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Tracking free-ranging sheep to evaluate interrelations between selective grazing, movement patterns and the botanical composition of alpine summer pastures in northern Italy

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Abstract

Extensive sheep pasturing in alpine regions has a long tradition and fulfils numerous sociological, economic and ecological functions. The effects of sheep grazing on the floristic composition and vice versa depend on various factors. Knowledge of potential interrelations is crucial to developing adequate management systems to maintain pasture productivity and its unique biodiversity. The aim of the present study was to discuss the potential interrelations between movement and selective grazing behaviour of free-ranging unherded sheep and the botanical composition of high-altitude mountain pastures in northern Italy. General movement patterns were determined by using GPS tracking. The floristic composition of areas roamed by the sheep was analysed by collecting physical data during the summer of 2022. The energy content of ingested herbage biomass was determined based on faecal samples. Ranging between 2296 and 3015 m above sea level (a.s.l.), the average altitude used by the sheep was 2654 m a.s.l. Correlation analyses showed that the sheep used significantly higher altitudes with increasing temperature and sunshine duration and with decreasing air humidity and rainfall. A clear selective grazing behaviour was revealed, namely a preference for species with better nutritional attributes. *Poa alpina* was the most preferred species, while areas dominated by *Nardus stricta* were avoided. Furthermore, the sheep showed an uphill migration over the season, possibly caused by the delayed start of grassland growth at higher altitudes. Analyses of faecal samples revealed sufficient energy contents, presumably as a result of the targeted selection of nutritious plant species. Future studies should evaluate the feeding value of herbage on offer in order to validate the current results. The study highlights the opportunity of animal tracking in remote areas and provides indications for selective grazing of sheep under conditions of free choice.

Keywords Extensive sheep grazing, GPS tracking, Alps, Pasture management, Energy requirement, Altitudinal use, Alpine plant species, *Nardus stricta*, *Poa alpina*

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Introduction

Sheep husbandry with freely ranged summer pastures in the mountains has a long tradition and historically promoted the establishment of mixed landscapes and highly unique biodiversity, thereby providing important ecological and sociological functions in the alpine region (Bätzing 2021; Garde et al. 2014). Alpine grasslands provide crucial regulating ecosystem services of high economic and social value such as climate regulation, carbon storage, water purification and erosion control (Liu et al. 2022). However, agricultural intensification and rural depopulation put semi-natural alpine grasslands at risk of degradation as an abandonment often leads to a gradual succession of shrubs and trees, resulting in a long-term decrease in biodiversity (Bonari et al. 2017; Bätzing 2021). Abandonment has also been found to promote the formation of soil tension fissures and consequently decreases soil stability (Cislaghi et al. 2019). Maintaining the traditional utilization of extensive pastures in the alpine region is important to the livelihood of rural communities, provides local high-quality products and contributes to the reduction of competition between human-edible food and animal feed (Guggenberger et al. 2014; Dentler et al. 2020).

By trampling, selective grazing, altering soil nutrients and relocating seeds, herbivores create heterogeneous habitat mosaics, prevent succession and thereby facilitate a broad range of plant species, particularly those associated with open habitats (Krahulec et al. 2001; Spatz 1994). Extensively stocked sheep are known to exhibit a patchy spatial use and repeatedly return to preferred areas. Such grouping behaviour as well as locally excessive herbivore densities can have detrimental effects on phytodiversity and pasture productivity (Stadler and Wiedmer 1999; Parnell et al. 2022; Porzig and Sambraus 1991). Strong selectivity for distinct plant species and asymmetrical nutrient transfer towards frequently used areas affect species composition (Boggia and Schneider 2012; Jewell et al. 2007). These patterns depend strongly on pasture management, in particular on the stocking rate (Parnell et al. 2022). In addition, the movement and grazing behaviour of livestock have been found to be also dependent on several other factors, in particular on climatic conditions (Mysterud et al. 2007), spatial experience of the animals (Bailey et al. 1996) and forage availability (Dumont et al. 1998). Even though there are a number of studies dealing with drivers of grazing distribution patterns on extensive rangelands and investigating sustainable pasture use based on stocking rates, herbage quality and possible impacts on the botanical composition, those are mostly experimental set-ups in lower altitudes (Pittarello et al. 2017; Scotton and Crestani 2019), with higher stocking rates

(Austrheim et al. 2008; Parnell et al. 2022) or different animal species (Raynor et al. 2021; Raniolo et al. 2022). However, case studies on very extensively stocked, unherded sheep on large high-altitude alpine pastures (>2500 m a.s.l.) are lacking.

In order to gain sufficient knowledge of potential interrelations between grazing behaviour and botanical composition, it is necessary to investigate the patterns and drivers of movement and selective grazing of sheep. Such data can provide useful information for the development of pasture management systems that are adapted to specific local conditions, to maintain good pasture productivity while protecting valuable alpine grassland ecosystems. Global Positioning Systems (GPS) as a means of tracking animal movement are among the first and most applied technologies used for studying foraging strategies and decision-making processes of livestock. Animal tracking has been proved an effective way to understand interactions between grazers and their resources (Hamidi et al. 2021), which can be beneficial for animal welfare, ecosystem protection and the farmers' workload (Aquilani et al. 2022; Gordon 1995).

For the purpose of this study and to discuss potential interrelations between animal behaviour and botanical composition, the following research questions were identified:

Q1: Are patterns of altitude used by the sheep stable over the season and to which extent are they driven by climatic conditions and/or characteristics of the grassland vegetation?

Q2: Do inventories of the botanical composition indicate a selective grazing behaviour of sheep under conditions of free choice?

Q3: What is the energy content of ingested herbage?

Study area and animals

The present study took place in the Vinschgau Valley ('Val Venosta'), located in the western part of the province of South Tyrol, Italy. Situated in the Southern Alps, the study area is characterized by a mountainous landscape and heterogeneous climate conditions. Hence, different practices of specialized agriculture are performed, depending on climate and altitude level. While the valley lowlands are primarily used for fruit cultivation and viticulture, alpine livestock pasturing is traditionally dominant in the higher altitudes. In 2021, approximately 37,000 sheep were kept in South Tyrol (Auton. province of Bolzano 2021), most of which are kept in the districts of Vinschgau and Meran, which makes the study area a typical region for alpine sheep husbandry. Traditionally, sheep are kept in extensive

production systems, with alpine pasturing during the months of May until September. Alpine pastures cover 14.8% (approx. 110,000 ha) of the land area of South Tyrol (Auton. province of Bolzano 2021).

The study was conducted during summer 2022 (June–August) on alpine pastures of the Langtaufers Valley (46° 51′ 19.1″ N, 10° 40′ 06.5″ E, municipality of Graun) at an altitude level ranging from approx. 2200 to 3000 m above sea level (a.s.l.). The average temperature during the study period of June, July and August was 13.4 °C, measured in the valley at an altitude of 1842 m a.s.l. (Eurac institute 2022). Hence, according to the atmospheric temperature gradient (Roedel and Wagner 2018), corrected average temperatures for the study site ranged from approximately 10.8 °C at 2200 m a.s.l. to 5.6 °C at 3000 m a.s.l. The average precipitation sum in the valley was 78.1 mm per month (Eurac institute 2022). The long-term average temperature for the same 3 months is 10.8 °C at 1842 m a.s.l., and the long-term precipitation sum is 108.2 mm per month (years 1990–020, Eurac institute 2022). Hence, the climatic

conditions during the study period were substantially warmer and drier than the long-term values.

The summer pasture (Fig. 1) comprised roughly 3350 ha, even though explicit borders in the form of fences were not present. The area was grazed for 133 days between 01 May 2022 and 10 September 2022 by several sheep flocks totaling 900 heads of different ages and breeds (main breed “Tiroler Bergschaf”). The majority of ewes were lactating during the study period. Between 19 and 22 June, the animals were collected by the shepherd and actively herded into the back part of the valley. Apart from that, the animals could roam freely across the pastures and were only controlled by the shepherd when they were about to cross the mountain ridge into another valley. There was no other herding intervention.

Methods

Recording and editing of animal movement using GPS collars

A number of sheep with several years of experience in the valley were chosen by the shepherd to be equipped

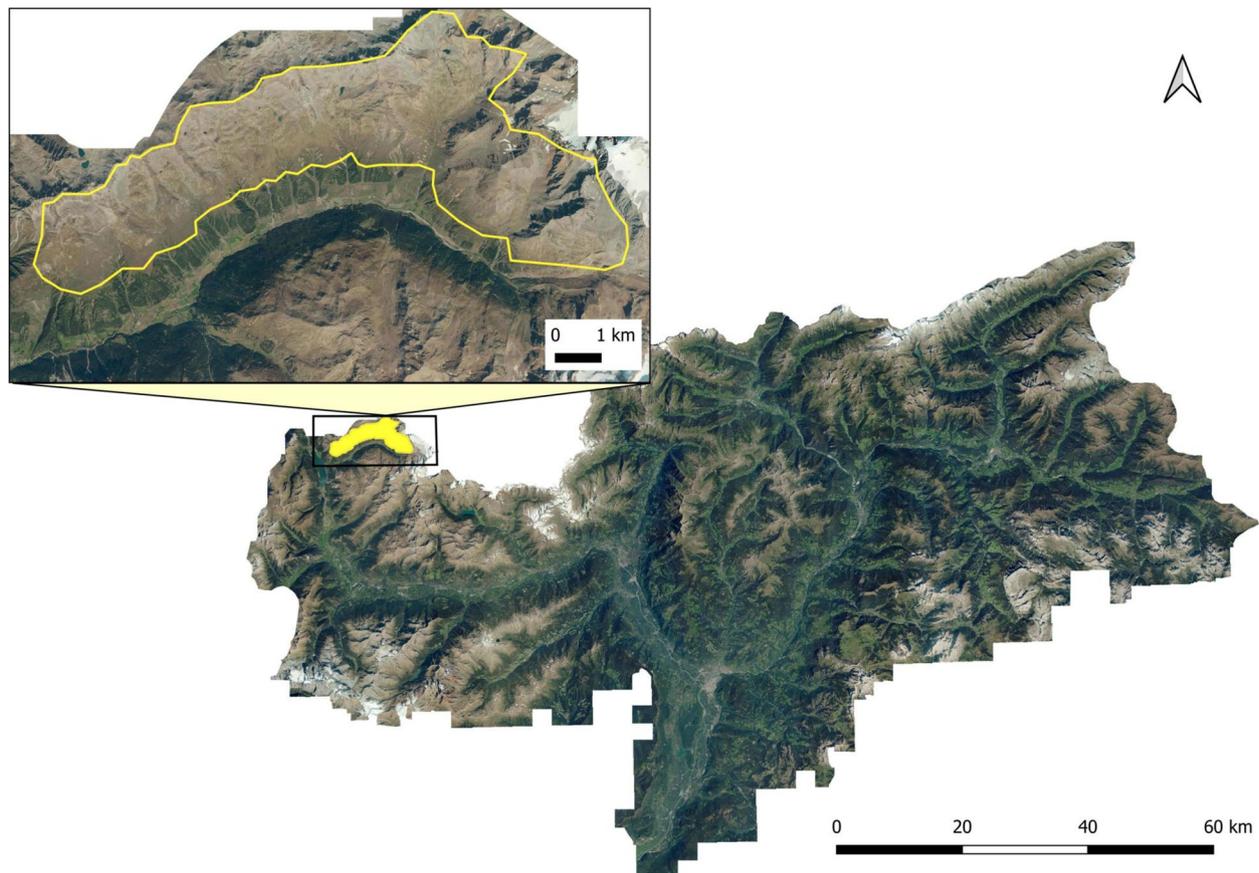


Fig. 1 Map of South Tyrol (northern Italy). The location and approximate extent of the investigated pasturing area in the Langtaufers Valley are highlighted in yellow

with GPS tracking devices, as a means of accurately locating the animals. The trackers were based on a long-distance radio system called 'LikeM13-System' (LikeM13-IoT Solution Provider, Ulrich Stecher). The devices were attached to a collar around the neck of the sheep, similar to bells that are traditionally used in alpine livestock farming. With a weight of 250–280 g, the tracking technique can be considered as non-invasive as it does not influence the sheep's natural behaviour (Hulbert et al. 1998). Besides a GPS module, the devices were endowed with a small solar panel for recharging the battery. Thus, the trackers did not need to be replaced during the study period. The frequency of transmitted positions depended on the battery charge level and consequently on adequate light conditions for the solar panel and varied from 2 to 60 min, with intervals during nighttime usually being wider than during the day. The GPS error of the sensors under optimal conditions was 5 m, although the error depended on satellite constellations and was not reached at all times during the study period.

For the purpose of this study, four of the equipped ewes were selected to be tracked throughout the study period of 3 months (June 1–August 31, 2022). After 1 month, the tracker of one of the chosen animals failed due to battery issues, whereupon another animal of the same flock was used for data collection thereafter. The animals were chosen with attention to their representability, as they belonged to four separate sheep flocks, each totaling around 15–25 heads, and their initial datasets of transmitted positions consisted of at least 8000 data points each. This way, a total of 60,984 initial position records were obtained. The datasets were implemented into the open-source geographic information system software QGIS (version 3.24.3 Tisler), in which clearly visible outliers were omitted manually (meaning locations that were obviously not within reach for the animal by reason of inaccessibility or available time window). The few days with pronounced shepherding activities were neglected as well, as they would have caused falsifications of the natural movement behaviour. Since the shepherding activities did not affect the overall altitude range and pasture area available to the sheep nor their grazing choices, all patterns observed in the present study are consequently attributed to the free-roaming sheep's natural behaviour. The adjusted total dataset comprised 56,666 records from four sheep. Z-coordinates for all data points were derived using a digital terrain model. Base maps and spatial layers were taken from the official 'geobrowser' website, operated by the province of South Tyrol (Auton. province of Bolzano 2022). The used coordinate system was 'ETRS89 – UTM zone 32N'.

Design of the on-site data collection

Besides the analysis of GPS data, three blocks of on-site field data collection were conducted during the study period: 6–12 June, 11–17 July, and 3–10 August. For this purpose, one of the tracked animals, representing a stable group of about 15 individuals, was chosen and the design of the recording sites was stratified according to known areas of sheep activity as retrieved from the GPS positional data of that individual. A recording spot was selected for data collection when the sheep group repeatedly returned to it during the 7 days prior to an on-site data collection block. A repeated return was considered when the group sojourned in the area at least twice. Cases in which the sheep only walked through an area were not considered. A total of 19 spots were selected, 6 in June and August each, and 7 in July. At each site, one transect of 100-m lengths was placed across the area and data was collected every metre within each transect. Figure 2 shows the exact locations of the transects as retrieved from a GNSS device (GPSMAP 64 s, Garmin, USA), the overall areas used by the sheep group during each month and the approx. total available pasturing area. The GPS coordinates, altitude and date of survey for each spot are listed in Table S1.

Vegetation survey

Vegetation surveys for botanical data collection were performed at 1-m intervals along the transects, resulting in 100 measuring points (MP) per transect. For this purpose, the extended sward height was measured using a sward stick (Farruggia et al. 2006) at first contact with the vegetation at every MP. A 2×3 cm big rectangle-shaped window was attached to the end of the stick, through which the vegetation was observed. At each MP, the phenology (vegetative/generative/mixed) and the condition (alive/dead/mixed) of the vegetation were determined. The phenological stages 'generative' or 'vegetative' were assigned to a MP, when more than 90% of the vegetation within the rectangle met the respective criterion. When neither of them was the case, the given attribute was 'mixed'. The approach was the same for the condition with dead and alive representing >90% of dead brown or live green herbage biomass, respectively.

The dry-weight-ranking (DWR) method was used to determine the botanical composition (Mannetje and Haydock 1963). Firstly, the three most dominant species at each of the 100 MP along each transect were identified to the taxonomic rank of species, except for species of the genus *Taraxacum*. Thereafter, they were ranked from 1 to 3 with regard to their approximate contribution to the dry matter yield inside the 2×3 cm rectangle, where the first rank refers to the most dominant species. The DWR method is based upon the assumption that

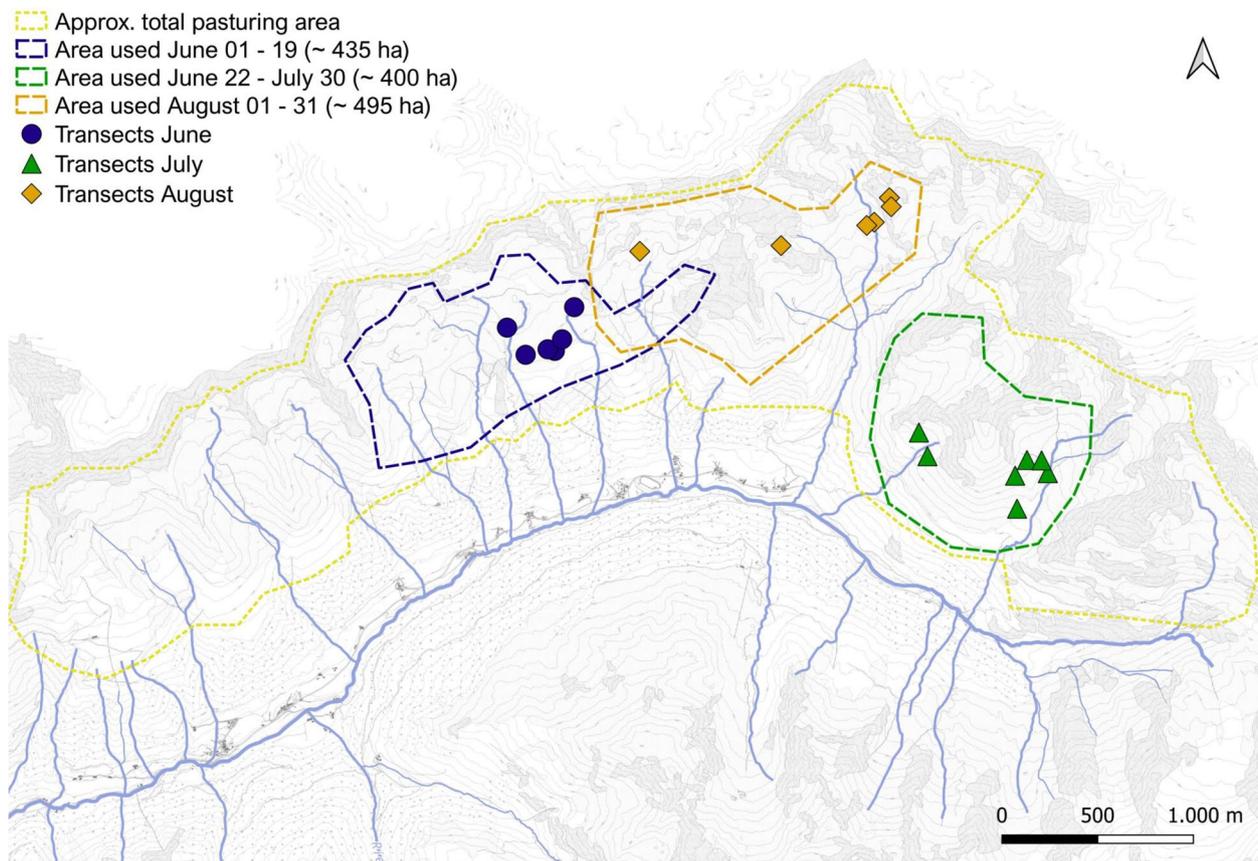


Fig. 2 Pasture areas roamed by the studied group of sheep during the study period and locations of the investigated transects. Extents are indicated approximately. Water courses are depicted in pale blue lines

the first-ranked species contributes a share of 70.2% to the total dry weight, rank 2 contributes 21.1% and rank 3 8.7%. These weighting factors are derived from long-term empirical studies validated on a large gradient of grassland conditions (‘t Mannelje and Haydock 1963). It is used in grassland vegetation analyses as one of the quick-to-implement and easy-to-learn approaches (Obermeyer et al. 2023) with low inter-operator variability (Friedel et al. 1988). Slightly modified weighting factors of 70, 20 and 10 were applied in this study, as Smith and Despain (1991) have validated that this has only marginal effects on the accuracy, while a major advantage is the simpler translation from percentages into the multipliers 7, 2 and 1. When only one or two species were present in the rectangle, the method of *multiple ranks* was applied, which implies the attribution of more than one rank to one species (Smith and Despain 1991). To obtain the botanical composition of the whole transect, the counts of ranks 1, 2 and 3 for each species were summed up separately, the sums were multiplied by 7, 2 and 1, respectively, before the thereby weighted sums of all three ranks were totaled to the group sum of each species. Lastly, the percentages

of contribution were calculated by dividing the weighted value of each species by the sum of all weighted values and multiplying the quotient by 100. The contributions of all species to a transect then equaled 100% (Smith and Despain 1991). The respective functional group (grasses, herbs or legumes) for each species was recorded and ranked accordingly and the same calculation was performed as it was for species.

The attribute ‘open’ was given when a MP contained stone, open soil or moss. In those cases, the previously described procedure was not conducted. For analysing ecological characteristics of the sites, four ecological indicator values (iv) were assigned to each species, which are based on the species’ ecological niches along certain environmental gradients and arranged on scales from 1 to 5 (Landolt 2010). These indicators were namely ‘nutrient iv’, measuring the species’ demand and tolerance of soil nutrients; ‘moisture iv’, referring to the species’ optimal soil moisture content; ‘cutting tolerance iv’, which serves as an indication for the species’ tolerance to mechanical disturbance; and ‘soil reaction iv’, which is closely related to the tolerated soil pH range. Mean

indicator values were attributed to each MP by weighting and averaging the respective indicator values of the three most dominant plant species according to the DWR multipliers 7, 2 and 1.

Additionally, in July and August, each of the 100 MP per transect was given one of the attributes 'grazed' or 'non-grazed', as based on visual assessments: When more than 50% of the vegetation within the 2×3 cm rectangle were obviously defoliated by grazing, the MP was given the attribute 'grazed'. Where it was not defoliated, the point was attributed as 'non-grazed'. This way the selection and distinct defoliation within frequently used sites could be assessed with confidence. The first block of fieldwork in June was needed for adequate overview and understanding of the actual on-site conditions, for which reason an attribution of 'grazed' and 'non-grazed' was not yet done at that time. Thereafter, the method for data collection was adjusted, consequently leading to separate analyses of two datasets. The first dataset with 19 transects across all 3 months, hereinafter referred to as 'whole observation period', consisted of 1900 MP, of which 223 contained open soil or stone. The second dataset, including only the data from July and August and referred to as 'selection observation period', comprised 1300 MP, of which 163 contained stone or open soil. This way, a total of 449 grazed and 688 non-grazed MP were sampled across 13 transects during the selection observation period. After calculating the composition of species and functional groups, as described above, DWRs were also performed separately for grazed and non-grazed MP within each transect of the selection observation period. This way, different botanical compositions were obtained, representing selection decisions made by the sheep.

or UV/VIS spectrophotometer (P) (San System, Skalar, Netherlands). The soil magnesium (Mg) content was determined with the CaCl₂ method using atomic absorption spectrometry (AAnalyst 400, Perkin Elmer Inc, Waltham, USA).

Faecal samples

On the last day of each block of field-data collection, ten randomly chosen faecal samples were taken from the sheep group ($n=30$ samples in total). The samples were taken without the sheep individual being known. Nevertheless, by checking the GPS software on-site, it was ensured that the faeces did originate from the respective group. Only fresh faecal samples based on still visible moisture of the outer surface were chosen. The samples were put into plastic bags and stored at +4 °C for a maximum of 24 h until being transported to the laboratory. After that, the samples were stored at -18 °C. For further processing, the samples were defrosted, dried at 60 °C for 48 h and weighed after each step. To determine the crude ash content, samples were milled to pass through a 1-mm screen, then the dry matter content was determined by drying at 105 °C for 24 h and weighing. Subsequently, the same sample was incinerated at 550 °C for 3 h in a muffle furnace (Nabertherm, Lilienthal). Another subsample was milled to pass through a 0.2-mm screen for total carbon and nitrogen (C/N) analysis using elemental analysis (vario EL cube, Elementar, Langenseibold). Referring to the faecal-nitrogen method by Schmidt et al. (1999), the faecal N content was used as an internal marker to calculate the digestibility and the metabolizable energy content of ingested herbage as a means of estimating the selected energetic feeding value. The following equations were used (Schmidt et al. 1999):

$$\text{DOM} [\%] = 95.90 - \frac{460}{N_{\text{faeces}} \left[\text{g kg}^{-1} \text{OM} \right]} - 0.1582 \text{GD} + 0.00062 \text{GD}^2 \quad (1)$$

$$\text{ME} \left[\text{MJ kg}^{-1} \text{DM} \right] = 0.1520 \text{DOM} [\%] - 0.0029 \text{XA}_{\text{faeces}} \left[\text{g kg}^{-1} \text{DM} \right] - 0.46 \quad (2)$$

Soil samples

To obtain information on the soil chemical composition of the study site, samples of the topsoil layer, down to 10 cm of depth, were taken across each transect (Fig. 2). The 19 soil samples taken in total were slowly dried by the sun for 1 week. The contents of plant available phosphorus (P) and potassium (K) in the soil were determined with the calcium-acetate-lactate (CAL) method in continuous flow analysis coupled to a flame photometer (K)

where *DOM* is the digestibility of organic matter, *ME* is the metabolizable energy, N_{faeces} is the faecal nitrogen content, $\text{XA}_{\text{faeces}}$ is the faecal crude ash, *DM* is the dry matter and *OM* is the organic matter of faeces. The OM was determined after subtracting XA from the faecal dry matter. The *GD* refers to the number of growing season days after April 30, thereby implementing a correction term that improves the accuracy of estimation by considering seasonal fluctuation.

Weather data

Daily information on the following weather parameters during the study period were taken from the 'meteorologist' website, operated by the Eurac Research Institute on Alpine Environment in South Tyrol (Eurac institute 2022): mean temperature, precipitation sum, mean air humidity, sunshine duration sum and mean wind speed. Temperature, air humidity and wind speed were taken from the meteorological station 'Melago Monte Pratzen', located at 2450 m a.s.l., thus being most suitable for representing the altitude level of the study site. Since data on precipitation and sunshine duration is lacking for this station, the station 'Vallelunga Grub', situated at 1842 m a.s.l. (valley bottom), was used for those. Both stations were located directly in the Langtaufers Valley, close to each other and to the study site (< 500 m and 1500 m apart from the study site, respectively). Long-term weather data was taken from the station 'Melago' (1915 m a.s.l.) for the period 1990–2020.

Statistical analyses

All statistical analyses were performed using the R Studio software (version 4.0.2, R Core Team 2020). First, descriptive analyses were carried out using the package 'psych' (Revelle 2022). Diagrams were produced with the 'ggpubr' package (Kassambara 2020). The significance level was set at $p \leq 0.05$ for all statistical tests. For all linear-mixed effects models listed below, data were visually tested for normal distribution of residuals using quantile–quantile plots from the 'car' package (Fox and Weisberg 2019), and for variance homogeneity by plotting residuals versus fitted values and residuals versus each predictor value. All variables expressed in proportions were logit-transformed. Significant main or interaction effects were tested post hoc for differences between means using the package 'emmeans' (Lenth et al. 2022), with a p -value adjustment according to the Bonferroni multiple testing correction method. Lastly, compact letters for all pairwise comparisons were produced with 'multcomp' package (Hothorn et al. 2008).

GPS data

For assessing the target variable 'altitude used by the sheep', linear-mixed effects models were calculated, using the 'nlme' package (Pinheiro et al. 2020). The model included the fixed effects of month (June, July, August) and daytime (day, night) as well as their interaction and the individual animals served as random effect. According to the observed sheep behaviour, daytime was calculated as the time between 5 a.m. and 10 p.m. (day) and between 10 p.m. and 5 a.m. (night). Variance adjustments were allowed for animal individuals. Subsequently, two-way repeated ANOVAs were calculated from the model.

Vegetational data

Linear-mixed effects models were computed for each outcome variable separately. The functional groups of grasses (G) and herbs (H); proportions of generative (PG), vegetative (PV) and mixed (PM) phenology; proportions of alive (CA) and mixed (CM) conditions; and ecological indicator values of nutrient iv (NIV), moisture iv (MIV), soil reaction iv (RIV) and cutting tolerance iv (CIV) constituted outcome variables. For the functional group 'legumes' and the condition 'dead', no statistical tests were performed, as their proportions were close to zero. Using the dataset of the whole observation period, the first set of models included the fixed main effect of the month (June, July and August) and the random effect of transects. Variance adjustments in the models were allowed for month for the variables H, PG, CA and CM. Data for NIV was log-transformed in order to improve the normal distribution. Subsequently, one-way repeated measures ANOVAs were calculated from the produced models. A second set of models was computed using the dataset of the selection observation period, including the fixed effects of defoliation (grazed and non-grazed) and month (July and August) as well as their interaction, and the random effect of transects. Variance adjustments in the models were allowed for month for the variables H, PV, PG, PM and RIV, and combined variance adjustments were allowed for month and defoliation for the variables G, CA, CM, CIV, MIV and NIV. Data for CIV and MIV were log-transformed for an improved normal distribution. Two-way repeated ANOVAs were calculated subsequently.

Data from faecal samples

Linear-mixed effects models were calculated for assessing the two outcome variables 'digestibility' (DOM) and 'metabolizable energy' (ME). Month was implemented as the fixed effect (June, July, August) and sample number (1–10) served as the random effect. Variance adjustments for the month were allowed for both variables. No transformation of data took place. Subsequently, one-way repeated measures ANOVAs were calculated.

Weather data

Pearson's product-moment correlation tests were applied using the 'rstats' package (R Core Team 2020) to test for linear correlations between mean daily weather variables and mean daily altitude (m a.s.l. day⁻¹). Normality was visually inspected using quantile–quantile plots. All parameters were tested for the absence of correlation with the date (all correlation coefficients $r < 0.15$, all p -values > 0.05). Additionally, all weather parameters were tested pairwise to account for between-variable correlations.

Results

Soil properties

Soil chemical analyses of the sites revealed an average plant available phosphorus content (CAL method) of $0.047 \pm 0.050 \text{ g kg}^{-1}$ (mean \pm SD), a mean potassium content (CAL method) of $0.21 \pm 0.151 \text{ g kg}^{-1}$ and a mean magnesium content (CaCl_2 extraction) of $0.13 \pm 0.097 \text{ g kg}^{-1}$. Due to the siliceous bedrock, the soil reaction is acid with a pH (CaCl_2) of 4.2 ± 0.35 and soil types consisting of silty loam, sand and loamy sand.

GPS tracking results

Ranging between a minimum of 2296 and a maximum of 3015 m a.s.l., the sheep used an average altitude of $2654 \pm 0.46 \text{ m a.s.l.}$ (mean \pm SE). Analysis of variance revealed a significant interaction effect of month and daytime ($F_{2,56659} = 26.76$, $p < 0.0001$): The sheep used increasingly higher altitudes over the season, with the lowest mean altitudes used in June and highest in August (2606 ± 0.68 vs. 2693 ± 0.75 , mean \pm SE) (Fig. 3a). Independently from the month, the sheep used significantly lower altitudes during the day than during the night (2649 ± 0.49 vs. 2703 ± 1.16 , mean \pm SE) (Fig. 3a) as evident from the hourly patterns during the course of a day as well (Fig. 3b).

Vegetation

Whole observation period

The overall proportions of different phenological stages throughout the study period of 3 months were 31.8% generative, 54.9% vegetative and 13.3% mixed vegetation. All three variables were affected by the month (generative: $F_{2,10} = 15.17$, $p = 0.0009$, vegetative: $F_{2,10} = 15.17$, $p = 0.0009$, mixed: $F_{2,10} = 7.31$, $p = 0.0111$): The proportions of generative vegetation were significantly smaller

in June than in July and August, whereas proportions of vegetative herbage were largest in June and lowest in July (Fig. 4a).

The total proportions of conditional stages in the vegetation were 77.5% alive, 1.4% dead and 21.1% mixed herbage. Analyses of variance revealed no significant effect of month on both alive and mixed herbage (Fig. 4b).

Across all 19 transects, a total of 64 species were found, of which the eight most dominant species accounted for two thirds of the estimated yield proportion. On average, each 100 m transect contained 23 ± 1.0 (mean \pm SE) plant species. The mean extended vegetation height was $6.8 \pm 0.6 \text{ cm}$ (mean \pm SE). Out of the 64 species, 19 were grasses, accounting for 55.1% of the estimated yield proportion. The 42 dicotyledonous herb species accounted for 42.2% and three leguminous species for 2.7% of the yield proportion (see Table S2 for species list). No significant effect of the month on the proportions of functional groups was found (Fig. 4c).

An average weighted nutrient iv of 2.5 ± 0.07 (estimated mean \pm SE), a moisture iv of 3.02 ± 0.04 , a cutting tolerance iv of 2.4 ± 0.05 and a soil reaction iv of 2.2 ± 0.04 were found. Nutrient iv, moisture iv and soil reaction iv were significantly affected by the month (nutrient iv: $F_{2,10} = 12.55$, $p = 0.0019$, moisture iv: $F_{2,10} = 7.93$, $p = 0.0086$, soil reaction iv: $F_{2,10} = 31.34$, $p < 0.0001$), all of them following an ascending order from June to August (Fig. 4d). No significant effect of the month on the cutting tolerance iv was found.

Selection observation period

Analyses of variance of the selection observation period revealed a significant interaction effect of defoliation \times month on the proportion of generative vegetation

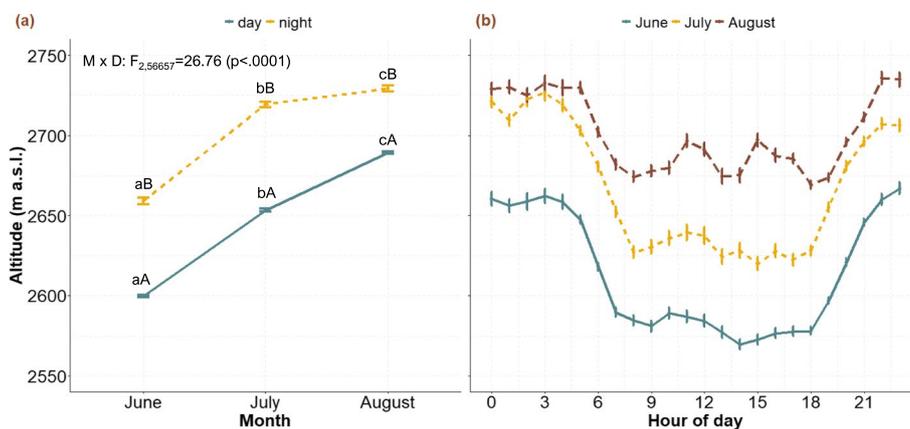


Fig. 3 **a** Mean altitude (m a.s.l.) used per month, as affected by the daytime. Different lowercase letters indicate significant differences of means among months within daytime. Uppercase letters indicate significant differences of means among daytimes within a month ($p < .05$). **b** Mean altitude (m a.s.l.) used per hour of day, as affected by the month. Means \pm standard errors of means (SE) were generated from the raw data

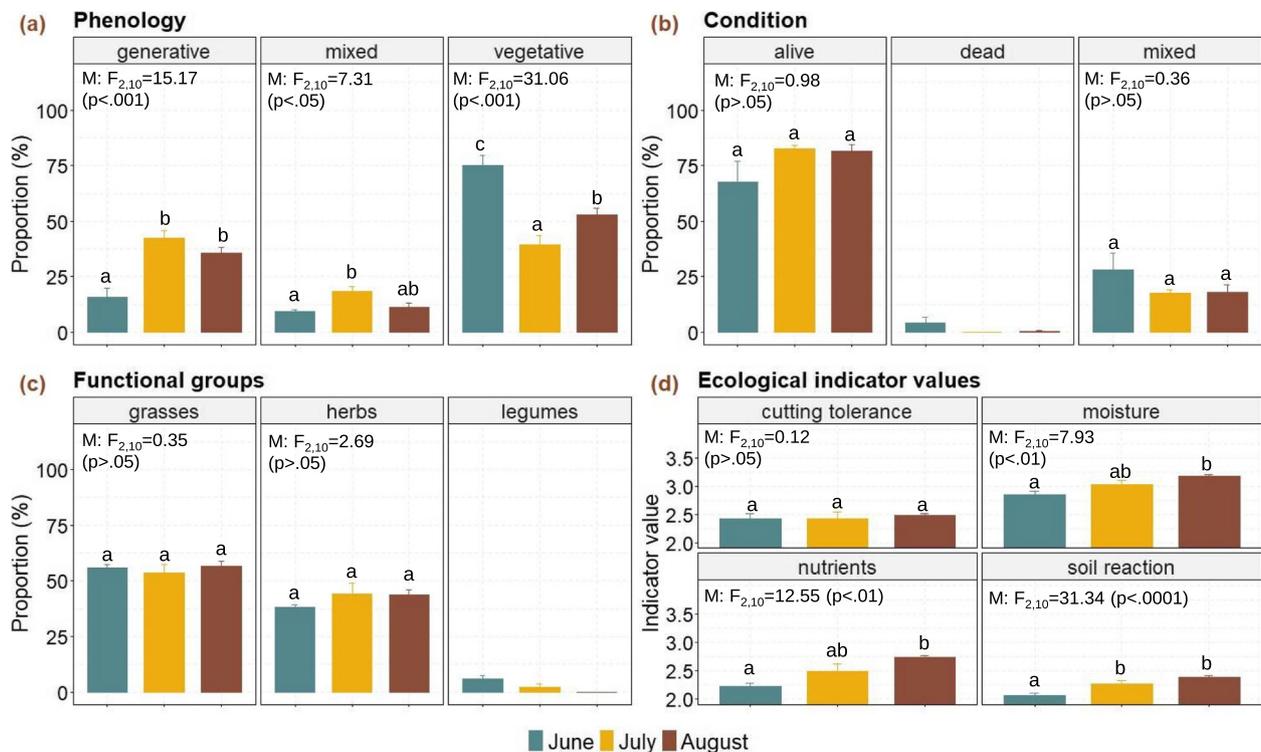


Fig. 4 Mean proportions (%) of **a** phenological and **b** conditional stages as well as of **c** functional groups, and **d** mean indicator values, as affected by the month for the data of the whole observation period. ANOVA outputs of the month's main effect (M) are shown with F-values, degrees of freedom and p -values. Bars represent arithmetic means \pm standard errors of means (SE), as calculated from the raw data. Different lowercase letters indicate significant differences between means among months ($p < .05$)

($F_{1,16}=7.31$, $p=0.0156$): Proportions were significantly larger at non-grazed than at grazed MP, with the effect being stronger in August than in July (Fig. 5a). The proportion of vegetative herbage differed significantly among grazed and non-grazed MP ($F_{1,16}=5.85$, $p=0.0427$), with a significantly larger proportion at grazed than at non-grazed MP (Fig. 5a). Mixed phenology did not differ significantly between grazed and non-grazed MP.

No significant interaction effects were found for the conditional stages, but there was a main effect of defoliation on the proportions of both alive and mixed herbage (alive: $F_{1,16}=56.77$, $p<0.0001$, mixed: $F_{1,16}=56.74$, $p<0.0001$): The proportion of alive biomass was significantly larger at grazed than at non-grazed MP. Significantly smaller proportions of mixed vegetation were found at grazed than at non-grazed MP (Fig. 5b).

Significant interaction effects of defoliation \times month were also found for the proportions of grasses and herbs (grasses: $F_{1,16}=14.32$, $p=0.0016$, herbs: $F_{1,16}=8.66$, $p=0.0096$): The proportions of grasses were generally larger at grazed than at non-grazed MP, although the difference was significant only in August ($75.5 \pm 1.9\%$ vs. $42.1 \pm 3.8\%$, mean \pm SE). In contrast, grazed MP

contained significantly smaller proportions of herbs than non-grazed MP throughout both months (Fig. 5c). Even though no statistical test was applied for legumes, as their overall proportion during the selection observation period was only 1.5%, the proportion at grazed MP was slightly larger than at non-grazed MP (2.7 ± 1.5 vs. 0.3 ± 0.2 , mean \pm SE) (Fig. 5c).

Analyses of variance also revealed a main effect of defoliation on all indicator values (nutrient iv: $F_{1,16}=21.01$, $p=0.0003$, moisture iv: $F_{1,16}=11.45$, $p=0.0038$, cutting tolerance iv: $F_{1,16}=11.37$, $p=0.0039$, soil reaction iv: $F_{1,16}=33.43$, $p<0.0001$), with all values being significantly larger at grazed than at non-grazed MP (Fig. 5d).

The eight most dominant plant species in the botanical survey of the selection observation period accounted for two thirds of the estimated yield proportion (Fig. 6). With an overall proportion of 15.7%, *Nardus stricta* was the most dominant plant species and showed a substantial discrepancy between its contribution to grazed and non-grazed MP (2.2% vs. 25.3%). The contrary was true for the second most dominant species *Poa alpina*, which contributed proportions of 30.7% to grazed and 3.7% to non-grazed MP. *Ligusticum*

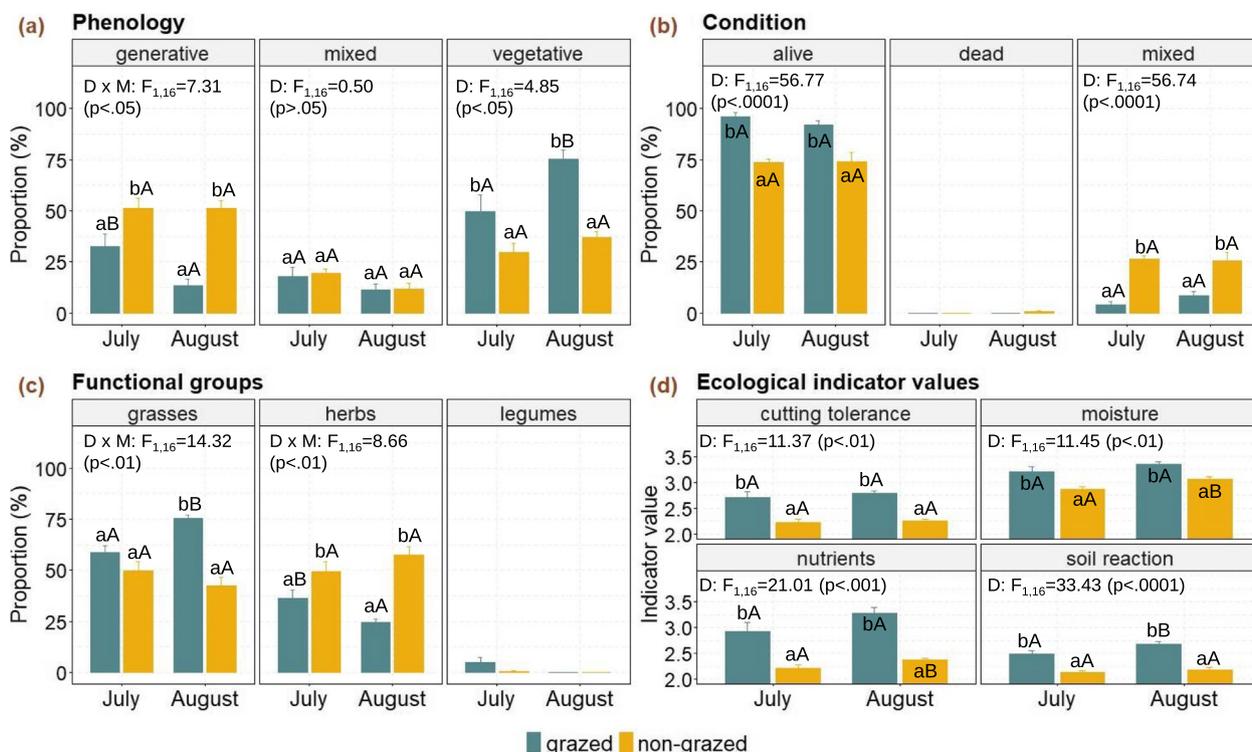


Fig. 5 Mean proportions (%) of **a** phenological and **b** conditional stages as well as of **c** functional groups, and **d** mean indicator values, as affected by the interaction of defoliation and month throughout the selection observation period. ANOVA outputs of interaction effects (D x M) are shown for generative phenology, grasses and herbs, and outputs of the defoliation main effect (D) for all other variables where the interaction was not significant. Indicated are F-values, degrees of freedom and p-values. Bars represent arithmetic means ± standard errors of means (SE) as calculated from the raw data. Different lowercase letters indicate significant differences among means of defoliation within month. Uppercase letters indicate significant differences of means among months within defoliation ($p < .05$)

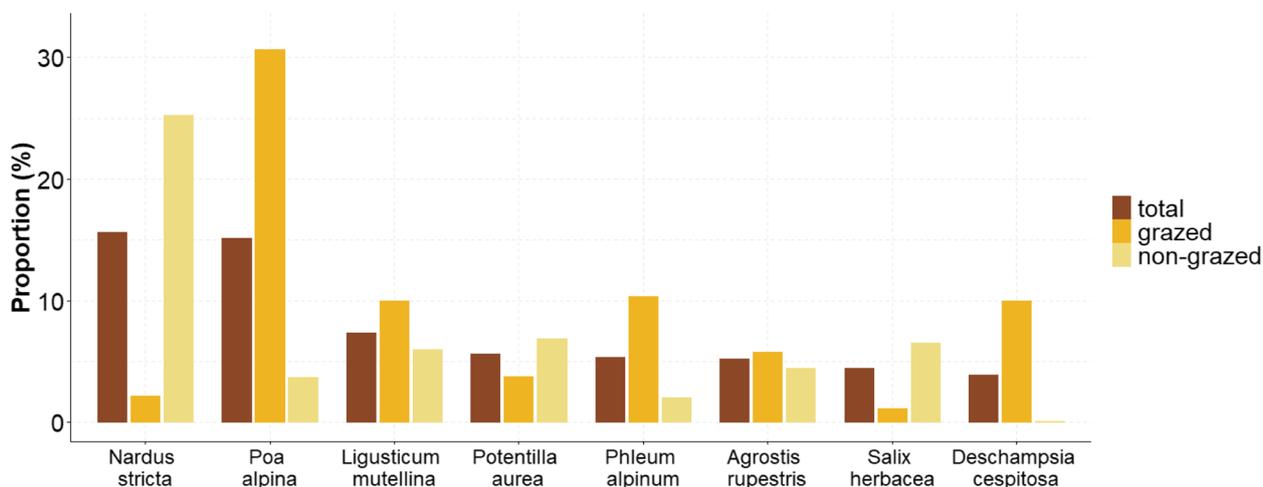


Fig. 6 Mean proportions (%) of the eight most dominant plant species in the botanical survey during the selection observation period. Bars represent arithmetic means of the contribution of each species to the overall botanical composition of the estimated yield proportion as well as to grazed and non-grazed measuring points

mutellina, *Phleum alpinum* and *Deschampsia cespitosa* also showed considerably larger proportions in grazed than in non-grazed MP.

Digestibility and energy content of ingested herbage

The mean DOM throughout the study period of 3 months was $73.3 \pm 0.74\%$ (mean \pm SE). As revealed from the analysis of variance, DOM was significantly affected by the month ($F_{2,18} = 233.09, p < 0.0001$), as faecal samples showed that the diets ingested by sheep in June had a significantly larger DOM than herbage ingested during July and August (Fig. 7a).

The overall mean metabolizable energy was 10.36 ± 0.11 MJ kg^{-1} DM. Similar to the DOM, the ME was significantly affected by the month ($F_{2,18} = 202.93, p < 0.0001$). Herbage ingested by the sheep in June contained significantly more ME than samples from July and August (Fig. 7b).

Correlations of altitude used by the sheep and weather parameters

Moderately positive correlations were revealed between the altitude used by the sheep and both temperature and sunshine duration (Table 1). Moderately negative correlations with the altitude used were found for air humidity as well as precipitation sum (Table 1).

Discussion

Our study goes beyond previous attempts, as it links the animal movement and grazing behaviour to climatic conditions and facets of the grassland vegetation and indicates potential consequences for the botanical composition and for the energy balance of the sheep. A seasonal trajectory of sheep movement towards higher altitudes was shown, as has already been found in other studies (Zanon et al. 2022; Myrsterud et al. 2007). The sheep also showed a clear selective grazing behaviour towards plant species with higher nutritional values.

Weather conditions and vegetation characteristics as possible drivers of movement patterns

With regard to our first research question (Q1), which aimed to understand the interrelations between animal movement, climatic conditions and grassland vegetation on very extensively stocked remote alpine pastures, we found that the mean daily altitude used by the sheep increased significantly with rising air temperature and sunshine duration and decreased with rising air humidity and precipitation. These findings are consistent with related literature (Myrsterud et al. 2007). Usually, exposure to heat and intensive solar radiation prompts sheep to seek out shade (Stafford Smith et al. 1985; Taylor et al. 2011). As located above the tree line, the lack of

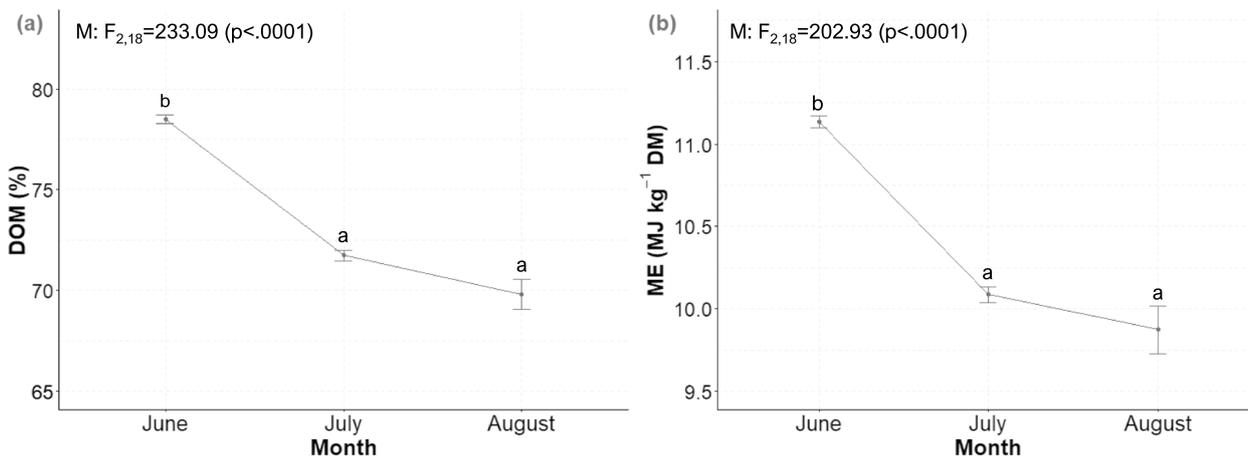


Fig. 7 a Mean DOM (digestibility of organic matter, %) and b mean ME (metabolizable energy, MJ kg^{-1} DM) \pm standard errors of means, as affected by the month. ANOVA outputs of month main effect (M) are shown with F-value, degrees of freedom and p-value. Different lowercase letters indicate differences between the means of months

Table 1 Pearson’s product-moment correlations of selected weather parameters, averaged per day and mean daily altitude (m a.s.l. day^{-1}) used by the sheep across the study period of three months. Indicated are r-value and p-value. Significant coefficients are shown in bold

	Temperature (°C)	Sunshine duration (s)	Wind speed (m/s)	Air humidity (%)	Precipitation sum (mm)
Altitude used by the sheep (m a.s.l. day^{-1})	0.41 ($p < .0001$)	0.39 ($p < .001$)	0.03 ($p = .775$)	-0.42 ($p < .0001$)	-0.35 ($p < .001$)

shade as a strong predictor for animal locations (Parnell et al. 2022) may have caused the sheep in this study to climb high altitudes instead, which provide lower temperatures and cooling wind. The use of higher altitudes may in addition serve as an insect-repelling strategy, as the number of biting insects has been found to decrease with wind speed (Mooring et al. 2003). Ridges and high altitudes were also chosen for bedding sites during the night (Taylor et al. 2011; Mooring et al. 2003), which might also indicate a predator-repelling strategy. The provision of shading options might have prevented the sheep from the upward movement. Further studies are needed in this respect. Furthermore, the sheep used significantly increasing altitudes over the season (June 2606 vs. August 2693 m a.s.l.). This is in line with other studies. The observed pattern of a steep increase between June and July and a flattening from July to August indicates that the altitudes used may have started to decrease again towards the end of the season (Mysterud et al. 2007; Zanon et al. 2022). Although delayed plant phenology and changing plant compositions cause the herbage biomass production and nutritional value of pastures to decline with increasing altitude (Dierschke and Briemle 2008; Gruber et al. 1998), the quality of single plant species has been repeatedly found to increase (Gruber et al. 1998). This seems to be particularly true for *Ligusticum mutellina* (Stählin 1971) (Fig. 6). Thus, the uphill migration of sheep over the growing season is possibly a result of the delayed start of vegetative growth and is in line with the sheep's preferences for young and leafy herbage in early phenological stages (Parnell et al. 2022). The significantly higher proportions of vegetative and alive vegetation at grazed MP, as found in the present study, support this explanation.

The recorded botanical composition is in accordance with a survey on similar altitude and siliceous bedrock by Blank-Pachlatko (2022). Those results underline that the proposed method of recording plant species with the dry weight rank method was an adequate way to characterize the botanical composition. However, the large proportions of *Poa alpina*, *Phleum alpinum* and *Ligusticum mutellina* in most transects (Table S2) do not entirely match the characteristic vegetation types. Instead, they can be assigned partly to *Poion alpinae* (alpine milkweed pasture), a plant community that usually develops under occasional fertilization and associated accumulation of nutrients in the soil (Prunier et al. 2019). The uncontrolled grazing and the oversupply of herbage quantity are assumed to promote a heterogeneous distribution of the sheep flocks and the formation of repeatedly frequented hotspots with associated nutrient carry-over. This is already reflected in the significant difference in all ecological indicators between grazed and non-grazed MP.

While the nutrient indicator at non-grazed MP clearly shows low supply, grazed MP show rather moderate nutrient contents (2.3 ± 0.04 vs. 3.1 ± 0.10 , means \pm SE). The high nutrient indicator values at grazed MP were mainly accounted for by *P. alpina*, *P. alpinum* and *L. mutellina*, which constitute three of the most dominant species in the survey and have a high agronomic value in terms of animal nutrition.

Clear selective grazing behaviour towards high-nutritional plant species

With regard to our second research question (Q2), the botanical composition of grazed MP showed, in accordance with other studies, that the sheep selected plant species of higher herbage quality (e.g. *Poa alpina*, *Phleum alpinum*, *Ligusticum mutellina*) (Bovolenta et al. 2008; Bossi 2022; Schubiger et al. 1998), whereas the poorly digestible and unpalatable *Nardus stricta* was clearly avoided (Kaulfers 2009; Widmer et al. 2020). *P. alpina* contributed about 30% to the estimated yield proportion of grazed MP and was by far the most selected species, which is in line with a previous study (Bowns 1971). The dominant cover of *N. stricta* could provide another explanation for the use of high altitudes by the sheep, as its proportion in the botanical composition has been found to decline with increasing height (Ellenberg and Leuschner 2010). The present study also found that the sheep clearly preferred grasses over herbs, which is consonant with other studies (Hofmann 1989; Pittarello et al. 2017). Moreover, the proportion of grasses at grazed MP increased significantly from July to August (Fig. 5c), whereas the overall proportion of grasses remained constant (Fig. 4c), which indicates an even stronger preference for grasses in August than in July. An explanation could be that the continuous defoliation of grasses, in contrast to dicot species, has been found to promote vegetative regrowth, thus countervailing the seasonal loss in herbage quality and increasing the sheep's preference for grasses over the season (Mysterud et al. 2011).

Do alpine pastures supply sufficient herbage quantity and quality?

Referring to our third research question (Q3), we aimed to evaluate the energy balance of sheep over the season using faecal data. The digestibility of grassland herbage declines over the course of the growing season in lowland (Hopkins 2000) and alpine vegetation (Bovolenta et al. 2008; Schubiger et al. 1998; Kronberg and Malechek 1997). Consequently, successive declines in DOM and ME contents of ingested herbage were observed in the present study (June: 78.5% DOM, 11.13 MJ ME kg⁻¹ DM vs. August: 69.8% DOM, 9.87 MJ ME kg⁻¹ DM). The pastures of the present study were stocked with ewes

and their offspring. Referring to the method by Baker (2004), a total ME requirement of 25.59 MJ day⁻¹ was calculated for a 70-kg model ewe (representing a light to average ‘Tiroler Bergschaf’ ewe) with a milk yield of 2 kg day⁻¹, that walks an average of 5000 m and 450 height metres per day, as based on findings of the present study. These energy requirements are in line with early findings using ewes which had an energy requirement of 25–30 MJ day⁻¹ (Robinson 1980). Given the average ME content of ingested feed of 10.36 MJ kg⁻¹ DM, a herbage dry matter intake of 2.5 kg per day and animal is assumed (Baker 2004). This value is close to the one reported by Luo et al. (2022), who recommended an energy content of 10.52 MJ ME kg⁻¹ DM in their study using ewes with twin lambs. Zanon et al. (2022) estimated an energy content of 7.68 MJ ME kg⁻¹ DM for the pastures of the present study area and assumed a negative energy balance. Other studies support the conclusion that the energy content of extensive alpine pastures is often not sufficient for lactating sheep (Leberl et al. 2012; Guggenberger et al. 2014). However, the results of the present study indicate that the sheep were likely able to ingest herbage with sufficient ME contents. These energy contents, as obtained through the selection of highly nutritious species, are probably higher compared to what is on average available from the pasture (Zanon et al. 2022).

The estimation of the amount of consumed herbage allows an extrapolation into the stocking rate and the sustainability of alpine pasture use. The gross pasture area under consideration had a size of approximately 3350 ha. After subtracting the area that is predominantly covered by bare rock (based on a land cover layer, Auton. province of Bolzano (2022)), approx. 1500 ha of vegetated pasture remains. Given an estimated annual DM yield of 600 kg ha⁻¹ (scaled down after Ellenberg and Leuschner (2010) and Gruber et al. (1998)), approx. 900 tons of herbage yield is available for the sheep across the 1500 ha. Based on the calculated individual mean daily intake of 2.5 kg and a total of 130 grazing days, the herd of 900 sheep uses roughly one third of that amount (300 tons). Thus, the stocking rate on the studied pastures is rather low and an oversupply in terms of herbage quantity is assumed. The potential herbage on offer left aside from grazing can support other ecosystem services benefitting from extensive management or point to the fact that more intensive grazing pressure could be applied thereby promoting livestock performance (Grinnell et al. 2023).

Conclusion

The present study with sheep on large, high-altitude alpine pastures reveals that defoliation was clearly and significantly targeted at plant species with higher

nutritive value, pointing at distinct selection that enables sufficient energy intake. The obtained energy balance exceeded estimations from previous studies and points to the fact that the sheep were most likely able to obtain diets of sufficient quality although they grazed at very high altitudes of up to 3000 m a.s.l. Future studies should include herbage biomass samples to compare ME contents offered against actually ingested herbage. Based on the present study, the 900 sheep consumed potentially only a fraction of the total dry matter herbage available from the pasture. However, little knowledge is available on the actual amount of grassland herbage accumulation at these very high altitudes. The movement towards higher altitudes under warmer conditions and increased exposition to sunshine points to the fact that the provision of shade might reduce energy expenditure for climbing and cause sheep to stay at lower altitudes.

Supplementary Information

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Additional file 1.

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Authors' contributions

MW: data collection, formal analysis, investigation, data curation, writing—original draft, review and editing. MG: resources, investigation, conceptualization, writing—review and editing. TZ: conceptualization, methodology, writing—review and editing. JI: funding acquisition, conceptualization, methodology, resources, writing—review and editing, supervision. MK: methodology, supervision, conceptualization, writing—review and editing.

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Availability of data and materials

Kindly contact the author for data requests.

Declarations

Consent for publication

All authors have read the final version of this manuscript and agree upon its publication.

Competing interests

The authors declare that they have no competing interests.

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