Greater impact of energy expenditure over harvest rate on resource conversion efficiency as herbivores grow

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April 19, 2024

Abstract

1. Herbivores adopt foraging strategies to maximize efficiency in diverse, resource-constrained environments. However, the effectiveness of these strategies may be more constrained by their capacity for energy cost rather than their ability to acquire resources. The swift utilization of resources during acquisition is crucial for optimizing energy conversion efficiency in animals. Nonetheless, the energy expended in this process inherently limits food conversion efficiency (FCE), an aspect that remains insufficiently explored in current research. 2. In this study, we introduced a concept framework that integrates harvest rate (HR) and energy expenditures (EE) into evaluating herbivore FCE. Utilizing high-resolution tri-axial accelerometry within a grazing treatments platform, we analyzed the behaviors of herbivores (Ovis aries) to determine the energy costs and time allocation for both lamb and dry ewe groups. 3. Our analysis demonstrated an inverse correlation between HR and EE, exhibiting both positive and negative influences on FCE. Notably, the impact of EE was more pronounced in larger-sized grazers (dry ewes), while HR significantly influenced smaller-sized grazers (lambs). However, the interaction effects between these variables tended to neutralize the variations in FCE observed across both groups. 4. Our research highlights how the behavioral patterns of grazers, in terms of resource acquisition and relative energy costs, are pivotal in determining resource utilization efficiency. Additionally, it reveals the trade-offs in these behaviors, which transition from being beneficial to restrictive as the body grows. This finding substantiates the theory that the behavior of herbivores is a reliable predictor of their efficiency in resource utilization.

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Abstract

Herbivores adopt foraging strategies to maximize efficiency in diverse, resource-constrained environments. However, the effectiveness of these strategies may be more constrained by their capacity for energy cost rather than their ability to acquire resources. The swift utilization of resources during acquisition is crucial for optimizing energy conversion efficiency in animals. Nonetheless, the energy expended in this process inherently limits food conversion efficiency (FCE), an aspect that remains insufficiently explored in current research. In this study, we introduced a concept framework that integrates harvest rate (HR) and energy expenditures (EE) into evaluating herbivore FCE. Utilizing high-resolution tri-axial accelerometry within a grazing treatments platform, we analyzed the behaviors of herbivores (*Ovis aries*) to determine the energy costs and time allocation for both lamb and dry ewe groups. Our analysis demonstrated an inverse correlation between HR and EE, exhibiting both positive and negative influences on FCE. Notably, the impact of EE was more pronounced in larger-sized grazers (dry ewes), while HR significantly influenced smaller-sized grazers (lambs). However, the interaction effects between these variables tended to neutralize the variations in FCE observed across both groups. Our research highlights how the behavioral patterns of grazers, in terms of resource acquisition and relative energy costs, are pivotal in determining resource utilization efficiency. Additionally, it reveals the trade-offs in these behaviors, which transition from being beneficial to restrictive as the body grows. This finding substantiates the theory that the behavior of herbivores is a reliable predictor of their efficiency in resource utilization.

Keywords: harvest rate, energy expenditure, food conversion efficiency, tri-axial accelerometry, foraging strategy

Introduction

Understanding the mechanisms underlying food conversion efficiency (FCE) is crucial in determining how herbivores convert ingested resources into energy for growth, reproduction, and maintenance (Belovsky, 1986; Illius and Gordon, 1992; Oonincx et al., 2015; Roehe et al., 2016). A key aspect of this process is how resource availability supplements the energy harvested by herbivores (Sollenberger et al., 2012; Vallentine, 2000; Venter et al., 2019). The uneven distribution of resources has prompted territorial herbivores to develop time-minimizing strategies to balance physiological constraints from handling and digestion (Bergman et al., 2001a; Zubieta et al., 2021). Thus, for field-grazing or wild herbivores, the time spent foraging becomes a limiting factor in resource acquisition rates, subsequently impacting the rate at which food can be converted into energy consumption. However, herbivores are not only limited by their ability to rate of acquiring energy but also by their capacity to expend it efficiently (Hudson, 2018; Speakman et al., 2021). Thus, how both harvest rate (HR) and energy expenditure (EE) collectively influence FCE in herbivores remains unclear (Fig. 1).

The dynamics of foraging behavior and dietary intake in herbivores are intricately linked to the availability and constraints of resources (Illius and Gordon, 1992; Pyke, 1984). This relationship plays a pivotal role in shaping their energy acquisition strategies. In environments abundant with resources, herbivores primarily focus on minimizing the time spent foraging, and optimizing their energy intake within the shortest possible duration (Gross et al., 1995; Norberg, 2021). Conversely, scarcity of resources prompts a shift in strategy. In this case, herbivores may extend their foraging time, thereby increasing their energy intake to meet the necessary demands, albeit at the cost of reducing time for other vital activities (Bayliss and Choquenot, 2002; Bergman et al., 2001a). Crucially, the adaptability of herbivores in altering their time strategy in response to fluctuating resource availability is modulated by their energy consumption needs (Fig.1a). In each feeding bout, grazers exhibit muscle contractions to sustain motion conservation, markedly affecting energy costs (Gleiss et al., 2011). The step-level foraging active (consuming energy cost) did not vary proportionally to the time in foraging, as the intense and strength differed from thousands of biting activities each day in response to the resources conditions (Fig. 1a), which accrued significant energetic cost over prolonged period-ranging corrected to the interaction to the resources conditions (Shipley, 2007). Thus, the energy cost not only consumes the physiological energy of herbivores but also reflects the strategies selection in response to resource conditions which is linked to the how rate of grazers consume in the given time. However, how the resource conditions varied in changing the relationship between EE and HR and further interaction on FCE remains unclear.

The advent of bio-logging technology, specifically herbivores-borne bio-loggers, allows for the precise measurement of movement and dynamic body acceleration on a fine temporal scale (Gleiss et al., 2011). Consequently, this enables researchers to develop indices of EE that are directly tied to body movement (Gregorini et al., 2008), as well as to calculate absolute values of EE that correlate with specific animal behaviors (Williams et al., 2014).

Our research was conducted on a controlled grazing platform, tailored to minimize dispersal effects and focus on the intrinsic dynamics of grazing (Bonte et al., 2012; Van Dyck and Baguette, 2005). We first examine the relationship between HR and EE. It is hypothesized that a negative correlation exists between these two variables; we anticipate that herbivores expend less energy and time harvesting when resources are abundant. Conversely, we expect a rise in EE with diminished resource availability, reflecting increased foraging effort (Fig. 1a). Our second objective was to investigate the influence of both HR and EE on FCE, considering the physiological states of our two subject groups: lambs and dry ewes. We hypothesized that FCE in the dry ewe group is more significantly impacted by EE with the assumption that energy costs scale linearly with the metabolic body weight of herbivore ungulates (Hudson et al., 2013; Nagy, 2005). Despite facing similar resource conditions in the grazing plots, we proposed that HR presents a greater challenge for the lamb group, given the comparative inexperience and lower resource-harvesting efficiency of these younger animals (Fig. 1b).

Materials and Methods

2.1 Study area

The present study was conducted in the northeast of Eurasian steppes, Xilinhot City, China. The area experiences continental precipitation with an average of 350 mm (200-500 mm) over 30 years, with 60 to 70% falling between July and August. The average monthly temperature varies from -21.6 in January to 19.0 in July, annual mean temperature of 0.3. Approximately 150 to 180 days per year are considered favorable for plant growth (Bai et al., 2010). The most prevalent plant species in the area are *Stipa grandis* P.A. Smirn., and *Leymus chinensis* (Trin.) Tsvel. (Li et al., 2015).

2.2 Grazing treatments and plant survey

The manipulative experiment was conducted with all 15 plots consisting of three herd compositions: lamb plots with light, moderate, and heavy grazing intensities, mixed lamb and dry ewe, dry ewe plots (Fig. 2a, c). We individually fitted sensors to one lamb and one dry ewe in each lamb and ewe grazing plot, while both a lamb and a dry ewe were fitted with sensors in each mixed plot. We monitored the accelerations of 17 sheep, comprising 11 lambs and 6 dry ewes, for a total of 53,280 tri-axis accelerations per sheep using accelerometer loggers to collect the behavioral data of grazers.

To monitor vegetation resources quality and quantity, the above-ground biomass (AGB), five quadrats of 1 m^2 were randomly placed within each plot on June 20th, August 15th, and September 10th, 2022. In addition, the aboveground plants were collected and then oven-dried at 105 °C for 15 min and then at 65 degC for 48 h until constant weight. The nitrogen content in the dried plant samples was measured using the Kjeldahl method and then multiplied by a conversion factor of 6.25 to obtain the crude protein content (CP) of the plants (Sanna et al., 2019).

2.3 Herbivores behavior monitoring

We selected sheep (Ovis aries; one of the most extensively kept livestock breeds in the grassland of Mongolia Plateau) attached with sensors to monitor the strength of actives (Fig. 2d). The accelerations of sheep were monitored using accelerometer loggers from Druid Technology Co., Ltd (Chengdu, China; https://www.ecotopiago.com). The collars were programmed to record three-axial acceleration at a frequency of 25 Hz for 1.5s every minute (i.e., 37 data points per axis and 111 data points per ACC burst) during the grazing period between the end of July and September. We conducted a correlation analysis between the frequency tri-axial of acceleration obtained for 1.5 seconds and those obtained by the device automatically calculating the values for every 6 seconds. The results showed a significant correlation, indicating that the 1.5-second frequency can represent the animal's behavior within that minute (Supplementary Fig. 2).

The data obtained from the study were stored in a device containing an nRF52840 SoC (system on a chip) that boasts a 64 MHz microprocessor, 1 MB Flash, and 256 kB RAM. The SoC features BLE (Bluetooth Low Energy), which facilitates data transfer between the logger and personal cell phones over a range of 70 m. The device also incorporates a 3G module for data communication via the mobile network, as well as sensors for capturing temperature and light intensity in addition to the three-axial ACC sensor. A solar panel was fitted onto the logger to recharge a 200 mAh rechargeable lithium battery.

The acceleration data initially collected in millivolts was converted into gravitational acceleration units (g), which represent the rate of change of velocity concerning gravity, using tag-specific calibration values. Subsequently, each of the three signals was subject to individual smoothing through running means over a period of 1.5 seconds. Following this, the corresponding smoothed data were subtracted from the unsmoothed data for each axis. The resulting sum of all three axes yielded a value for the Overall Dynamic Body Acceleration (ODBA) experienced by the animal given by

ODBA = |Dynamic acceleration (x)| + |Dynamic acceleration (y)| + |Dynamic acceleration (z)|

2.4 Behaviors classification

We utilized the XGBoost algorithm, a boosting ensemble algorithm that efficiently implements the Gradient boosting decision tree algorithm (Van Soest, 2018), to classify sheep behaviors about energy expenditure and foraging strategies. Specifically, we classified behaviors into grazing (feeding, walking-feeding, walking) and nongrazing behaviors (standing, lying, ruminating-standing, ruminating-lying), as the ODBA was more accurately related to the active status of animals. During the grazing period, actual observed behaviors were conducted for 3-5 days every month, and we eliminated data with multiple behaviors or behavioral changes within 1 minute to ensure the monotonicity of behavioral data (Wang et al., 2020). Ultimately, 2500 individual behavior segments (each segment lasting more than 30 s) were included for analysis.

We acquired 27 features from motion sensors using the 'rabc' package (Yu and Klaassen, 2021), including mean, variance, standard deviation, max, min, range, and ODBA for each ACC axis separately (denoted with prefix*x*, *y*, *z* in the output data frame), except for ODBA. After filtration, we used 70% of the data combined with actual observed behavior data to develop the behaviors classification model based on the XGBoost algorithm. The remaining 30% was used to validate the classification filter and report the classification accuracy. The results showed more than 90% accuracy for behavior classification (Supplementary Fig. 1a). Similarly, using only ODBA as a classification criterion, we were able to accurately classify feeding behavior (> 0.1 g) and non-feeding behavior (< 0.1 g) (Supplementary Fig. 1b).

2.5 Derivation of foraging parameters

2.5.1 Calculating the dry matter intake (DMI)

Sheep were weighed on June 20th, August 15th and September 10th to calculate DMI and energy expenditure. We estimated the daily DMI of collared sheep by using the measured live body weight and previously derived

relationships between live body weight data and daily intake from experimental trials of various studies for farm ruminant animals (Van Soest, 2018), which was given by

$$DMI = M^{0.75}(CF)$$

Where DMI is the dry matter intake (kg/day), M (kg) is the live body weight of the sheep, and CF is a constant factor that represents the intake coefficient, which depends on the sheep's physiological stage, breed, sex, and environmental factors. Generally, the CF was selected as 3% of the body weight of sheep (Van Soest, 2018). We computed the FCE by dividing the dry matter intake (DMI) by the body weight gain. FCE is a measure of how efficiently an animal converts feed into body weight gain.

2.5.2 Calculating the energy expenditure

We calculated the EE of collared sheep using previously derived relationships between triaxial accelerometer data and animals' energetics from experimental trials of various types of animal species as well as farm ruminant animals (Halsey et al., 2011; Miwa et al., 2015). The link between sheep energetics and collar data is given by

$$VO_2 = 15.139M^{0.794} + 38.467M^{0.835}(ODBA)$$

 $r^2 = 0.908$

here VO₂ (ml/min) amount of oxygen consumed over 1 min, and overall dynamic body acceleration ODBA (g) is the sum of the absolute value of each accelerometer axis summed over 1 min (Miwa et al., 2015). Oxygen consumption was then converted to kilojoules expended per 20.46 J/ml (McLean, 1972). We then estimated the sum of energy expenditure (kilojoules) as the sum of kilojoules expended per minute over each 1-min period between successive data collection.

2.5.3 Calculating the harvest rate

In this study, the rate of energy acquisition by grazers is quantified using the product of the harvest rate, as described by Holling's disc equation (a type II functional response), and the energy content of the harvested resources (Brown et al., 2017). The formula for this calculation is given as

$$H = \frac{\alpha EP}{M}$$

english $(1+\alpha R)$

where α represents the probability of encounter, denotes handling time, R symbolizes resource abundance, and E signifies the energy yield per unit of food. Considering the relatively small size of the grazing plots (2 hectares), it is assumed that each herbivore individual encounters resources with uniform probability. However, total resource availability varies, as the number of sheep units differs across plots (Fig. 2c). Consequently, the resource abundance per plot (R_{plot}) is modified to:

$$R_{\rm plot} = \frac{1}{\rm SU}R$$

Here, E is represented by the crude protein percentage (CP%) of herbage, and resource abundance is indicated by the above-ground biomass (measured in grams). The handling time () is quantified through the use of tagged sensors that record foraging time (in seconds). This leads to the revised equation:

$$H = \frac{ER_{\rm plot}}{(1+R_{\rm plot})}$$

2.6 Statistical analysis

In this study, we employed Ridge Regression to explore the connections between HR, EE, and FCE, addressing the multicollinearity issue evident between HR and EE. Ridge Regression, chosen for its L2 regularization, effectively manages predictor intercorrelations in our small sample size with multicollinearity. A key methodological step was determining the optimal regularization strength (alpha) through cross-validation using RidgeCV. This algorithm automatically tunes alpha, searching logarithmically scaled alpha values to minimize Mean Squared Error (MSE). To ensure model robustness, we conducted a sensitivity analysis, focusing on variations in Root Mean Squared Error (RMSE) across different alpha values, indicating model stability under varying regularization levels. The final Ridge Regression models for the Lamb and Dry Ewe datasets were refined using alpha values from cross-validation. Model performance was evaluated based on RMSE, which measures the standard deviation of prediction errors. Our analyses utilized Python's scientific computing libraries: Pandas for data manipulation, Scikit-learn for machine learning modeling and cross-validation, and Matplotlib for visualizations.

Results

The HR and EE show a negative corrected relationship in lamb group (Y = -3E-06X + 1.3112; $R^2 = 0.6613$; p < 0.001; Fig. 3) and dry ewe group (Y = -1E-06X + 1.5233; $R^2 = 0.8539$; p < 0.001; Fig. 3).

The FCE was negatively correlated with EE across all studied herbivores (Y = -7E-07X + 0.4145; $\mathbf{R}^2 = 0.8098$; p < 0.001; Fig. 4a), and negatively correlated with EE in dry ewe group (Y = -4E-07X + 0.2963; $\mathbf{R}^2 = 0.7152$; p < 0.001; Fig. 4a), there was no significant association relationship in lamb group. The FCE positively correlated with harvest rate in the lamb group (Y = 0.2266X + 0.0906; $\mathbf{R}^2 = 0.4214$; p < 0.001; Fig. 4b) and in the dry ewe group (Y = 0.3349X - 0.1943; $\mathbf{R}^2 = 0.8376$; p < 0.00; Fig. 4b).

Using the ridge regression model, we found that FCE was more positively affected by the HR than negatively affected by energy expenditure, and the interaction effects show slightly negative effects on FCE in the lamb group (Fig. 5a). In the dry ewe group, we found that FCE more negatively affected by energy expenditure than positively affected by the harvest rate, and the interaction effects show slightly negative effect but more than that in lamb group (Fig. 5b)

Discussion

Grazing or wild herbivores meet their physiological requirements for growth and survival by rapidly harvesting resources (Mysterud, 2006; Stigter and Van Langevelde, 2004), which serve as substrates for digestible and utilizable energy (Kamra et al., 2012; Van Soest, 1996). Our study extended beyond merely assessing the behavioral rate of resource acquisition to also include an evaluation of the functional costs associated with the foraging process. Typically, the home range within which animals acquire resources is limited by their energy expenditure (Fagan et al., 2013). By restricting the diffusion process using experimental exclusion plots, grazers effectively minimized energy losses associated with searching for food. Consequently, our focus shifted to examining the influence of individual behavioral characteristics on resource acquisition and corresponding energy expenditures, specifically in terms of the feed conversion efficiency. Most vertebrates possess a digestive storage organ like the stomach or crop to balance rapid food intake with slower energy utilization, indicating that energy food harvest from their environment at a much faster rate than they can process and utilize it (Speakman and Król, 2010).

4.1 The contrasting relationship between HR and EE

Our findings confirm the hypothesis grazers increased energy investment in foraging results in a lower harvest rate from available resources (Fig. 3), when herbivores optimize their harvest rate, akin to time-minimizing grazers that prioritize high energy gain within shorter handling times (Bergman et al., 2001a; Hazen et al., 2015), they also demonstrate a preference for energy efficiency. This is exemplified by the foraging behaviors of wood bison, which balance residence time and patch quality for efficient energy utilization (Bergman et al., 2001). The novelty of our study lies in illustrating that grazers' foraging strategies encompass not only a preference for harvest rate efficiency but also for optimizing energy expenditure.

The observed as the harvest rate increase a more pronounced decrease in energy expenditure in larger herbivores compared to smaller ones (Fig. 3). Despite the lack of significant size-related differences in harvest rates among grazers, larger sheep demonstrate notably higher energy consumption during foraging than their smaller counterparts, ODBA does not directly measure variation in physiological performance "capacity" but rather the combination of intrinsic physiological constraints and behavioral decisions made in a dynamic environment (Payne et al., 2016), likely due to their overall posture and activity patterns (Chimienti et al., 2020; Halsey et al., 2011). Furthermore, the impact of energy expenditure on harvest rate is markedly greater in larger sheep, implying that smaller sheep exhibit higher foraging efficiency (Fig. 4). This conclusion is drawn from observable differences in harvest rate and energy costs, highlighting behavioral distinctions in foraging efficiency. Although, our study did not delve into physiological aspects such as digestive efficiency in grazers, where higher basal metabolic rates might lead to increased energy consumption and thus reduced foraging efficiency (Nagy, 2005; White et al., 2009). Regarding the differences of biting behaviors in response to resources conditions larger herbivore due to their capacity for larger bite sizes, generally consume more food (Spalinger and Hobbs, 1992; Wilmshurst et al., 2000). However, smaller grazers exhibit a higher relative consumption compared to their larger counterparts in low-biomass grasslands. Smaller animals have shown greater proficiency in maintaining high food intake in environments where resources are limited or dispersed (Fortin, 2006). This efficiency is particularly notable in low productivity or patchy environments, where smaller herbivores can sustain higher food intake levels more effectively than larger herbivores (Fortin, 2006). This finding underscores the adaptive foraging strategies of smaller herbivores in resource-scarce ecosystems.

4.2 The effect of both EE and HR on FCE

In this study, we employed two indicators to assess the FCE of grazers. Our results demonstrate that FCE increases with harvest rate but decreases with energy costs (Fig. 4). Notably, we defined foraging efficiency as the ratio of harvest rate to energy costs, which significantly enhanced the FCE (Fig. 4). Both harvest and energy expenditure are predictive of FCE. Of these, physical activity can cause the greatest variation in the rate of energy expenditure (Wilson et al., 2018). For instance, foraging has been shown to elevate energy consumption in wapiti and moose by 33% and 28-39%, respectively (Karasov, 1992), while an improved harvest rate has been linked to increased body weight gain (Van der Graaf et al., 2005). In addition, our findings reveal that estimating energy costs provides a more comprehensive prediction of FCE across both groups, as opposed to the harvest rate, which only predicts FCE within each group individually (Fig. 4). This suggests that the harvest rate is not directly proportional to energy consumption, pointing to underlying physiological differences in energy expenditure. Our analysis further clarifies that FCE is more influenced by harvest rate in the lamb group compared to the dry ewe group (Fig. 5), in the case of larger sheep. harvest rate contributes to FCE but is offset by the energy expenditure required, leading to a contrasting conclusion in the lamb group. The interaction effects in lambs neutralize the impact, although they do not eliminate the negative effect (Fig. 5). Energy expenditure during foraging includes step-level feeding strategies (Supplementary Fig. 1) and unique fluctuation patterns (gut throughput rate: foraging-runniating), akin to those observed such as the tail-beat oscillations of sharks during swaying, the wing-beat cycle of birds, and the push-off by limbs in terrestrial animals (Gleiss et al., 2011).

Although our controlled experiments enabled us to assess the relationship between harvest and energy expenditure across different-sized animals and their impact on FCE, they did not fully capture the optimization of behavioral strategies during the diffusion process (Benoit et al., 2020; Klarevas-Irby et al., 2021). The grazers may seek more efficient resources to improve their harvest rate or adopt more efficient diffusion strategies, both of which can influence foraging efficiency. Therefore, we hypothesize that grazers in a free-ranging environment may exhibit altered relationships between harvest rate and energy costs, subsequently affecting FCE.

Conclusions

Our study introduces an ecological research framework that links observable foraging behaviors of herbivores to their proficiency in converting resources into energy. The rapid utilization of resources during acquisition is pivotal for optimizing energy conversion efficiency in animals. However, the energy expended in this process inherently restricts the efficiency of resource acquisition. A significant finding of our study is that animals of varying sizes demonstrate distinct differences in energy expenditure and resource acquisition rates. Typically, smaller animals, such as lambs, are more heavily influenced in terms of resource acquisition efficiency, whereas larger animals, like adult sheep, are predominantly affected by energy consumption. This distinction provides a novel approach for inferring the internal physiological states of animals, including foraging behavior and energy transformation, by observing their behavioral patterns. Conclusively, comprehending and forecasting the energy conversion efficiency of terrestrial herbivores is crucial for evaluating their survival and development in ecological habitats. Furthermore, insights into the growth stages of these animals enhance the precision of growth rate assessments.

References

Bai, Y., Wu, J., Clark, C.M., Naeem, S., Pan, Q., Huang, J., Zhang, L., Han, X., 2010. Tradeoffs and thresholds in the effects of nitrogen addition on biodiversity and ecosystem functioning: evidence from inner Mongolia Grasslands. Glob. Change Biol. 16, 358–372.

Bayliss, P., Choquenot, D., 2002. The numerical response: rate of increase and food limitation in herbivores and predators. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 357, 1233–1248. https://doi.org/10.1098/rstb.2002.1124

Belovsky, G.E., 1986. Optimal foraging and community structure: implications for a guild of generalist grassland herbivores. Oecologia 70, 35–52.

Benoit, L., Hewison, A.M., Coulon, A., Debeffe, L., Gremillet, D., Ducros, D., Cargnelutti, B., Chaval, Y., Morellet, N., 2020. Accelerating across the landscape: The energetic costs of natal dispersal in a large herbivore. J. Anim. Ecol. 89, 173–185.

Bergman, C.M., Fryxell, J.M., Gates, C.C., Fortin, D., 2001a. Ungulate foraging strategies: energy maximizing or time minimizing? J. Anim. Ecol. 70, 289–300.

Bergman, C.M., Fryxell, J.M., Gates, C.C., Fortin, D., 2001b. Ungulate foraging strategies: energy maximizing or time minimizing? J. Anim. Ecol. 70, 289–300. https://doi.org/10.1111/j.1365-2656.2001.00496.x

Bonte, D., Van Dyck, H., Bullock, J.M., Coulon, A., Delgado, M., Gibbs, M., Lehouck, V., Matthysen, E., Mustin, K., Saastamoinen, M., Schtickzelle, N., Stevens, V.M., Vandewoestijne, S., Baguette, M., Barton, K., Benton, T.G., Chaput-Bardy, A., Clobert, J., Dytham, C., Hovestadt, T., Meier, C.M., Palmer, S.C.F., Turlure, C., Travis, J.M.J., 2012. Costs of dispersal. Biol. Rev. 87, 290–312. https://doi.org/10.1111/j.1469-185X.2011.00201.x

Brown, J.S., Kotler, B.P., Porter, W.P., 2017. How foraging allometries and resource dynamics could explain Bergmann's rule and the body-size diet relationship in mammals. Oikos 126, oik.03468. https://doi.org/10.1111/oik.03468

Chimienti, M., Desforges, J.-P., Beumer, L.T., Nabe-Nielsen, J., van Beest, F.M., Schmidt, N.M., 2020. Energetics as common currency for integrating high resolution activity patterns into dynamic energy budgetindividual based models. Ecol. Model. 434, 109250. https://doi.org/10.1016/j.ecolmodel.2020.109250 Fagan, W.F., Lewis, M.A., Auger-Methe, M., Avgar, T., Benhamou, S., Breed, G., LaDage, L., Schlagel, U.E., Tang, W., Papastamatiou, Y.P., 2013. Spatial memory and animal movement. Ecol. Lett. 16, 1316–1329.

Fortin, D., 2006. The Allometry of Plant Spacing That Regulates Food Intake Rate in Mammalian Herbivores. Ecology 87, 1861–1866. https://doi.org/10.1890/0012-9658(2006)87[1861:TAOPST]2.0.CO;2

Gleiss, A.C., Wilson, R.P., Shepard, E.L., 2011. Making overall dynamic body acceleration work: on the theory of acceleration as a proxy for energy expenditure. Methods Ecol. Evol. 2, 23–33.

Gregorini, P., Gunter, S.A., Beck, P.A., 2008. Matching plant and animal processes to alter nutrient supply in strip-grazed cattle: Timing of herbage and fasting allocation1. J. Anim. Sci. 86, 1006–1020. https://doi.org/10.2527/jas.2007-0432

Gross, J.E., Zank, C., Hobbs, N.T., Spalinger, D.E., 1995. Movement rules for herbivores in spatially heterogeneous environments: responses to small scale pattern. Landsc. Ecol. 10, 209–217.

Halsey, L.G., Shepard, E.L., Wilson, R.P., 2011. Assessing the development and application of the accelerometry technique for estimating energy expenditure. Comp. Biochem. Physiol. A. Mol. Integr. Physiol. 158, 305–314.

Hazen, E.L., Friedlaender, A.S., Goldbogen, J.A., 2015. Blue whales (Balaenoptera musculus) optimize foraging efficiency by balancing oxygen use and energy gain as a function of prey density. Sci. Adv. 1, e1500469. https://doi.org/10.1126/sciadv.1500469

Hudson, L.N., Isaac, N.J., Reuman, D.C., 2013. The relationship between body mass and field metabolic rate among individual birds and mammals. J. Anim. Ecol. 82, 1009–1020.

Hudson, R., 2018. Body size, energetics, and adaptive radiation, in: Bioenergetics of Wild Herbivores. CRC Press, pp. 1–24.

Illius, A.W., Gordon, I.J., 1992. Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. Oecologia 89, 428–434.

John R., S., Krol, E., 2010. Maximal heat dissipation capacity and hyperthermia risk: neglected key factors in the ecology of endotherms. J. Anim. Ecol. 79, 726–746. https://doi.org/10.1111/j.1365-2656.2010.01689.x

Kamra, D.N., Pawar, M., Singh, B., 2012. Effect of plant secondary metabolites on rumen methanogens and methane emissions by ruminants. Diet. Phytochem. Microbes 351–370.

Karasov, W.H., 1992. Daily energy expenditure and the cost of activity in mammals. Am. Zool. 32, 238–248.

Klarevas-Irby, J.A., Wikelski, M., Farine, D.R., 2021. Efficient movement strategies mitigate the energetic cost of dispersal. Ecol. Lett. 24, 1432–1442. https://doi.org/10.1111/ele.13763

Li, C., Alatengdalai, Xue, S., Tajima, A., Ishikawa, N., 2015. Estimation of herbage intake and digestibility of grazing sheep in Zhenglan Banner of Inner Mongolia by using n-alkanes. Anim. Nutr. 1, 324–328. https://doi.org/10.1016/j.aninu.2015.11.004

McLean, J.A., 1972. On the calculation of heat production from open-circuit calorimetric measurements. Br. J. Nutr. 27, 597–600.

Miwa, M., Oishi, K., Nakagawa, Y., Maeno, H., Anzai, H., Kumagai, H., Okano, K., Tobioka, H., Hirooka, H., 2015. Application of overall dynamic body acceleration as a proxy for estimating the energy expenditure of grazing farm animals: relationship with heart rate. PloS One 10, e0128042.

Mysterud, A., 2006. The concept of overgrazing and its role in management of large herbivores. Wildl. Biol. 12, 129–141.

Nagy, K.A., 2005. Field metabolic rate and body size. J. Exp. Biol. 208, 1621–1625.

Nagy, K.A., Girard, I.A., Brown, T.K., 1999. ENERGETICS OF FREE-RANGING MAMMALS, REP-TILES, AND BIRDS. Annu. Rev. Nutr. 19, 247–277. https://doi.org/10.1146/annurev.nutr.19.1.247

Norberg, R.A., 2021. To minimize foraging time, use high-efficiency, energy-expensive search and capture methods when food is abundant but low-efficiency, low-cost methods during food shortages. Ecol. Evol. 11, 16537–16546.

Oonincx, D.G.A.B., Broekhoven, S. van, Huis, A. van, Loon, J.J.A. van, 2015. Feed Conversion, Survival and Development, and Composition of Four Insect Species on Diets Composed of Food By-Products. PLOS ONE 10, e0144601. https://doi.org/10.1371/journal.pone.0144601

Pyke, G.H., 1984. Optimal foraging theory: a critical review. Annu. Rev. Ecol. Syst. 15, 523–575.

Roehe, R., Dewhurst, R.J., Duthie, C.-A., Rooke, J.A., McKain, N., Ross, D.W., Hyslop, J.J., Waterhouse, A., Freeman, T.C., Watson, M., Wallace, R.J., 2016. Bovine Host Genetic Variation Influences Rumen Microbial Methane Production with Best Selection Criterion for Low Methane Emitting and Efficiently Feed Converting Hosts Based on Metagenomic Gene Abundance. PLOS Genet. 12, e1005846. https://doi.org/10.1371/journal.pgen.1005846

Sanna, F., Re, G.A., Piluzza, G., Campesi, G., Sulas, L., 2019. Forage yield, nutritive value and N-fixation ability of legume based swards are affected by light intensity in a Mediterranean agroforestry system. Agrofor. Syst. 93, 2151–2161.

Shipley, L.A., 2007. The influence of bite size on foraging at larger spatial and temporal scales by mammalian herbivores. Oikos 116, 1964–1974. https://doi.org/10.1111/j.2007.0030-1299.15974.x

Sollenberger, L.E., Agouridis, C.T., Vanzant, E.S., Franzluebbers, A.J., Owens, L.B., 2012. Prescribed grazing on pasturelands.

Spalinger, D.E., Hobbs, N.T., 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. Am. Nat. 140, 325–348.

Speakman, J.R., Chi, Q., Ołdakowski, L., Fu, H., Fletcher, Q.E., Hambly, C., Togo, J., Liu, X., Piertney, S.B., Wang, X., Zhang, L., Redman, P., Wang, L., Tang, G., Li, Y., Cui, J., Thomson, P.J., Wang, Z., Glover, P., Robertson, O.C., Zhang, Y., Wang, D., 2021. Surviving winter on the Qinghai-Tibetan Plateau: Pikas suppress energy demands and exploit yak feces to survive winter. Proc. Natl. Acad. Sci. 118, e2100707118. https://doi.org/10.1073/pnas.2100707118

Speakman, J.R., Król, E., 2010. Maximal heat dissipation capacity and hyperthermia risk: neglected key factors in the ecology of endotherms. J. Anim. Ecol. 79, 726–746. https://doi.org/10.1111/j.1365-2656.2010.01689.x

Stigter, J.D., Van Langevelde, F., 2004. Optimal harvesting in a two-species model under critical depensation: the case of optimal harvesting in semi-arid grazing systems. Ecol. Model. 179, 153–161.

Vallentine, J.F., 2000. Grazing management. Elsevier.

Van der Graaf, A.J., Stahl, J., Bakker, J.P., 2005. Compensatory Growth of Festuca rubra after Grazing: Can Migratory Herbivores Increase Their Own Harvest during Staging? Funct. Ecol. 19, 961–969.

Van Dyck, H., Baguette, M., 2005. Dispersal behaviour in fragmented landscapes: Routine or special movements? Basic Appl. Ecol. 6, 535–545. https://doi.org/10.1016/j.baae.2005.03.005

Van Soest, P.J., 2018. Nutritional ecology of the ruminant. Cornell university press.

Van Soest, P.J., 1996. Allometry and ecology of feeding behavior and digestive capacity in herbivores: a review. Zoo Biol. Publ. Affil. Am. Zoo Aquar. Assoc. 15, 455–479.

Venter, J.A., Vermeulen, M.M., Brooke, C.F., 2019. Feeding ecology of large browsing and grazing herbivores. Ecol. Brows. Grazing II 127–153.

Wang, J., Bell, M., Liu, X., Liu, G., 2020. Machine-learning techniques can enhance dairy cow estrus detection using location and acceleration data. Animals 10, 1160.

White, C.R., Blackburn, T.M., Seymour, R.S., 2009. Phylogenetically informed analysis of the allometry of mammalian basal metabolic rate supports neither geometric nor quarter-power scaling. Evolution 63, 2658–2667.

Williams, T.M., Wolfe, L., Davis, T., Kendall, T., Richter, B., Wang, Y., Bryce, C., Elkaim, G.H., Wilmers, C.C., 2014. Instantaneous energetics of puma kills reveal advantage of felid sneak attacks. Science 346, 81–85. https://doi.org/10.1126/science.1254885

Wilmshurst, J.F., Fryxell, J.M., Bergman, C.M., 2000. The allometry of patch selection in ruminants. Proc. R. Soc. Lond. B Biol. Sci. 267, 345–349. https://doi.org/10.1098/rspb.2000.1007

Wilson, R.P., Neate, A., Holton, M.D., Shepard, E.L.C., Scantlebury, D.M., Lambertucci, S.A., Di Virgilio, A., Crooks, E., Mulvenna, C., Marks, N., 2018. Luck in Food Finding Affects Individual Performance and Population Trajectories. Curr. Biol. 28, 3871-3877.e5. https://doi.org/10.1016/j.cub.2018.10.034

Yu, H., Klaassen, M., 2021. R package for animal behavior classification from accelerometer data—rabc. Ecol. Evol. 11, 12364–12377.

Zubieta, A.S., Marín, A., Savian, J.V., Soares Bolzan, A.M., Rossetto, J., Barreto, M.T., Bindelle, J., Bremm, C., Quishpe, L.V., Valle, S. de F., 2021. Low-intensity, high-frequency grazing positively affects defoliating behavior, nutrient intake and blood indicators of nutrition and stress in sheep. Front. Vet. Sci. 8, 631820.

Data Availability

Source Data will be freely available upon acceptance.

Code Availability

The code will be freely available upon acceptance.

Acknowledgements

This study was financially supported by the National Key R&D Program of China (2021YFD1300503) and the National Natural Science Foundation of China (42203077, 32192462).

Contributions

J.L., Y.R., X.G. and Y.C. conceived the study. X.G., H.Z., Z.Z. and P.L. performed the fieldwork. X.G., Z.Z., T.H. and G.L. analyzed the data. X.G. drafted the paper and all authors approved the final manuscript.

The authors declare no conflict of interest.

Supplementary Information

Supplementary Fig. 1. Confusion matrix plot of between grazing and non-grazing behavior cross-validation results.

Supplementary Fig. 2. Correlation of recorded ODBA in the time window of 1.5 s and 6 s.

Figure legends

Fig. 1. Conceptual framework for the impact of harvest rate (HR) and relative energy expenditure (EE) on feed conversion efficiency (FCE).

(a) To compare herbivores' activity levels using ODBA in three distinct types of grasslands located in Inner Mongolia: meadow steppe, typical steppe, and desert steppe. At each of these sites, we selected sheep equipped

with sensors to monitor their foraging activity. To ensure consistency, we maintained similar grazing densities and body weights across all sites in the designated plots for each grassland treatment. The methodology for calculating ODBA indicators was consistent with that outlined in the main manuscript, specifically in section '2.3 Herbivores Behavior Monitoring'.

(b) The dynamics of HR and EE relative to resource availability. When resources are scarce (represented by a light green color, symbolizing low resource availability), HR decreases due to limited food availability, alongside an increase in EE due to intensified foraging efforts. Conversely, in conditions of resource abundance (illustrated with a deep green color, denoting high resource availability), HR increases with a corresponding decrease in EE, as a result of reduced needs for extensive foraging.

Fig. 2. Grazing Plot Treatments and Herbivore Behavior Monitoring.

(a) Depiction of grazing plot treatments showcasing variations in grazing density and herd composition. (b) Image showcasing the experimental grassland area utilized in the study. (c) Comparative analysis of grazing densities expressed in sheep units (SU) across different treatment plots. (d) Dry ewes and lambs fitted with tri-axis acceleration sensors for behavioral data collection. Grazing plot treatments: LL, light grazing plot with lambs; LM, moderate grazing plot with lambs; LH, heavy grazing plot with lambs; Mix, mixed plot with both lambs and dry ewes; E, ewe grazing plot with dry ewes; *Note:*Grazing densities are standardized to a 50-kg sheep equivalent (SE) for uniformity in measurement.

Fig. 3. Relationships between harvest Rate (HR) and energy Expenditure (EE) in Lamb and Dry Ewe groups.

Fig. 4. Herbivores' FCE in relation to EE (a) and the HR (b).LL, Lambs in the light grazing plots; LM, Lambs in moderate grazing plots; LH, lambs in the heavy grazing plots; Lmix, Lambs in the mixed grazing plots; E, dry ewes in the ewe grazing plots.

Fig. 5 . Predicted effect of HR and EE on FCE. The effects on the Lamb group (a) and Dry ewe group (b).

Figure 1

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Figure 2

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Figure 3

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Figure 4

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Figure 5

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