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Invited review: Disentangling residual feed intake—Insights and approaches to make it more fit for purpose in the modern context

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ABSTRACT

Residual feed intake (RFI) is an increasingly used trait to analyze feed efficiency in livestock, and in some sectors such as dairy cattle, it is one of the most frequently used traits. Although the principle for calculating RFI is always the same (i.e., using the residual of a regression of intake on performance predictors), a wide range of models are found in the literature, with different predictors, different ways of considering intake, and more recently, different statistical approaches. Consequently, the results are not easily comparable from one study to another as they reflect different biological variabilities, and the relationship between the residual (i.e., RFI) and the underlying true efficiency also differs. In this review, the components of the RFI equation are explored with respect to the underlying biological processes. The aim of this decomposition is to provide a better understanding of which of the processes in this complex trait contribute significantly to the individual variability in efficiency. The intricacies associated with the residual term, as well as the energy sinks and the intake term, are broken down and discussed. Based on this exploration as well as on some recent literature, new forms of the RFI equation are proposed to better separate the efficiency terms from errors and inaccuracies. The review also considers the time period of measurement of RFI. This is a key consideration for the accuracy of the RFI estimation itself, and also for understanding the relationships between short-term efficiency, animal resilience, and long-term efficiency. As livestock production moves toward sustainable efficiency, these considerations are increasingly important to bring to bear in RFI estimations.

Key words: feed efficiency, biological processes, individual variation, resilience

INTRODUCTION

Improving feed efficiency is of major interest for livestock production, and thus it is not surprising that there has been an increasing number of publications reporting efficiency results. This is especially the case for studies using the residual feed intake (RFI) method. The RFI method is designed to quantify between-animal variation in efficiency, and it is well suited to use in genetic evaluation and breeding schemes because it does not derive efficiency as a ratio between production and intake. However, as has been reviewed elsewhere (Berry and Crowley, 2013; Kenny et al., 2018), there is a confusing array of RFI results, correlations, and heritabilities that are not easy to compare because of differences in the RFI models used, which often makes biological interpretation impossible.

The variability in feed efficiency may hide different biologic realities (Cantalapiedra-Hijar et al., 2018). As shown in Figure 1, animals may vary in their digestive efficiency (i.e., the conversion of feed into nutrients) or in their metabolic efficiency (i.e., the conversion of nutrients into products). It can be envisaged that (in a given feeding environment) the same overall efficiency may be achieved by different combinations of digestive and metabolic efficiencies. Within that feeding environment, these differences may be of no consequence, but may well become important in other environments. For instance, an animal that has a higher metabolic efficiency because it partitions more of its energy to milk and less to maintaining body reserves may not be penalized in abundant nutritional environments, but will probably not cope well in nutritional environments with feed shortages where it needs its body reserves.

A further limitation of most RFI models is that they typically calculate RFI for a fixed time interval, usually a short one (typically a few months), and are not adapted to characterizing long-term RFI (the entire productive life) or time-trends in RFI. These longer-term measures are important in the context of selecting for sustainable efficiency. Indeed, gains in short-term efficiency have been associated with negative conse-

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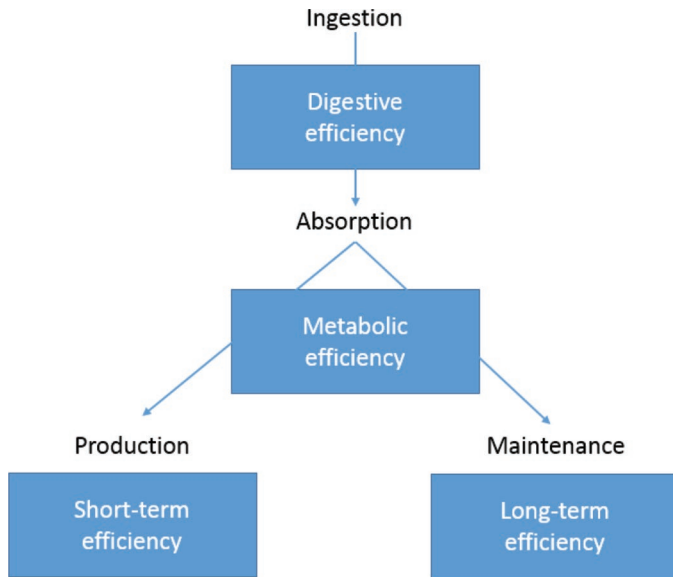


Figure 1. Classes of efficiency. “Maintenance” is considered to include all the nonproductive life functions that can contribute positively to longevity.

quences in the longer term, for instance on fertility and length of productive life (Vallimont et al., 2013; Puillet et al., 2016). As can be seen in Figure 1, favoring higher production can cause a trade-off with the other life functions that underpin animal robustness and lifetime efficiency. The issue of trade-offs is more fully discussed in Friggens et al. (2017).

Accordingly, the aim of this paper is to first examine the RFI method from a biological and theoretical basis to clarify the key questions related to the interpretation of RFI results, before then tackling some of the more pragmatic and statistical considerations. Approaches that overcome the current limitations of RFI methods are identified, and specific focus is given to making the RFI method more adapted to the modern context of precision livestock data and to the need to improve efficiency in a sustainable way. Readers looking for full reviews of the existing RFI literature and its comparison with other efficiency metrics are referred to Berry and Crowley (2013) or Cantalapiedra-Hijar et al. (2018).

BASIS OF THE RFI EQUATION AND KEY QUESTIONS

The RFI equation is generally constructed from the following base:

$$\text{Intake} = \text{intercept} + a \times \text{predictor}_a + b \times \text{predictor}_b + c \times \text{predictor}_c + [\dots] + \text{RFI}, [1]$$

where RFI is the residual of the model. Linear regression is used to determine, for a given group animals on a given diet, the values of the regression coefficients a , b , c ... as well as the intercept, but typically with only 1 observation per animal. In theory, the residual (i.e., RFI) captures differences in efficiency. Animals with a negative value of RFI have an observed intake that is less than that predicted for the group and, as such, are deemed to be more efficient because they have eaten less for a given production level (or produced more for a given intake level). Following the same logic, animals with a positive RFI are deemed to be less efficient.

The different predictors (i.e., factors considered in the intake prediction) are energy sinks. These include processes that consume energy such as milk production, growth, and maintenance, or internal energy sources such as use of body reserves. Because it provides a good biological context for highlighting most of the key issues concerning RFI, the rest of this paper focuses on RFI estimation in lactating animals. The RFI equation raises several questions:

- What is actually contained in the residual? As a residual, it is expected to contain both the biological variability in intake not explained by the model and any errors in measurement or in the model structure. The biological part of the residual, which equates to true differences in efficiency, is the part we wish to isolate. Is it possible to distinguish these different components, and if so, how best to do this? Alternatively, can we reduce the error component of RFI? This is explored in the section “Nature of the residual.”
- What is the biological meaning of the intercept? From a theoretical point of view, the RFI equation should not have an intercept. This is evident if we consider it on an energy basis because the sum of true energy outputs is always equal to the true energy input. However, in practice there may be reasons to include an intercept in this kind of model, which are discussed in more detail in the section “Nature of the residual” (and “Intake and digestive efficiency”) below.
- Which predictors for the intake should be included in the equation? In other words, which predictors do we consider as being “required or essential energy sinks” for an animal, and which of these are likely to be the major determinants of feed efficiency differences? When more predictors are included in the model, the model performs better in terms of properly accounting for resource usage. However, when more is explained with the equation, less variability remains in the residuals

Table 1. Abbreviations used in this article

Abbreviation	Meaning
BCS	Body condition score
BW	Body weight
<i>ed</i>	Energy density (assumed digestive efficiency)
<i>ded</i>	Deviations from the assumed digestive efficiency
DMI	Dry matter intake
<i>ef</i>	Errors in fitting
<i>eim</i>	Errors in measurement
FI	Feed intake
<i>imf</i>	Individual variability in metabolic efficiency from the identified energy sinks
<i>ues</i>	Unidentified energy sinks
Δ BW	Changes in body weight (gain or loss)
Δ BCS	Changes in body condition score (gain or loss)

as well as a greater proportion of the residuals that is simply noise (the error). In addition, many predictors are not easy to measure (e.g., heat production, gestation). How do we include them in the equation? Where do we stop? This issue is detailed in the section “Nature of the predictors.”

- An issue that emerges when considering how to rationalize the predictors relates to how they change with time. As the animal moves through different physiological stages, the relative importance of different predictors in the RFI estimation will change, and this may impact between-animal variation in these changes. For example, animals vary in the extent and duration of body reserves mobilization in early lactation, which has significant consequences on their subsequent reproductive efficiency. Capturing these time-trends requires time-series measures of the predictors, intake, and an expansion of the classical RFI model to deal with these repeated measures. Having such measures offers considerable opportunities for quantifying the relative importance of the different biological components of RFI. Approaches to do this and the benefits of so doing are discussed in the section “Incorporating time-trends in predictors.”
- Another key question is: how do we consider and incorporate intake data? This is especially important if data from multiple feeds or feeding situations are being used. If we use kilograms of DM, then the coefficients a , b , c . . . are composite values of both digestive and metabolic efficiency (because they include the conversion from DM to energy equivalents). If net energy (NE) is used, then, in theory, the digestive efficiency disappears from the coefficients. However, as the conversion of kilograms of DM to megajoules of NE assumes a constant digestive efficiency for all, then any interindividual variability for digestibility would

“pollute” the residual, and maybe the other coefficients. A reflection on digestibility and its inclusion into the equation is presented in the section “Intake and digestive efficiency.”

As several abbreviations are used in the development of the ideas and equations, their meanings are listed in Table 1 for ease of understanding.

NATURE OF THE RESIDUAL

As previously said, the RFI is the residual of the equation (Eq. 1); therefore, it contains not only the feed efficiency variability, but also all of the errors and imprecisions in the data and the RFI model. The residual can be considered to consist of the following: errors in measurement (*eim*), errors in fitting (*ef*), unidentified energy sinks (*ues*), deviations from the assumed average digestibility (*ded*), individual variability in metabolic efficiency from the identified energy sinks (*imf*), and a possible nonexplained part (ε_i). We will start by ignoring *ded* because this is more conveniently treated on the left-hand side of the RFI equation, which contains information about intake. Thus, the equation for the residual is as follows:

$$\text{Residual} = eim + ef + ues (+ ded) + imf + \varepsilon_i \quad [2]$$

where the properties of each of these components of the residual are discussed below.

The *eim* should be random noise with a population mean of zero, but there may be a nonzero mean if there is a global bias in (one of) the measures. There may be individuals with systematic measurement errors (e.g., a cow who systematically spills more feed than the rest of the group or who systematically steals feed from others). The *ef* would be due to 1 of 3 issues. The first would be ignoring a nonlinear response to 1 of the predictor energy sinks, which implies variable

efficiencies for that process. This is more complex to deal with and should only be considered when the possibilities below have been discounted. The second issue is an unclear calculation of an energy sink that then gives the illusion of a variable efficiency. An example of this, discussed more in the following section, is using the change in body weight (ΔBW) as an energy sink rather than separating it into the underlying changes in body lipid and body protein. Such a separation would then resolve the apparent *eif*. This example is really due to an *ues* (changes in body lipid and body protein are not explicitly considered as energy sinks), and it is to be expected that approximately all *eif* issues can be reconsidered as *ues*. The third issue is real *eif* (i.e., efficiencies differ according to performance level). These could result in a nonzero population mean of *eif* and may include individual differences (e.g., high vs. low producers). Real *eif* would imply a need for nonlinear RFI models. However, as shown subsequently, the 2 main sources of *eif* identified in the literature—an effect of intake level on digestibility and changing maintenance requirements as the proportion of metabolically active tissues increases with performance level—can be accommodated without the need for nonlinear models. The *ues* can give a nonzero population mean (e.g., when ignoring animal activity levels) and may include individual differences (e.g., an animal with systematically a greater activity than the population mean). Given the technical difficulty of measuring all energy sinks, *ues* cannot be ignored and may include some “true” components of feed efficiency. For the *imf*, the individual variability in metabolic efficiency is what is sought to be captured with RFI; it is a “true” component of feed efficiency. The population mean per definition is zero.

Given these considerations, it is now possible to look at the residual in terms of these components and specifically identify systematic elements (mean values, indicated by a bar) and animal-specific elements (indicated by subscript i). Thus, the residual is defined as follows:

$$\text{Residual} = \overline{eim} + \overline{eif} + \overline{ues} + eim_i + eif_i + ues_i + imf_i + \varepsilon_i. \quad [3]$$

By definition, the mean value of *imf* is zero. By including Eq. 3 in Eq. 1, a new intercept is created equal to $\overline{eim} + \overline{eif} + \overline{ues}$, and the residual term is now centered on zero:

$$\text{Intake} = \overline{eim} + \overline{eif} + \overline{ues} + a \times \text{predictor1} + b \times \text{predictor2} + [\dots] + eim_i + eif_i + ues_i + imf_i + \varepsilon_i, \quad [4]$$

Thus, the intercept adjusts for systematic errors in the RFI data and equation based on a mean value common among all individuals. Its presence is not mandatory (we hope for a zero intercept), but it may help to deal with reality, and, as such, can be useful to provide a meaningful term for these unaccounted systematic effects.

It is interesting to differentiate the components of RFI with a subscript i , and in particular to isolate the “true” individual variation in efficiency (i.e., ded_i and imf_i). However, in practice, it is hard to see how to do this (the special case of ded_i is dealt with in the “Intake and Digestive Efficiency” section), and the appropriate alternative approach would be considering them all in one. Considering them all in one assumes that all these individual deviations can be considered, in practice, as elements of global differences in efficiency between individuals. This is pragmatic, but may be dangerous if the size of these elements is affected by the local production environment. For example, ues_i may include the costs of feeding behavior or activity. These will clearly differ in extensive grazing versus indoors feeding situations, and would probably be considered as beneficial to the efficiency of the grazing animal but not to the housed animal. In the same way, an animal that is systematically good at sorting its diet (resulting in its intake having a higher energy density than that of an animal on the same feed who does not sort) could be considered as being more efficient when the environment provides a heterogeneous feed (i.e., with an opportunity to sort), but would lose this advantage when on homogeneous feeds. Thus, even if no differentiation is done between the components of the residual in RFI calculation, it remains important to keep them in mind together with a detailed description of the environment (and the measurement methods). This applies not just to the interpretation of animal variability in RFI, but also to how farm, year or experiment effects are fitted in these models.

NATURE OF THE PREDICTORS

The predictors of intake in our equation are, by definition, all energy sinks (or supplies in case of body reserve mobilization) that explain changes in intake. If some appear obvious to consider, such as milk production, growth, or body reserves changes, it is not as simple to consider other predictors such as activity and heat diffusion, or other effects such as fertility needs. To deal with this fact, we can propose that energy sinks can be of 2 types: those that are part of production (e.g., milk, meat, fetus) and those that are part of fighting entropy (e.g., maintaining the machinery, protein turnover, immune function). In both cases, the benefits

of including additional predictors should be weighed against the methodological difficulties of measuring them and the associated measurement errors that they may bring to the estimation of RFI.

From a biological perspective, it is a useful simplification to postulate that every production is either lipid or protein. This is because the underlying biological efficiencies of protein and lipid production are quite different from each other. Therefore, lipids and proteins can be divided into milk lipid and milk protein (considering that milk lactose is tightly linked to milk protein, and thus can be merged with the protein cost), growth lipid and growth protein, and body lipid reserves and body protein reserves. The second possible simplifying assumption is that the cost of creating 1 g of lipid is the same, regardless of the production it is associated with (e.g., milk, growth). The assumption is also to a large extent the same for protein (we ignore possible minor differences in costs between growth and milk production), but it has been known for a long time that the efficiency of synthesis is much lower for proteins than for lipids (e.g., 0.45 vs. 0.75 in rats; Pullar and Webster, 1977; and 0.35 vs. 0.60 in cattle; Geay, 1984).

Using the assumption above, we accept that a production cost corresponds to the energy of the production itself (39.6 MJ/kg of lipid and 23.8 MJ/kg of protein) plus the work of building and disassembling the product (i.e., the efficiencies of these processes). However, as the work of building and disassembling molecules have different costs (for lipid and protein in ruminants see Friggens et al. 2007b), the equation should differentiate between accretion (\oplus) and catabolism (\ominus) as follows:

$$\text{Intake} = a \times \text{lipids}^{\oplus} + b \times \text{lipids}^{\ominus} + c \times \text{proteins}^{\oplus} + d \times \text{proteins}^{\ominus} + \text{maintenance} + \text{RFI}. \quad [5]$$

For a product such as milk, a well-established approach to deal with its variation in lipid and protein content is to express milk as fat- and protein-corrected milk (i.e., adjust milk volume to a standard fat and protein content). Alternatively, and in coherence with the above postulate, we could use milk fat yield and milk protein yield in Eq. 5. For growth, where it is much more difficult to precisely measure the composition of growth, it is useful to use BCS in combination with BW to indirectly obtain body protein change and body lipid change. Other methods exist (e.g., calorimetry), but only on limited data. Changes in body protein and especially body lipid will also capture usage of body reserves (by definition, catabolism only occurs for body

reserves). The details for doing this are developed elsewhere (e.g., Friggens et al., 2007b), but this boils down to having changes in BW and BCS (Δ BW and Δ BCS), and their interaction in the following equation:

$$\begin{aligned} \text{Intake} = & a \times \text{BW}^{\oplus} + b \times \text{BW}^{\ominus} + c \times \text{BCS}^{\oplus} \\ & + d \times \text{BCS}^{\ominus} + e \times \text{BW} \times \text{BCS}^{\oplus} + f \times \text{BW} \times \text{BCS}^{\ominus} \\ & + g \cdot \text{MLY} + h \cdot \text{MPY} + \text{maintenance} + \text{RFI}, \end{aligned} \quad [6]$$

where MLY = milk fat yield, MPY = milk protein yield, and a through h are regression coefficients.

Equation 6 raises a problem with respect to its resolution, as 6 different terms need to be estimated from only 2 different measures (BW and BCS). This will cause obvious correlations among the predictors and make resolution difficult, if not impossible. In addition, for any given time interval between 2 consecutive measures, it is not possible to distinguish what was gained and what was lost in that interval, with only the net difference (Δ) between those 2 being accessible. In classical RFI approaches, this will very likely lead to an unwanted *ues* in the residual, affecting the RFI estimates as it has been shown that there are differences between individual cows in their patterns of body reserve change (Banos et al., 2005; Kessel et al., 2008). This problem is revisited in the section “Incorporating time-trends in predictors.”

With respect to the second component, fighting entropy, the only function routinely considered in the literature is maintenance. Maintenance is usually included through the metabolic weight. But in terms of energy, similar to production, the maintenance costs are different between lipids and proteins; therefore, as a minimum, the maintenance should not only be a function of the metabolic weight but also of the BCS. The equation for adjusting BW to a standard body fat content is

$$\text{EBW}_{\text{std}} = \text{EBW} \times \frac{1 - 2(\text{BCS} - \pm)}{1 - 2(\text{BCS}_{\text{std}} - \pm)}, \quad [7]$$

where EBW is empty body weight (i.e., the animal weight without the digestive content), and std implies a given standard BCS (e.g., 2.75). The assumptions needed to do this (linear relation between BCS and body lipid content) are outlined in Friggens et al. (2007b). In Eq. 7, the coefficients α and β are assumed to be known but depend on the mature size of the breed and on the condition score scale used (Zygoiannis et al., 1997; Roche et al., 2004). Typical values estimated

from dairy cattle data are $\alpha = 0.5$ and $\beta = 0.1$ (Friggens et al., 2007b). If the reasonable assumption is made that gutfill is a constant proportion of empty BW, then the equation above is exactly the same for BW. Thus, the predictor for maintenance, $BW^{0.75}$, in the RFI equation can be replaced by $BW_{\text{std}}^{0.75}$, thereby eliminating spurious variation in maintenance requirements due to differences in body fatness.

There is also an issue related to maintenance costs associated with “more active than average” tissues or organs, which emphasizes the importance to finding ways to estimate the size of these tissues relative to the whole animal. Maintenance includes the maintenance of the digestive tract, but metabolic BW does not account for the changes in digestive tract size happening throughout the lactation nor the changes in digestive protein secretion. The intake capacity of the cow increases significantly during the first weeks of lactation (i.e., the size of the digestive tract increases), which, as a highly active tissue, implies an increase of maintenance requirements (Tulloh, 1966; Smith and Baldwin, 1974). In practice, this issue is in some way going to be linked to intake levels. This will be dealt with below (section “Intake and Digestive Efficiency”).

The question arises: what other aspects of “fighting entropy” could be included (or to what extent they are indexed on maintenance)? From a physiological perspective, it would seem reasonable to include variables such as immunity costs, resilience mechanisms, and activity. However, there is currently almost no quantitative basis for including these specific components, with the possible exception of activity. The extent to which differences in RFI can be explained by accelerometer and body temperature measures can be approached from 2 perspectives, purely in terms of energetics or as proxies for resilience. From the energetics perspective, differences in overall activity will be associated with a direct energy cost of movement, and, likewise, differences in the mean temperature of animals reflect a higher thermodynamic cost. As such, activity and temperature measures could be expected to explain a part of the variance in RFI. From the resilience perspective, high-frequency time-series measures of activity, milk yield, BW, and other indicators such as animal temperature are currently being explored as proxies to estimate the numbers of perturbations an animal experiences during a given time period (Adriaens et al., 2020; Poppe et al., 2020). Assuming that the animal responses to these perturbations have an energetic cost for the animal (i.e., activating the underlying physiological and immunological resilience mechanisms), then it is expected that such proxies (e.g., number of perturbations, cumulated loss, residual standard deviation of production

records) may be usefully incorporated into efficiency considerations (Berghof et al., 2019).

Although this offers avenues for including resilience aspects in the efficiency method, it will not cover all aspects as is. For instance, the potential negative effect of increased production on probability of successfully reproducing would not be captured. Intuitively, it does not seem reasonable to directly include these in RFI. However, if RFI is measured over long enough periods, a penalty emerging via those animals that drop out of the herd early should be seen. In other words, resilience comes into the picture via productive lifespan when considering long-term efficiency. With respect to short-term efficiency, especially the case of growing animals reared for meat production, it is harder to see how to incorporate the notion of resilience. The question is important because the aim is to avoid selecting traits that favor short-term efficiency to the detriment of resilience. The issues of resilience and long-term efficiency are discussed in the final section of this paper.

INCORPORATING TIME TREND IN PREDICTORS

Because RFI requires individual data of feed intake, usually expressed as DMI, most of the pre-existing discussion on the time period over which RFI is estimated has focused on how short a time period can be used. These discussions typically pit the negative effect of a shorter period of measure on the accuracy of estimates against the high cost of phenotyping DMI for a longer period. The repeatability of intake measurements is indeed not that high, often ranging from 0.5 to 0.7 in early lactation for weekly measure in dairy (Potts et al., 2015; Li et al., 2016; Connor et al., 2019). We can consider from the literature on beef cattle that 5 wk of measurement is a minimum for intake data (Archer et al., 1997; Archer and Bergh, 2000; Wang et al., 2006), with a consensus that a measurement period of around 70 d is a reasonable length for RFI, corroborated by dairy studies (Connor et al., 2019). Furthermore, intake data are not the only sensitive measurements that have an effect on the RFI. Body weight is also a key and tricky measurement. Depending on the feed inside the digestive tract, the live weight may vary up to 40 to 50 kg, enough to hide real changes in body condition, and hence body reserves.

Within the classical RFI model, there are also biological considerations for limiting the measurement period. If the measurement period is sufficiently short to be able to assume that it is not containing a mix of body accretion and mobilization, then the problem of Eq. 6 having too many correlated predictors can be addressed through the following simplification:

$$\begin{aligned} \text{Intake} = & (a + \text{BW}_{\text{SIGN}} \times b) \times \Delta\text{BW} \\ & + (c + \text{BCS}_{\text{SIGN}} \times d) \times \Delta\text{BCS} \\ & + \text{other predictors} + \text{RFI}, \end{aligned} \quad [8]$$

where BW_{SIGN} is a 0/1 variable, which is 1 when ΔBW is negative, and BCS_{SIGN} is the same but applied to ΔBCS . Clearly, if the intervals over which these deltas are measured are short enough, then in any one interval, there will be no significant mixing of gain and loss. Assuming this was feasible (i.e., that measurement error is adequately dealt with), it allows to simplify further:

$$\begin{aligned} \text{Intake} = & a' \times \Delta\text{BW} + b' \times \Delta\text{BCS} \\ & + \text{other predictors} + \text{RFI}, \end{aligned} \quad [9]$$

with the consequence that the values of a' and b' [(that correspond to $(a + \text{BWSIGN} \times b)$ and $(c + \text{BWSIGN} \times d)$ at a given time, respectively] differ at different times (e.g., stages of lactation). All potential interactions would be included in the term “other predictors.” The possibility of comparing coefficients across different stages of lactation has been explored further (DEFFILAIT project, unpublished; www.deffilait.fr). However, the results suggest that with manual recording of BW and BCS, typically on a weekly or even monthly basis, it is not realistic to expect that the estimates of ΔBW , and especially ΔBCS , are sufficiently accurate for this approach. However, if high-frequency automated BW and BCS recording is done (e.g., at

each milking; Fischer et al., 2015), then the approach becomes feasible. The logical conclusion of this is to describe these coefficients as function of time (e.g., dependent on the days in milk).

Because precision livestock technologies provide high-frequency repeated measures, it becomes possible to move from classical methods where RFI is a point-measure for a given period to methods that explore the differences between animals in their trajectories of RFI through time. For example, Martin et al. (2020) have recently shown that animal variation in RFI trajectories over the entire lactation can be derived from a multitrait random regression model using repeated measures of milk yield, BW, BCS, and DMI (in this case described by third-order Legendre polynomials). As shown in Figure 2, this enables the estimation of the correlations between the predicted intake and each of its predictors (milk, BW, and BCS) at each time point. Therefore, it is possible to have an indication of the relative importance of the different energy sinks in RFI at different stages of lactation. Because of the smoothing of the time-series within the model, and the continuous daily estimates of RFI, the whole problem of the length of measurement periods is circumvented, as is the problem of mixing body reserve accretion and mobilization. Considering the massive changes expected in early lactation, it could be more efficient to use splines rather than Legendre polynomials. The number of knots and degrees of polynomials between each knot would need to be defined, but there are precedents for this (Friggens et al., 2007a).

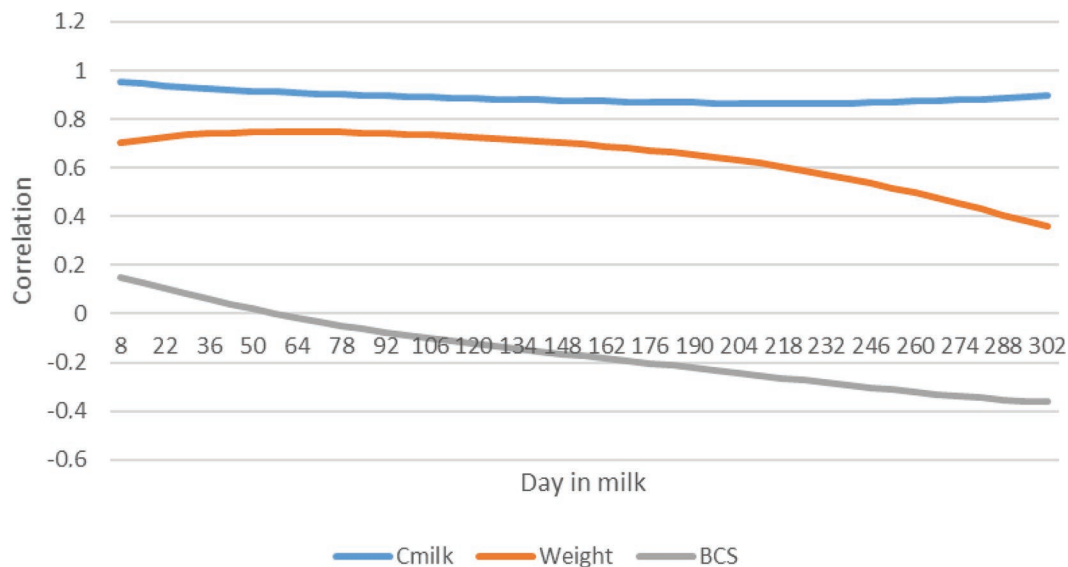


Figure 2. Correlation between the predicted intake and the animal effects of its predictors [fat- and protein-corrected milk (Cmilk), BW (Weight), and BCS] across the lactation. Figure adapted from Martin et al. (2020).

Models of this type also open the door to a better biological interpretation of RFI. Classical RFI allows identification of animals that are more, or less, efficient (assuming that the errors described in the section “Nature of the residual” are properly dealt with), but cannot shed light on which biological components of the efficiency complex contribute to differences in feed efficiency. The paper of Fischer et al. (2018), building on previous studies (Aggrey and Rekaya, 2013; on birds; and Savietto et al., 2014; on beef), explored a new method to isolate the cow-specific part of residual energy intake from the residual. It consists of including a random component to the coefficients in the RFI equation, and thus capturing the interindividual variation in efficiency. In theory, models of this type, which exploit the repeated measures structure of precision livestock data, can quantify which biological components are underpinning differences in efficiency. Although the approach is promising, it has shown itself to present some statistical challenges with difficulties to fit the equation because of correlations among the factors. The papers listed above have been able to overcome some of the issues by normalizing the predictor measures, by exploiting different correlation structures, and by using more powerful software. Fischer et al. (2018) used SAS, which is not able to easily take correlations into account; Martin et al. (2020) used Wombat (Meyer, 2007), which allows the user to better estimate them, and eventually restrict the rank of the matrix. However, these methods are also data hungry, requiring large numbers of animals and large numbers of measures per animal.

INTAKE AND DIGESTIVE EFFICIENCY

The base measure of intake is DMI per day (we assume here that the methods for converting fresh matter intake into DM do not introduce bias in the RFI calculations; Seymour et al., 2019), but of course when efficiency is considered, consideration should be given to the energy density of the diet. If the aim is to pool data sets from different trials or locations—this would certainly be needed in the context of large-scale genetic evaluation of RFI—then the differences in energy density of the feed need to be accounted for. The literature offers ideas on how to deal with this issue [e.g., Tempelman et al. (2015) and Lu et al. (2017) use random ration-specific regressions of DMI on milk energy and BW], but to get a comprehensive understanding of the point, let us go into details. Even within a given situation where the feed is the same for all animals, there are important issues for the RFI method.

Energy intake can be described in terms of gross energy, digestible energy, metabolic energy, and NE as follows [see Emmans (1994) for full details]:

$$\begin{aligned} \text{Gross energy (GE) intake} &= \text{intake} \\ &\times \text{heat of combustion of the feed,} \end{aligned}$$

$$\text{Digestible energy intake} = \text{GE intake} - \text{gas} - \text{feces},$$

$$\begin{aligned} \text{Metabolic energy intake} &= \text{GE intake} \\ &- \text{gas} - \text{feces} - \text{urine,} \end{aligned}$$

$$\begin{aligned} \text{Net energy intake} &= \text{GE intake} - \text{gas} \\ &- \text{feces} - \text{urine} - \text{heat.} \end{aligned}$$

We can have individual variation in each step of the conversion from one energy level to another, and thus differences in (digestive) efficiency already present (see Phuong et al., 2013). If the feed is described in terms of NE, then it is in the currency that is directly used by the processes that are the energy sinks included as predictors in the RFI equation. This means that the resulting estimated coefficients (a , b , c in Eq. 1) can be interpreted as the metabolic efficiencies for the different energy consuming processes. However, using NE, it is very difficult to isolate any between-animal variation in digestive efficiency. If, on the other hand, the feed measures used in the RFI equation are DMI, then each predictor coefficient becomes a combination of the metabolic efficiency of that process and the overall digestive efficiency. This can make interpretation tricky. It is for these reasons that up until this point in the paper, the left-hand side of the equation has always been called “intake” without any detail.

To deal with this, the effect on the RFI equation of the transformation of the intake into a given energy unit needs to be considered (i.e., the accounting for digestibility and metabolizability). Generally, this value, called energy density (ed), usually comes from literature based on the feed composition or digestibility measures. A priori, it should be assumed that this number is incorrect in 3 ways:

- It can be systematically off for a given feed [i.e., a mean deviation (\overline{ded}) exists from ed].
- It ignores true individual variability in digestive efficiency (i.e., ded_i , which is a “true” component of feed efficiency). It should be noted that the individual variability in digestive efficiency may be due to variation in the digestive processes within

the digestive tract, but may also come from systematic differences in an animal's ability to select the most digestible parts within the feed offered (i.e., in feed sorting). It is considered here that this variation in feed sorting is one element of the animals feed efficiency.

- It ignores the effect of level of intake on digestive efficiency. Let's call this ded_{FI} . When expressing intake as digestible energy intake, this term is, in theory, considered by the conversion into digestible energy. However, assuming ded_{FI} to be zero would be to assume that the digestible energy conversion is perfect across all feeds, which is not done here.

Taking the above into account, the energy density of the feed for a given animal becomes

$$(ed + \overline{ded} + ded_{FI} \times DMI_i + ded_i),$$

and thus, when expressing intake in energy terms, the left-hand side of Eq. [1] becomes:

$$(ed + \overline{ded} + ded_{FI} \times DMI + ded_i) \times DMI. \quad [10]$$

Given that the aim of RFI is to isolate the individual variation in "true" efficiency (i.e., imf_i and ded_i), the rest of this section will first deal with this aspect within a uniform feeding situation, and then will look at possibilities to extend this for multiple feeding situations. In both cases, the aim is that the RFI equation includes the estimation of the energy density of the feed, as well as isolating ded_i . Accordingly, DMI can be split into the mean value (indicated with a bar) plus the individual deviations (i.e., $DMI = \overline{DMI} + DMI_i$)

Thus [10], the left-hand side of Eq. 1, becomes:

$$(ed + \overline{ded} + ded_{FI} \times DMI + ded_i) \times \overline{DMI} + (ed + \overline{ded} + ded_{FI} \times DMI + ded_i) \times DMI_i. \quad [11]$$

It would be logical to expand the DMI part of $ded_{FI} \times DMI$ in the same way. However, let's simplify by assuming that the feeding level effect on ed is sufficiently accounted for by the correction on the mean DMI (this effectively means any individual differences in ded_{FI} are moved into the individual component of ded_i). In other words, in the following, $ded_{FI} \times \overline{DMI}$ will be used rather than $ded_{FI} \times (\overline{DMI} + DMI_i)$, giving:

$$(ed + \overline{ded} + ded_{FI} \times DMI + ded_i) \times \overline{DMI} + (ed + \overline{ded} + ded_{FI} \times \overline{DMI} + ded_i) \times DMI_i, \quad [12]$$

where ed , \overline{ded} , and $ded_{FI} \times \overline{DMI}$ are all constants that can be grouped in one ed_{true} as follows:

$$(ed_{true} + ded_i) \times \overline{DMI} + (ed_{true} + ded_i) \times DMI_i. \quad [13]$$

We can now expand the original Eq. 4 to specify these elements in the full RFI equation:

$$(ed_{true} + ded_i) \times \overline{DMI} + (ed_{true} + ded_i) \times DMI_i = \overline{eim} + \overline{eif} + \overline{ues} + a \times predictor1 \times b \times predictor2 + [...] + eim_i + eif_i + eus_i + imf_i + \varepsilon; \quad [14]$$

$$(ed_{true} + ded_i) \times DMI = \text{int} + (ed_{true} + ded_i) \times -\overline{DMI} + a \times predictor1 \times b \times predictor2 + [...] + eim_i + eif_i + eus_i + imf_i + \varepsilon. \quad [15]$$

If DMI is expressed on the left-hand side of the equation as deviations from the mean (DMI_i) and include mean DMI among the predictors with a fixed and a random coefficient $(ed_{true} + ded_i) \times -\overline{DMI}$, a considerable way is covered toward isolating individual variability in digestive efficiency. For example, a difference between 2 cows in ded_i of 0.025 (relative to a typical ed_{true} of 0.66) would give a difference in DMI_i of 1 kg of DM/d (for cows eating on average 21 kg of DM/d with identical BW and milk production). To our knowledge, this reformulation of the RFI equation has not been reported in the literature, and thus it remains to be seen if it has practical utility. It should be noted that the above equation includes an animal performance component in the true digestibility (ed_{true}), the effect of the mean DMI on digestibility ($ded_{FI} \times \overline{DMI}$). To avoid

this, we could redefine ed_{true} as being only $ed + \overline{ded}$. This does not change Eq. 15 and the resolution described above; it simply means that the individual variation in digestibility (ded_i) accounts for the variation in DMI in absolute terms rather than as a deviation from the mean DMI.

The second issue deals with the fact that different experiments will use different feeds, and thus the energy density of the feed, ed , and the error associated with its

estimation will differ between experiments, as illustrated by the results of Tempelman et al. (2015). Ignoring this could create the situation where the regression coefficients estimated for the pooled data set are markedly different from those estimated within each feed or feeding situation (Simpson's paradox). Clearly, RFI models should be structured to avoid this problem. The idea is to include an element that allows the true value of ed , ed_{true} , to be estimated for each feed or feeding situation within the RFI model. This may be possible, in a relatively straightforward way, by extending the random regression model of Martin et al. (2020) to include the "experiment" factor among the fixed effects. This relies on the assumption that the average differences in ed can be removed by a linear adjustment, as suggested by the term $(ed_{true} + ded_i) \times -\overline{DMI}$ in the above equation. However, this assumption should be carefully examined and validated on real data to avoid oversimplification. Another option would be to explore the use of recursive models (Gianola and Sorensen, 2004; i.e., analyzing one effect after the other iteratively with the aim of having a final convergence).

TOWARD SUSTAINABLE EFFICIENCY: SHORT-VERSUS LONG-TERM EFFICIENCY

So far, the details of the RFI equation have been discussed to contribute to making the RFI method more adapted to the modern context of precision livestock data. In doing this, the technical issues related to the time periods of measurement have been dealt with. Here, the focus is back to the important issue concerning time periods of measurement (i.e., the value and interpretation of short- vs. long-term efficiency measures). The underlying idea is that sustainable efficiency should be the goal of any efficiency improvement strategies. This means considering the longer-term consequences of any efficiency gains. To do this, 2 notions must be considered at the animal level: trade-offs and productive longevity (at the animal level; it gets more complicated at the herd or farm levels; Faverdin and Van Milgen, 2019).

As described above, the most efficient animals are those able to produce more at a given level of intake (or those eating less at a given level of production). It seems obvious that animals that put a greater proportion of their acquired resources into product will be more efficient, but this implies a reduced proportion of these resources will go to other life functions, which is known as a trade-off. A trade-off between productive and "fighting entropy" life functions would have possible negative consequences on animal robustness. In dairy cows, a critical function for staying in the herd

is reproduction, and it is now well-documented that a negative (phenotypic and genetic) correlation exists between milk production and reproduction (Boichard and Manfredi, 1994; Pryce et al., 2004), and thus intensive selection for milk production has degraded reproductive performance (Miglior et al., 2017). There has also been a strong reduction in the average productive lifespan over the same period (Hare et al., 2006). More generally, the majority of evidence suggests that high levels of performance, be it milk, meat, or egg production, are associated with decreased robustness (Rauw et al., 1998). Loyau et al. (2016) reported a negative genetic correlation between egg weight and surface body temperature under heat stress in laying hens (see also review of Mignon-Grasteau et al., 2015). In rabbit lines divergently selected for reproductive intensity or reproductive longevity, high reproductive intensity does were less resilient to an environmental perturbation and were less able to use their body reserves (Theilgaard et al., 2007). Gilbert et al. (2017) reported that a pig line selected for low RFI had significantly less body fat and a decreased fasting heat production relative to the high RFI line, although there were no clear differences in the growth between lines when exposed to a sanitary challenge (Chatelet et al., 2018). More recently, studies are emerging that seek to characterize resilience to environmental perturbations (Ben Abdelkrim et al., 2019; Adriaens et al., 2020) and to relate variation in these resilience measures to frequency of health events and productive longevity (Berghof et al., 2019). Poppe et al. (2020), building on work of Elgersma et al. (2018) and using the residual variance in milk yield from daily milk records as a resilience measure, found favorable genetic correlations between resilience and health, fertility, and longevity. Taken together, this literature suggests that short-term efficiency is unfavorably correlated with resilience, and that resilience contributes positively to a longer productive lifespan, at least in adult producers. From the dairy cattle data of the DEFFILAIT project, we have recently been able to look at the relation between RFI and resilience, measured as the accumulated loss in milk yield during perturbations (based on 237 lactations; unpublished). Because the losses in milk yield were matched by losses in intake during these short-term perturbations (Figure 3; Bareille et al., 2003), whole lactation RFI was barely affected. This suggests that the link between resilience and efficiency is mainly through the effect of resilience on productive lifespan.

Returning to consideration of the time-span over which efficiency is measured and going to the extreme of considering lifetime efficiency, it is probable that the more efficient animals may be the resilient ones (i.e., those able to cope well with environmental

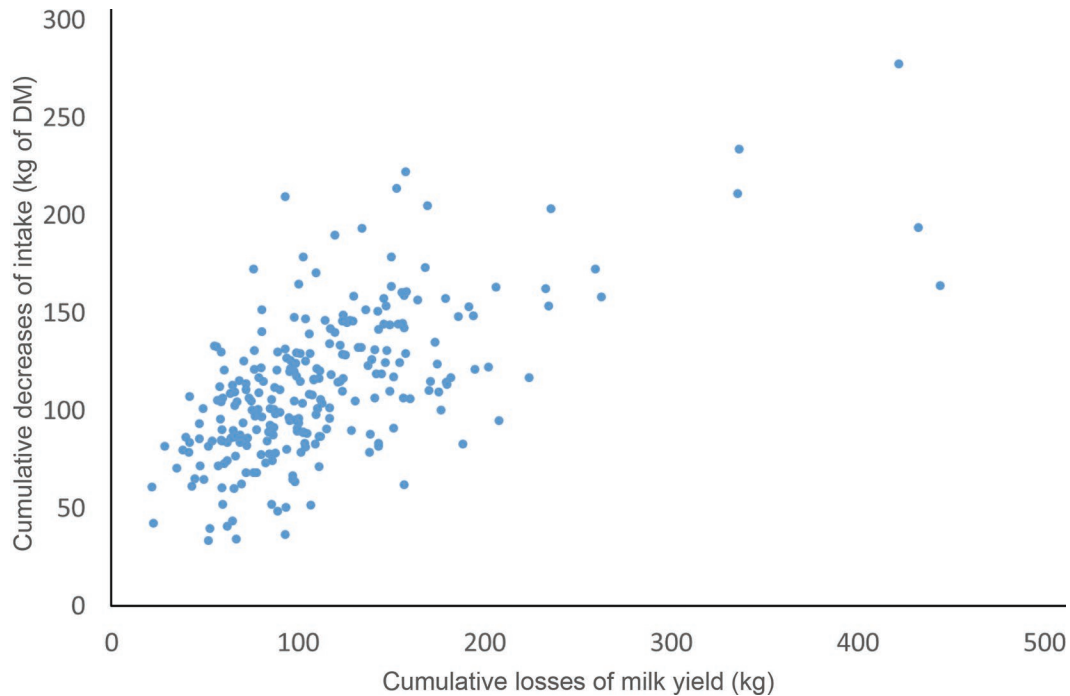


Figure 3. Relationship between the cumulative decreases in DMI during feed intake perturbations and the cumulative losses of milk yield during milk perturbations (average of 250 first days of 237 lactations, DEFFILAIT project data, www.deffilait.fr).

perturbations and thereby minimize effects on both production and other life functions such as health and reproduction). These longer-lived animals will increase the proportion of their lifespan that is productive, and thereby dilute the efficiency cost of the nonproductive rearing period. Accordingly, as shown in Figure 4, we could hypothesize that the correlation between feed efficiency and resilience changes with the duration of the measurement period. Indeed, results of simulations using a model designed to represent resource allocation between life functions suggest that different resource allocation characteristics underpin short-term efficiency and long-term efficiency (Puillet et al., 2016, 2021). However, these results remain to be validated with animal data. Such data would also allow quantification of what measurement duration is needed to avoid a negative correlation between efficiency and resilience. This is important for knowing the period over which we need to measure efficiency (i.e., defining the appropriate phenotypes that would allow selection for sustainable efficiency).

A key question is then, what kind of feed efficiency do we want to select for? Do we want an animal that is highly efficient for a specific period of its life (a few weeks around the peak of lactation for example), or do we want it to have a better accumulated efficiency over its life? Selection for a short-term feed efficiency may select for a switch in the resource allocation that will

benefit production but deteriorate resilience and the key life functions that contribute to longevity. On the other hand, if selection for a longer productive lifespan degrades production too much, then the lifetime efficiency of such animals may be not better than that of short-lived high producing animals. In this context, the idea of selecting for sustainable efficiency seems promising. These issues need to be explored not just

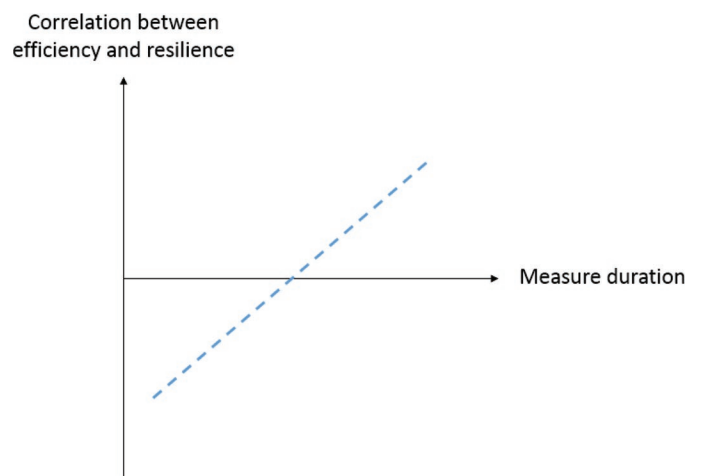


Figure 4. Schematic representation of the possible effect of residual feed intake measurement period on the correlation between efficiency and resilience.

for adult producers, but also in the context of growing animals reared for meat production. This opens up for consideration of efficiency not just at the animal level, but also at herd or farm level. A final point that should be considered when coming to selection decisions is that in this article the interest was the biological nature of RFI, and thus it was defined at the phenotypic scale. However, it is possible to model RFI to be genetically (and not phenotypically) independent from the energy sinks that are used as predictors (Kennedy et al., 1993), which ensures the absence of undesired genetic correlations between these traits in selection programs.

SUMMARY

Until very recently, the notion of measuring feed efficiency over a whole lactation, and even more so over a whole lifespan, seemed beyond reach. It is therefore not surprising that data sets with long-term measures of intake, and thus long-term efficiency, are very rare, especially if good resilience measures are also required. However, the burgeoning field of precision livestock technologies, with its promise of automated high-frequency measures, has now developed to the point where not only milk production but also body reserve (weight and condition score) changes (Thorup et al., 2018; Fischer et al., 2020), and more recently intake measures (Lassen et al., 2018), are becoming available as a commercial reality that can be used on sufficient scale to allow phenotyping of large populations of animals for long-term efficiency.

The increasing availability of such time-series data brought into focus several limitations of the traditional RFI methodology, particularly in relation to the time periods of measure and the ability to evaluate the importance of the different biological components of overall feed efficiency. We believe that the technical advances proposed above will contribute to resolving these limitations, and thus to making the RFI method fit for purpose in the precision livestock future. This should allow the relationships between short- and long-term efficiency to be evaluated and to be reframed in terms of sustainable efficiency goals that can be included in future selection and management strategies.

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