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Seasonal dynamics of cattle grazing behaviors on contrasting landforms of a fenced ranch in northern China

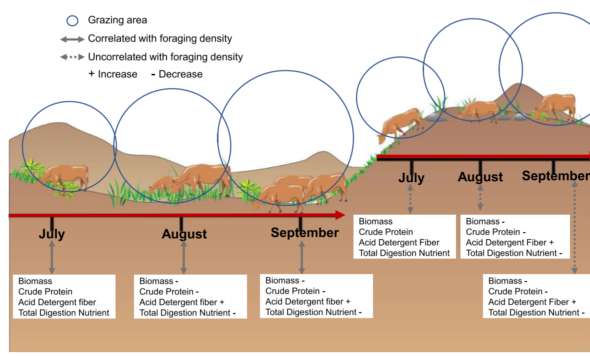
Xiaowei Gou [a], Atsushi Tsunekawa [b], Mitsuru Tsubo [b], Fei Peng [c,d,*], Jian Sun [e], Yulin Li [f], Xueyong Zhao [f], Jie Lian [f]

[a] The United Graduate School of Agricultural Sciences, Tottori University, 4-101 Koyama-Minami, Tottori 680-8553, Japan
[b] Arid Land Research Center, Tottori University, 1390 Hamasaka, Tottori 680-0001, Japan
[c] International Platform for Dryland Research and Education, Tottori University, 1390 Hamasaka, Tottori 680-0001, Japan
[d] Key Laboratory of Desert and Desertification, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, Lanzhou 73000, China
[e] Synthesis Research Centre of Chinese Ecosystem Research Network, Key Laboratory of Ecosystem Network Observation and Modelling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences (CAS), 11A, Datun Road, Chaoyang District, Beijing 100101, China
[f] Naiman Desertification Research Station, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, Tongliao 028300, China

HIGHLIGHTS

- Cattle foraged longer as resource availability declined from July to September.
- In low-land areas, the area used by cattle and foraging density increased over time.
- In sand-dune areas, only the area used by cattle increased over the grazing season.
- Low-land herbage quantity and quality declined over the grazing season.

GRAPHICAL ABSTRACT



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ABSTRACT

The number of livestock per unit area is commonly used as a proxy of grazing pressure in both experimental studies and grassland management. However, this practice ignores the impact of landform heterogeneity on the spatial distribution of grazing pressure, leading to localized patches of degraded grassland. The spatial distribution of actual grazing density thus needs to be examined. Owing to the corresponding changes in resource availability and energy consumption as livestock move across an elevation gradient, we predict that livestock will preferentially use low-land and that different temporal patterns of grazing pressure will occur in the contrasting landforms. GPS location data and a machine learning technique were used to identify the seasonal pattern and the factors driving grazing pressure on a fenced ranch. Over both low-land and sand-dune landforms, the proportion of time that livestock spent on foraging increased from 63% in July to 67% in August and 69% in September, and non-foraging behavior decreased correspondingly. In low-land, the log-transformed average foraging density significantly increased from 0.61 (i.e., total foraging behaviors in 5 days measured at 50-s intervals per 10×10 m grid) in July to 0.66 in August and 0.88 in September, whereas there was no significant change on sand-dunes. From July to September, the relative area of low-land foraged by cattle accounted for 31%, 35%, and 36%, respectively, and in sand-dunes the proportions increased from 45% to 47% to 51%. In low-land, the foraging density was negatively correlated with biomass ($P = .07$), total digestible nutrients ($P < .05$), and crude

* Corresponding author at: International Platform for Dryland Research and Education, Tottori University, 1390 Hamasaka, Tottori 680-0001, Japan.
E-mail addresses: d17a4006h@edu.tottori-u.ac.jp (X. Gou), tsunekawa@tottori-u.ac.jp (A. Tsunekawa), tsubo@tottori-u.ac.jp (M. Tsubo), pengfei@tottori-u.ac.jp, pengfei@lzb.ac.cn (F. Peng), sunjian@igsnrr.ac.cn (J. Sun), liyl@lzb.ac.cn (Y. Li), zhaoxy@lzb.ac.cn (X. Zhao), lianjie@lzb.ac.cn (J. Lian).

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protein ($P = .06$) and positively correlated with acid detergent fiber ($P < .05$), whereas no such relationships were observed in sand-dunes. Our results indicate that topographic features should be considered when managing livestock, especially during periods with adverse conditions of herbage quality and quantity.

1. Introduction

The total desertified land area is estimated to be 3.6 billion ha in arid and semi-arid regions around the world (Daily, 1995). Overgrazing is believed to be one of the primary driving forces of degradation (Schlesinger et al., 1990; Van De Koppel and Rietkerk, 2000). Overgrazing can lead to marked reductions in nutritive value and yield of herbage (Chaneton et al., 1988; Ayantunde et al., 1999; Gutman et al., 1999) and result in severe grassland degradation. With the surging numbers of livestock in arid and semi-arid lands, understanding how to manage livestock grazing both temporally and spatially is crucial for preventing degradation and restoration of degraded grassland as well as for maintaining livestock production (DeYoung et al., 2000; Briske et al., 2008; Hao et al., 2018).

Many field grazing experiments have been carried out (Lunt et al., 2007; Hanke et al., 2014; Eldridge et al., 2016) to clarify how livestock grazing affects grassland productivity (Huang et al., 2016), species diversity (Pour and Ejtehadi, 1996), soil quality (Hiernaux et al., 1999), and desertification (Weber and Horst, 2011). In these experiments, researchers used different grazing density gradients indicated by the number of livestock per unit area (Okayasu et al., 2010; Wang and Wesche, 2016). The effects of different livestock behaviors such as foraging and resting were ignored across space. However, grazing density varies temporally and spatially with the availability of resources and the changing environments across a grassland (Chillo and Ojeda, 2014). Therefore, monitoring and modelling different livestock behaviors and investigating the seasonal dynamics of the spatial distribution of livestock would improve the management of livestock grazing and help to prevent grassland degradation (Bailey et al., 1996; Kohler et al., 2006).

Estimating the spatial distribution and temporal dynamics of grazing density is difficult because of the spatial heterogeneity and temporal dynamics of resource availability and differences in livestock energy consumption across various landforms (Butt, 2010). Grazing activities, including foraging and non-foraging activities, comprise various interactions between livestock and the environment (Baumont et al., 2004). Complex interactions among biotic factors, such as forage quantity and quality, and abiotic factors, such as elevation and distance to a watering point (Von Müller et al., 2017), determine the spatial distribution of different livestock behaviors on a ranch (Hirata et al., 2010). In a ranch with abundant vegetation and flat terrain, livestock generally concentrate in several areas that have good-quality forage at the beginning of the grazing season and then expand over a broader area to achieve an even spatial distribution with relatively low grazing density late in the season (Evans et al., 2004; Pelster et al., 2004). On a ranch with spatially homogenous resources, the livestock's use of herbage resources also shows selective grazing and a mosaic pattern that balances the nutrient demand and energy supply for livestock (Andrew, 1988; Barnes et al., 2008; Okayasu et al., 2010). The spatial expansion across a ranch is moderated by the trade-off between the area's forage quality and productivity. Livestock instinctually avoid walking long distances to save energy given abundant herbage resources (Sejian et al., 2012). Otherwise, the spatial range of livestock movement will be constrained by the energy gained at the expense of energy consumption (Fierro and Bryant, 1990).

Spatial differences in the quality and quantity of herbage due to rugged terrain on a ranch will lead to a heterogeneous distribution of livestock (Henkin et al., 2012). Livestock prefer to spend more time in relatively flat areas where lower energy consumption is required for grazing activities (Parker et al., 1984). As compared to that on flat terrain, grazing capacity was 30% lower in areas with slopes between 11% and 30%, and 60% lower in areas with slopes between 31% and 60% (Holechek, 1988). Moreover, elevation differences can lead to a heterogeneous distribution of available resources and differences in plant community composition and soil type (Miyasaka et al., 2011). Livestock forage longer in a nutrient-rich patch in an area with heterogeneous topographic features, but they rarely forage in the same patch for several consecutive days in a homogeneous environment (Bailey, 2005).

The Horqin Sandy Land of northern China has suffered from serious desertification (Chen and Su, 2008). Despite many national and regional restoration projects, such as fence construction and the provision of cash subsidies to reduce the livestock number per household, desertification of grasslands in the Horqin Sandy Land is still ongoing (Miao et al., 2015). Several researchers have investigated plant communities under different grazing densities in the Horqin Sandy Land (Zhang et al., 2005; Li et al., 2012; Tang et al., 2016). The direct application of grazing density to arid and semi-arid pastoral systems has been criticized, however, because it neglects the spatiotemporal dynamics of actual foraging pressure (Bailey et al., 1996). Understanding these spatiotemporal dynamics may help ranchers to improve the efficiency of resource use and to respond effectively to the actual environmental conditions on a ranch (Anderson et al., 2012). Given the landform characteristics of the Horqin Sandy Land and the ongoing land degradation (Li et al., 2012), we expect that livestock should preferentially use low-land areas and that temporal patterns of grazing pressure should differ in areas with contrasting landforms.

The objectives of our study were (1) to quantify the ratio of foraging to non-foraging behaviors of livestock on a ranch in the Horqin Sandy Land; (2) to explore the spatial distribution of livestock grazing and its temporal dynamics on contrasting landforms (i.e., low-land vs. sand-dune); and (3) to understand the biotic factors determining the grazing spatial distribution.

2. Material and methods

2.1. Study site

The study was conducted in the western part of the Horqin Sandy Land (42°00′N, 119°39′E), Naiman County, Inner Mongolia, northern China (Fig. 1A). The area is characterized by interspersed low-land areas, fixed and semi-fixed sand dunes with an average height of 5–8 m, length of 400–600 m, and width of 20–40 m (Zhang et al., 2005). The fixed and semi-fixed dunes account for 70% of the total area (Zhang et al., 2012). From 1980 to 2014, the annual mean temperature was 7.3 °C, and the annual mean precipitation was 318 mm, with 70–80% of the precipitation occurring between June and August (Liu et al., 2014). The average annual wind speed ranged from 3.2 to 4.5 m s^{-1}, with most windy days and windstorms occurring between March and May (Zhang et al., 2012).

Sheep, goats, and cattle have been grazed in this region in recent decades. However, the carrying capacity of pasture has decreased from 1.81 to 0.19 sheep unit ha^{-1} owing to the continuously increasing number of livestock in the region (Jiang et al., 2003; Li et al., 2012). For this reason, a livestock exclusion policy has been extensively implemented in the Horqin Sandy Land (Li et al., 2012) since the mid-1980s to prevent grassland degradation (Baxter, 2007).

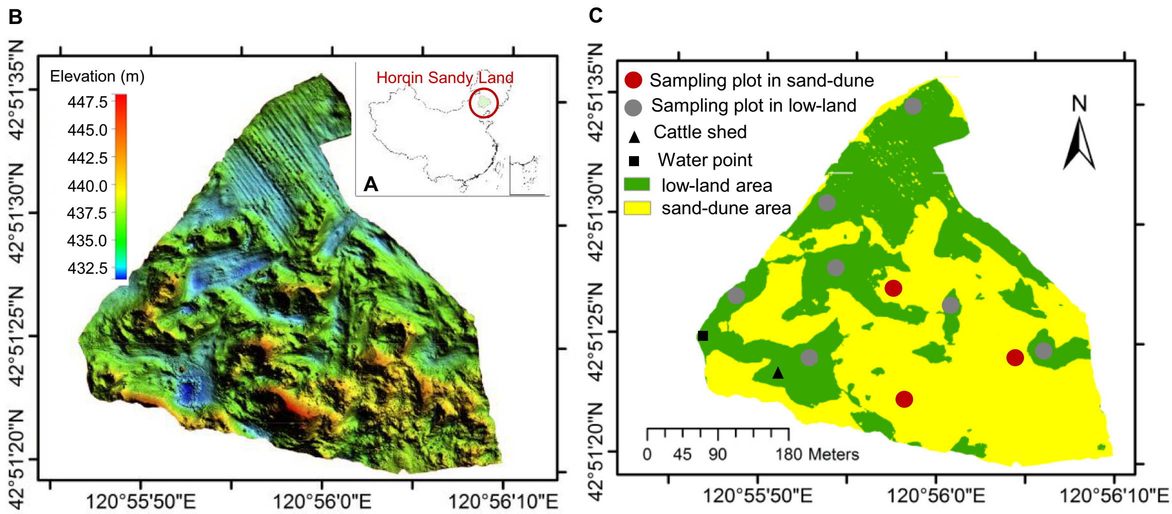

Fig. 1. (A) Location of the Horqin Sandy Land, (B) digital surface model of the study ranch, and (C) landform classification into low-land and sand-dune areas and sampling plot locations.

Before monitoring livestock movement and conducting the plant survey, we visited and inspected ranches of several households in this region and selected one (42°51′24.59″ N, 120°55′50.34″ E) of them as the research site (Fig. 1) for the following reasons. First, consistent with the prevailing management practices in this region, livestock grazing at this ranch occurred without herdsman interventions, such as supplemental feed supplies. Second, landforms on the range included both fixed dunes and low-land areas, which are typical landforms in the Horqin Sandy Land (total area is 20.1 ha, with 8.04 ha of lowland and 12.06 ha of sand dunes; Fig. 1). Third, the ranch's use history was clear; low-land areas were used to grow corn and millet from 1995 until 2007, when fencing was erected and livestock grazing began across the ranch. Finally, the owner of the ranch communicated well with us, and good communication was essential for this experiment to be completed.

At the research site, livestock grazing usually occurs from early July to late September. The vegetation is typical of a temperate desert steppe; the dominant species are *Pennisetum centrasiaticum*, *Cleistogenes squarrosa*, and some dwarf shrubs (*Artemisia oxycephala* and *Artemisia halodendron*).

The low-land area characterized by Kastanozems, and sand-dune by Ustic Sandic Entisols (FAO, 2006). The Ustic Sandic Entisols are with a loose structure, and they are particularly susceptible to wind erosion (Li et al., 2009). Soils in the low-land areas have more nutrients and higher soil moisture level, as compared with soil property in dunes (Li et al., 2009).

2.2. Land survey

An elevation map of the study ranch was generated by using drone photogrammetry. A drone (DJI Phantom 4 Pro, https://www.dji.com/jp/phantom-4-pro) was used to capture photos covering the whole ranch by using an autopilot flight paths program. Since the total area of the study ranch was 20.1 ha, the fixed height and horizontal speed were set to 80 m and 3 m s^{-1} and the forward overlap (flying direction) and side lap (between adjacent flight lines) were set to 80%. With these parameters applied to the flight autopilot, the program was designed to obtain 400 images over a target area of 700 m × 700 m (Fig. 1B).

Pix4Dmapper Pro software (version 2.0) was used to process the acquired photographs and to automatically generate orthoimages, a 3D point cloud, and a digital surface model (DSM) with 2 cm × 2 cm ground resolution (Car et al., 2016). To refine the geolocation of the drone photographs and to assess the accuracy of the DSM, eight ground control points were evenly positioned across the study ranch. Geographic coordinates and elevation of the eight ground control points were measured with a Trimble RTK GPS (Real-Time Kinematic) within 1 m accuracy (UTM Zone 51 N, WGS84 horizontal datum). We then evaluated the spatial accuracy by comparing digitized and known coordinates from the ground and calculating the root mean square error (RMSE). Finally, we generated a DSM with a vertical resolution of 5 cm.

Landforms at the study site were classified as low-land or sand-dune by using field observations. We selected an elevation threshold of 438 m to distinguish the two landforms; if the pixel elevation was higher than 438 m, that DSM pixel was classified as sand-dune; otherwise it was classified as low-land (Fig. 1C).

2.3. Grazing behavior analysis

During the grazing season of 2018 (1 July to 30 September), 13 adult Simmental cattle (3 to 6 years old) grazed the ranch. Each animal had a GPS device (precision ±3 m; catalog no. GT-600, i-gotU, Mobile Action Technology, Taipei, Taiwan) attached to a collar around its neck with a battery that allowed the GPS device to operate for more than 5 days. The GPS device continuously recorded the animal's location at 50-s intervals for five consecutive days; then it was removed, recharged, and re-attached. This procedure was followed throughout the grazing season.

During the grazing season, we observed cattle activities for around 15 days (09:00 to 17:00 UTC + 8) per month and found that the 13 animals moved together around the ranch. However, the number of available GPS devices declined through the sampling period due to rainfall damage and loss. Because the objective of the study was to compare cattle behaviors and distribution patterns among three grazing periods in both the low-land and sand-dune areas, the GPS recordings should have the same time length, a fixed date-interval corresponding to the timing of the herbage survey (15th of each month), and the same number of cattle among the 3 months. In September, GPS recordings were available only for two cattle on 5 consecutive days (11 to 15 September). Therefore, we calculated the foraging density for 5 consecutive days in each month using the GPS recordings of two cattle, and the GPS data of two cattle were used for the following analysis.

Every 5 days, there were around 8550 GPS position data for each animal. The predicted metrics of distance (linear distance, cumulative distance) and turning angle were calculated by using the focal locations from 100- to 800-s time intervals. We applied the random forest algorithm to classify livestock behaviors by using predicted metrics and field-observed behavioral data. To evaluate the performance of the random forest model, we used 10-fold (i.e., performed 5 times) cross-validation to separate the data into smaller training data sets and testing data sets. The overall accuracy of the random forest model was 87% (95% CI = 85–90%), and the accuracy of foraging behaviors was 95% (95% CI = 92–98%) in the model.

Then, we randomly selected two cattle for each grazing period and imported these data into the constructed algorithm to classify foraging and non-foraging behaviors (Gou et al., 2019).

The few and similar precipitation occurred during these periods; 1.2 mm of rain fell in July, 5.6 mm in August, and 0.2 mm in September (Fig. S1). The mean air temperature was 25.6 °C in July, 23.8 °C in August, and 20.7 °C in September (Fig. S2). Few precipitation events occurred in the 3 months.

As explained in Section 2.4, we surveyed plant communities and collect biomass in mid-July, mid-August, and mid-September of 2018. Thus, only the GPS recordings covering 11–15 July, 11–15 August, and 11–15 September 2018 were used for further analysis.

2.4. Herbage production and quality measurement

For the plant community surveys and biomass collection, we selected seven low-land sites that were evenly distributed and three typical sand dunes on the ranch. As there were small variations in the species composition across the low-land areas, we selected three small and four large low-land sites to investigate the herbage community. Most sand-dunes on the ranch were distributed along the edges of ranch fences, and we selected three sand dunes evenly distributed in the center of the ranch to investigate the sand dune plant community.

On 15 July, 15 August, and 15 September 2018, three (1 m × 1 m) quadrats were randomly established at each selected low-land site along the diagonal of a 10 m × 10 m plot, and three quadrats were established on each sand-dune, one at the top, one on the leeward slope, and one on the windward slope (i.e., 21 low-land quadrats and 9 sand-dune quadrats in each month). We recorded every species that occurred in the quadrats, cut the aboveground part of each plant, and put the material in envelopes separated by species. The plant samples were dried to constant weight (55 °C for 48 h) and then weighed to obtain the biomass of each species. The biomass of each quadrat is the summed biomass of all plants in the quadrat. Then the same species from different low-land or sand-dune quadrats were mixed. The crude protein (CP), neutral detergent fiber (NDF), acid detergent fiber (ADF), and total digestible nutrients (TDN) of each species per month were determined by chemical analyses performed by Cumberland Valley Analytical Services (Tongzhou District, Beijing, China). The CP, NDF, ADF, and TDN of each quadrat were the means of CP, NDF, ADF, and TDN of each species in the quadrat weighted by the relative abundance of each species.

2.5. Cattle density

The boundary of the study ranch was recorded by a real-time differential hand-held GPS (GPS PRO XR, Trimble Navigation Ltd., Sunnyvale, CA, USA), which we moved along the fence boundary while recording GPS position at 10-s intervals. The DSM was clipped by the boundary data to cover the study ranch. The GPS position data of the two selected cattle were classified as foraging or non-foraging behaviors by using a random forest algorithm (Gou et al., 2019). In our study, 80% of the moving distance in the 50-seconds interval was less than 10 m (Fig. S3). Thus, to examine the spatial distribution of cattle behaviors, we analyzed the foraging density at the 10 × 10 grid. Thus, each livestock behavior at each point had position information. Then, the summed number of foraging behaviors in each 10 m × 10 m grid was considered as the foraging density of the grid. The average foraging densities in the low-land and sand-dune areas each month were the means of the foraging density of the low-land and sand-dune grids, respectively.

2.6. Data analysis

The foraging density at each elevation was the average of foraging densities at that elevation throughout the 3 months of grazing. The foraging area was the sum of grids in which foraging occurred in low-land and sand-dune areas, respectively. The proportional low-land foraging area was the ratio of low-land grids in which foraging occurred to the total number of ranch grids. The same method was used to calculate the proportional sand-dune foraging area.

The number of GPS points was considered to represent the total time that cattle stayed on the ranch every 5 days. The number of foraging behaviors in the same period was considered to represent the foraging pressure on the ranch. The ratio of summed foraging behaviors to the total number of GPS points was the proportion of foraging during the period. This way of calculating proportional foraging is the same as using the ratio of foraging time to the total time cattle stayed on the ranch because the time interval for each GPS point is the same. The calculation of the proportion of non-foraging behavior was done in the same way.

After log-transformation, the foraging densities in all 10 m × 10 m grids in low-land and sand-dune areas during the 3 months were tested for normal distribution and variance equality by using the Kolmogorov–Smirnov and Levene's tests, respectively; data normal distribution and homogeneity of the variances were considered at a $P > .05$. The foraging densities during this period were not normally distributed, and heteroscedasticity was observed in both low-land and sand-dune areas. Therefore, differences in foraging density between the two landforms during the 3 months were tested by using the non-parametric Kruskal–Wallis test (*rstatix* package in R). Log-transformation of the raw data does not affect the results of the Kruskal–Wallis test. Thus, the log-transformed foraging density data were used in the following analyses. For multiple comparisons of foraging densities among the 3 months in both low-land and sand-dune areas, the Kruskal–Wallis test and Dunn's post hoc test were used to analyze the differences between pairs of months and between the landforms. The foraging density in all grids during the 3 months was used to assess the frequency distribution in low-land areas and in sand-dune areas. Two-way ANOVA (*ANOVA.TFNs* package in R) was used for comparing the herbage quality (CP, NDF, ADF, TDN) and quantity (biomass, species diversity) among the 3 months between low-land and sand-dune areas; significance levels were set a $P < .05$. Species diversity was calculated by using the Shannon diversity index in the *vegan* package in R.

A multiple linear regression model (*lme4* package in R) was used to analyze the relationships between foraging density and herbage quality and quantity in the study. First, the data from both low-land and sand-dune areas were included. The dependent variable in the model was the foraging density in grids of field plots where biomass and forage quality had been determined. The independent variables in the model were herbage quality and quantity at plots on the ranch. In the analysis, the "period of July" was a dummy reference category compared with the "period of August" and "period of September" for effects of seasonal grazing density.

Also, to evaluate the effects of landform on the cattle behaviors and distribution pattern, the variable "sand-dune" was a dummy reference category compared with "low-land". In the second step, two multiple linear regression models were calculated to assess the relationship between cattle density and herbage conditions in low-land and sand-dune separately; significance levels were set at $P < .05$. In both analyses, the independent variables were the same as in the first step except for the variable of "landform". All analyses were conducted in RStudio v.1.2.1335 with R 3.6.1 and ArcGIS 10.2 (Environmental Systems Research Institute, Olympia, WA, USA).

3. Results

3.1. Dynamics of the spatial distribution pattern of livestock behavior

We observed a significant difference ($P < .05$) in the summed log-transformed foraging density in July, August, and September (number of total foraging behaviors in 5 days measured at 50-s intervals per grid cell of 10 m × 10 m) between low-land and sand-dune areas (Fig. 2A). The average log-transformed foraging density ranged from 1.5 to 2.8 in low-land areas during the grazing season and from 1.2 to 2.0 in sand-dune areas (Fig. 2B). The average foraging density decreased with increasing elevation (Fig. 2C).

The spatial distributions of grazing density in July, August, and September are presented in Fig. 3. During the grazing season, the proportion of time spent foraging across the entire ranch increased from 63% to 67% to 68% in July, August, and September, respectively, with a corresponding decrease in time spent not foraging. Likewise, the proportion of time spent foraging increased from 41% to 43% to 44% in the low-land areas and from 21% to 23% to 24% in the sand-dune areas in the July, August, and September grazing periods, respectively (Fig. 3A).

The log-transformed foraging density significantly increased from 0.61 in July to 0.66 in August to 0.88 in September in low-land areas ($P < .05$), whereas no differences were observed in sand-dune areas (0.44, 0.44, and 0.66, respectively; Fig. 3B). The detailed distribution of foraging behavior showed that higher foraging density (1.2–2.5) was mainly confined to the low-land area around the cattle shed in July (see Fig. 1C for this location), but cattle spread to other areas of the ranch in August and September (Fig. 3E). The proportion of area foraged by cattle increased in both low-land and sand-dune areas. Of the entire low-land area on the ranch, 31%, 35%, and 36% was used for foraging in July, August, and September, respectively; similarly, the relative area of sand dunes used increased in those months (45%, 47%, and 51%, respectively; Fig. 3C). Low- and high-density foraging decreased whereas medium-density foraging increased from July to September in both low-land and sand-dune areas (Fig. 3D).

3.2. Temporal changes in forage quantity and quality

The average biomass of the 21 low-land quadrats was 144, 87, and 44 g m^{-2} in July, August, and September, respectively; these values are higher than those in the nine sand dune quadrats in those months (66, 50, and 30 g m^{-2}, respectively; Fig. 4A). The decreasing trend of biomass in both low-land and sand-dune areas was significant ($P < .05$; Fig. 4A). Species diversity was also higher in low-land than in sand-dune areas and declined from July to September in both (Fig. 4B). The value of NDVI decreased significantly from July (0.41) to August (0.38) and September (0.23) in low-land areas. The same trend was observed in sand-dune areas (0.37 in July, 0.28 in August, and 0.22 in September). A significant difference of NDVI between low-land and sand-dune was observed in July and August, but not in September (Fig. S4).

The CP and TDN significantly declined from July to September in both the low-land and sand-dune areas (Fig. 4C, E). The ADF did not differ significantly between July and August in low-land areas, but it increased significantly from August to September; the same trend was observed in sand-dune areas (Fig. 4D). The biomass, species diversity, and TDN in low-land was significantly higher than those in sand-dunes (Fig. 4A, B, E). More detailed information is given in Tables S1 and S2.

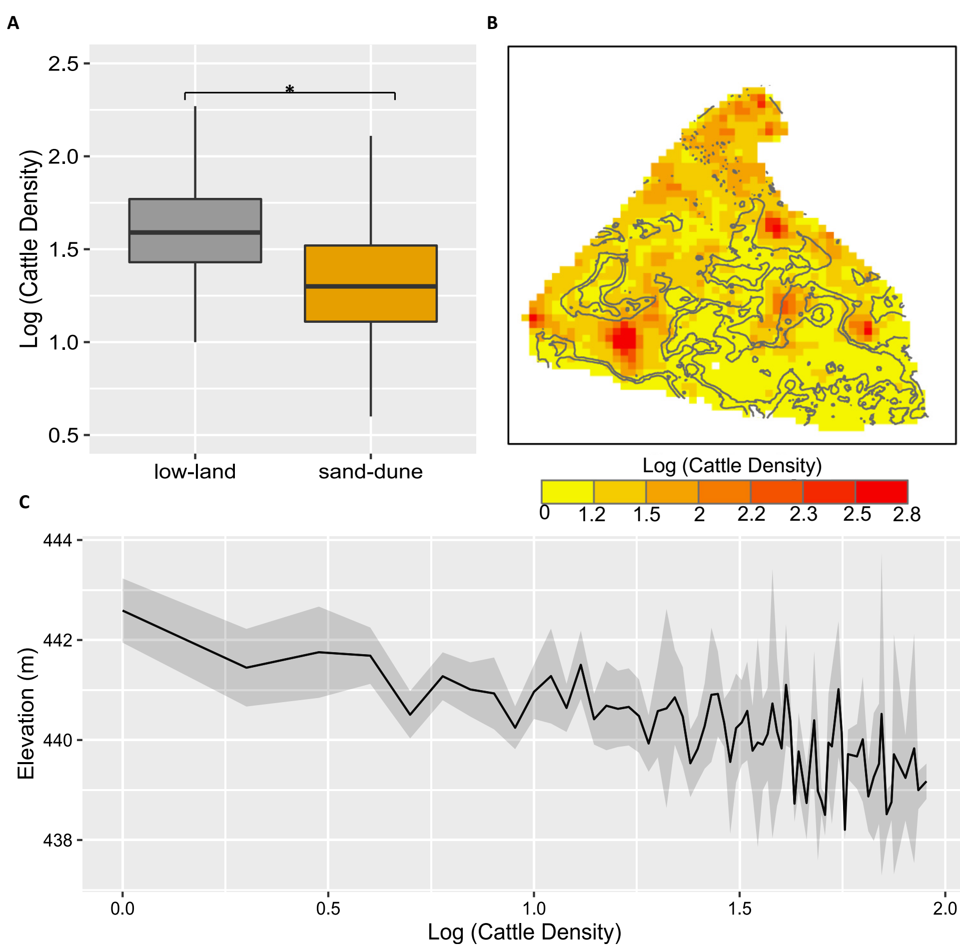

Fig. 2. (A) Seasonal summed cattle foraging density (log-transformed) in low-land and sand- dune areas (*$P < .05$), (B) the foraging density summed across the entire grazing season in each grid of the ranch, and (C) the relationship between cattle density and elevation (shading indicates the standard error of foraging density of grids at the same elevation; number of grid-cells = 1200). In the box plots, bounds of the box spans from 25 to 75% percentile, center line represents mean, and whiskers visualize 5 and 95% of the data points.

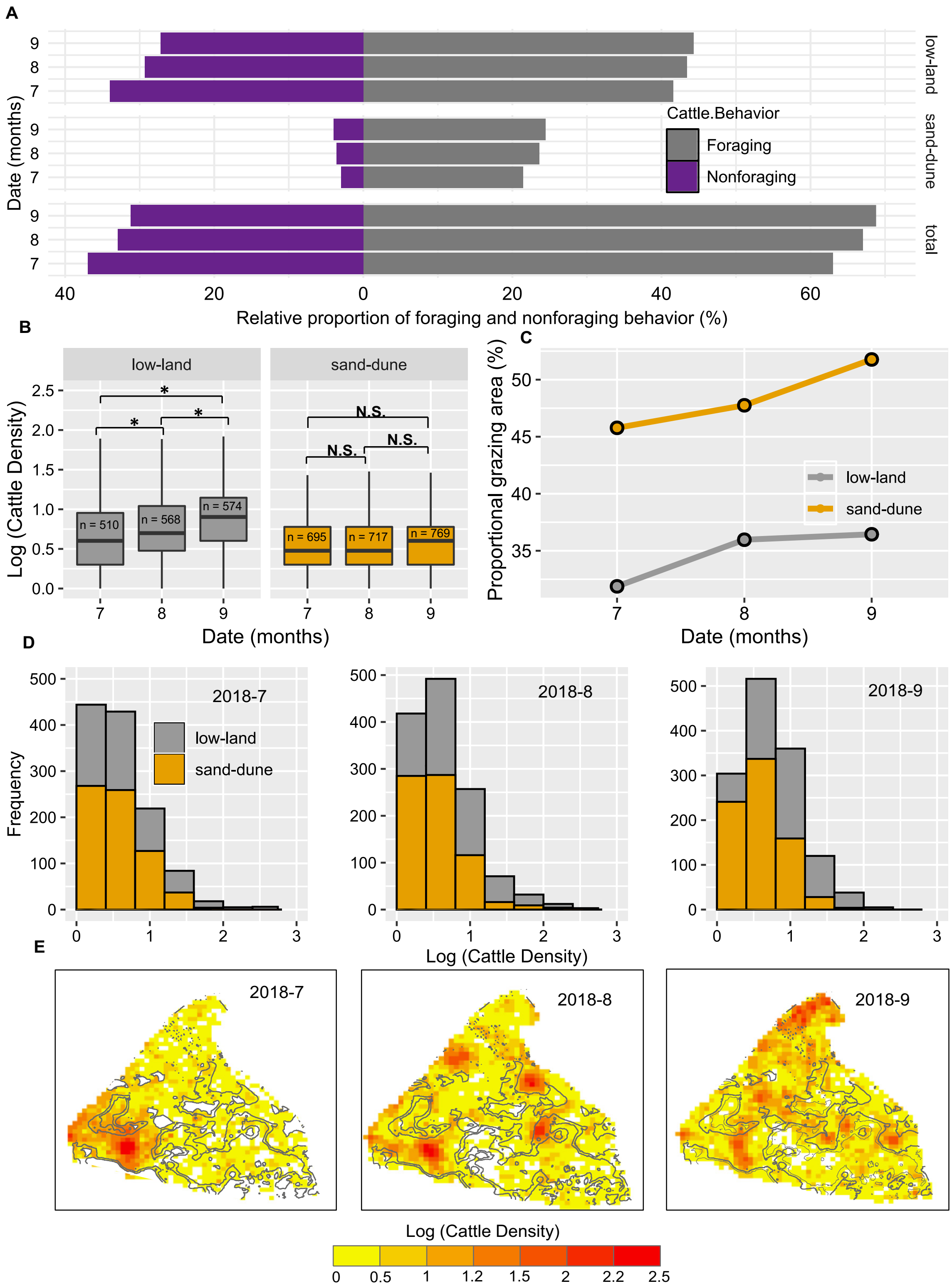

Fig. 3. Seasonal dynamics of cattle behavior. (A) Relative proportions of foraging and non-foraging behaviors in the low-land and sand-dune areas and in the whole ranch area, (B) spatial averages of monthly foraging density (log-transformed) in low-land and sand-dune areas (*$P < .05$), In the box plots, bounds of the box spans from 25 to 75% percentile, center line represents mean, and whiskers visualize 5 and 95% of the data points, (C) proportion of total low-land and sand-dune areas used for foraging, (D) foraging density frequency in low-land and sand-dune areas in each month, and (E) spatial distributions of foraging density (log-transformed) in each grid in July, August, and September.

The adjusted R^2 of the multiple regression for the whole ranch was 0.34 ($P = .06$). The results showed that landform, rather than forage quality and quantity, significantly affected the foraging density: cattle foraging significantly increased ($P = .05$) in low-land but decreased in sand-dune areas. The adjusted R2 of the multiple linear regression for the low-land was 0.62 ($P = .034$). In the low-land, biomass ($P = .053$), CP ($P = .055$), and TDN ($P = .017$) were negatively related and ADF ($P = .025$) was positively related with foraging density (Table 1).

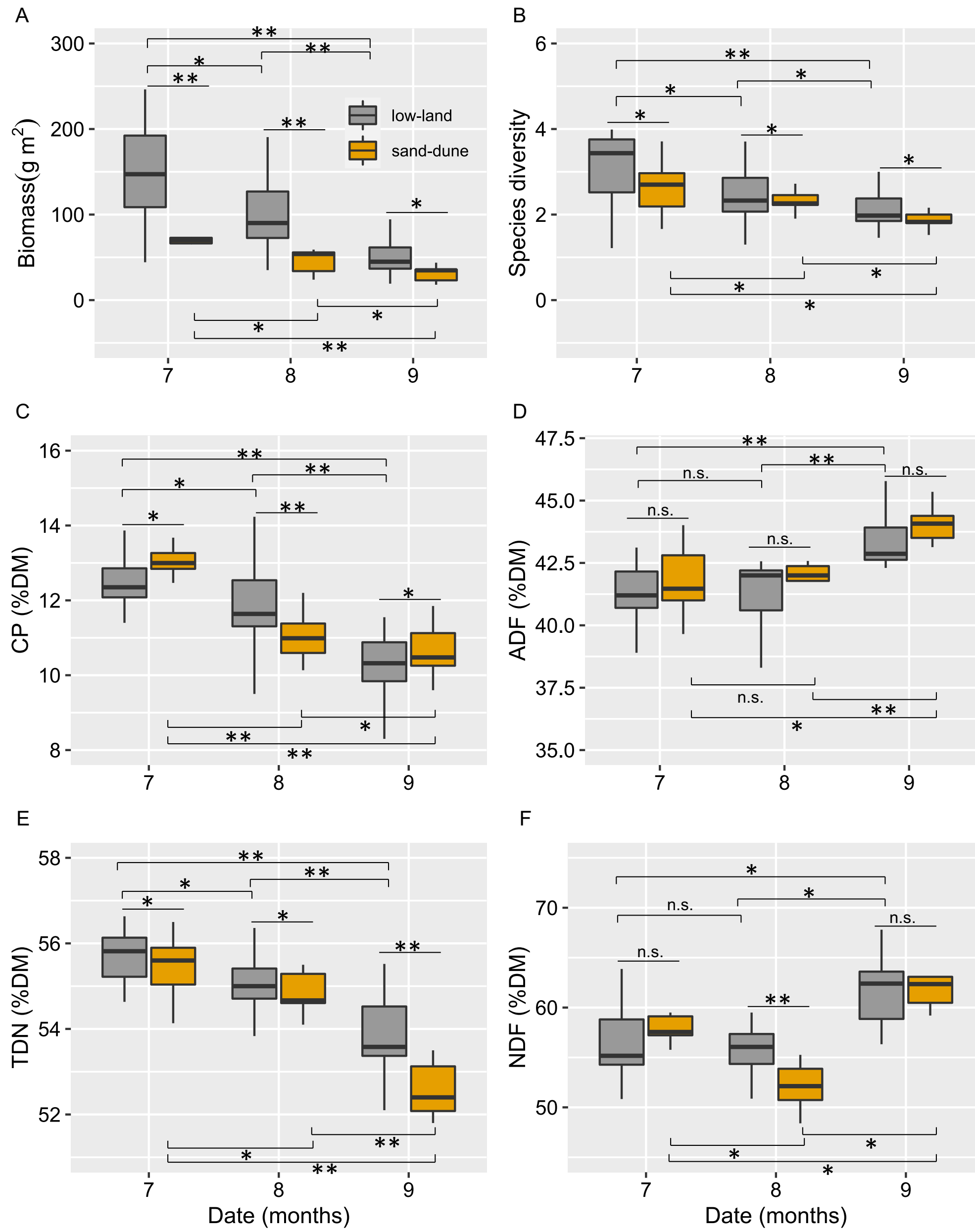

Fig. 4. Comparison of herbage quantity and quality in different grazing periods between low-land and sand-dune. The box plots show the values of (A) pasture aboveground biomass, (B) species diversity, (C) crude protein (CP), (D) acid detergent fiber (ADF), (E) total digestible nutrients (TDN), (F) neutral detergent fiber (NDF). In the box plots, bounds of the box spans from 25 to 75% percentile, center line represents mean, and whiskers visualize 5 and 95% of the data points. (*$P < .01$, **$P < .001$).

No significant relationships were observed between foraging density and herbage nutrient contents in sand-dune areas.

4. Discussion

4.1. Cattle distribution pattern in low-land and sand-dune areas

Generally, livestock prefer gentle terrain and adjust their grazing strategies to avoid higher elevations (Roath and Krueger, 1982). The greater proportion of foraging behaviors in the low-land areas than in sand-dune areas (Fig. 3A) supports the grazing habits of livestock in an undulating landscape, which led to higher foraging densities in the low-land areas (Fig. 2A, B). Our study also demonstrated a negative relation between foraging density and elevation (Fig. 2C). High energy costs are associated with cattle moving about a rugged terrain. A previous study reported that the cost of lifting one kilogram one vertical meter is 5.9 kcal for wild and domestic ungulates, regardless of body weight or species (Parker et al., 1984), and the oxygen consumption rate increases when they walk on steep slopes (Yousef et al., 1972).

Moreover, herbage quality and quantity are also associated with the different cattle distribution patterns between low-land and sand-dune areas (Sanaei et al., 2019). With respect to pasture quantity, our results showed greater biomass and species diversity in low-land areas than in sand-dune areas throughout the grazing period from July to September. These results are consistent with a previous works that reported livestock tend to lengthen their foraging time in plant communities that offer abundant quantities of preferred forages (Provenza, 1995; Launchbaugh and Howery, 2005). With regard to herbage quality, although the nutrient contents of forage species did not differ between low-land and sand-dune areas throughout the grazing period (Fig. 4), the livestock probably could gain more nutrients from forage species in low-land areas because the they were more abundant (higher

Table 1
Multiple linear regression results for whole ranch, low-land and sand-dune areas.

Variable	Total ranch		Low-land		Sand-dune	
	Regression coefficient	P value	Regression coefficient	P value	Regression coefficient	P value
Biomass (g m^{-2})	−0.064	0.091	−0.157	0.053	−0.133	0.877
CP (% DM)	−0.7	0.078	−2.377	0.055	−0.641	0.771
ADF (% DM)	0.15	0.071	3.093	0.025*	1.026	0.795
NDF (% DM)	0.07	0.102	1.42	0.102	0.184	0.815
TDN (% DM)	−0.41	0.06	−5.731	0.017*	−2.512	0.811
August (dummy)	−0.508	0.143	−0.612	0.143	−3.81	0.653
September (dummy)	−0.806	0.147	−0.736	0.147	−1.541	0.915
Low-land (dummy)	1.328	0.05*				
R Square	0.45		0.75		0.379	
Adjusted R square	0.34		0.624		−3.966	
F-statistic	2.86		5.74		0.087	
P value	0.064		0.034*		0.988	

Notes: The variables used in the regression of cattle density was the dependent variable, and biomass, crude protein (CP), acid detergent fiber (ADF), neutral detergent fiber (NDF), and total detergent nutrient (TDN) were independent variables for the fixed effects in the model. August, September and low-land are the dummy variables for fixed effects of seasonal grazing periods, the variable of July and sand-dune were reference group in the model. In analysis, each dummy variable is compared with the reference group.
* Indicates a significant relationship ($P < .05$).

biomass) (Sebata and Ndlovu, 2012). Cattle prefer to forage in plant communities with higher species diversity because a mixture of forage species can supply more nutrients and energy (Rosiere et al., 1975). Thus, the higher species diversity in low-land areas (Fig. 4) might be one possible reason for the higher foraging density there (Rosiere et al., 1975).

4.2. Variation of cattle behavioral activity and foraging density

Previous studies revealed a trade-off between livestock grazing time and intake rate per bite, which is determined by the pasture condition (Gordon and Lascano, 1993). The intake rate per bite declines with a reduction in forage availability, which results in at least partially compensatory changes in foraging time (Davies and Southey, 2001; Lachica and Aguilera, 2003). Cattle can meet their necessary energy requirement in a shorter foraging time with a high intake rate per bite (Prache et al., 1998). In our study, at the beginning of the grazing season in July, less foraging time and lower foraging density were observed both in low-land and sand- dune areas (Fig. 3A, B). During this period, the biomass and nutrients of herbage were higher (Fig. 4), consistent with there being a higher intake mass per bite and a higher nutrient intake per bite in a relatively small area (Fig. 3C). Moreover, the relatively small foraging areas of cattle in both low-land and sand-dune areas supports the idea that livestock can gain the necessary energy in a relatively short period without moving to other areas for foraging.

Foraging time increased from July to September (Fig. 3A), while the foraging density increased in August and September by cattle in the low-land areas (Fig. 3B). The probable reason is that herbage quantity and quality both gradually decreased from July to September (Figs. 4; S4), as the herbage was consumed by cattle (Butt, 2010) and reached maturity (Schönbach et al., 2009). Cattle density was negatively related with herbage quantity and quality in low-land areas (Table 1). The maturation process of herbage can lead to a decline in CP and an increase in ADF because the proportion of stems and leaves increases (Benvenutti et al., 2008). Therefore, the maturation of plants increases their tensile strength and causes the cattle to spend more time chewing and alters their biting position as they select more nutritious parts of the herbage (Tjardes et al., 2002). When forage availability is low and herbage quality is poor, cattle can improve their intake by taking smaller bites (Lyons and Machen, 2000), but they need a longer grazing time to compensate for the decline of intake mass and nutrients per bite (Baumont et al., 2007). The relative increase of foraging time from August to September was greater than that from July to August in both the low-land and sand-dune areas; this result can be explained by the decline of herbage quality, which caused the cattle to spend more time ruminating to absorb the nutrients from the herbage. The foraging density also increased as the proportion of low-land areas foraged increased. This finding implies that as the grazing season progresses, cattle spend more time foraging on herbage in a given area and they acquire more cumulative nutrients by foraging on different herbage communities by increasing the proportion of low-land areas foraged.

The variation of foraging behaviors on the ranch supports previous findings that cattle have the ability to alter their behaviors to cope with the balance between nutrient demand and energy consumption by using various spatiotemporal distribution patterns (Fierro and Bryant, 1990; Butt, 2010). In our study, there was no change of foraging density in sand-dune areas (Fig. 3B) even though the proportion of sand-dune area foraged sharply increased from July to September given the elevated foraging time during this period. While the cattle foraged in sand-dune areas, they consumed more energy to maintain a standing posture and to walk on the soft sandy soils of the dunes (Relton, 2015). We also observed no relationship between cattle density and herbage nutrient content in sand-dune areas (Table 1), possibly because sand-dunes offer relatively lower cumulative herbage nutrients throughout the grazing period and because a larger grazing area is required to gain sufficient nutrients from sand-dune herbage communities.

In addition to the different distribution of cattle foraging between low-land and sand-dune areas, a heterogeneous distribution was observed in the low-land areas (Fig. 3E). Generally, cattle can readily travel across gentle terrain while grazing (Bailey, 2005), but in rugged topography, the movement of cattle from one feeding site to another is restricted (Bailey, 1995). Livestock always show a concentrated distribution early in the grazing season and a more dispersed distribution as the season progresses (Evans et al., 2004). We observed a high density near the cattle shed at the beginning of the grazing season, but subsequently cattle spread to other areas; the decline in both high and low foraging density and the increase in medium foraging density (Fig. 3D) indicated widely dispersed and evenly distributed foraging late in the grazing season (Fig. 3E). The exploration of new grazing areas forces the cattle to pass through rugged terrain. Thus, the movement route for foraging might cross dunes on the ranch, thus increasing the foraging area in sand dunes later in the season.

4.3. Limitations of the study

Our study has several limitations, including insufficient data for the experiment design, and the results were affected by biotic and abiotic factors involved in the cattle behavior and distribution pattern. First, the cattle behaviors and distribution pattern varied under different climate conditions, such as extreme air temperature, which could increase the cattle's core body temperature and respiration rate and reduce activity, feed intake, and milk yield (Hahn, 1999; Ominski et al., 2002; West, 2003). Daily air temperature and precipitation were monitored at a meteorological station 20 km away from the study site. Few and similar precipitation events occurred during the recording periods of cattle behaviors in our study, and the difference in temperature among the grazing periods hardly affected the cattle behaviors and distribution during the experimental periods (Figs. S1 and S2). Therefore, the results of our study may not be generalized to ranches affected by extreme climate conditions that would influence the cattle's normal behaviors and distribution pattern. In future studies, it will be critical to include longer grazing times under different climate conditions to broaden the scope of our findings.

Another limitation was that we obtained GPS data for only two cattle and used them to represent the behaviors and distribution pattern of the entire cattle population. The size of a herd will vary with resource conditions on a ranch (Howery et al., 1998). When resources are relatively abundant, cattle in a herd usually feed and rest together, and dominant animals displace subordinates less frequently. A previous study showed that as cattle herds extend their home ranges, they divide into several small groups in winter and spring but form a large group and concentrate near water and feed at other times (Lazo, 1994). Our study period was from July through September. Because the forage resource of this period was relatively abundant, the cattle congregated in a large group. Our field observations during the period also provide evidence of group behaviors where cattle foraged together in the same low-land area and sand-dune area. Therefore, the behavior of two cattle might actually be representative of the population. However, in our study, the recorded grazing density might be higher than the actual density because we used the grazing density of just two cattle to represent the whole population in September. The home range of the cattle herd in September might be larger because of the low quality and quantity of herbage (Venter et al., 2019). Therefore, location data obtained from more cattle over a longer period are needed to clarify cattle behaviors and distribution patterns.

4.4. Implications for land management

The spatial and temporal variation of livestock foraging density can affect ecosystem functions (Venter et al., 2019). Our results indicate that higher foraging density occurred in low-land areas than in sand-dune areas (Fig. 2A), especially when the herbage quantity and quality were low (Fig. 3B). In the grazing periods with poor herbage conditions, foraging in low-land areas tended to occur at high density because of the reduction in forage quality and availability. Thus, ranchers should initiate interventions such as a rotational grazing system, in which a ranch is delineated into two grazing areas, such as low-land and sand-dune areas.

The essential role of rotational grazing is to decrease the grazing time in the area with higher grazing density (Heitschmidt and Taylor Jr, 1991). Continuous grazing may lead to ranch degradation over the long term (Venter et al., 2019). For policymakers, when recommending the management practice of rotational grazing to herdsman, low-land and sand-dune areas should be recognized as two grazing camps. The management of grazing duration at each camp is determined by the herbage conditions; for example, cattle might be moved to the sand-dune camp once the herbage condition at the low-land camp fell as a result of poor herbage weather conditions.

5. Conclusion

The cattle preferred to forage in low-land areas compared to sand-dune areas, probably reflecting the greater energy consumption required and poorer herbage conditions in the high-elevation areas. The temporal dynamics of foraging pressure showed different patterns in low-land and sand-dune areas from July to September. The foraging pressure and proportional area used by cattle both increased from July to September in low-land areas, whereas only the proportional area foraged increased in the sand-dune areas. As the grazing season progressed, the foraging time increased in both low-land and sand-dune areas. The foraging density increased as herbage quality and quantity declined in low-land areas.

Our results indicate that microtopographic variation facilitates uneven and patchy foraging distributions on the ranch, and that high foraging density is likely to occur in low-land areas of an undulating landscape. When making grazing policies in this region, the microtopography of a ranch and seasonal dynamics of the spatial distribution of foraging density should be considered to manage grazing density. Ranch owners should consider using a rotational grazing system in which cattle are shifted from a low-land grazing camp to a higher elevation camp during periods of herbage decline.

CRediT authorship contribution statement

Xiaowei Gou: Conceptualization, Methodology, Software, Writing-original draft preparation, Data curation. **Atsushi Tsunekawa**: Conceptualization, Methodology, Funding acquisition, Supervision. **Mitsuru Tsubo**: Methodology, Data curation. **Fei Peng**: Methodology, Data curation, Writing-Review and Editing. **Jian Sun**: Data curation, Software. **Yulin Li**: Methodology. **Xueyong Zhao**: Methodology. **Jie Lian**: Resource.

Declaration of competing interest

The authors declare no conflict of interest regarding the publication of this article.

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Appendix A. Supplementary data

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