintain cattle production (Fig. 7B, C, D). According to the optimal foraging theory, livestock spends the least time foraging and moves the shortest distances under light grazing while maintaining a maximum weight gain (secondary productivity). Logically, a stocking rate should be carefully controlled around 0.23– 0.34 Au/ha in the meadow steppe to effectively improve livestock production; otherwise, supplementary feeding is required to maintain a stable secondary productivity.

4.2. The interactions between cattle and the vegetation

The significant correlations between plant and animal behaviour indicate their joint influences on animal production. However, livestock weight gain has a weaker relationship with vegetation than livestock behaviour, which implies that livestock may be quite flexible to changes in vegetation and may modify their intake strategy to make up for the deficit. We found plant height was negatively correlated with UAR, travel distance and foraging time of the cattle, which was likely associated with the intake rate and amount of feed per bite of cattle (Penning et al., 1991). There also appears a very strong correlation between plant height and aboveground biomass, suggesting a similar relationship between cattle behaviour and the aboveground biomass. Plant height and density affect, and are affected by, the intake rate and quantity per bite of the animals — highly sensitive to grazing and positively influenced by feed intake (Arnold, 1987; Penning et al., 1991; Laca et al., 1994). Grazing also altered the vegetation; heavy grazing reduced the canopy height, cover, biomass, and productivity, and it increased the CP content of the vegetation (Liu et al., 2009; Liu et al., 2015; Zhu et al., 2018; Zhang et al., 2022). In addition, the community structure changed due to livestock preferentially foraged on more palatable species, with the dominant species changing from graminoids to short perennial forbs under heavy grazing (Zainelabdeen et al., 2020). These changes were consistent with our findings.

Plant diversity is another critical feature of plant community, which may be related to the function and major process of grasslands. The resource concentration hypothesis states that plant diversity influences animal behaviour and habitat complexity, with the latter affecting the spatial behaviour of herbivores (Root, 1973). We found that plant community diversity was highest under moderate grazing (Table S1), which is consistent with the intermediate disturbance hypothesis (Connell, 1978). Li et al. (2017) also found that plant species diversity and productivity were highest under light grazing conditions. Collectively, livestock species, grassland type, climate conditions, and disturbance cycles all affect grazing-vegetation interactions. However, it is worth noting that the thresholds of light-to-moderate grazing are not easy to identify, because a low grazing intensity for one specific land area may be regarded as a medium-to-high grazing intensity in another. We found a significant correlation between the cattle travel distance and the Margalef index. Here community species richness increased foraging preferences for livestock, which in turn increased movement distances. Another study reported that increasing plant diversity improved livestock learning, memory, and recognition, reduced grazing selectivity, and promoted uniform grassland resource utilization. Plant diversity was another important exogenous factor affecting animal foraging dynamics, improved appetite, and stimulated foraging and foraging time (Wang et al., 2010).

The underlying mechanisms for the interactions between livestock behaviour and forage nutrients is complex because plant nutrient composition undergoes dramatic changes across seasons and plant physiological stages (including phenology). We also detected the correlations between cattle behaviours and forage nutrient contents. The cattle foraging times and travel distances were negatively correlated with DM, ADF, NDF, OM, C, and GE, and positively correlated with CP (Fig. 6, Table S2). This was partially due to the fact that the higher the grazing intensity, the lower the DM, ADF, NDF, C, OM, and GE of the forage and the higher the CP content (Table S1) when grasses were low in fibre under heavy grazing, which will cause the livestock to move farther distances and forage longer to obtain the same energy. LWG was negatively correlated with cattle foraging time, movement distance, and UAR simultaneously (Fig. 6), which is consistent with prior analyses of calves based on observations of herbage intake and ingestive behaviour (Jamieson and Hodgson, 1979), but we found a weak relationship between vegetation and livestock LWG, suggesting that vegetation may directly influence livestock behaviour and thus indirectly influenced livestock production. In contrast, Gou et al. (2020) found that cattle foraging density was negatively correlated with CP and positively correlated with ADF, presumably because the CP and ADF contents gradually decreased and increased from July to September. But we found that the CP and ADF contents were the highest in August, when forage growth and nutrient content are at their peak at Eurasian meadow steppes. This indicates that cattle movement and foraging times increase with forage freshness. These discrepancies may be explained by relative differences between the studies in terms of terrain, grassland type, and vegetation conditions. Understanding these drivers is critical to predict livestock production in grassland ecosystems under different grazing intensities, forage quality and quantity.

4.3. Implications and limitations

Grazing is the most significant human practice in northern China and the Eurasian steppe, and grazing strategy is a key issue in the adaptive management of grassland ecosystems. Our findings underscore the importance of livestock production at different grazing pressures when spatial and temporal behaviour of grazing livestock are included. We found that grazing intensity significantly altered both vegetation characteristics and animal behaviours and ultimately determined the secondary production of grazing ecosystems. According to optimal foraging theory, animals acquire the highest secondary production under suitable grazing intensity when they spend the least time and travel the shortest distance in foraging. Logically, a stocking rate should be carefully controlled around 0.23– 0.34 Au/ha in the meadow steppe to improve livestock production; otherwise, supplementary feeding is required to keep a stable secondary production and maintain the ecosystem's health. Beyond this grazing intensity, the longer browsing distance for foraging increases the energy consumption of livestock and decreases the feed conversion ratio overall.

In terms of spatial characteristics of livestock behaviour, we found that habitat selection adheres to the Ideal Free Distribution model at lower population density, which provides a theoretical basis for the spatial allocation and matching of grassland and livestock resources. To incorporate livestock habitat selection behaviour into grazing practice is helpful for better planning and management of grassland ecosystems, especially in vegetation types with strong spatial heterogeneity, such as sandy scattered grassland and alkalized patchy grassland in northeast China. The spatial aspects of animal behaviour also serve as a theoretical foundation for smart grazing, which is being developed simultaneously with 3S and AI technology and has just been applied in the grassland of northern China.

The present study had several limitations. Firstly, limited by the battery life of the GPS collars, the record frequency of livestock position in this study is 10 min and is not accurate enough to reveal more detailed trajectory, habitat occupation, and foraging behaviours of livestock. We hope future development of technology will fill this gap and provide better approaches for animal behaviour observation. Secondly, extreme climatic events such and severe drought, heavy rainfall, or heat waves may have a strong impact on the spatiotemporal characteristics of livestock behaviour; however, two years of research duration is too short to likely encounter and factor extreme conditions. Thirdly, this experiment was conducted on in temperate meadow steppe which is characterized by a semi-arid climate, and the livestock behaviour and their response to grazing intensity may be different in typical steppe or alpine grasslands. Nevertheless, we hope that our findings provide a guidance for future research and serve to improve understanding and adaptive management of grassland ecosystems.

5. Conclusions

Grazing intensity has a strong impact on grazing animal behaviours and grassland ecosystems. Under heavy grazing, cattle spent more time foraging, moved longer distances for food, and utilized a higher proportion of paddock compared with moderate and light grazing. The changes in these behaviours with increasing grazing pressures are likely attributable to increased intraspecific competition among cattle under limited resources, but this does not compensate for the impact on cattle production. Grazing intensity also changed vegetation characteristics, particularly plant height, aboveground biomass, species diversity, and pasture chemical composition, which in turn affected animal behaviour. Other animal behaviours such as egestion/excretion also influence grassland soil, which should be considered in the future studies.

Understanding livestock grazing behaviour can provide a better knowledge of livestock foraging mechanisms and contribute to the sustainable development of grassland ecosystems and livestock husbandry while accommodating optimal foraging theory and ideal free distribution.

CRediT authorship contribution statement

Lulu Hou: Methodology, formal analysis, writing - original draft, writing - review & editing. Ahmed Ibrahim Ahmed Altome and Yousif Mohamed Zainelabdeen Hamed: Sample collection & screening, writing - review & editing. Haixia Sun, Yi Tao, Jiquan Chen, Ruirui Yan, Xiang Zhang, Beibei Shen, Xu Wang, Serekpaev Nurlan, Nogayev Adilbek, Akhylbekova Balzhan, Maira Kussainova, Amartuvshin Amarjargal, Wei Fang and Alim Pulatov: Writing - review & editing. Xiaoping Xin: Resources, data curation, writing - review & editing, supervision, funding acquisition. All authors contributed critically to the drafts and gave final approval for publication.

Data availability

The authors do not have permission to share data.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.164191.

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