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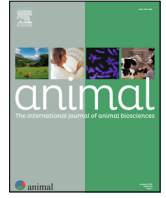
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A framework to estimate the environmentally attainable intake of dairy cows in constraining environments



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ABSTRACT

Most intake models for dairy cows have been developed to make predictions under normal conditions, in which animals can meet their nutritional requirements. To estimate intake under constraining conditions, i.e. when intake is defined by the environment and not by the animal's requirements, it is necessary to develop models that take into account environmentally driven effects. The aim of this work was to develop a framework to represent the links between environmental variables (food quality and quantity, as well as ambient temperature, season, and farm type) and intake. The framework integrates time as the major constraint on intake and proposes the environmentally attainable intake (**EAI**) as the product of the Eating Rate (**ER**) and the Eating Time (**ET**). ER is the maximum sustainable rate (gr DM/min) at which animals bite the food, and ET is the daily time (min/d) that animals have to eat. The architecture of the framework is easily extensible to add constraints such as predation pressure, reproductive costs, competition, parasitism, or diseases. Data from grazing and indoor dairy farms were used to test the usability of the framework. The results show that a time use-based framework is a reliable approach to estimate intake considering environmental variables with minimum use of animals' characteristics. In conclusion, a high-level framework of feeding behaviour, that captures the main underlying mechanisms of intake in constrained environments, can be used to predict the EAI and the effects of the environment on animal performance.

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Implications

The computational tool described in this paper can help researchers to study animal performance in constraining environments, breeders to improve breeding programmes to face future adversities, and farmers to evaluate management strategies that optimise animal production, especially time-dependent decisions.

Introduction

Knowing intake allows the formulation of rations that meet the nutritional requirements of the animals, and allows evaluation of their efficiency both in terms of economics (cost of food relative to production) and biological variation (identifying the most efficient animals). However, measuring individual feed intake requires large investments and structural changes on farms. For housed cows, individual and automatic feeders are expensive and have particular technical challenges. For grazing cows, only indirect

methods can be used, such as the average difference in pre- and postgrazing herbage mass of a group of animals or the use of markers in individuals. As an alternative to those expensive and laborious activities, mathematical models can be used to predict intake. These models range from equations that only include animal factors (e.g. BW, daily weight gain, milk production, milk composition, milk days, parity, body condition score) to more complex models that encompass food characteristics (e.g. particle size or composition).

By definition, the majority of intake models are developed and used under normal farm conditions where animals have free access to food and water, and the farm management aims to guarantee health and welfare by minimizing exposure to harsh conditions. In these models, to simplify, intake corresponds to a situation where animals can express their full potential to eat and meet nutritional requirements or to a situation where they are only limited by feed quality. However, it is also very important to predict intake under constrained environmental conditions, where animals simply cannot express their full potential to eat because of environmental constraints, for instance, under conditions of climate change (Simpkin et al., 2020).

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In this work, we develop a framework to predict the environmentally attainable intake (EAI) of dairy cows under environmentally constrained conditions, that is to say, to estimate the intake that animals can reach when it is conditioned by the prevailing environmental conditions and not by animal inherent capacity. The view taken here is that actual intake corresponds to the minimum value between the cow's innate capacity to eat and the intake defined by the environmental conditions. In this view, the animal side of intake is conceptually separated from the environmental side of intake, which allows the study of complex phenotypes such as feed efficiency, especially for understanding genetic basis, and genetic by environment interactions.

We present (1) an approach to calculate the Eating Rate (ER, g DM/min) and the Eating Time (ET, min/d). We use (2) reported data of housed and grazing Holstein cows, and a Bayesian algorithm to test both the usability of the framework and the parameter sensitivity. Finally, we discuss (3) the regulatory processes underlying intake that were considered during the framework development. We hope that this framework will become a complementary tool that allows the estimation of intake in those situations where traditional models cannot be used due to the feeding restrictions generated by the environment.

Material and methods

Framework development

For constraining environments, we propose that EAI is the product of the maximum sustainable rate at which animals eat a given food (i.e. ER) and the daily time available to eat this food (i.e. ET) (Eq. (1) in Table 1). In building these two components, four principle criteria were identified:

- Criterion 1 is to minimise the complexity of the framework structure by minimizing the use of assumptions about the functioning of animals. In particular, we chose to minimise the effect of animal characteristics on intake and the use of detailed explanations of the feeding behaviour. Structurally, the framework does not have internal feedback.

Table 1
Description of the equations used to estimate the environmentally attainable intake of Holstein cows in constraining environments.

Equation	Expression
Eq. (1)	$EAI = ER \times ET$
Eq. (2)	$\text{mature ER} = a + (b / (1 + \exp(-c \times (d - \text{peNDF}))))$
Eq. (3)	$\text{proportion of the mature ER} = 1 / (1 + \exp(0.015 \times (200 - \text{age})))$
Eq. (4)	$ER = \text{mature ER} \times \text{proportion of the mature ER}$
Eq. (5)	$MST = 0.13 + (0.35 / (1 + \exp(-0.007 \times (20 - \text{age}))))$
Eq. (6)	$TCT = 1 / (1 + \exp(-a \times (b - MDT)))$
Eq. (7)	$SDA = (-0.14 \times \text{dayL}) + 0.20$
Eq. (8)	$\frac{dS_{(i)}}{dFAD_{(i)}} = -(S_{(i)} * k1) - (S_{(i)} * k2)$
Eq. (9)	$\frac{dET_{(i)}}{dFAD_{(i)}} = (S_{(i)} * k1) + (Rumination_{(i)} * k3) - (ET_{(i)} * k4)$
Eq. (10)	$\frac{dRumination_{(i)}}{dFAD_{(i)}} = (S_{(i)} * k2)$
Eq. (11)	$\frac{dAddPro_{(i)}}{dFAD_{(i)}} = (ET_{(i)} * k4) - (Rumination_{(i)} * k3)$
Eq. (12)	$k4 = a + (b / (1 + \exp(c \times (d - FAD))))$
Eq. (13)	$\text{proportion of the AddPro} = 1 / (1 + \exp(a * (b - \text{proportion of the day for feeding activities})))$

Variables: environmentally attainable intake (EAI, gr DM/d), eating rate (ER, gr DM/min), proportion of the day for minimum sleep time (MST, d/d), proportion of the available day (24 hours minus MST and minus the time when farm operations prevent access to food) for thermally comfortable time (TCT, d/d), proportion of the TCT for season-dependent activities: mainly resting (SDA, p/p), proportion of the feeding time for: seek for food time (S), eating time (ET), rumination, and additional processing time (AddPro). Inputs: physical NDF content of food (peNDF, % of DM), age of the animal (days), maximum daily temperatures (MDT, °C), daylight length (dayL, d/d), and food area density (FAD, Kg DM/ha).

- According to the second criterion, the framework must be solid in concepts and assumptions, with the ability to provide a mechanistic view of the results.
- The third criterion dictates that the framework must generate realistic predictions and have the ability to predict patterns of reported intake data of Holstein cows at individual level.
- Finally, the fourth criterion is that the framework is designed to be flexible allowing it to be expanded to consider additional environmental constraints (by adding factors such as predation pressure, reproductive costs, competition, parasitism, or diseases), and to be adaptable allowing to incorporate more complex representations of the processes (by adding or changing the mathematical relationship between variables).

For ER, we assume that in constraining environments, animals have a constant, maximum sustainable ER depending on the food quality. In this manner, animals make efficient use of the time they have to eat without compromising the balance between the energy ingested and the cost of harvesting and processing of food. In addition, we take into account that ER has an anatomical component, which we assume to be proportional to animal size (i.e. breed and age) rather than animal BW (which is more sensitive to effects of prior feed availability). Therefore, in this framework, the ER is defined by the fibre content of the food and by the oral capacity (size and force) of each animal. Obeying our first criteria, ER is defined by the physical NDF content of food (peNDF, percentage of DM particles retained on an 8-mm sieve, Mertens, 1997), and by the animal's age (days). We chose these two variables to operationalise our ER definition because peNDF is a good proxy for both the ease of harvesting and the digestible energy content of food, and because the oral capacity increases with age.

We propose two steps to estimate the ER. The first step is to calculate the ER in the adult animal (i.e. mature ER), for which the peNDF is used as a predictor (Eq. (2) in Table 1). Here, maturity refers to the age at which animals reach their full oral capacity to eat. The second step is to calculate the proportion of the mature ER according to the age of the animal (Eq. (3) in Table 1). The left plot in Fig. 1 shows the assumed change in mature ER given the peNDF content of the food, and the right plot shows the assumed change in the proportion of the mature ER (p/p) from birth to maturity in Holstein cows.

In this framework, ET refers solely to the time spent prehending, chewing, and swallowing feed. It does not include the time used to move between feeding stations. To estimate ET, the total time in the day when intake can occur is 24 hours minus the sleep time and the time when farm operations prevent access to food. The time when animals can eat is divided into these activities: thermoregulation, season-dependent activities, and feeding activities (seek for food (i.e. foraging), eating (i.e. ET), rumination, and additional processing). The environmental variables used to estimate ET and the activities considered in this framework are presented in Fig. 2.

To use this approach, we assume that:

- Animals need a mandatory minimum amount of time to sleep soundly (Siegel, 2008).
- Some farm activities prevent animals from accessing food.
- If there is heat stress, animals need time for thermoregulation. During thermoregulation, animals cannot do another activity.
- Some animals' activities (e.g. resting, sexual behaviour, parental care) depend on the season (Mastromonaco and Gonzalez-Grajales, 2020). However, we assume that resting is the most relevant season-dependent activity to be considered in this framework.
- The proportion of time used for seek for food, eating, rumination, and additional processing is a function of food availability.

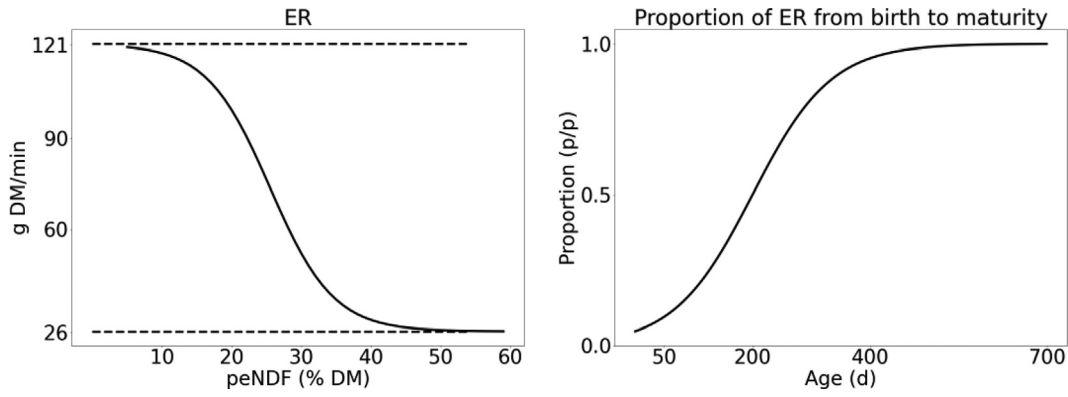


Fig. 1. The left plot shows the assumed change in mature eating rate (ER, gr DM/min) given the physical NDF content of food (peNDF, % DM), and the right plot shows the assumed change in the proportion of ER (p/p) from birth to maturity in Holstein cows.

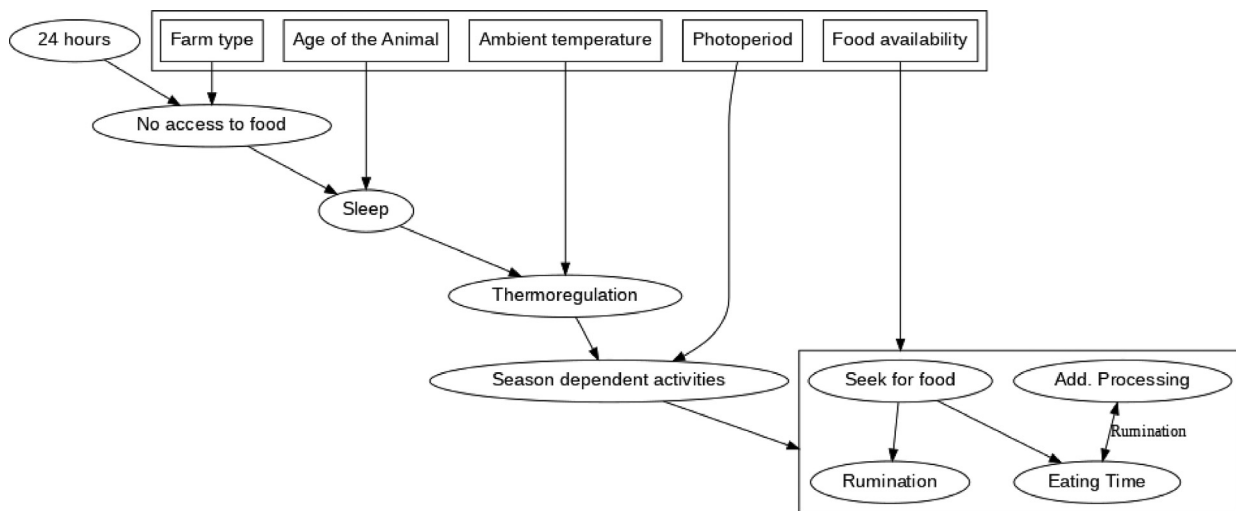


Fig. 2. Environmental variables and time components used to estimate the eating time in a framework to study the environmentally attainable intake of dairy cows in constraining environments.

With this assumption, we considered that: (1) Rumination is more influenced by the level of intake than by the quality of the diet (e.g. % NDF), (2) when the food availability is high (e.g. housed conditions), intake rate exceeds the stomach emptying rate, in which case animals need an additional time to process food before eating again (additional processing).

- For simplicity, we assume that there is no overlap between activities. This means, for instance, that animals cannot perform any other activity (e.g. rumination) while they do not have access to food or during thermoregulation.

Although sleep is the most vulnerable state, animals need a minimum sleep time (**MST**) to prevent welfare problems. In cattle, sleep can be divided into three parts: rapid closed eyes side-to-side movements sleep (**REM**), non-rapid eye movement sleep (**NREM**), and drowsiness. During REM, there is no physical activity; and during drowsiness and NREM, it is accepted that cattle can ruminate (Ternman et al., 2019). To avoid overlapping between sleep and rumination, we assume that drowsiness and NREM are vigilance states in which animals are unable to ruminate. Additionally, we assume that young animals need more time to sleep than adults because of the effect of sleep on hormone release, brain development, and growth (Siegel, 2008). Because it is difficult to establish what proportion of drowsiness and NREM time can be used for rumination, and based on the fact that some authors report that

adult cattle sleep 4 h/d, of which less than an hour is REM sleep (Ruckebusch, 1972; Ternman et al., 2019), we assume that adult Holstein cows need 12.5% of the day (180 min/d) for MST. We propose Eq. (5) (Table 1) to use the animals' age to estimate the proportion of the day used for MST. Fig. 3 shows the proposed Sleep-Wake life changes in Holstein cows.

Management strategies may be different between farms and represent a significant reduction in ET because they prevent access to food. On dairy farms, travel time to the milking parlour and waiting time to be milked prevent access to food. Other farm activities, such as feed delivery, weighing, counting, deworming and vaccination, could also be taken into account to calculate the time animals spend on-farm activities that prevent them from eating. To use this framework, the user needs to estimate the daily time spent on these types of activities. We assume that Holstein cows need, for example, 8.3% of the day (120 min/d) for these activities, and that animals cannot perform any other activity while they do not have access to food.

Four assumptions are used to represent the effect of heat stress on intake. First, feeding activities are heat-producing, this means that during heat stress, these activities are absent. Second, cows cannot rest during heat stress because as the ambient temperature increases, they spend less time lying down to increase the body surface area exposed to air (Berman, 2005). Third, high temperatures do not affect sleep because heat spikes occur around noon.

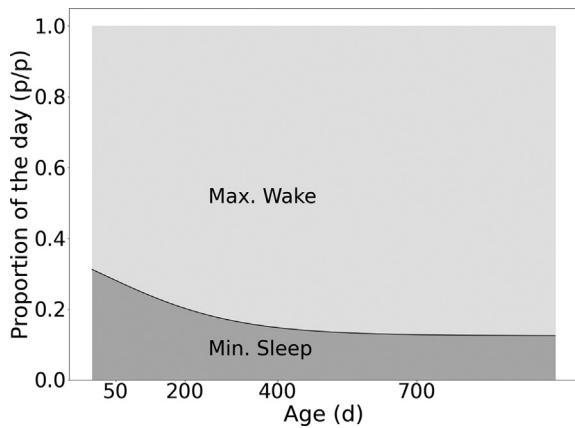


Fig. 3. Sleep-Wake proportion of the day from birth to maturity in Holstein cows.

Fourth, although animals may try to thermoregulate when they do not have access to food (e.g. increase the time spent drinking), this is not significant. It would likewise be possible to include the effects of cold stress on intake in the framework but we chose not to do this here because the lower critical temperature for fully fed cattle does not seem relevant in the farmed animal context.

After subtraction of MST and no access to food time, animals have a thermally comfortable time (TCT) for seasonal- and feeding-related activities if the maximum daily temperature (MDT, °C) does not exceed 25 °C (i.e. there is no heat stress) (Hahn, 1999). If this limit is exceeded, the TCT decreases as MDT increases. We propose Eq. (6) (Table 1) to estimate the proportion of TCT by using the MDT as a predictor. We assume that animals use the reduction of TCT for thermoregulation. In Fig. 4, the left plot shows the assumed change in the proportion of TCT given the MDT. For simplicity, and because it is not always possible to measure other factors involved in heat stress (humidity, solar radiation and wind speed), we assume that these factors are strongly correlated with temperature, and that the MDT is the most relevant factor to estimate heat stress effects on intake.

Although photoperiod also affects social and reproductive behaviours, we assume that resting is the only seasonally dependent activity (SDA) that has a significant effect on intake in constraining environments. It is important to mention that in this framework, sleep and resting are different concepts. For these activities, we assume that sleep is not affected by environmental factors, while resting is a flexible activity influenced by the season. It has been shown that when the length of the day decreases (e.g., winter in

temperate countries), animals decrease ET (Munksgaard et al., 2020). We assume that this reduction in ET is time that can be used for seasonal activities (e.g. resting). We propose Eq. (7) (Table 1) to proportionally divide the TCT into two parts: a) SDA (mainly resting), and b) Time for feeding activities. We assume that the proportion of TCT used for SDA is linearly related with the daylight length (d/d). In Fig. 4, the right plot shows the change in the proportion of TCT used for SDA, given the daylight length (d/d).

After subtraction of MST, no access to food, thermoregulation and SDA, animals have time available for four feeding activities: Seek for food (S), Eating Time (ET), Rumination and Additional Processing. In our framework, the time for feeding activities can be split into these four activities by using the food area density (FAD, Kg of DM/ha) as a predictor in an Ordinary Differential Equation (ODE) system (Eqs. (8)–(11), Table 1). We assume that FAD can be used to describe both thickness of grass in uniform pastures and the distances between patches in patchy landscapes. Fig. 5 shows the dynamics of the four feeding activities given the FAD.

The ODE system consists of four state variables and four fluxes. To develop Eqs. (9) and (11) (Table 1), we assume that there is a food processing time per unit of food ingested (time to transit through the gastro-intestinal tract). When FAD is low, this processing time is accommodated within the time budget of the other feeding activities. However, when FAD is high (typically housed cows eating a total mixed ration), there is a need for additional food processing time. This fits with the observation that eating time in housed cattle is reduced relative to grazing cows (Charlton and Rutter, 2017). To incorporate a simple representation of this phenomenon into the framework, we propose that with increasing FAD, ET reduces because animals need an additional time to process the food before eating again. We call this: Additional Processing (AddPro) time. The flow dynamics (parameter k_4 in Eqs. (9) and (11), Table 1) from ET to AddPro is defined by an auxiliary equation (Eq. (12), Table 1). In this equation, the value of k_4 increases as the FAD increases. Another auxiliary equation (Eq. (13), Table 1) is used to define the effect of the proportion of the day available for feeding activities on the ET. We assume that as the proportion of the day for feeding activities decreases, the ET/AddPro ratio increases because animals need to optimise intake. In this logic, when the daily time for feeding activities decreases, the proportion of the time used for both ET and rumination increases. The impacts of the modifiers of the AddPro time (Eqs. (12) and (13)) within the time available for feeding activities are shown in Fig. 6.

FAD has a restrictive effect on ET because scattered food increases the seek for food time. In our framework, this time accounts for both patchy and uniform landscapes. In patchy

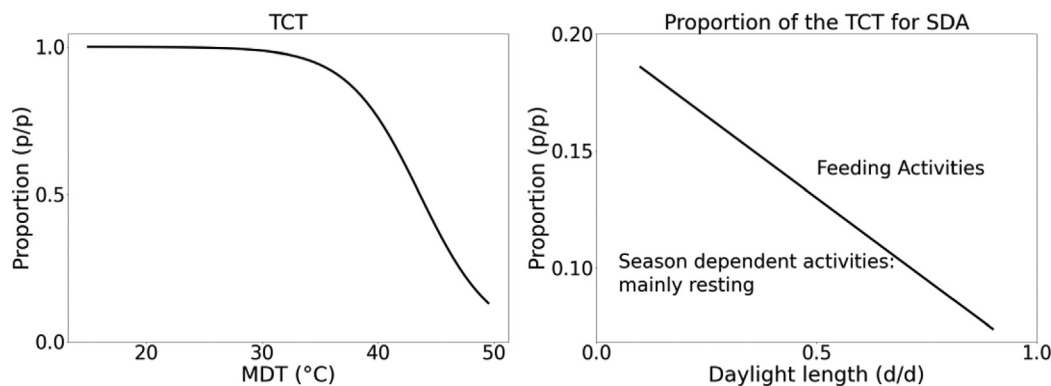


Fig. 4. For Holstein cows, the left plot shows the change in the proportion of the available day (24 hours minus sleep and minus the time when farm operations prevent access to food) that is Thermally Comfortable Time (TCT) given the maximum daily temperature (MDT, °C). The right plot shows the change in the proportion of the TCT used for season-dependent activities (SDA, mainly resting) given the daylight length (d/d).

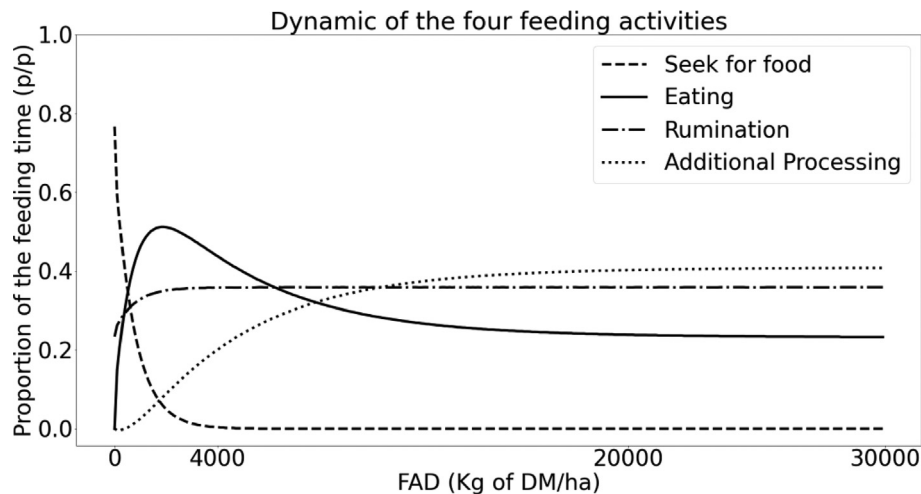


Fig. 5. Dynamic of the four feeding activities (seek for food, eating, rumination, and additional processing time) relative to the food area density (FAD, Kg DM/ha) for Holstein cows.

landscapes, the distances between feeding stations define the cumulative daily time that the animal spends travelling through these stations. While in uniform landscapes, the seek for food time corresponds to the time that animals use to move through the feeding landscape as they eat. The seek for food time is zero when the FAD is high (e.g. housed cows with no competition at the feed bunk). The current framework does not account for competition at the feed bunk in housed cattle (which would imply an increase in seek for food time with increasing competition). Finally, the time spent ruminating is an important part of feeding behaviour. However, as discussed later, we assume that the rumination time is defined relative to the level of intake. This assumption seems reasonable given the dataset we compiled (see below).

Framework simulation and validation

The framework was implemented, simulated and validated using Python (v3.7). It is available on request to the corresponding author. Sargent (2010) describes various techniques and tests used in model validation. From Sargent's description, we chose the parameter variability (i.e. Sensitivity Analysis) as validation techniques. Traditionally, Sensitivity Analysis consists in changing the values of the inputs and/or parameters of a model to determine which of them have the most significant effect on outputs. To generate these variations in the parameters, we chose Bayesian Inference (BI), as described in Ramirez et al. (2022). Briefly, we performed BI using the Delayed Rejection Adaptive Metropolis (DRAM) algorithm (Miles, 2019) to compute the posterior distributions of 18 parameters. These distributions describe the range of plausible parameter values and the consequence of these values on the fit of the model to the validation data. We used Geweke's value (Geweke, 1992) to check both convergence of the BI procedure, and the sensitivity of the error to the parameter values (i.e. their variability across the Markov chains). We assume that the framework is more sensitive to those parameters with higher Geweke's value.

During BI, the DRAM algorithm uses Euclidean distances between observed and predicted data (DMI, ER and ET) for parameter generation, by rejecting those parameters that increase said distances. To compute these distances, a validation database was built using data from 21 papers when adult Holstein cows were used (Supplementary Materials S1–S3). The parameters related to MST, proportion of the mature ER, and the proportion of the TCT

used for SDA (parameters in Eq. (3), (5) and (7) in Table 1, respectively) were not included in the Sensitivity Analysis because no articles were found with the necessary information for BI. The parameters of these equations were manually identified prior to BI using some reported data (Supplementary Table S2).

Results

Data base

The papers (Supplementary Table S1) report information on 48 and 31 treatments for grazing and housed cows, respectively. Table 2 presents the characteristics of the animals in these papers. It is noteworthy that housed cows were heavier (+142.3 Kg) and with higher milk production (+10.4 Kg) than grazing cows. A total of 638 and 267 animals were used in grazing and housed studies, respectively. The mean, minimum and maximum value of the variables used for BI are presented in Tables 3 and 4. As shown in Table 3, the mean values of ER and ET are very different between both systems, while there is no marked difference for the rumination time. As shown in Table 4, the mean value of peNDF is higher (+21.6%) in grazing than in housed diets. All the papers correspond to research carried out with lactating Holstein cows in Ireland, New Zealand, France and Chile for grazing cows, and in UK, Germany, USA, Iran and Canada for housed cows.

Sensitivity analysis

After 10 000 iterations of the BI, the median, SD and Geweke's value of each parameter were calculated (Table 5). A Geweke's value close to one indicates that the first part of a Markov chain is very similar to the last part of the same chain. We assume that the framework is sensitive to parameters with a high Geweke's value because this means that, during the BI, the algorithm was unable to explore other areas of the parameter space without increasing the error (i.e. the distances between the observed and predicted values). The Geweke's values greater than 0.9 indicate that the framework is sensitive to six of the 18 inferred parameters: two parameters used to estimate the ER, two parameters used to estimate the heat stress effects, and the initial condition of seek for food and rumination in the ODE system.

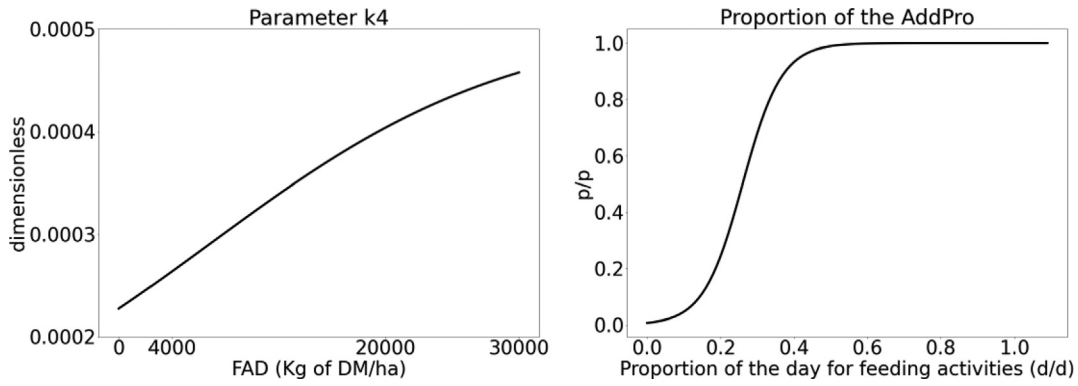


Fig. 6. Modifiers of the additional processing (AddPro) time. For Holstein cows, the left plot shows the changes in the value of the parameter k4 given the food area density (FAD, Kg DM/ha). The right plot shows the change in the proportion of AddPro time given the proportion of the day available for feeding activities.

Table 2

Statistics for BW, milk yield (MY) and composition, and days in milk (DIM) in the database of Holstein cows used for validation of the framework.

System	BW (Kg)			MY (Kg/d)			Milk protein (%)			Milk fat (%)			DIM		
	Mean	min	max	Mean	min	max	Mean	min	max	Mean	min	max	Mean	min	max
Grazing	511.5	460	621	22.5	16.1	28.6	3.3	3.0	3.6	4.0	2.8	4.7	97.2	34	211
Housed	653.8	570	710	32.9	20.0	41.1	3.2	2.8	3.8	3.5	2.9	4.0	98.5	19	195

Table 3

Statistics for eating rate, eating time, and rumination in the database of Holstein cows used for validation of the framework.

System	ER (g DM/min)			ET (min/d)			Rumination (min/d)		
	Mean	min	max	Mean	min	max	Mean	min	max
Grazing	31.2	20.2	48.9	479	263	677	431	327	531
Housed	86.6	37.6	143.4	276	174	412	434	236	606

ER: Eating rate, ET: Eating time.

Table 4

Statistics for physically effective NDF and food area density for diets in the database of Holstein cows used for validation of the framework.

System	peNDF (% DM)			FAD (Kg DM/ha)		
	Mean	min	max	Mean	min	max
Grazing	44.2	33.9	58.3	1 853.4	935	3 362
Housed	22.6	14.1	27.7	NA	NA	NA

Physical NDF content of diet (peNDF), food area density (FAD). All studies with housed cows present peNDF values measured with the same methodology (Mertens, 1997). For the works in grazing, it was assumed that 100% of the NDF of the pasture is peNDF. In housed studies, it was assumed that the FAD was always greater than 20 000 Kg DM/ha.

Simulations

The effects of heat stress, season, and food availability on daily time splitting are presented in Fig. 7. The left plot shows how the thermoregulation time increases as the MDT increases above 25 °C, which reduces the TCT and, consequently, the ET. The middle graph represents the changes in SDA in animals that inhabit the northern hemisphere. In these countries, ET is expected to increase during the summer due to seasonal changes in SDA. The graph to the right shows that seek for food time increases when food is scarce, and that additional processing time increases as food availability increases.

The left plot in Fig. 8 shows the observed intake reported in some papers (Supplementary Table S1) versus the EAI estimated by the framework. The middle plot in the same figure shows a comparison of observed intake reported in heat stress papers (Supplementary Table S2) and the EAI. Finally, the right plot shows a comparison of observed intake reported by Munksgaard et al.

(2020) and the EAI throughout the year. Although the plots in Fig. 8 show that the framework adequately describes some reported data, it is important to point out that these data were used during the BI. This indicates that a formal test, with independent data, is necessary to evaluate the framework.

Discussion

Our framework is not the first approach to predict environmentally constrained intake, indeed the concept has existed at least since the formulation of Conrad et al. (1964), who proposed that as the digestibility of the food increases, there is a point where the physical limitations on the ability to eat fade and the influence of animal production become dominant. Allen et al. (2019) have shown that if intake equations also include the effects of nutritional environment, models would yield better predictions than models based only on animal effects. This partially explains why equations that include only animal factors, and do not account

Table 5
Sensitivity analysis of the parameters in the framework to estimate the environmentally attainable intake of Holstein cows in constraining environments.

Equation	Parameter	Description	Mean	SD	Geweke value
Eq. (2)	a	Minimum mature eating rate	26.3	2.8	1.00
Eq. (2)	b	Maximum mature eating rate = a + b	94.9	16.9	0.89
Eq. (2)	c	Control of the curvature of the sigmoid function	0.22	0.05	0.82
Eq. (2)	d	Inflection point of the curve	25.5	1.9	0.95
Eq. (6)	a	Control of the curvature of the sigmoid function	0.32	0.14	0.90
Eq. (6)	b	Inflection point of the curve	43.6	3.75	0.97
Eqs. (8)–(11)	k1	Flux from seek for food to eating time	1.09e–03	1.41e–04	0.86
Eqs. (8)–(11)	k2	Flux from seek for food to rumination time	2.12e–04	4.64e–05	0.67
Eqs. (8)–(11)	k3	Flux from additional processing to eating time	1.49e–04	2.16e–05	0.75
Eqs. (8)–(11)	k4	Flux from eating to additional processing time	See Eq. (12)		
Eq. (8–11)	Seek[0]	Initial proportion of the feeding time for seek for food	0.77	0.015	0.97
Eq. (8–11)	Rum[0]	Initial proportion of the feeding time for rumination	0.23	0.005	0.94
Eq. (12)	a	Minimum “k4” value	7.25e–05	6.51e–05	0.05
Eq. (12)	b	Maximum “k4” value = a + b	4.4e–04	1.9e–04	0.46
Eq. (12)	c	Control of the curvature of the sigmoid function	8.7e–05	6.4e–05	0.07
Eq. (12)	d	Inflection point of the curve	6 797.2	3 409.5	0.62
Eq. (13)	a	Control of the curvature of the sigmoid function	18.8	11.9	0.22
Eq. (13)	b	Inflection point of the curve	0.26	0.12	0.41

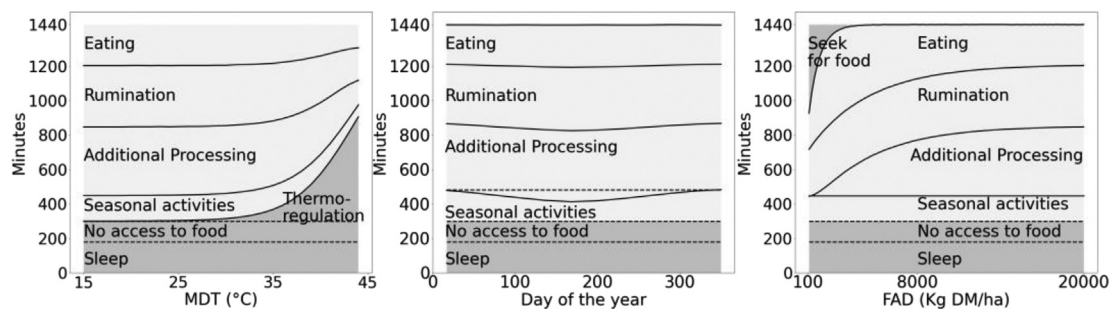


Fig. 7. Changes in the dynamics of animal activities according to changes in environmental conditions. For Holstein cows, the left, middle and right plots show the changes in the time used for each of the activities considered in this framework (min/d), according to the maximum daily temperature (MDT, °C), the day of the year (northern hemisphere), and the food area density (FAD, Kg DM/ha), respectively.

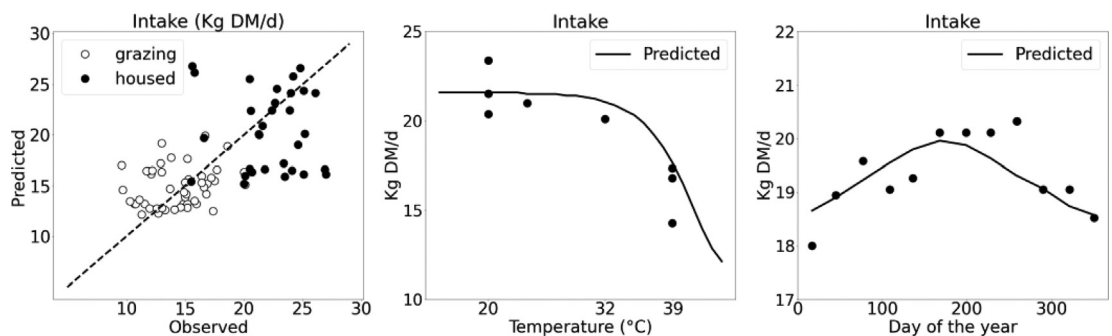


Fig. 8. Environmentally attainable intake (EAI) predicted by the framework relative to literature data. For Holstein cows, the left plot shows the actual intake (open and closed circles for grazing and housed cows, respectively) reported in papers (Supplementary Table S1) versus the EAI estimated by the framework. The middle plot shows a comparison of actual intake (closed circles) reported in heat stress papers (Supplementary Table S2) and the EAI estimated by the framework. The right plot shows a comparison of actual intake (closed circles) reported by Munksgaard et al. (2020) and the EAI estimated by the framework throughout the year.

for e.g. the effects of fill, are likely to over-predict intake for high-producing cows.

Other models that have looked at environmental factors have almost exclusively focused on fill (Allen et al., 2019) or thermal stress (Tao et al., 2020) but to our knowledge, none have combined these and other environmental factors on a time budget available for eating. We acknowledge that in non-constraining environments, animal factors are of major importance for predicting intake, and thus that any complete intake prediction model should include both environmental and animal modules (Poppi, 1996).

However, it is useful for breeders to have a clear distinction between the EAI, and the intake that is required by the animals' genetic potentials. This was the motivation for developing the present framework. As discussed below, it is a necessary prerequisite for prediction models to explore questions such as, which genotypes are best suited to which environments?

Not having a clear distinction between EAI and animal genetics creates unwanted correlations between the underlying physiological mechanisms of resource acquisition and resource allocation in models that aim to characterise the relative importance of such

mechanisms (Puillet et al., 2016). Indeed, such models suggest that animals with different combinations of acquisition and allocation genetics (i.e. not correlated) are better suited to different environments, and these different combinations are beneficial in terms of resilience and efficiency (Puillet et al., 2021; Bouquet et al., 2022). Thus, being able to predict intake in constraining environments independently of animal characteristics is of value. However, a minimal representation of animals is necessary as clearly cows and chickens differ in their 'design', for this, we use the animal type (i.e. Holstein cows) and the animal's age. The framework we developed allows us to estimate the EAI of dairy cows across a range of feeding environments spanning from grazing systems to indoors feeding with total mixed ration. We assume that this framework is valid for both short-term and long-term adverse conditions, since adaptations by animals are not considered.

Our framework is designed to operate with few entries, and to have a simple and generic structure that can be adapted to use more complex representations of environmental effects on intake, should one wish. Although, as described below, each of the framework components can be treated as a complex process in itself, involving many factors (e.g. optimal foraging theory to describe feed harvesting), we chose a usable framework with a minimal representation of the environment, avoid double counting (i.e. each environmental variable is used to calculate only one process in the framework) and minimal process explanation for generic application. In the following section, we discuss the main reasons why the framework structure was chosen.

In the literature, ER has been defined in various ways, including the number of bites per minute or the number of meals per day (Forbes, 2007). When intake is not restricted, this is fast at the beginning of the meal, slows as eating progresses, and plateaus when maximum food intake is reached (Thomas et al., 2017). In this S-shaped dynamic of ER, satiety plays an important role in reaching a plateau at the maximal food intake. Instead, when intake is restricted, we can assume that ER does not follow the dynamic described above because animals are always hungry, the stimulus to compete for food and eat is maximal, and there is no satiety at play.

For grazing cattle, ER has been calculated using bite density, leaf size, spatial arrangement of plant leaves and stems, and the effect of thorns or other physical barriers to eating (Brink and Soder, 2011; Boval and Sauvant, 2021). However, estimating ER using these variables is not easy because often not all this information is available. For simplicity, we chose the peNDF as a predictor for ER because this variable allows the development of a generic equation that can be used in a wide range of situations (from grazing to housed cows), with less complexity than other multivariable methods. For a certain animal, we assume that ER is defined by the food quality, and that food peNDF largely represents this quality. In this manner, when the peNDF is used to estimate ER, this estimation accounts for both the energy value of the food and its ease of harvesting and processing.

To propose the ER equations, we take into account that the motivation to eat is governed by the animals' internal state (Gregorini et al., 2013), and we assume that in constrained environments, animals are always, by definition, hungry. Some authors (Chilibroste et al., 2007; Gregorini et al., 2011) suggest that hunger reduces the oral processing of food through a reduction in mastication. This is a compensatory mechanism to increase short-term intake rate, swallowing boluses with larger particles and thus increasing rumen retention time. Although greater bite rates for hungrier cows have been reported (Chilibroste et al., 2007; Gregorini et al., 2009), we assume that this behaviour is not sustainable for a long time because the balance between the energy cost of eating and the energy gained from eating is important for

animals facing adverse conditions. These animals will only increase their ER if this represents an increase in energy gained.

On the other hand, ER is age-dependent because the chewing force depends on the animal's craniofacial morphology, which increases with age. We assume that biting force can be explained by the hard structures of the animal's mouth, in particular, the incisor arcade breadth because this is a determinant animal factor for bite area and hence for bite mass. Boval and Sauvant (2021) found that arcade has the lowest error among some predictive equations of bite mass. Additionally, we assume that animals of the same age have the same oral capacity. In heifers and multiparous lactating cows, Cangiano et al. (2002) found that differences in incisor arcade breadth between animals of the same weight were minimal.

The second main component of our framework, the ET, is not entirely new. The use of time to estimate intake has been previously used. For example, Nørgaard and Mølbak (2001) presented a linear model to estimate the energy intake using the dietary chewing index value of diets, proposed by Balch (1971), for dairy cows and steers. This model was adapted by Nielsen et al. (2015) to study the relationship between energy intake and chewing index of diets fed to pregnant ewes. In this model, the chewing index expressed as minutes per kilogram of DM of a feed is estimated as the sum of the eating index (min/Kg of DM) and the rumination index (min/Kg of DM).

To develop the ET component in the framework, we follow the idea that feeding time is highly correlated with intake (Pahl et al., 2016). This implies that estimating ET is a useful aspect of intake estimations. We assume that the daily time that animals have for eating is restricted by some farm activities that prevent free access to food and by the trade-offs between feeding and other vital functions (sleep, resting, sexual and social behaviour, etc.). We classified these functions into two groups: seasonal and non-seasonal. In our framework, resting does not include sleep because, as well as sexual and social behaviours, resting is considered as a seasonal dependent function while that changes in sleep are more associated with the animals' age.

Sleep is one of the essential behaviours in mammalian health and welfare. In general, prey sleep less than predators, since prey need to spend more time searching for and processing food. Measuring the minimum time that dairy cows need to sleep is not easy. The recognised gold standard for assessing sleep is polysomnography (Van De Water et al., 2011) but it is a time-consuming and impractical method for sleep identification in dairy cows managed under standard farm conditions (Hunter et al., 2021). In our framework, we assume that regardless of environmental conditions cows need a minimum daily time to sleep and this time changes with age (Hänninen, 2007).

Heat stress is an important factor that must be considered in challenging environments because rising ambient temperature is one of the most relevant factors that reduces intake in calves and heifers (Wang et al., 2020), and adult cows (Tao et al., 2020). To represent the effect of heat stress, we assume that thermoregulation occurs at the expense of seasonal and feeding activities, because during heat stress, cows prefer to stand to increase the body surface available for cooling (Wang et al., 2018). Although the maximum ambient temperature is used in our framework to represent the effect of heat stress on intake, it is possible to adapt the equation to use multiple variables (e.g. temperature-humidity index, THI), and even thermal radiation and air fluxes. In our framework, heat stress does not affect the time when animals do not have access to food, nor their sleep time. This simplification is needed to avoid double counting time. We judged that this was an acceptable simplification because when animals are constrained by farm management, they generally are limited in their ability to deal with heat stress, and sleep is minimally affected

because animals usually sleep at night when heat stress is less pronounced. In practice, for a framework user, this would mean adjusting their input values for these times to take into account any observed overlap.

The remaining time, that is the thermally comfortable time with access to food, can be used by animals to carry out seasonally dependent and feeding activities. Although sexual and social behaviours are part of the seasonal functions, we consider that resting is the most relevant. Cow behaviour is known to have seasonal variations. Munksgaard et al. (2020) found that the lying time was longer during winter than during summer, and both the duration of eating per day and activity were influenced by the month of the year. Although these changes could be attributed in part to variations in temperature, the photoperiod and endogenous circannual rhythms also play an important role in determining dairy cow behaviour throughout the year (Chemineau et al., 2007). In our framework, the resting time increases linearly as the length of the daylight decreases. This approach allows us to represent the changes in seasonal activities throughout the year.

Following the logic of our framework, the time available for feeding activities, and therefore the time available to eat, is that which remains after subtracting the time in which animals do not have access to food, sleep, control their body temperature and rest (i.e. non-feeding activities). It would have been possible to simplify even further by requesting as an input only the time available for feeding activities within the day (the lower left-hand box in Fig. 2). However, by including the non-feeding activities in the framework, we have provided significant flexibility to recalibrate to other species and also provided entry points into the framework for more detailed descriptions of these classes of activities. Either way, the resulting time available for feeding activities provides the basis for estimating intake in constrained environments. The final equations (Eqs. (8)–(13) in Table 1) are devoted to apportioning the feeding time between the feeding activities: seek for food, eating, rumination, and additional processing. In this approach, seek for food is only relevant at low food densities (e.g. grazing), rumination is proportional to intake, and animals need an additional processing time when the ER is high (i.e. indoors feeding with total mixed ration).

With respect to seek for food, some authors (Anselme and Güntürkün, 2019) suggest that the low motivation to eat when food is available at high density is an adaptation to remain fast and agile to escape from predatory attacks. In contrast, the higher motivation to eat when food is scarce is an adaptation to get the energy required to stay alive. These concepts indicate that when food is scarce, animals cover large areas to support life. Utsumi et al. (2009) found that the travel speed of dairy cows between patches, patch residence time, and depletion increased with increasing distance between patches. Gregorini et al. (2011) found that the restriction of time at pasture affects the eating step length, the velocity of walking, the distance walked and the area explored, while cows are grazing. All these behaviours can be explained by the “incentive hope” concept. This is a motivational state in which animals increase their behaviours of seeking, hoarding, and/or consuming food to avoid the risks of starvation (Clark, 2019). The uncertainty in the size, frequency, and delay with which the food will be found increases the value of the food found and instills hope that this reward will be reached once again in the near future (Robinson, 2019).

We assume that under adverse conditions, animals try to use their maximum food-seeking capacity to maximise intake. However, this condition cannot be sustained for a long time because food search requires both energy and time. The selection of speeds between feeding patches is affected by the energy costs of movement, the probability of detecting predators or being detected by one, and the energy costs of losing opportunities to eat while

travelling (Wilson et al., 2015). According to the marginal value theorem (Charnov, 1976), in a “patchy habitat”, the animal must make decisions about which patches to visit and how long to stay in each one. The animal should leave the patch it is presently in when the marginal gain rate in the patch drops to the average gain rate for the habitat. In the present study, we chose to simplify by representing a drop-off in seek for food with increasing food area density.

Finally, it is well accepted that rumination depends on the hardness, rigidity and density of the particles present in the rumen and the speed at which they break into small pieces. If all these food characteristics are largely explained with the peNDF content of food, it is expected that the rumination time increases with increasing peNDF in the diet (Yang and Beauchemin, 2006). However, as explained above, we chose to use peNDF to estimate ER and not rumination because we assumed that, under challenging conditions, the time spent ruminating is primarily defined by the level of intake (i.e. ET) rather than the quality of intake. For simplicity, we also assumed that rumination could not occur during resting time. This is because the resting time is defined as the minimum resting time; i.e. it is an active need for pure rest and thus not used for rumination. The same was assumed for sleep and non-access to food time. It would not be difficult to adjust the framework to assume that a proportion of these times was available for rumination but that requires data to estimate this parameter, which were not readily available in the literature.

Conclusion

A time-based framework for predicting intake in constraining environments has been developed and shown to adequately describe EAI in both grazing and housed cows. The mean absolute errors for intake were 2.4 and 4.2 Kg DM/d for grazing and housed cows, respectively. The framework minimises correlations between animal and environmental characteristics suitable. It is simple, suitable for use with resource acquisition-allocation models, and could be readily adapted for use in other livestock species.

Supplementary material

Supplementary material to this article can be found online at <https://doi.org/10.1016/j.animal.2023.100799>.

Ethics approval

No approval is needed for this study.

Data and model availability statement

The data that support the study findings are publicly available as [supplementary material](#), and the Python code for the framework is accessible upon request to the corresponding author.

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Author contributions

JFRA, LP and NCF drafted the paper. JFRA developed the database and code for BI. All authors read and approved the final manuscript.

Declaration of interest

The authors declare that they have no competing interests.

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