Quantifying energy dissipation by grazing animals in harsh environments

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Abstract

Grazing systems in harsh environments are common throughout the world, and animal production is the mainstay of the livelihoods of many resource-poor farmers. The energy cost of the various activities involved in the process of harvesting the pasture to transform it into animal product can be estimated through an energy balance. This cost would be the difference between the metabolizable energy intake ($\text{MEI}$) and the energy expenditures for maintenance ($\text{MEM}$), temperature regulation ($\text{METr}$), and the energy for production ($\text{MEp}$). Each of the $\text{ME}$ has its own net energy ($\text{NE}$) and its associated efficiency ($\text{K}$). When $\text{MEI} > \text{MEM + METr + MEp}$, the difference is attributable to the energy dissipated during grazing. The efficiency of converting the energy consumed into animal products depends on the magnitude of the dissipation. The inefficiency is associated with the energy spent in locomotion and the stress produced when there is low availability of energy in the pasture. This paper presents a method to quantify the dissipation of energy by grazing animals by considering it as a function of available energy. Such an understanding is required in order to develop management strategies to increase conversion efficiency.

Keywords: Grazing; Stressful environment; Energy dissipation; Entropy; Animal behavior

1. Introduction

In grazing systems, animal production is obtained, indirectly, from solar energy produced in an abiotic environment. Attributes of the ecotope such as water, light, temperature, and nutrients characterize and determine pasture production that, in turn, governs animal production. Grazing animals harvest the energy from the pasture by concentrating and transforming it into product in a thermodynamically open and dissipative system that is not in equilibrium.

The first law of thermodynamics—which states that energy cannot be created or destroyed but can be converted from one form to another is fundamental to ecosystems analysis and in particular to the analysis of grazing systems. This law is applied in order to describe how much energy is in a food, as well as in the quantification of how much work an animal can do or how much milk or meat it can produce.

On the other hand, the second law of thermodynamics—which states that the entropy increases in the irreversible processes and remains constant in the reversible processes—has been less used to explain the processes which occur in biological systems or in their modeling (Kohn and Boston, 2000). In grazing systems, a direct implication of this law is that not all the energy provided by the pasture is available for carrying out work or for producing milk or meat.

The energy from the pasture that is extracted and concentrated by the grazing animal is not totally available for transformation into animal products. Animals expend energy for metabolic maintenance, temperature regulation (homeothermic), grazing, and production. Each one of these processes has its own heat increment ($\text{HI}$) and their magnitudes depend on the metabolic pathway followed from the metabolite in the feed intake to the product depot. This dissipation of energy corresponds to the negative entropy that is
exchanged with the environment, in an irreversible process. Under free grazing conditions this dissipation has been traditionally lumped into the maintenance requirement. The maintenance requirement of grazing animals, compared to confined ones, has been reported to be from 0% to 100% (see review by Lachica et al., 1997). This increment is associated to extra energy expenditure in physical activities: walking (Di Marco and Aello, 1998) locomotion (Lachica et al., 1997, 1999), and biting rate (Di Marco et al., 1996). Less attention has been given to other extra energy expenditures such as the weather (Armstrong and Robertson, 2000) and other stress producing factors.

The present article describes a way to estimate the energy costs incurred by a grazing animal as it tries to meet its energy demands. These costs include both the energetic cost directly associated with physical activities such as walking, eating and foraging as well as the costs associated with non-physical activities. This measure of energy dissipation associated with grazing is assessed for different animal species, pastures and grazing systems.

2. Materials and methods

In order to calculate the energy cost of grazing for sheep and cattle, different experiments were done and relevant data from a number of previously published studies were compiled and utilized. The data included information on types of grazing systems—rotational and continuous—in different pasture types, in addition to information on the level of stress. The methodology is based on the energy expenditure of an animal when grazing (Cañas and Gastó, 1974). The method consists of balancing the metabolizable energy consumed through grazing (MEI) with the energy expenditures for maintenance (MEm) and production (MEp), and with the energy expended in temperature regulation (MEtr). When MEI > MEm + MEp + MEtr, the difference is attributable to the energy required for grazing (MEgr).

Previously conducted experiments (Cañas and Paladines, 1967; Rojas and Paladines, 1967), with Corriedale sheep under four grazing-pressure treatments in mixed pastures of Phalaris tuberosum and white clover Trifolium repens were re-analyzed to estimate the energy spent by grazing animals. Healthy animals with similar weight and body condition were used in the experiments. The results were obtained in a thermal neutral environment, where the temperature ranged from 8.1°C to 18.5°C (Ensminger and Olentine, 1978). A continuous grazing system was utilized, and the consumption of dry matter was calculated from measurements of total amount of feces produced per animal (for 6 animals) and from a determination of the digestibility of the dry matter consumed. In vitro digestibility was determined weekly in extrusa samples collected through esophageal cannulated animals. Extrusa samples were used to determine the digestibility of the selected diet by the in vitro method (Tilley and Terry, 1963).

Using data from another research program (Hull and Meyer, 1957, 1967; Hull et al., 1961) a comparative energy balance was calculated for sheep and Hereford cattle grazing a pure stand of alfalfa (Medicago sativa) and a mixture of white clover (Trifolium repens) and dactylis (Dactylis glomerata). It was then possible to compare the energy requirement for grazing of these two animal species for two pasture types.

Data from experiments carried out by Salas and Paladines (1988) were also used. In those experiments, Merino sheep grazed mixed pasture composed of Trifolium pratense, Trifolium repens, and Tetroune sp. under two grazing systems, continuous or rotational (the paddocks were grazed for 1d and rested 3d). Organic matter intake was estimated, individually, for 5 animals using measurements of total feces produced per animal and of the in vitro digestibility of the organic matter (assessed from extrusa samples obtained from esophageal cannulated animals). Other response variables measured were grazing time and the weight of adrenal glands. These measurements allowed an assessment to be made of the stress associated with grazing. Analysis of these data enabled the development of hypotheses about the physiological bases of the non-physical component of grazing’s energy requirement.

Cañas and Gastó (1974) proposed that the magnitude of the ME required for grazing depends on the availability of forage per unit area, expressed as the metabolizable energy density per pasture area. This concept requires a measure of the concentration of the energy contained in the pasture per unit of volume. Measuring this is complicated since, in addition to the availability of forage per unit area, the height of the canopy is also needed in order to obtain a real

<table>
<thead>
<tr>
<th>Nomenclature</th>
</tr>
</thead>
<tbody>
<tr>
<td>Y MEgr: (kJ/kg body weight)</td>
</tr>
<tr>
<td>A the value of (Y−B) when X tends to 0</td>
</tr>
<tr>
<td>B the asymptotic value of Y when X tends to +∞</td>
</tr>
<tr>
<td>λ the rate of exchange of Y in relation to X</td>
</tr>
<tr>
<td>X the availability of metabolizable energy per hectare (MJ ME/ha)</td>
</tr>
<tr>
<td>K0 the value of λ when the availability approaches zero MJ/ha</td>
</tr>
<tr>
<td>K1 the exchange rate</td>
</tr>
</tbody>
</table>

### Equation

\[
\left( 1 + \lambda Y NMEI \right) = K1 Y NMEI + K0 + B Y NMEI + A Y NMEI \]

### Approximation

The asymptotic value of Y tends to zero when the availability approaches zero MJ/ha. This increment is associated to extra energy expenditure in physical activities: walking (Di Marco and Aello, 1998) locomotion (Lachica et al., 1997, 1999), and biting rate (Di Marco et al., 1996). Less attention has been given to other extra energy expenditures such as the weather (Armstrong and Robertson, 2000) and other stress producing factors.

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evaluation of the volume of forage per unit area. In the present study, a simpler method is proposed for assessing the energy requirement for grazing. The concentration of energy in the pasture is expressed as the amount of metabolizable energy of the pasture available per unit area. This caloric availability is used as a proxy for the metabolizable energy density of the pasture.

### 3. Results and discussion

#### 3.1. Quantifying the energy requirement for grazing ($ME_{gr}$)

Table 1 shows the estimated mean values of dry matter intake ($DMI$) per animal per day (g/day) and the average daily weight gain for sheep (g/day). In spite of the fact that all the controllable animal factors were maintained as constant as feasible across the treatments and that the coefficient of variation of $DMI$ was around 7%, there was no direct relationship between $DMI$ and weight gain. This is explained by the high variation in the availability of metabolizable energy ($ME$) per hectare, which ranged from 5750 to 15,100MJ ME/ha, in spite of the close digestibility range (78–82%). Consequently, the variation in availability of forage of between 747 and 1901kg of dry matter per hectare seems to constitute the critical factor.

It was thus deduced that, in some treatments, the animals had extra energy expenditure. A direct consequence is a decrease in the availability of metabolizable energy for production. This difference was attributed to the portion of the energy dissipated or exchanged with the environment, what we have termed the $ME_{gr}$.

Fig. 1 shows a graphic representation of the metabolizable energy (kJ) required for grazing per live weight unit (kg), and expressed as a function of the availability of metabolizable energy per hectare (MJ ME/ha).

The equation is of the exponential type:

$$Y = A e^{-\lambda X} + B,$$

where $Y = ME_{gr}$; (kJ/kg body weight), $A$ is the value of $(Y - B)$ when $X$ tends to 0, $B$ the asymptotic value of $Y$ when $X$ tends to $+\infty$, $\lambda$ the rate of exchange of $Y$ in relation to $X$, $X$ the availability of metabolizable energy per hectare (MJ ME/ha).

The exchange rate $\lambda$ decays exponentially with the availability of metabolizable energy in the pasture. This rate is expressed as

$$\lambda(X) = K_0 e^{-K_1 X},$$

where $K_0$ = The value of $\lambda$ when the availability approaches zero MJ/ha, $K_1$ = The exchange rate.

By substituting Eq. (2) in Eq. (1), Eq. (3) is obtained. This equation describes the $ME_{gr}$ in relation to the availability of metabolizable energy in the pasture, per

![Fig. 1. Functional relationship between the $ME_{gr}$ and the available energy for Corriedale sheep grazing on mixed Phalaris tuberosum and Trifolium repens pastures.](image-url)
hectare:

\[ Y = A e^{(-K_0 e^{(K_1 * x)})} + B. \]  

(3)

Using Eq. (3) with the data, the following parameters were obtained using the marquart procedure of SAS: \( A = 108.78 \pm 13.92 \) (kJ ME/kg BW), \( K_0 = 1.13 \times 10^{-2} + 9.31 \times 10^{-3} \) (per MJ/ha), \( K_1 = 3.89 \times 10^{-4} + 0.76 \times 10^{-4} \) (MJ/ha), \( B = 33.47 \pm 6.53 \) (kJ ME/kg BW).

As a result, the equation that makes the most biological sense, and that best describes the data is

\[
ME_{gr}(\text{kJ ME/kg BW}) = 33.47 + 108.78 \\
\times e^{(-1.13 \times 10^{-2} \times e^{1.89 \times 10^{-4} \times 100(MJ \text{ 1 ha})})} \\
R^2 = 0.97.
\]  

(4)

In the biological interpretation of Eq. (4) it is proposed that, when the availability of \( ME \) is very small (values approaching 0), the \( ME_{gr} \) remains approximately constant (with a left asymptotic value of 142 kJ/kg BW). For an energy availability of less than 11,534 MJ/ha, the exchange rate is \( 1.13 \times 10^{-2} \) per unitary increase in available energy (MJ/ha). When energy availability falls within the range of 11,534–18,000 MJ/ha, the change rate is \( 3.89 \times 10^{-4} \) per unit of increase in available energy. For values of availability greater than 18,000 MJ/ha (1507 kg DM/ha, under the conditions found in the experiment), the \( ME_{gr} \) tends to be constant (right asymptotic). That is, the energy requirement for grazing becomes constant and parallel to the \( x \)-axis, with a value of 33.5 kJ per kg of body weight.

In addition, the constant value \( A + B \) represents the maximum amount of energy the animal exchanges with its environment. The component \( B \) seems to be associated with physical work, attributable to physical activity during grazing. The value of 33.5 kJ/kg BW is valid when considering flat land. This quantity represents an approximate 12% of the \( ME_m \). Similar figures for locomotion were reported for free ranging sheep (Blaxter, 1964) and goats (Lachica et al., 1997). If the topography of the land under grazing is irregular (hilly), the asymptotic value of 33.5 may be increased. The component \( A \) is thus an additional source of energy dissipation during grazing. We propose to relate this energy dissipation to the stress produced by low forage availability. When the availability of \( ME \) is less than 7000 MJ ME/ha, the total dissipation of energy reaches its highest value, which tends to be constant. Even though we are pooling \( A \) and \( B \) into what we termed \( ME_{gr} \), it is probable that the efficiencies (\( K_A \) and \( K_B \)) would differ. It is worth mentioning that, in this work, it is proposed that for a particular animal specie when \( B \) increases due to the topography of the land, the value of the term \( A + B \) remains constant.

It can thus be inferred that the grazing system studied could maximize the animal product only when the energy availability in the pasture is equal to, or greater than, 18,000 MJ/ha. Lower energy availabilities produce an increase in the energy dissipation of the system. In order to return to the level of order required, there is a need to introduce exogenous energy, in the form of feed supplementation.

3.2. The type of animal effect

Fig. 2 shows a graphic comparison of the energy requirements of different species. In general, it can be observed that the shape of the response is broadly similar for all species, although the values are different. The shifts are due to particular attributes of each species, some of which are addressed below.

Cattle and sheep. Comparing the \( ME_{gr} \) of sheep and cattle, grazing the same pasture, it was found that the Hereford cattle had a \( ME_{gr} \) 1.4 and 1.6 times greater than that of Corriedale sheep for the legume and grass pastures, respectively. Therefore, although the shape of the curves is similar for both species, the cattle response is shifted upwards. This means that, for the same energy availability, the \( ME_{gr} \) is increased by a factor of approximately 1.5 (Table 2).

Pigs. Using data from Cañas (1999), an \( ME_{gr} \) was estimated for pigs (Landrace and Large White crosses), with body weights \( (BW) \) of 60 kg, that were scavenging on Jerusalem artichoke (Helianthus tuberosum). The energy availability of the tuber alone was 88,000 MJ ME/ha and the \( ME_{gr} \) 64.4 kJ/kg of live weight. This number is greater than the right asymptotic value obtained for Corriedale sheep (33.5 kJ/kg) at the same availability of \( ME \). This value is also larger than that estimated for Hereford cattle (50.2 kJ/kg live weight).

Alpacas. Arce et al. (1994) applied the energy requirement equation developed for grazing Corriedale

![](image-url)

Fig. 2. Theoretical curves for \( ME_{gr} \) as a function of available energy for different animal species.
sheep to a simulation model that considered alpacas grazing in mixed grasslands in the South American Altiplano. The validation of the model indicates that the developed equation would overestimate $ME_{gr}$. This overestimation indicates that the equation that should be used for alpacas might require a factor of less than one. This holds true if the response is parallel to that of Corriedale sheep, as was shown for Hereford.

The original hypothesis was that if the $ME_{gr}$ was expressed as units of BW (kg) we could arrive at a general equation suitable for several animal species. We found that while the shape of the function seems to be similar, the equations (the parameters describing the functions) are different, regardless of anatomical similarities.

### 3.3. Components of the energy requirement for grazing

It has long been known that grazing animals use more energy than confined animals, due to additional expenditures of energy on activities such as eating and walking for most of the day. Arnold (1981) proposed that the degree of the physical activity undertaken by grazing sheep varies as a function of the conditions of the pasture. Graham (1964), Osuji (1974), Osuji et al. (1975), and Blaxter (1964) indicated that the maintenance requirement of grazing sheep could increase by up to 18%. Langlands et al. (1963) proposed that this value can reach as high as 25%, and Van Hes (1974) proposed that grazing dairy cows could increase their maintenance requirement by up to 12%. All these data are obtained assuming that the energy expenditure of walking on flat land is from 2 to 2.5 J per kg of live weight per meter traveled, a value that can increase to 28 J/kg/m in hilly land. This implies that the energy requirements of a cow of 500 kg, walking on flat land, could increase by 1 MJ of ME/day. In hilly conditions, this increase could vary from 7.1 to 8.5 MJ of ME/day, which is only a small proportion of the animal’s total energy requirement (Holmes and Wilson, 1984). That is, this animal is expected to increase its energy expenditure up to 75% of the $ME_m$.

Recent studies revisiting this old paradigm have produced more reliable data. Di Marco and Aello (1998) monitoring the CO₂ production of cattle with the $^{14}$C-entry rate technique evaluated the energy cost of walking. They found that steers walking on a level surface increased in 11–41% the energy expenditure as a function of the walking pace (1–4 km/h) when compared to animals at rest. When the animals walked at 2 km/h over a 6% gradient the energy expenditure increased in 39%. In a separate experiment Di Marco et al. (1996) showed that the energy expenditure during grazing was a function of the biting rate which in turn increases as the availability of forage decreases.

Lachica et al. (1997, 1999) combined readings from pedometers and altimeters with calorimetry to estimate energy expenditure by grazing goats. The extra energy cost for locomotion increased up to 47% of the maintenance requirement. The highest values were obtained during the summer and when the animals walked near 13 km. They also showed that the use of tabulated values tend to over estimate the dissipation of energy due to locomotion.

In the experiments with Corriedale sheep reported by Cañas and Paladines (1967) the estimated energy dissipation values ranged from 20% to 90% of $ME_m$. Much larger proportions were found in the analysis of literature data (Table 2). This would indicate that for very low available energy in the pasture, the energy expenditure seems to be higher than the portion attributable only to locomotion. The portion not accounted for is hypothesized to be associated with energy expenditure due to the stress the animals suffer when grazing pastures with low energy availability.

The term ‘stress’ was utilized for the first time by Selye (1936). It refers to an animal’s response to external factors such as cold, heat and, in this case, low

<table>
<thead>
<tr>
<th>Live weight (kg)</th>
<th>Weight gain (kg/day)</th>
<th>$MEI$ (kJ/day)</th>
<th>Energy requirement (kJ ME/day)</th>
<th>$ME_{gr}$ as proportion of:</th>
<th>$ME_{gr}$ per BW (kJ/kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>$ME_m$ (kJ/day)</td>
<td>$ME_p$ (kJ/day)</td>
<td>$ME_{gr}$ (kJ/day)</td>
<td>$MEI$</td>
</tr>
<tr>
<td>Alfalfa</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Young bulls</td>
<td>272</td>
<td>0.755</td>
<td>99,872</td>
<td>36,430</td>
<td>12,824</td>
</tr>
<tr>
<td>Sheep</td>
<td>34</td>
<td>0.155</td>
<td>15,029</td>
<td>7657</td>
<td>2916</td>
</tr>
<tr>
<td>White clover-rye grass</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Young bulls</td>
<td>272</td>
<td>0.800</td>
<td>125,261</td>
<td>36,430</td>
<td>14,079</td>
</tr>
<tr>
<td>Sheep</td>
<td>34</td>
<td>0.141</td>
<td>15,866</td>
<td>7657</td>
<td>2565</td>
</tr>
</tbody>
</table>

$MEI$, metabolizable energy intake.  
$ME_m$, energy requirement for maintenance.  
$ME_p$, metabolizable energy requirement for production.  
$ME_{gr}$, metabolizable energy requirement for grazing.
availability of food. The animal's response involves a process of general adaptation, by which means it avoids the effect of the stressor. In this process of adaptation, the suprarenal cortex plays a very important role. This gland produces catecholamines, which are responsible for increasing the animal's metabolism, and so the animal manages to compensate for the effect of the stress factor.

In experiments by Salas and Paladines (1988), animals that were permanently faced with a scarcity of forage had the heaviest adrenal glands, the greatest proportions of suprarenal cortex within the gland, and the lowest thymus weights. All these factors suggest that these animals were subjected to stress (Table 3). In the low forage availability treatments, a clear lysis of the thymus was observed. Furthermore, frequent acts of aggression were observed in those animals subjected to a continuous grazing regime in which there was a low availability of forage. These animals clearly displayed competitive behavior, in which some animals took on a dominant attitude and others a subordinate one.

It can thus be suggested that grazing, when forage is scarce, results in energy dissipation that is generated by an endocrine effect, and which is associated with a stress causing situation produced by competition for food. This extra expenditure is in addition to the expenditure associated with higher biting rate (Di Marco et al., 1996). It can be stated that, when the availability of forage is high, the energy invested in the MEgr is explained by the muscular work that grazing implies. However, when food becomes scarce, in addition to the greater physical effort the animals have to make, they are subject to a situation of stress that demands a substantial quantity of additional energy. More research is required to further elucidate this matter. If the components A and B of Eq. (3) have different efficiencies of conversion from ME to NE (i.e. $K_A \neq K_B$), then it would not be adequate to pool both components as MEgr.

### 3.4. Effect of the grazing system

As well as having a suprarenal cortex that was of relatively larger proportions, animals in continuous grazing systems were found to have greater energy dissipation than those in rotational grazing systems (Table 3). This could be explained by the greater stress suffered by animals under continuous grazing. Salas and Paladines (1988) observed that animals in continuous grazing systems, with high grazing pressures (as defined by Mott, 1960), exhibited behavior patterns that were different from animals in rotational grazing systems.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Continuous grazing availability</th>
<th>Rotational grazing availability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forage availability (kg DM/ha)</td>
<td>5105</td>
<td>884</td>
</tr>
<tr>
<td>Energy availability (kJ ME/ha)</td>
<td>48,442</td>
<td>8389</td>
</tr>
<tr>
<td>Average animal weight (kg)</td>
<td>41.4</td>
<td>31.2</td>
</tr>
<tr>
<td>Energy consumption (kJ ME)</td>
<td>12,878</td>
<td>13,322</td>
</tr>
<tr>
<td>Weight gain (kg/day)</td>
<td>0.27</td>
<td>0.01</td>
</tr>
<tr>
<td>ME_{gr} (kJ/day)</td>
<td>2326</td>
<td>894</td>
</tr>
<tr>
<td>ME_{gr} (kJ/kg BW)</td>
<td>54.4</td>
<td>272</td>
</tr>
<tr>
<td>ME_{gr} (% ME_{in})</td>
<td>39</td>
<td>176</td>
</tr>
<tr>
<td>ME_{gr} (% ME_{m})</td>
<td>0.041(b)</td>
<td>0.016(c)</td>
</tr>
<tr>
<td>Suprarenal (% empty weight)</td>
<td>0.0052(c)</td>
<td>0.0008(b)</td>
</tr>
<tr>
<td>Suprarenal cortex (% total gland)</td>
<td>53.06(b)</td>
<td>76.4(a)</td>
</tr>
<tr>
<td>Heart (% empty weight)</td>
<td>0.48(c)</td>
<td>0.56(a)</td>
</tr>
<tr>
<td>Liver (% empty weight)</td>
<td>1.95(ab)</td>
<td>1.77(bc)</td>
</tr>
<tr>
<td>Kidneys (% empty weight)</td>
<td>0.31(b)</td>
<td>0.36(a)</td>
</tr>
<tr>
<td>Spleen (% empty weight)</td>
<td>0.19(a)</td>
<td>0.19(a)</td>
</tr>
<tr>
<td>Thymus (% empty weight)</td>
<td>0.016(c)</td>
<td>0.0057(a)</td>
</tr>
<tr>
<td>Suprarenal (% empty weight)</td>
<td>0.0080(b)</td>
<td>0.0035(c)</td>
</tr>
<tr>
<td>Suprarenal cortex (% total gland)</td>
<td>76.4(a)</td>
<td>43.26(b)</td>
</tr>
<tr>
<td>Heart (% empty weight)</td>
<td>0.56(a)</td>
<td>0.50(bc)</td>
</tr>
<tr>
<td>Liver (% empty weight)</td>
<td>1.77(bc)</td>
<td>1.97(a)</td>
</tr>
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<td>Kidneys (% empty weight)</td>
<td>0.36(a)</td>
<td>0.29(b)</td>
</tr>
<tr>
<td>Spleen (% empty weight)</td>
<td>0.19(a)</td>
<td>0.19(a)</td>
</tr>
<tr>
<td>Total observation time (h)</td>
<td>16</td>
<td>16</td>
</tr>
<tr>
<td>Standing w/o eating (h)</td>
<td>4.52(c)</td>
<td>10.31(a)</td>
</tr>
<tr>
<td>Lying down (h)</td>
<td>8.3(a)</td>
<td>3.8(b)</td>
</tr>
<tr>
<td>Shutdown without eating (h)</td>
<td>3.18(a)</td>
<td>1.89(b)</td>
</tr>
<tr>
<td>Grazing (% of the animals)</td>
<td>27.1</td>
<td>61.7</td>
</tr>
<tr>
<td>Organ weights</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Thymus (% empty weight)</td>
<td>0.016(c)</td>
<td>0.0057(a)</td>
</tr>
<tr>
<td>Suprarenal (% empty weight)</td>
<td>0.0080(b)</td>
<td>0.0035(c)</td>
</tr>
<tr>
<td>Suprarenal cortex (% total gland)</td>
<td>76.4(a)</td>
<td>43.26(b)</td>
</tr>
<tr>
<td>Heart (% empty weight)</td>
<td>0.56(a)</td>
<td>0.50(bc)</td>
</tr>
<tr>
<td>Liver (% empty weight)</td>
<td>1.77(bc)</td>
<td>1.97(a)</td>
</tr>
<tr>
<td>Kidneys (% empty weight)</td>
<td>0.36(a)</td>
<td>0.29(b)</td>
</tr>
<tr>
<td>Spleen (% empty weight)</td>
<td>0.19(a)</td>
<td>0.19(a)</td>
</tr>
</tbody>
</table>

Different letters appearing on the same line indicate significant differences ($P<0.05$).

ME_{gr}; metabolizable energy required for grazing; average digestibility = 70% & ruminating time = 4h.
even though the grazing pressure was similar. Animals in the continuous grazing system were constantly moving for more hours of the day, while seeking their food (Table 3). The suprarenal glands of these animals also exhibited a greater mean weight, indicative of a physiological response to the continual stress suffered. It was also reported that, when the availability of forage was less than 400 kg DM/ha, the animals in the rotational grazing system lay down as if they expected to be moved to another site where there was more forage. By contrast, the animals under the continuous grazing system, which had similar forage availability, experienced greater stress and consequently had greater energy dissipation. The results indicate that, under high grazing pressures, the use of rotational grazing has advantages over continuous grazing systems. However, this difference is not observed under low grazing pressures, where there seems to be no advantage inherent in the rotational system.

Thus, rotational grazing is recommended when high grazing pressures are used. Shepherds are usually employed in such a situation. The other option allows for the adaptation of animals to environmental changes. Under the above grazing conditions, it is recommended that animals that exhibit the lowest symptoms of stress be selected for breeding. This recommendation is based on the hypothesis that the behavioral response to stress might be heritable and that habituation does not occur with regard to this effect. Thus, a modification of the pattern asserted as a reaction to stress could be achieved if selection is carried out on this basis.

With regard to this fact, farmers living in stress causing environments traditionally select their animals based on the production achieved under these environmental conditions. As a result, it is evident that in conditions of low forage availability, as is the case in the South American Altiplano or in the high plateau area of Tibet, centuries of selection has resulted in animals well-adapted to such conditions. The aim of farmers was to select animals that perform better and that experience less stress under conditions of low forage availability, rather than to select those that perform better under conditions of maximum forage availability. That is why programs that introduce new breeds have seldom succeeded. Corriedale sheep or Hereford steers, selected for maximum production under conditions of high forage availability, have greater energy dissipation than local breeds of sheep on the Andean Altiplano or Tibetan Yaks.

3.5. Equations for different species

We hypothesize that the relationship describing the change of energy dissipation, as a function of energy availability is unique; however, the parameters of this relationship will depend on the species and on the animal breed. This hypothesis implies that when evaluating animal performance, one should be able to separate architecture from functioning. In our particular case, where the response of different animals could be described with one equation with different parameters implies that the animal species studied presented similar function but different architecture (Fig. 2).

It is assumed that the inflection point of all the species considered share a common tangent line. The distance between the inflection points is, thus, an indication of the ability of a particular animal species to harvest forage at low levels of availability, relative to other species. The column labeled “factor” in Table 4 indicates, with respect to the Corriedale sheep, the relative adaptability of the species considered in this paper. If these assumptions hold true, the derivative of each equation, with respect to the available energy (Fig. 3), shows, for each of the species, the change in energy dissipation that results from stress. It is worth noting that the levels of stress experienced by animal species that have been selected for survival under harsh environments, such as the criollo sheep, yaks or wild boar, are smaller than those of animals selected for better environments more suitable for supporting high animal production.

High producing animals selected under stall-fed or improved pasture conditions will not perform well in grazing systems that have energy availability values below 18,000 MJ ME/ha. Indicators that measure the level of stress should be defined, in order to test the adaptability of crossbred animals to harsh environments.

3.6. Implications for management

Animals grazing grasslands in stressful environments tend to dissipate a high proportion of the energy they
consume, due to the low energy availability. The level of dissipation might be reduced through grassland improvement in a few small areas by means of expensive interventions. An in situ quantification of the level of stress experienced by the grazing species might be an approach useful in developing strategic management systems. For example, rotational or shepherd-guided grazing seems to substantially reduce the level of stress experienced by the animals, and thus the amount of energy dissipated. The use of animals that have been selected to perform satisfactorily under prolonged energy shortages is highly desirable in some environments. Experience and theory indicate that the common practice in some developing countries of introducing high producing breeds in peasant communities is not an effective strategy.

The use of selected animals entails a management dilemma. On one hand, the manager requires animals that perform well in stressful environments, but on the other hand, the number of suitable animal types is limited. The genetic base for selection must be increased, and the selection process should not be carried out with a single objective in mind, as it appears to be now. This calls for the development of indicators, for example, metabolic indicators, that could provide early signals regarding selection potential. This seems to be a pragmatic way of increasing animal productivity under harsh conditions.

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