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A simple model for the effect of thermal stress on the productivity of small ruminants

G. Pardo[a], A. del Prado[a*]

[a]*Basque Centre for Climate Change (BC3), Edificio Sede Nº 1, Planta 1ª, Parque Científico de UPV/EHU, Barrio Sarriena s/n, 48940 Leioa (Bizkaia)*

*Corresponding author: Agustin del Prado. Email: agustin.delprado@bc3research.org

Abstract

Projected climatic changes are expected to change temperature and precipitation patterns and to increase the frequency of extreme events in many regions of the world. This will affect livestock systems through direct effects on animal performance as a result of thermal stress. The purpose of this work is to develop a model that is able to estimate the potential impact of thermal stress on the productivity of small ruminants. To do so, a semi-mechanistic model is proposed, based on an energy balance perspective and the application of the temperature-humidity index (THI) as an indicator of the heat stress severity level. The effect of thermal stress on animal's energy balance is captured by two main mechanisms: i) an increase in energy maintenance requirements and ii) a modification on feed intake. As a result of energy imbalance, the decline on animal productivity is estimated (i.e. milk yield, tissue growth). The different components of the model have been tested against available experimental data, showing that it is able to capture non-linear productivity losses across a range of heat stress conditions and systems. Finally, the applicability of the model is tested with dfifferent examples, and limitations and strengths are discussed. Despite some

constraints, we highlight its relative simplicity and flexibility, so it would be feasible to be integrated into whole farm modelling approaches and/or feed requirement systems for small ruminants. This will help to predict the potential consequences of climate change on productivity, and to explore appropriate adaptation strategies.

Keywords: heat stress, sheep, goats, climate change

Introduction

Among the various consequences that climate change (CC) can induce for small ruminants, impaired productivity caused by heat stress (HS) is a major concern, due to its economic implications (e.g. Al-Dawood, 2017).

Sheep and goats are homeothermic species, but, environmental conditions, such as temperature, humidity and solar radiation, may affect their thermoregulation capabilities. When animals are within the limits of their thermoneutral zone (TNZ), they require keep their body in constant temperature without efforts and they can achieve their optimum production performance (e.g. milk yield, growth rate). However, when exposed to environmental conditions above or below the TNZ, a number of physiological and behavioural responses are triggered in an attempt to adapt to the thermal stress.

Decreased productivity under HS conditions has traditionally been attributed to the feed intake (FI) reduction usually observed in animals exposed to a high thermal load. However, some studies have pointed out that feed intake and production can sometimes have dissimilar responses to HS, indicating that both, direct and indirect (i.e. feed intake) mechanisms could be involved in the productivity reduction associated to HS (e. g. Mahjoubi et al., 2014).

Under HS conditions, feed intake (FI) is often reduced in an attempt to reduce heat production and feed transit through the digestive tract (Marai et al., 2007; Sevi and Caroprese, 2012). In addition, different heat dissipation mechanisms are activated by the animals in order to combat hot environments (e.g. increased respiration rate). All these mechanisms involve an additional consumption of energy. As a result, the dietary energy and the energy efficiency of the animal are significantly altered, which may be behind the decline on productivity in terms of growth rate or milk yield (quantity and/or fat and protein contents) (Abdalla et al., 1993).

Projected climatic changes indicate that the likeliness of HS conditions will increase in many regions of Europe, thus affecting the long-term sustainability of farms. Average temperatures are tending to increase and all scenarios tested using climate model projections indicate this trend will further continue in future decades together with an increased frequency of extreme high temperatures and heat waves across all over Europe (Kovats et al., 2014).

In comparison to other livestock species, small ruminants have features (e.g. thermal tolerance) that can provide them specific advantages when coping with HS. However, they could be particularly vulnerable to CC, as intensive production has prioritised productivity traits over resilience traits in the animals. Moreover, a large share of the production is held in arid areas with already severe climatic conditions that could worsen in the future.

Previous modelling efforts on this topic have focused on describing the interactions among climatic variables and physiological traits of livestock. To do so, a number of mechanistic models have been previously proposed to simulate the heat balance of ruminants under thermal stress conditions (Thompson et al., 2014, Mc Govern et al., 2000; Turnpenny et al., 2000). These kind of approaches are often based on dozens of parameters, which require precise calibration and often limit its applicability.

On the other hand, empirical/statistical modelling approaches (e.g. regression models) are based on direct observation and the use of extensive data records and measurements. Different regression models have been developed relating climatic variables and productivity on small ruminants (Ramon et al., 2016; Finocchiaro et al., 2015) with very contrasting results. Given recording of field data serves other purposes than measuring thermal load effects, many other factors are involved in the determination of the measured traits. As a result, field data contains lots of 'noise' that need to be adjusted using appropriate statistical modelling. Despite of correction for noisy factors, this approach may still yield inaccurate estimates of response (Freitas et al 2006).

As an intermediate approach, in the present work, a semi-mechanistic model is proposed that estimates the effect of thermal stress on sheep and goat productivity (milk yield, growth) following an energy balance approach. The incorporation of this model into whole farm modelling frameworks and/or feeding systems will allow exploring the subsequent effects of weather and site conditions on the productivity of small ruminant systems. Moreover, it will also help identifying appropriate adaptation practices and assess synergies and trade-offs between mitigation and adaptation strategies.

Material and methods

Model description

Approach, inputs and outputs.

The model is conceptualized to be integrated as a sub-model into whole farm models that predict meat (i.e. growth) and/or dairy production, but also into feeding systems usually applied to make energy requirements and/or feed intake calculations.

A number of nutritional requirements standards applicable to small ruminants exists. Among the most extensively used are the Agricultural and Food Research Council (e.g. AFRC, 1995, 1998), the National Research Council (e.g. NRC, 2001), the French National Institute for Agricultural Research (e.g. INRA: Jarrige, 1989) and the Commonwealth Scientific and Industrial Research Organisation (e.g. CSIRO, 2007). All of them share a similar structure based on the calculation of the energy requirements of the animal for the different physiological functions and an estimation of feed intake (FI) and feed value in order to match those energy requirements. In this work, the AFRC (1995) system, which is the default system for IPCC (2019) energy sheep calculations, have been used to calculate energy requirements for maintenance and for milk production or growth. However, other feeding systems would be also applicable.

The typical partitioning of feed energy within animals is schematically described in Figure 1. Intake energy (IE) is the energy ingested per day, and is determined from the feed voluntary intake and the energy density of the feed. As feed is not completely absorbed by the organisms, digestible energy (DE) represents the available portion of IE once energy loss through the faeces is accounted for. Metabolizable energy (ME) is the energy remaining after faecal, gases and urinary energy losses, and represents the energy available for productive functions, such as growth or reproduction, but also for supporting metabolic processes (i.e. maintenance) of an animal, such as activity for obtaining nutrients, respiration or thermoregulation mechanisms.

In the proposed model, two main mechanisms have been considered to capture the effects of thermal stress (Figure 1): the increase in the energy requirements for maintenance (E_m) and the change in the amount of feed intake (FI). Accordingly, the model has two different modules where a set of equations is proposed that relate thermal stress intensity with variation factors (%) that correct the values for both variables respectively.

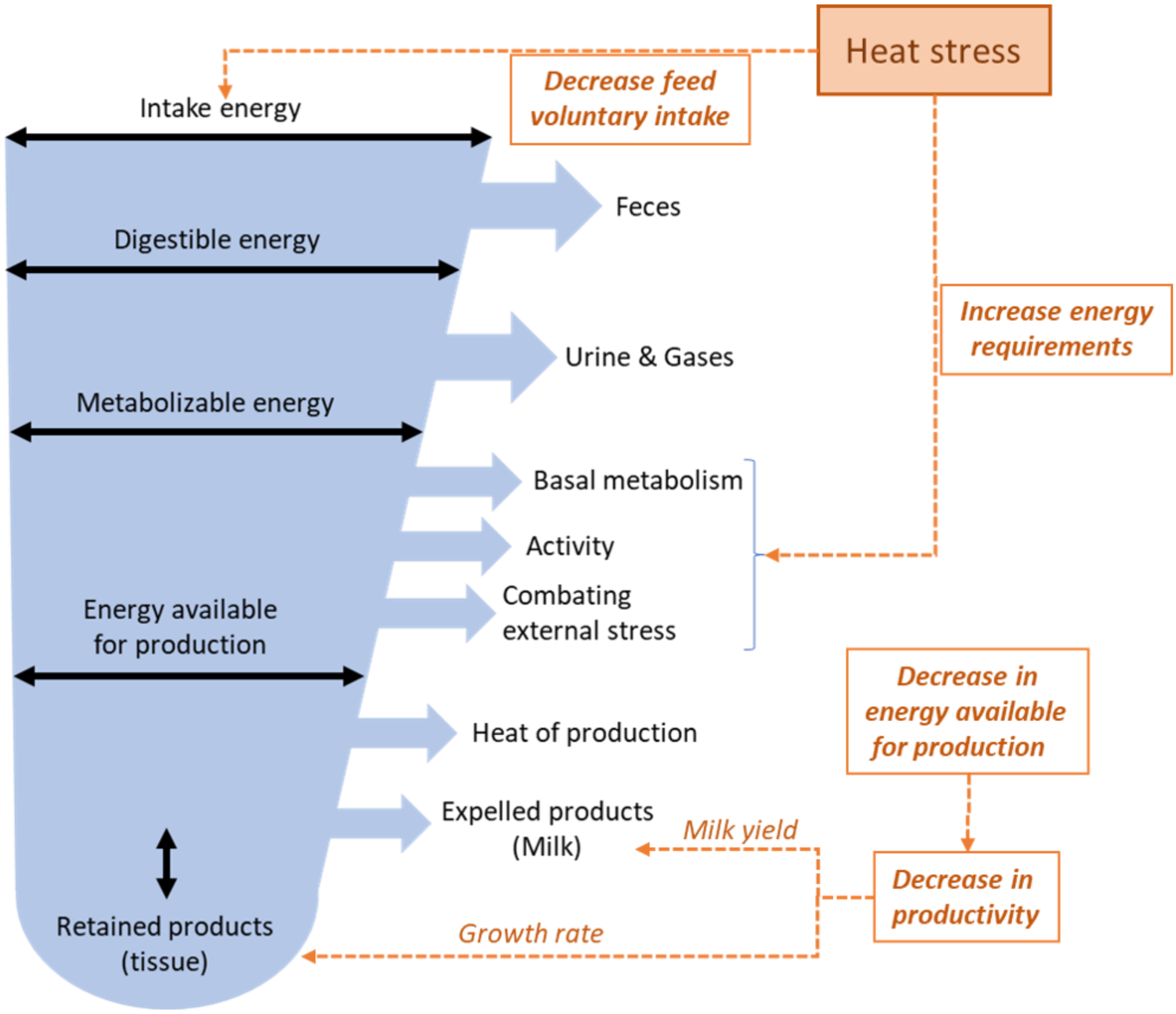

Figure 1 Partition of feed energy within the animal and potential effects of heat stress on the energy balance (Adapted from NRC 1981).

In order to estimate the thermal stress intensity from ambient conditions, the temperature and humidity index (THI) (as defined by Marai et al. 2007) was used as a proxy:

$$THI = (T_{db} - ((0.31 - 0.31 \cdot RH) \cdot (T_{db} - 14.4) \quad (1)$$

where T_{db} is the dry bulb temperature (ºC) and RH is the relative humidity (RH%)/100.

Energy requirements for maintenance: Correction for heat stress (HS)

Under HS conditions energy requirements for maintenance are expected to significantly increase (National Research Council (NRC), 2001)) mainly due to a rise in body temperature and respiration rate (Sevi and Caroprese., 2012).

The magnitude of this increase in energy requirements will depend on the severity of HS, which can be related to the increased energy cost for higher respiration rate (panting) (Hales, 1973). Hence, the type and intensity of panting has been proposed as a proxy to estimate the appropriate adjustment in energy requirements for maintenance according to the subsequent levels of HS (National Research Council (NRC), 1981; Silanikove, 2000).

When the animal is in the first stages of HS, modest panting (i.e. rapid shallow panting) is usually identified. An increase of about 7% in the maintenance requirements has been estimated during this phase. In contrast, severe HS conditions are associated with deep open-mouth panting, which may increase maintenance requirements in the range between 11-25% (NRC, 1981). As a rough approximation, we applied the THI thresholds indicated by Marai et al., (2007) for small ruminants (THI<22.2=absence of HS; 22.2 to <23.3 = mild HS; 23.3 to <25.6 = moderate HS; >25.6 severe HS) to delimit the subsequent HS stages which were related to the energy requirement estimations described from NRC (1981) (Table 1).

Table 1 *Relationship established among heat stress (HS) level, increases estimated for maintenance energy requirements (NRC, 1981, 2001) and THI thresholds for small ruminants proposed by Marai et al. (2007)*

Heat Stress level	Energy requirement increase[1]	THI thresholds for small ruminants[2]
Mild HS	0-7%	22.2-23.3
Moderate HS	7-11%	23.3-25.6
Severe HS	11-25%	25.6-30.0
Extreme HS	>25%	>30.0

[1] Based on NRC (1981) and NRC (2001)

[2] Based on Marai et al., (2007)

In contrast to cold exposure, a non-linear response of energy demands during hot conditions has been suggested (e.g. Ames et al., 1971). The cooling mechanisms of the animal are intensified exponentially with the external hot conditions and body temperature (Silanikove 2000), although other physiological and behavioural responses are also triggered that may partially counteract this effect. This exponential response has mainly been attributed to the effect of temperature in the rate of physiological processes, but also to the decline in the efficiency of evaporative mechanisms. In fact, during the transition from rapid shallow painting stage (moderate HS) to slower deeper breathing (severe HS) a decrease in the thermoregulatory efficiency of sheep have been reported (e.g. Hofman and Riegle, 1977).

Based on these considerations and the estimations from Table 1, an exponential relationship was developed in order to relate the different HS levels, represented through THI thresholds, with the expected increase in energy requirements (Figure S1):

$THI > THI_{HS}$ $VF_{Em(HS)} = 0.5657 \cdot \exp(0.0264 \cdot THI)$ (2)

where $VF_{Em(HS)}$ is the variation factor of energy requirements for maintenance under HS conditions, THI is the temperature-humidity index according to the ambient conditions in the site, and THI_{HS} is the THI threshold considered for HS. Based on that factor, the following equation can be used to adjust the maintenance energy requirements of small ruminants according to HS conditions:

$E_{m(HS)} = E_{m(TN)} \cdot VF_{Em(HS)}$ (3)

where $E_{m(TN)}$ (MJ/day) is the metabolizable energy (ME) required for maintenance estimated at thermoneutral conditions (TN) and $E_{m(HS)}$ (MJ/day) is the ME required for maintenance corrected for HS conditions.

Energy requirements for maintenance: Correction for cold stress (CS)

Two main factors determining the rate of heat loss, (and consequently the change in energy requirements for maintenance) can be pointed out in small ruminants: i) the thermal gradient between body core temperature and external ambient temperature, and ii) the insulation provided by the tissue, wool or hair of the animal.

Based on these two factors, the following linear equation can be used to estimate the effect of cold conditions on the maintenance energy requirements of small ruminants (based on NRC, 1981):

$$E_{m(CS)} = E_{m(TN)} + b \cdot \Delta T / I \qquad (4)$$

where $E_{m(CS)}$ (MJ/day) is the ME for maintenance corrected for cold stress (CS) conditions, $E_{m(TN)}$ (MJ/day) is the ME requirements for maintenance without thermal stress, ΔT (ºC) is the thermal gradient between animal's CS temperature threshold and ambient temperature, I (ºC·m^2·day/MJ) represents the total insulation provided by the hair or wool, and b (m^2) is the body surface area of the animal.

For estimating body surface area, the equation proposed by Bennett, (1973) can be applied:

$b = 0.094 \cdot BW^{0.67}$ (5)

According to Blaxter et al., (1959) wool insulation capacity is about 1.67 ºC·m^2·day /MJ per cm depth. Total insulation can be inferred from that coefficient and the estimated fleece depth (cm). As a result, insulation provided depending on fleece depth can have a significant effect on the energy requirements for maintenance under CS conditions, as shown in Figure S2.

Feed intake (FI)

Heat-stressed animals decrease FI in an attempt to reduce heat production, coming mainly from tissue metabolism but also from feed fermentation in the digestive tract, which is an important source of heat in ruminant animals (Kadzere et al., 2002). Although a number of studies have shown FI to decrease in ruminants under exposure to hot conditions, values for prediction of the interactions among temperature and FI for sheep and goats are limited, thus making it difficult to establish quantitative definitions of HS effects on that basis.

NRC (1981) developed some relationships for cattle describing the response on FI increase or decrease with Temperature (in comfort zone FI=100%). This work also suggest that the change in FI for small ruminants under thermal stress would follow a similar trend than in cattle (NRC, 1981).. For our purpose, equations relating temperature (ºC) and FI for lactating (dairy systems) and fattening cows (beef systems) were extracted from NRC (1981) using WebPlotDigitizer 4.2 (Rohatgi, 2019) and adapted for suggested CS and HS thresholds of small ruminants (Figure S3). To do so the extracted equations were modified by converting temperature into THI (assuming relative humidity of 50%), and then the TNZ was adjusted so it coincided with THI thresholds for CS (THI_{CS}<11.5) and for HS (THI_{HS}>22.2) according to small ruminants' literature (Ames and Brink, 1977; NRC, 1981, Marai et al., 2007). As a result, the following polynomial relationships were developed capturing the effect of thermal stress (HS or CS) on FI for dairy and meat production systems:

For dairy systems (lactating animals):

If $THI>THI_{HS}$: $VF_{FI(HS)} = -0.0018\cdot(THI - THI_{HS})^2 + 0.0014\cdot(THI - THI_{HS}) + 1.0017$ (5a)

If $THI<THI_{CS}$: $VF_{FI(CS)} = 0.0010\cdot(THI - THI_{CS})^2 - 0.0036\cdot(THI - THI_{CS}) + 1.0061$ (5b)

For meat systems (fattening animals):

If $THI>THI_{HS}$: $VF_{FI(HS)} = -0.0033\cdot(THI - THI_{HS})^2 + 0.0051\cdot(THI - THI_{HS}) + 0.9933$ (5c)

If $THI<THI_{CS}$: $VF_{FI(CS)} = 0.0001\cdot(THI - THI_{CS})^2 - 0.0039\cdot(THI - THI_{CS}) + 1.0099$ (5d)

where $VF_{FI(HS\ or\ CS)}$ is the variation factor for feed intake (FI) under HS or CS conditions (which values 1 under TN conditions), THI is the temperature-humidity index at the climatic conditions in the site and $THI_{(HS\ or\ CS)}$ is the temperature-humidity index thresholds of small ruminants for HS or CS respectively. Based on that factor, the following equation can be used to correct the effect of hot or cold conditions on the feed intake:

$FI_{(HS\ or\ CS)} = FI_{(TN)} * VF_{FI\ (HS\ or\ CS)}$ (6)

where $FI_{(TN)}$ (kg DM/day) is the daily feed intake estimated at thermoneutral conditions and $FI_{(HS\ or\ CS)}$ (kg DM/day) is the daily feed intake corrected for either HS or CS conditions

Productivity loss through energy balance

Energy is considered the first limiting factor upon the level of animal production achieved by feeding a specific diet (AFRC, 1995). As stated previously, with the aim to capture the effect of thermal stress on animal productivity in a semi-mechanistic manner, the approach described in this work is based on an energy balance, described as:

$E_{FI} = E_m + E_{liveweight\ change} + E_{prod}$ (7)

where E_{FI} is the metabolisable energy (ME) available through the feed intake, E_m is the ME required for maintenance of the animals, $E_{liveweight\ change}$ is the ME available through mobilisation of body reserves and E_{prod} is the ME required for growth or milk production. Under HS conditions, a reduction on the E_{FI} (i.e. feed intake reduction) is expected while an increase is projected on E_m (i.e. energy requirements for cooling mechanisms). As a result, the energy available for growth or milk production (E_{prod}) will be reduced, and consequently the productivity will decline. Following AFRC (1993), energy requirements for milk production or weight gain (E_{prod}) can be estimated through the following equations (analogous formulas exist in other feeding systems):

$E_{prod} = EV_{milk} \cdot Y_{milk}$ (8a) Lactating animals

$E_{prod} = EV_g \cdot \Delta W$ (8b) Growing animals

where EV_{milk} (MJ/kg) is the energy value of the milk, Y_{milk} (kg/day) is the milk yield, EV_g (MJ/kg) is the energy value of the liveweight gain of growing animals and ΔW (kg/day) is the daily liveweight gain.

The EV_g can be defined according to the type of animal and liveweight. Similarly, the EV_{milk} can be estimated from the fat and protein content, and can be even fixed assuming a normalised value of fat- and protein-corrected milk (FPCM). Consequently, in the proposed model, the effects of HS on the energy balance will directly affect milk productivity (Y_{milk}) or weigth gain (ΔW).

For EV_g we applied the equations proposed by AFRC guidelines. For EV_{milk} we used the equation proposed by Pulina et al 2005 (EVmilk = 251.7 + 89.6F + 37.8P). We normalised EV_{milk} to a set content of fat (6.5%) and protein (5.8%), translating milk yield losses into FPCM.

Nevertheless, stress conditions can cause a transient metabolic energy deficit, which will activate an increase in the mobilization of energy stored in body reserves during lactation. In order to capture this effect, based on AFRC guidelines, a function was developed that relates a gradual mobilization of energy through liveweight loss with HS level according to THI:

$$BW_{loss} = BW \cdot 0.0025 \cdot VF_{BW} \quad (9)$$

where BW_{loss} (kg/day) is the daily liveweight loss in sheep or goats due to HS, BW (kg) is the liveweight of the animal (which has a multiplier factor to set a maximum potential of 0.25% BW loss daily), and VF_{BW} is a factor from 0 to 1 that reflects a gradual effect of HS on the potential mobilisation of body reserves (Figure S4).

The maximum potential of 0.25% BW loss daily was extracted from AFRC guidelines based on INRA (1988) indicating a liveweight loss of 1kg/week (143g/day) for dairy goats during the first month of lactation. Considering early lactation stage as the period of maximum body reserves mobilisation, and assuming a BW of 55kg for dairy goats, we rounded 0.25% BW as a reasonable figure for the maximum daily loss for both sheep and goats.

Model validation

The different sub-modules described above were analysed separately by comparing the estimated values with independent datasets from published experiments in literature. The capability of the proposed equations was evaluated based on graphical comparisons and statistical analysis according to the goodness-of-fit of the observed vs predicted data.

A literature search and a selection of studies was carried out based on the following criteria: 1) the trials involved sheep or goats, 2) they analysed performance under thermoneutral (TN) and HS conditions, and 3) the studies provide information at least on one of these parameters: energy for maintenance, feed intake, milk production (lactating animals) or daily weight gain (fattening animals).

As a result, only one study was found indicating the increase of energy requirements for maintenance in small ruminants under HS (Mahjoubi et al 2014), thus limiting the independent validation process of the correspondent module. For feed intake, 14 studies were found (8 dairy and 6 meat systems). Further details are indicated in Supplementary Tables S1 and S2.

The validation of the productivity loss estimated by the model includes the application of the two previous sub-modules. Consequently, it involves an indirect validation of them, as they are applied in the energy balance estimations. To do this validation, we used those studies that provide details of the feed ingredients and composition (i.e. feed energy density), feed intake and decline of milk production (and composition) or daily weight gain, as those details were needed to estimate the effects on the net energy balance. As a consequence, we identified 3 studies for lactating animals (Abdalla et al., 1993; Hamzaoui, 2014; Leibovich et al., 2011) and one for fattening lambs (Ames and Brink 1977). Further details are indicated in Supplementary Tables S3 and S4.

Model test

We used the model to simulate the effect of thermal stress on two case studies: a sheep farming system producing lambs annually located in Aragon (north-eastern

Spain) (rasa-aragonesa breed) and a dairy sheep farm located in Castilla la Mancha (central Spain) (manchega breed).

For meat systems, rasa-aragonesa breed lambs, whose typical liveweight weights at weaning and slaughter are 13.9 kg and 22 kg, respectively, are fully housed and fed with concentrates, and forage after weaning (diet composition in Table 2). We selected weather from specific periods of different years in Zaragoza (Aragon) for simulating: (i) heat stress effect on born-in-May lambs weight gain for the whole period after weaning (summer 2017) and (ii) cold stress effect on born-in-December lambs extreme event (8 days on January 2010).

Table 2. *Diet characteristics for the growing lambs*

FEED	%	GE MJ/kg DM	DE MJ/kg DM	ME MJ/kg DM
Barley	33.6%	18.4	14.8	12.4
Maize	27.3%	18.7	16.1	13.6
Soybean Meal	23.7%	19.7	18.2	13.6
Wheat	6.4%	18.2	15.6	13.1
straw	9.0%	18.2	8	6.5

For dairy, we selected a heat wave extreme event of 7 days (in summer 2015) from Ciudad Real (Castilla la Mancha). Manchega ewes were simulated to be fully housed and were fed with alfalfa hay and corn as shown in Table 3. We tested the model considering (i) no effect of heat stress, (ii) simulated effect of heat stress and (iii) changing diet as a strategy to adapt energy requirements under heat stress conditions (replacing 10% DM of hay in the diet ration with soybean meal). Although calculating GHG emissions is beyond the scope of our study, we included a very simple complementary example to illustrate how the model would work on a heat stress adaptation strategy that could potentially result in a trade-off in climate change mitigation (i.e. increase in GHG emissions). For this, we simulated enteric CH_4

emissions using IPCC (2019) and estimated the C footprint of purchased feed for these days according to (Ecoinvent® 3.01 Database 2013) and calculated emissions as CO_2-e using a GWP of 28 for CH_4 (IPCC, 2013).

Table 3. *Diet characteristics for the manchega lactating ewes*

FEED		GE	DE	ME
	%	MJ/kg DM	MJ/kg DM	MJ/kg DM
Alfalfa hay	90%	18.2	10.6	8.4
Corn	10%	18.7	16.1	13.6

Additionally, we simulated for a Manchega breed dairy sheep, the potential impact of thermal stress (heat and cold) on milk productivity loss and changes in dry matter intake averaged over a whole lactation period. For this scenario, we simulated an ewe's typical lactation curve from Manchega breed lambing in February and milking for 6 months (February-July).

Results

Model validation

Energy requirements for maintenance

At the conditions of that pair-fed trial, the results estimated with the proposed equation (58%) seem in accordance with the values obtained in the study from Mahjoubi et al., (2014) (Figure S5); which suggested an increase by about 66% of energy maintenance costs in growing sheep under extreme severe HS conditions (THI>35).

Feed intake

Model predictions of decline on feed intake for dairy systems agreed reasonably well with measured data (Figures 2 a,b) (r^2=0.83). The slope value (0.64) may indicate that the model tends to overestimate the decline on feed intake under mild HS conditions (underestimation of calculated total FI), while it tends to understimate the decrease of feed intake under harsh conditions (in particular under severe HS).

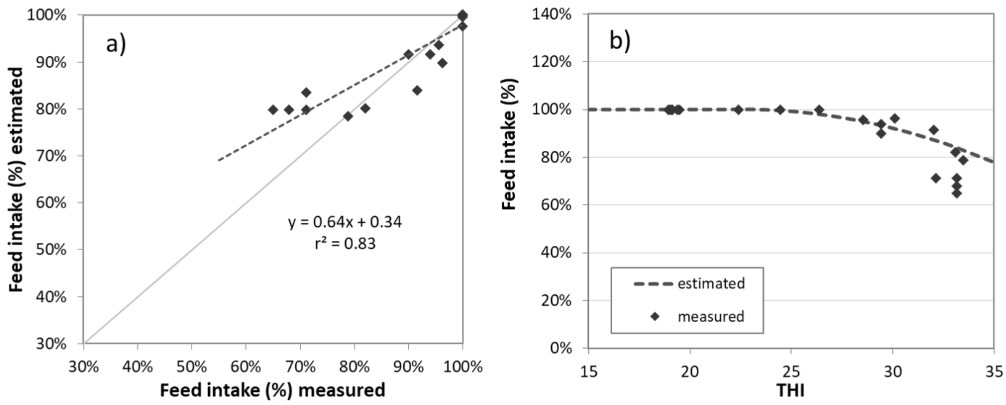

Figure 2 a, b Estimated vs measured reduction of feed intake of dairy sheep and goats under heat stress (Details of dataset in Supplementary Table S1).

For meat systems, although the model predictions on feed intake reduction seem to agree with the measure data moderately well (slope=0.68, r^2=0.44), there seem to be large uncertainty associated to the large variability of data (Figures 3 a,b). Again it appears the equation may under-predict slightly the decline on feed intake in certain conditions, but there are insufficient points at the low end of the range to confirm this trend.

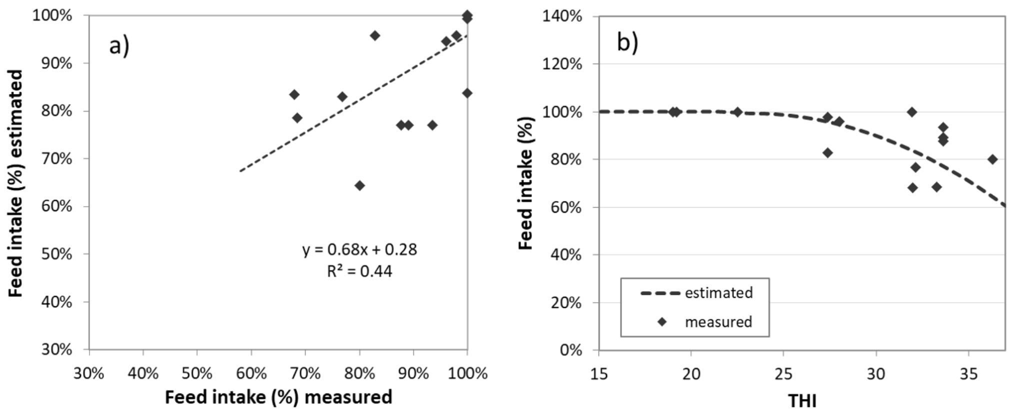

Figure 3 a, b Estimated vs measured reduction of feed intake of meat small ruminants under heat stress (Details of dataset in Supplementary Table S2).

Productivity

The model estimates FPCM decline with acceptable accuracy (r^2 = 0.51) (Figures 4 a b). The slope value (0.50) may indicate that the meta-model could tend to overestimate the decline on FPCM, particularly on the low range, but there are insufficient data at the low end to confirm this trend.

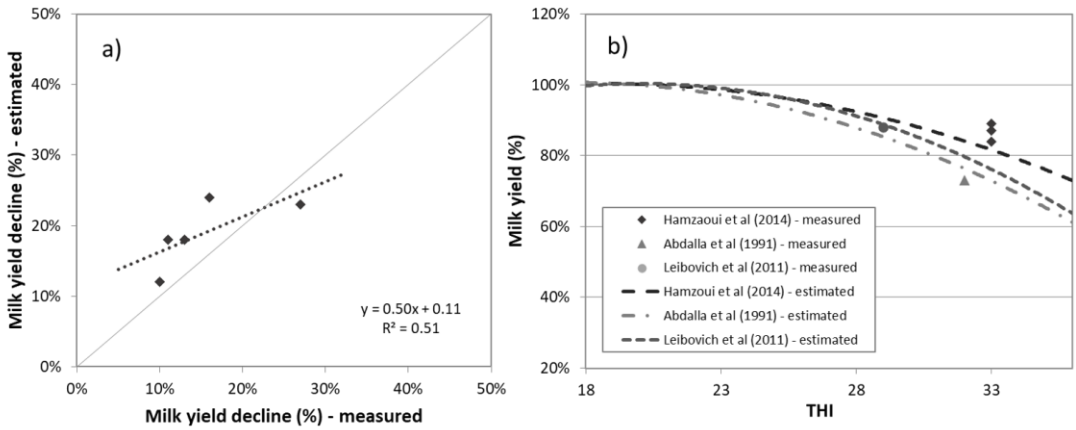

Figure 4 a, b Estimated (dotted lines) vs measured reduction (%) of milk yield of dairy small ruminants under heat stress (Details of dataset in Tables S3 and S4).

The model was also tested for meat systems by comparing the estimated values with observed measurements from the study of Ames and Brink (1977) on growing lambs exposed to different ambient temperatures (-5 to 35º). The model estimations for average daily gain (ADG) agreed reasonably well (r^2 = 0.92, slope=0.78) with the measured data (Figures 5 a,b) although it seems that the model generally tends to overpredict ADG.

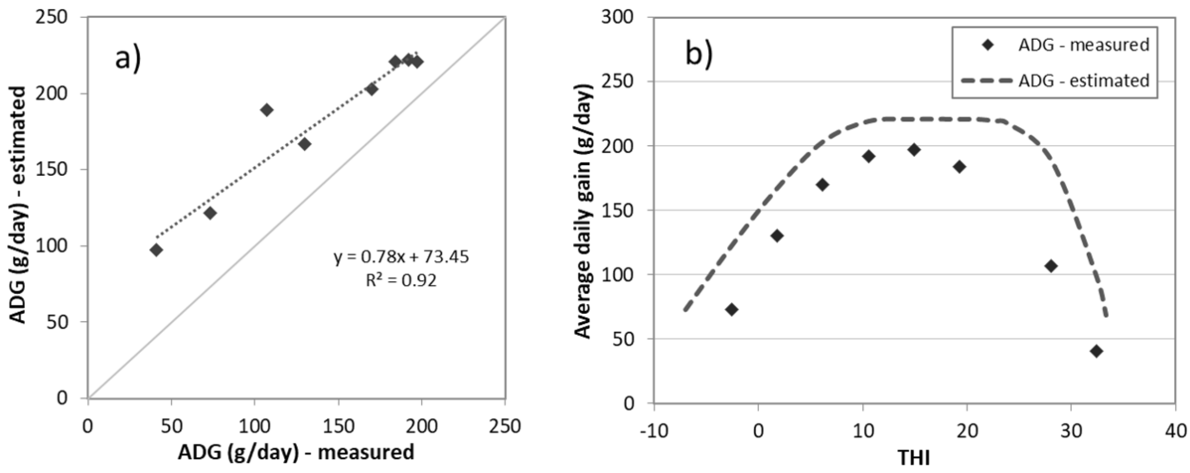

Figure 5 a, b Estimated (line) vs measured average daily gain (ADG) of growing lambs under heat stress (Details of dataset in Tables S3 and S4).

Model test

Effect of heat and cold stress on lamb growth and DM Intake in a meat sheep system

Simulated results show that daily DM lamb intake was reduced up to 16% due to heat stress, which led to a delay of about 2 days for reaching the expected slaughter weight (Figure 6 a). This implies that about almost half a kg of DM feed extra per lamb is required, which would equate to approximate 228 kg extra of concentrates for 260 lambs (*data not shown*).

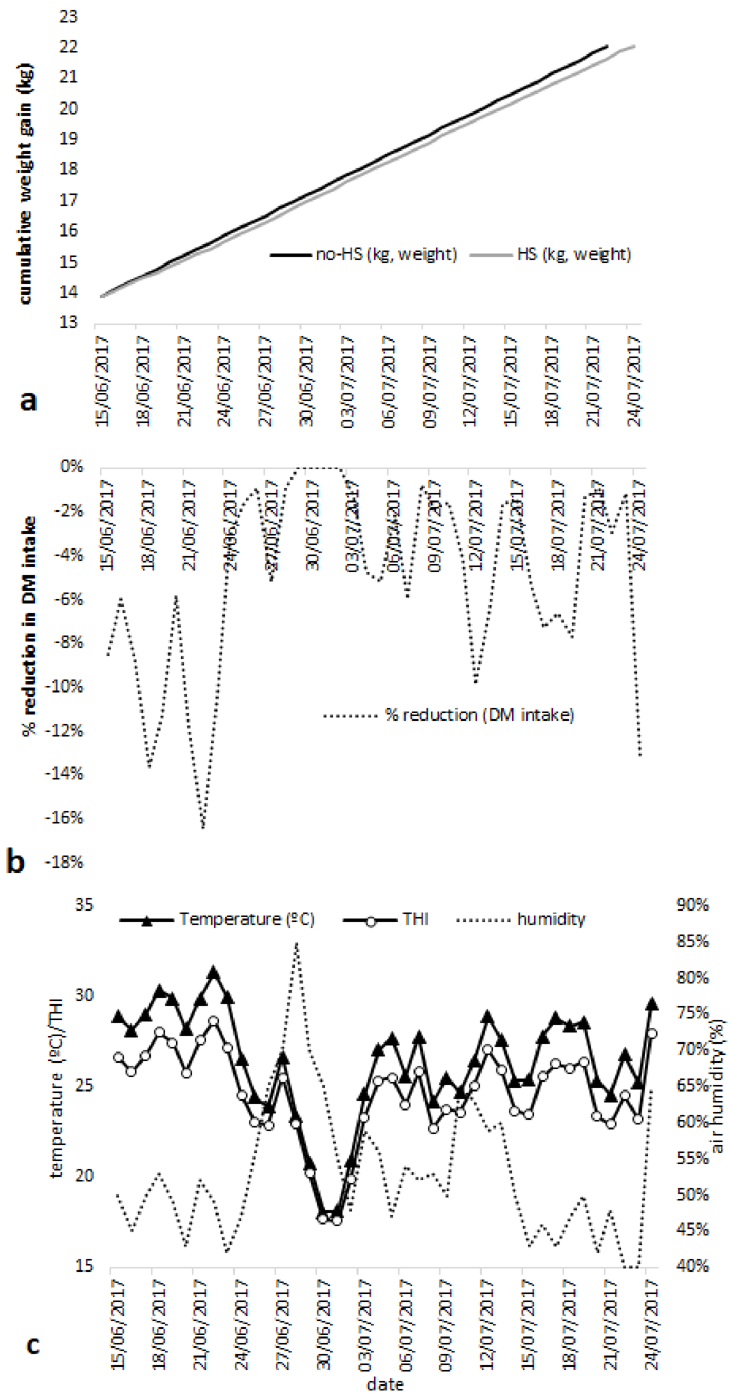

Figure 6 a, b, c Cumulative lamb growth (a) and daily DM intake reduction (%) (b) for the different days of lambs in the period between weaning and slaughter.Daily average temperature (ºC), THI and air humidity are shown (c).

Results of liveweight gain of lambs under cold vs. non-cold stress are shown in Figure 7. Cold stress affected lambs by reducing their expected weight gain (2-29%) and requiring extra DM intake (4-10%). Simulated results indicate that aggregated effect of 8 days' cold stress on lamb growth will result in a loss in efficiency of feed utilized for growth of about 50 g/kg DM intake (*data not shown*).

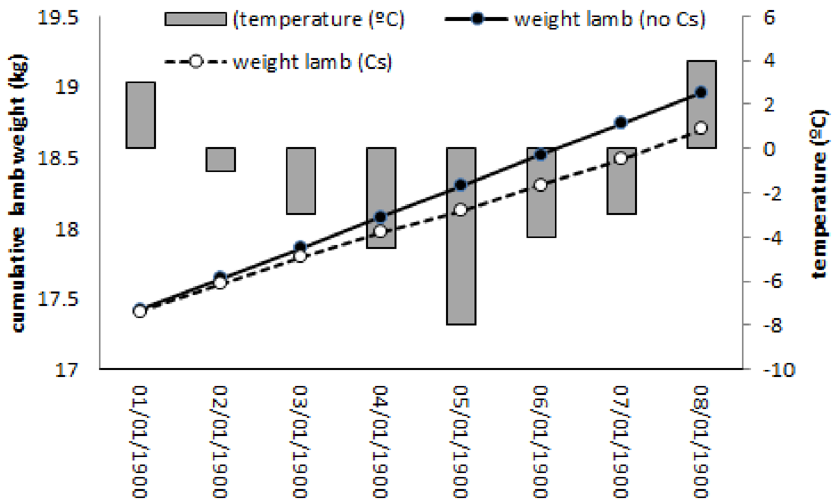

Figure 7 Comparison between lamb growth (kg) without and with cold stress effect for 5 days of cold. Daily average temperature (ºC) during this period is shown as grey bars.

Effect of heat stress on milk productivity and DM Intake, adaptation strategies and trade-off synergies with climate change mitigation in lactating ewes

Non-adapted simulated ewes resulted in losses of up to 23% milk production (3%-23%), which implied an average 11% reduction in milk yield and an extra of 0.12 kg DM intake required per L of milk produced (Figure 8 a). Higher density feed, used as an adaptation strategy, helped to ameliorate most of the effect of heat stress on DM intake (*data not shown*) and milk productivity (only about 2% reduction) (Figure 8 a). Enteric CH_4 emission intensity was about 3% and 8% lower for the adapted to heat stress compared with the scenarios without considering heat stress and considering heat stress without adaptation, respectively (Figure 8 b). However, when we include the embedded GHG emissions from purchased feed, the adapted scenario, i.e. using geed with a high energy content, resulted in much larger emission intensities due to the large C footprint of soybean ingredient (Figure 8 b).

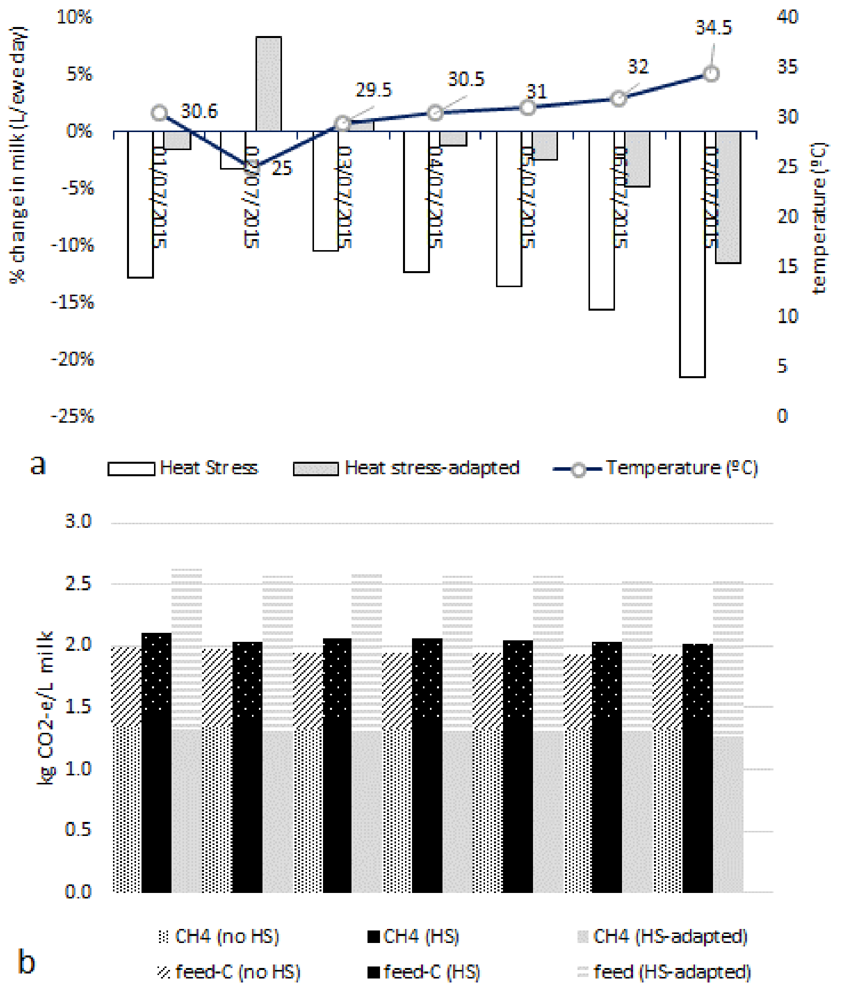

Figure 8 Reduction in daily milk productivity (%) for non-adapted and adapted (fed with higher energy supplementation) lactating ewes under heat stress lead by high temperatures (a) and their corresponding simulated GHG emissions intensity (as kg CO_2-e/L milk) for non-adapted (HS), adapted (HS-adapted) vs. without heat stress (no-HS) resulting from enteric CH_4 fermentation and embedded CO_2-e emissions from purchased feed (feed-C) (b).

When extending the simulation of the model to a whole lactation period, we found that milk yield (as FPCM) was affected by cold and heat stress (Figure 9c) during winter and summer periods, but these losses were moderate when averaged over the whole lactation period (3.7%) (Figure 9a). Whereas, the ewes required extra DM intake during the cold stress periods, the opposite was found during heat stress days (figure 9b). On average, reductions in DM intake by heat stress periods were compensated by increases in DM intake in cold stress periods (Figure 9b). As expected, when we combined both factors (DM intake and milk yield), the averaged feed conversion ratio for the whole period expressed as kg DM intake/ kg FPCM was slightly higher (about 6%) when thermal stress was considered (*data not shown*) (Figure 9ab).

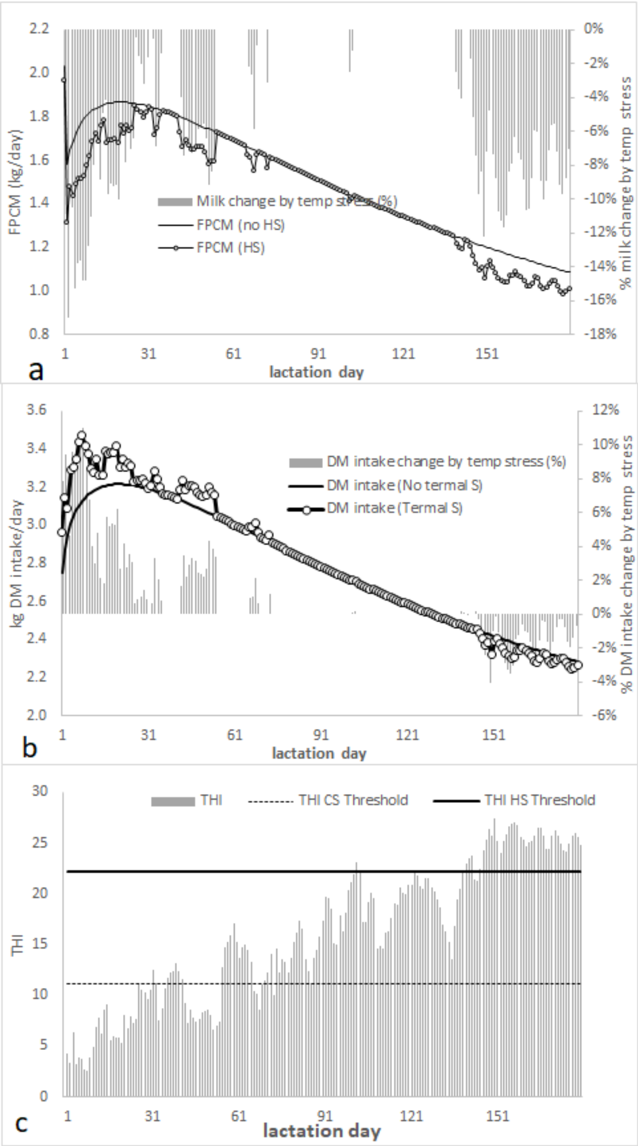

Figure 9a, b, c. Simulated daily Fat Protein Corrected Milk (FPCM) yield (kg/day and %) (a), and daily DM intake (kg/day and %) (b) of an average ewe milking during 6 months (lambing in February) and for either considering or not considering heat and cold stress induced by Central Spain THI values beyond THI cold and heat stress thresholds (c).

Discussion

Evaluation and limitations of the model

Mechanistic models aim to describe mathematically the relationships between the variables and components of a system. In this case, a mixed approach is followed. The effect of climatic conditions on every component has been captured in independent modules through the development of empirical relationships, but the components describing the system have been inter-related in the model in a mechanistic manner through the energy balance.

Mechanistic models are especially constrained by the level of understanding existing about the behaviour of the system, though. For small ruminants, the main effects and responses launched under HS have been identified, but there are still some knowledge gaps about the different mechanisms involved in the animal metabolism resulting in productivity loss (Mahjoubi et al., 2014; Salama et al., 2014). Therefore, while the two components considered in this model probably explain most of the decline in productivity, other mechanisms not included in the conceptual system could also have an influence, such as lowering blood flow to the udder (Lough et al., 1990) or decreasing the secretion of growth hormone (Mitra et al., 1972). As a result, the capability of the model to capture all the variability of results observed in literature could be limited at some extent.

The model seems to capture reasonably well the increase in energy requirements linked to heat dissipation mechanisms triggered under HS. However, the importance of this component in the system is still a topic in discussion. Studies in dairy cows under hot conditions concluded that reduced feed intake explains about 50% of milk yield decline (Baumgard and Rhoads, 2013), thus indicating that other mechanisms could have an important role in the productivity losses resulting from HS. In contrast, some authors suggest that feed intake decline could have a much more relevant role in the case of small ruminants under HS, where it alone could explain most of the productivity losses (Salama et al., 2014). This confronts with the results obtained from pair-fed trials in growing lambs though (Mahjoubi et al., 2014).

Analysing the behaviour of the model components, it seems that the importance of feed intake decline on productivity loss increases with HS. Hence, at low-mild levels of HS (THI=23-26) the effect of energy requirement increase for heat dissipation is more relevant, although at this stage the productivity losses predicted are usually low (rarely higher than 5%). However, at more severe HS levels (THI=27-35) the feed intake decline tends to be the component explaining most of the productivity losses predicted by the model (about 50% to 80%).

The model seems to predict reasonably well the decline in feed intake expected under HS (Figures 2 and 3). Differences observed among measured and predicted values of the FI component of the model may be related with other limitations, such as the difficulty to accurately define the specific TNZ for different species and breeds, and to capture other factors which also influence the level of response on feed intake, such as type of diet (forage:concentrate ratio) or animal productivity level (Hamzaoui et al., 2013; Hamzaoui, 2014). These limitations have been considered, and potential approaches are explored in the following section of the discussion to be implemented into the model if more accurate information become available (described in sections below). Other climate variables than temperature and relative humidity, such as wind speed and solar radiation, may also play a role, but have not been considered in our study.

The model has shown to be able to capture reasonably well productivity losses of the trials used in the validation process, although several discrepancies have been observed in some cases for both, dairy (Hamzaoui, 2014) and meat systems (Ames and Brink 1977).

As previously mentioned, this could be attributed, in part, to the uncertainty defining the TNZ. In this work the HS thresholds proposed by Marai et al. (2007) for small ruminants are applied, in a first attempt to demonstrate the capabilities of the model. However, the TNZ of small ruminants in every situation can be affected by a number of factors that may not always be fully reflected due to the lack of data.

For example, from the study of Ames and Brink (1977) it is observed a TNZ between 10ºC to 20ºC, suggesting a THI_{HS}=19.3 (60%RH) while in similar studies with lambs, higher values, up to 25ºC (THI_{HS}=23.7) have been reported (Ames et al, 1971). Moreover, differences among species can be relevant too. A higher HS threshold can be expected for goats, as they tend to tolerate hot conditions better than sheep, due to specific adaptation mechanisms (Lu, 1989; Al-Dawood, 2017). This could be behind the overestimation of FPCM production losses calculated from the dataset of Hamzaoui, (2014) which involves trials with Murciano-Granadina goats, a Mediterranean breed that could have a higher HS tolerance.

The feeding system applied to estimate energy requirements could also be an important source of discrepancies itself. In this case, the estimations are based on AFRC, (1995). Although it is a robust and internationally recognised method, it seems AFRC may underestimate energy requirements for small ruminants when compared to other feeding systems like NRC, INRA o CSIRO (Cannas, 2004). In our model this would lead to a surplus of energy available, and therefore, to an overestimation of daily weight gain or milk production.

In addition to this, the available literature on HS effects on small ruminants is limited, especially in comparison to dairy and beef cattle (Renaudeau et al., 2012). Because of this, in some aspects the model components rely on relationships developed from studies on cattle that have been adjusted to be applied on sheep and goats. As all of them are ruminants, they may follow the same principles, but the lack of specific data for sheep and goats in some particular aspects involves an additional source of uncertainty.

Applicability and strengths of the model

Our model test on real case studies provides a snapshot of potential applicability for climate change studies at different levels.

First, the model is relatively simple, and its components are based on common principles of animal production. This feature facilitates its adaptability and integration into already existing whole farm models. This is of particular importance for whole farm models that are used to assess CC mitigation and adaptation strategies, which very few of them incorporate thermal stress impacts on animals (Del Prado et al., 2013).This could also be extended to regional or national studies applied to the estimation of the effect of thermal stress on the livestock sector.

Among the most extended feeding systems applied for small ruminants (AFRC, NRC, CSIRO, INRA), most of them do not consider corrections for energy requirements or feed intake under HS conditions. In the case of CSIRO, a complex set of equations is provided to account for the effect of cold conditions, capturing the influence of different factors like temperature, rain or wind. For dairy sheep in Mediterranean conditions, Calsamiglia et al., (2009) recommended a linear decline correction in feed intake of 2% every ºC when THI>23, based on Finocchiaro et al., (2005). A linear relationship was also proposed by Fox, (1987) suggesting a reduction by 1% per ºC. In contrast, the polynomic relationship used in our model reflects a gradual effect of HS on FI reduction, declining about 1% per ºC at mild HS levels, and closer to 2% per ºC at severe HS conditions.

Another interesting feature of the model described in this work is its flexibility. This could be especially relevant when exploring future CC scenarios, involving higher temperatures and more frequent extreme events (e.g. heat waves). Studies from pure empirical approaches have been found to underestimate production losses linked to HS, particularly when they are based on monthly production data, as it is usually measured in the commercial milk recording systems (Ramón et al., 2016). Moreover, too simplistic linear approaches may not fully capture the range of variability of conditions expected due to CC, which may often result in non-linear responses. For example, Salama et al., 2014 indicated a decrease of 1% in milk yield for each 1-unit increment of THI in dairy goats under HS. Analysing the results from the present work for dairy systems, the proposed model describes a gradual decline of the FPCM productivity, in the range of 2-5% at mild HS levels, up to >20% at severe HS conditions, when an increase in 1 unit of THI can involve a decline of about 1.5% in milk yield. This behaviour seems to agree better with the results from literature when trials at different levels of HS have been conducted (Sano et al., 1985; Brown et al., 1988).

The adaptability of the proposed model also involves some other advantages in the context of CC, particularly in relation with the exploration of adaptation strategies as it has been shown in the model test. Moreover, these adaptation measures, as shown in the model test, can also be easily tested as potential climate change mitigation (or not) measure too. Specific modifications on animal diets and/or changes on forage composition could be potentially incorporated through the components of the model.

Other adaptation measures related to environmental modifications of the site (e.g. evaporative cooling) could be also potentially explored through the proposed model, although in this case, more information from literature would be required to support them.

The model structure and simplicity facilitates the TNZ to be easily updated and/or adapted, which allows to capture other factors that also influence the level of response on feed intake, such as type of diet (forage:concentrate ratio) or animal productivity level (Hamzaoui et al., 2013; Hamzaoui, 2014) if future advances and knowledge in the field allows to establish robust evidence.

Specific approaches have been considered that will allow to capture these effects in the model. For example, in the case of high productive animals or breeds from temperate regions, THI_{HS} threshold could be decreased accordingly in order to reflect a higher sensitivity to HS. Similarly, if robust data were available, THI_{HS} threshold could be increased accordingly in order to reflect the effect of measures that facilitate the heat dissipation from the animals, like ventilation or evaporative cooling. Other option could be modifying the polynomial relationship relating environmental conditions (i.e. THI) and FI, which could be disaggregated into a set of polynomic equations in order to capture the different effect depending on forage:concentrate ratio, or animal/breed sensitivy to HS. This modifications would add more complexity to the model, and the trade-offs between adaptability and applicability should be considered though.

Conclusions

This work describes a semi-mechanistic model for predicting productivity losses in small ruminant systems due to HS conditions. The model is based on capturing the effects of HS on the animal's energy balance, mainly through two mechanisms: the changes in energy maintenance and feed intake. Despite its limitations, according to the evaluation conducted, the model is able to capture potential productivity losses across a range of HS conditions and systems. We believe its relative simplicity, together with the ability to capture non-linear responses to different HS intensities, constitute a major strength and innovation of the proposed model. These features may enhance its incorporation into whole farm modelling approaches and existing feed requirement systems for small ruminants, thus allowing to integrate the potential consequences of CC on productivity, but also to assist with the identification of appropriate adaptation solutions in small ruminant systems.

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Declaration of interest

The authors declare they have no conflicts of interest.

Ethics statement

None

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Supplementary Tables:

Table S1. Studies reporting feed intake (FI) decrease (%) for dairy sheep and goats under heat stress.

Reference	System	Breed	THI range	FI loss (%)
Abdalla et al., 1993	Dairy sheep	Finn x Dorset x Rambouillet	19-32	29%
Bernabucci et al., 2009	Dairy sheep	Sardinian	19-30	4%
Brasil et al., 2000	Dairy goats	Alpine	22-32	8%
Brown et al., 1988	Dairy goats	Alpine	19-29	6%
Hamzaoui et al., 2014	Dairy goats	Murciano-granadina	19-33	29-35%
Hamzaoui et al., 2013	Dairy goats	Murciano-granadina	19-33	21%
Leibovich et al., 2011	Dairy sheep	Assaf	26-29	10%
Sano et al., 1985	Dairy goats	Saanen	19-33	18%

Table S2. Studies reporting feed intake (FI) decrease (%) for meat sheep and goats under heat stress.

Reference	System	Breed	THI range	FI loss (%)
Alhidary et al., 2012	Meat sheep	Merino	22-32	23%
Ames and Brink 1977	Meat sheep	Merino	19-32	4-35%
Bhattacharya et al., 1974	Meat sheep	Awassi	19-33	4%
Denek et al., 2006	Meat sheep	Awassi	11-27	2-17%
Dixon et al., 1999	Meat sheep	Merino x Border Leicester	15-34	7-12%
Indu et al., 2014	Meat sheep	Malpura	32-36	20%

Table S3. Overview of small ruminant studies selected to evaluate production losses. The reported results have been converted into fat and protein correct milk (FPCM) according to Pulina, Macciotta and Nuda (2004) and THI has been normalised based on Marai et al., 2007

Reference	System	Weight (kg)	THI range	Feed intake (kg DM/day)	FPCM loss (%)
Abdalla et al., 1993	Dairy sheep	75	19-32	2.7-1.9	27%
Hamzaoui et al., 2014 (1)*	Dairy goat	41	19-33	2.5-1.8	16%
Hamzaoui et al., 2014 (2)*	Dairy goat	41	19-33	2.3-1.5	12%
Hamzaoui et al., 2014 (3)*	Dairy goat	41	19-33	2.3-1.6	13%
Leibovich et al., 2011	Dairy sheep	69	26-29	2.8-2.5	12%
Ames and Brink 1977	Lambs	25	(-3)-32	1.9-0.9	-

*Corresponds to different trials from the same study

Table S4. Overview of the feed composition in the studies selected to evaluate production losses.

Reference	Ingredients	%	GE (MJ/kg DM)	DE (MJ/kg DM)	ME (MJ/kg DM)
Abdalla et al., 1993	Lucerne hay	96.0	18.2	10.6	8.1
	Corn	4.0	18.7	16.1	13.6
Hamzaoui et al., 2014	Lucerne hay	60.4	18.2	10.6	8.4
	Barley grain	15.0	18.4	14.8	12.4
	Beet pulp	9.1	17.1	13.9	11.4
	Corn	7.5	18.7	16.1	13.6
	Soybean meal	5.0	19.7	18.2	13.6
	Sunflower meal	3.0	19.4	11.8	9.1
Leibovich et al., 2011	Gluten feed	31.9	18.8	15.1	12.2
	Wheat silage	19.7	17.6	9.6	7.8
	Vetch hay	19.0	18.3	12.5	9.8
	Corn	9.9	18.7	16.1	13.6
	Barley grain	9.2	18.4	14.8	12.4
	Soybean meal	3.9	19.7	18.2	13.6
	Wheat grains	3.1	18.2	15.6	13.1
	Wheat bran	1.4	18.9	13.5	11.0
	Sunflower meal	1.3	19.4	11.8	9.1
Ames and Brink 1977	Lucerne	50.0	18.2	12.1	8.4
	Sorghum	40.0	18.8	16.0	13.0
	Molasses	5.0	17.0	14.5	12.1
	Soybean meal	5.0	19.7	18.2	13.6

Supplementary Figures:

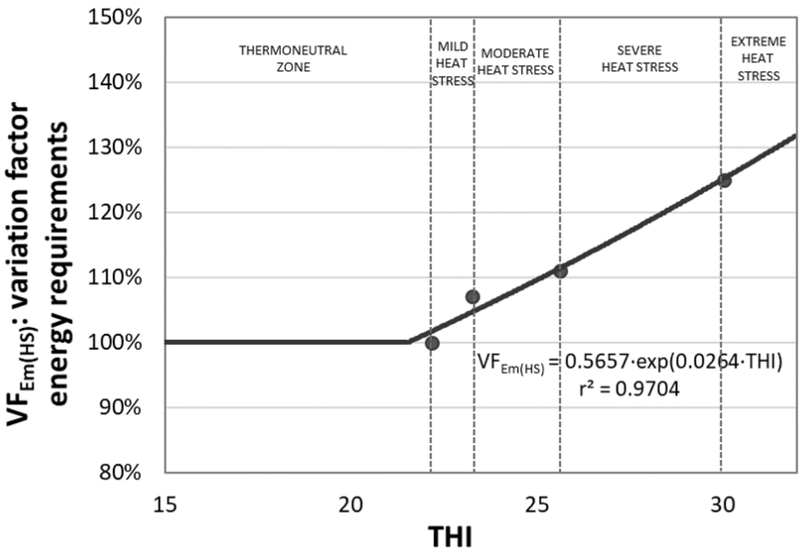

Figure S1. Equation developed to estimate the additional energy requirements for maintenance according to temperature-humidity (THI) conditions, related to different heat stress (HS) levels (Adapted from NRC 1981, 2001).

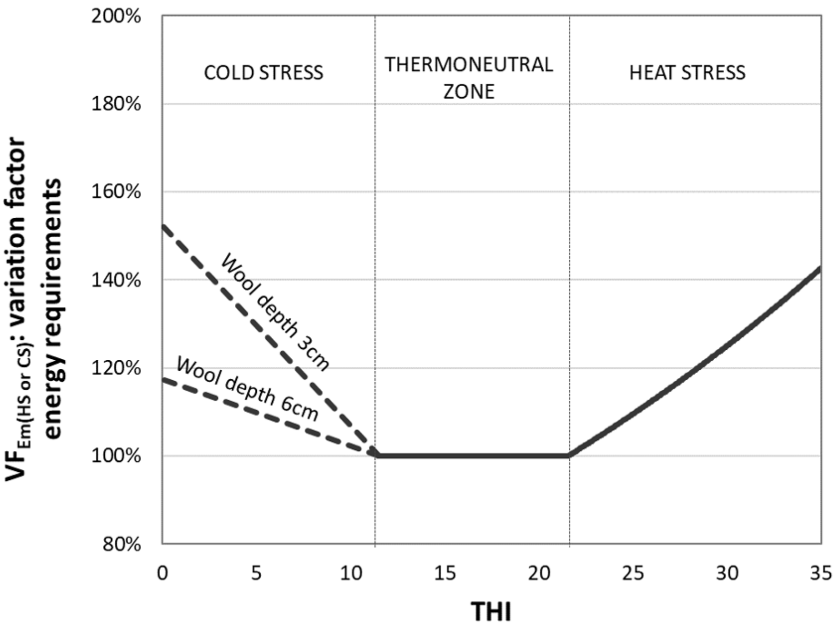

Figure S2. Estimation of increase on energy requirements for maintenance under cold stress (dotted lines) for sheep (assuming THI_{CS} threshold = 11.5 (T=11ºC, RH=50%)) and heat stress conditions (THI_{HS} threshold = 22.2 (based on Marai et al., 2007)).

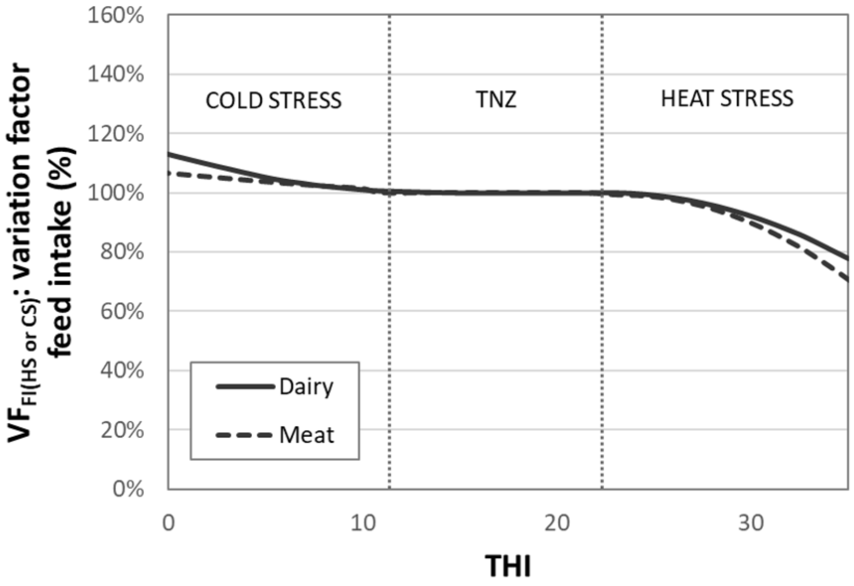

Figure S3. Effect of thermal stress conditions (THI) on feed intake of small ruminants for dairy and meat systems. (THI_{CS} threshold = 11.5; THI_{HS} threshold = 22.2)

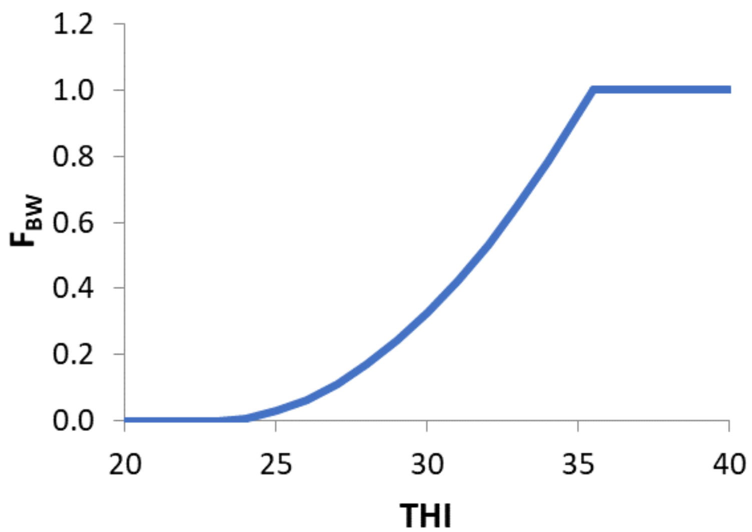

Figure S4. Factor F_{BW} captures a gradual effect of heat stress on BW loss to mobilise reserves on lactating animals under energy deficit.

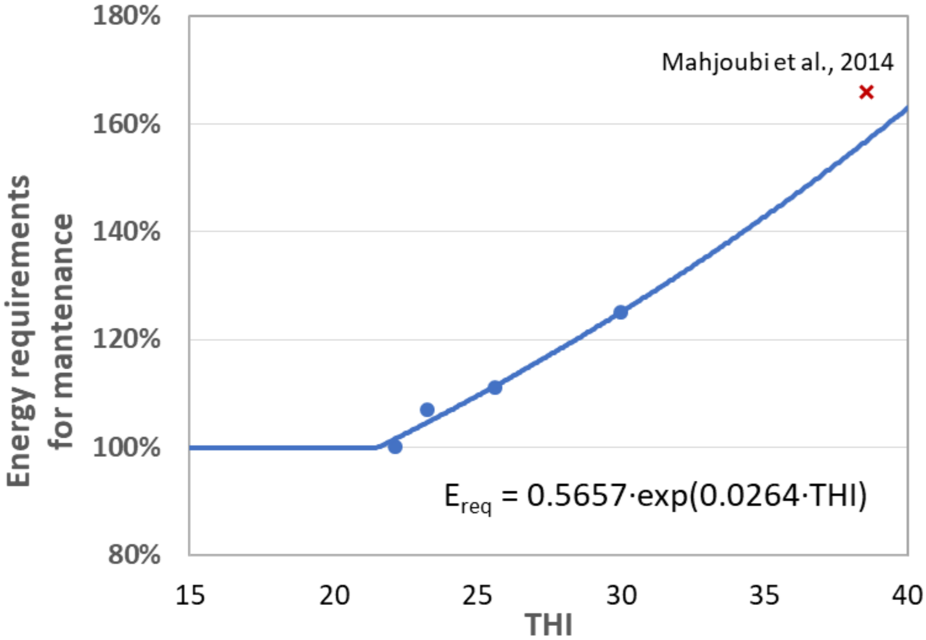

Figure S5. Validation of equation developed relating increase on energy requirements for maintenance with environmental conditions (THI) under HS. Estimated result under extreme HS conditions of THI=38.6 obtained through extrapolation (57%) are in accordance with reported value (66%) by Mahjoubi et al., 2014.

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