

Feed Efficiency in Growing and Mature Animals

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ABSTRACT: Interest in efficiency of production, particularly feed efficiency, is intensifying. Many alternative definitions of feed efficiency exist in growing animals and mature animals although most research on feed efficiency is on growing animals. Here we review the state of the art on the alternative definitions of feed efficiency, their genetic component, and discuss how such measures could be included in breeding goals. Selection index theory in growing beef cattle suggests an improvement in monetary response to selection for a terminal-based breeding goal of up to 20%, if measures of feed intake are available on the animal itself or a small number of progeny. The corresponding response to selection was considerably less ($\leq 5\%$) in mature dairy cows assuming feed intake was available on sires measured as growing bulls, and a genetic correlation of 0.67 existed between residual feed intake in a growing animals and lactating animal.

Keywords: heritability; definition; breeding goal

Introduction

Improved system efficiency is required to fulfill the protein and energy demands of an expanding and more affluent human population. Animal (feed) efficiency is one of the many components of overall system efficiency. There is still however debate on a) what is the best measure of feed efficiency in growing and lactating animals, b) how best to incorporate feed efficiency into a breeding program, as well as c) what impact selection on feed intake will have on other animal performance traits (e.g., reproductive performance) and what gains are realistically achievable.

This paper reviews alternative definitions of feed efficiency in growing and lactating animals, suggests other possible measures in lactating animals, summarizes genetic parameters for the alternative definitions and discusses alternative proposals on how to best include efficiency in a breeding goal as well as the potential gains achievable.

Feed Efficiency Definitions

Table 1 summarizes the plethora of definitions of (feed) efficiency that exist and also presents some novel potential definitions of (feed) efficiency in mature animals. Feed conversion efficiency (FCE) was the traditional measure of feed efficiency in growing animals but has now been replaced (in animal breeding research studies in ruminants in particular) by residual feed intake (RFI). Feed conversion efficiency in lactating animals is still, however, the most commonly used measure probably because of its ease of calculation and explanation. The numerator used to calculate FCE must somehow account for the differential in energy cost of producing milk fat, protein, and lactose and using some measure of total milk energy (Tyrrell and Reid,

1965) is one option to achieve this. Nonetheless, FCE in mature animals has serious shortcomings especially during periods of body tissue anabolism or catabolism such as in the immediate post-partum period (Roche et al., 2009). All else being equal, females mobilizing body tissue have greater energy available for production and other bodily functions but considerable body tissue mobilization can result in compromised health and fertility (Roche et al., 2009). Moreover, the lost body tissue will generally have to be replaced in late lactation or during the dry period; therefore any definition of efficiency in mature animals must be based on measurements over a long period of time. Here we suggest an alternative definition of FCE, FCE_{adj} , which includes body tissue gain (e.g., growth) in the numerator and body tissue mobilization in the denominator. The coefficients applied to both parameters could be derived from nutritional tables or estimated from the data (e.g., coefficients from an RFI equation). Table 2 gives an example of three different cows (similar for other mature animals) with the same traditional FCE but different FCE_{adj} .

Analogous to partial efficiency of growth (PEG) used in growing cattle (Table 1) we define partial efficiency of milk production (PEMP) as energy corrected output divided by feed intake after accounting for energy required for maintenance (Table 1). Again the regression coefficient on metabolic live-weight could be from nutritional tables or derived from the RFI multiple regression model. Kleiber ratio (KR) in growing cattle is defined as average daily gain divided by metabolic live-weight (Table 1); in dairy cattle we defined kleiber ratio as 1) milk energy output divided by metabolic live-weight, or 2) milk energy output plus the cost of body weight gain (i.e., total energy out) all divided by metabolic live-weight. A similar trait to KR described above in lactating animals has been used previously to evaluate differences among lactating dairy cows (Coleman et al., 2010). Furthermore, a similar trait, offspring weight weaned (i.e., function of offspring daily gain) divided by weight of the mature animal, has been advocated as a measure of efficiency in beef herds. The advantage of this measure of efficiency is that measures of feed intake are not required. Coleman et al. (2010) defined a feed efficiency trait as kg dry matter intake (DMI) relative to kg live-weight which is similar to the feed to weight (FtW) trait defined in Table 1. This trait can give an indication of the intake capacity of an animal.

Residual feed intake (RFI) is increasing in popularity as a proxy for feed efficiency in growing cattle (Berry and Crowley, 2013), sheep (Knott et al., 2008), and pigs (Gilbert et al., 2007). Residual feed intake is defined as the difference between energy intake and demand and is usually estimated as the residuals from a least squares regression model regressing feed intake on the various energy sinks. Figure 1 gives an example of a two-

Table 1. Definitions of (feed) efficiency in growing and lactating/mature animals; analogous definitions of feed efficiency in growing and mature animals are on the same row

Growing animals	Lactating/mature animals
$FCE = \frac{ADG}{FI}$	$FCE = \frac{ECM}{FI}; FCE_{Adj} = \frac{ECM + b_{1a}\Delta WT^+}{FI - b_{1b}\Delta WT^-}$
$PEG = \frac{ADG}{FI - FI_{Maintenance}}$	$PEMP = \frac{ECM}{FI - b_1 WT^{0.75}}$
$RGR = \frac{100 \cdot (\log_e WT_{END} - \log_e WT_{START})}{Days\ on\ test}$	
$KR = \frac{ADG}{WT^{0.75}}$	$KR = \frac{ECM}{WT^{0.75}}; KR = \frac{ECM + b_{1a}\Delta WT^+}{WT^{0.75}}$
	$FtW = \frac{FI}{WT^{0.75}}$
$RFI = FI - (b_1 WT^{0.75} + b_2 ADG + b_3 (\Delta) FAT + b_4 WT^{0.75} \cdot FAT + b_5 ADG \cdot \Delta FAT)$	$RFI = FI - (Parity \cdot \sum_{i=1}^n DIM^n + b_1 WT^{0.75} + b_2 ECM + b_3 (\Delta) BCS + b_4 \Delta WT + b_5 WT^{0.75} \cdot BCS + b_6 \Delta WT \cdot \Delta BCS)$
$RG = ADG - (b_1 WT^{0.75} + b_2 FI + b_3 (\Delta) FAT + b_4 WT^{0.75} \cdot FAT)$	$RSP = ECM - (Parity \cdot \sum_{i=1}^n DIM^n + b_1 WT^{0.75} + b_2 FI + b_3 (\Delta) BCS + b_4 \Delta WT + b_5 WT^{0.75} \cdot BCS + b_6 \Delta WT \cdot \Delta BCS)$
$RIG = RG - RFI$	$RISP = RSP - RFI$

FCE=feed conversion efficiency, ADG=average daily gain, ECM=energy corrected milk; FI=feed intake, $[\Delta WT]^+ =$ live-weight gain; $[\Delta WT]^- =$ live-weight loss; PEG= partial efficiency of gain, PEMP=partial efficiency of milk production; WT=live-weight; RGR=relative growth rate; KR=Kleiber ratio; RFI=residual feed intake; FAT=fat depth; BCS=body condition score; FtW=feed to weight ratio; RG=residual gain; RIG=residual intake and gain; ECM=energy corrected milk; PEMP=partial efficiency of milk production; DIM=days in milk; RSP=residual solids production, RISP=residual intake and solids production.

dimensional plane predicting, from the average of the population, the expected feed intake for each combination of metabolic live-weight and average daily gain; the RFI model in this instance included just metabolic live-weight and average daily gain as the energy sinks and is typical of most RFI models fitted (Berry and Crowley, 2013). Animals above the plane (i.e., dots) eat more than predicted based on their performance (i.e., positive RFI) and are therefore deemed to be inefficient. Animals below the plane (i.e., triangles) eat less than predicted based on their performance (i.e., negative RFI) and are therefore considered to be efficient relative to the average population. The variation in RFI reduces as the complexity and completeness of the RFI statistical model increases. However, as the complexity of the statistical model increases, the contribution of measurement error and errors due to an inaccurate model to the residual term also increases. Savietto et al. (2014) outlined some of the deficiencies of the commonly used RFI models including the lack of measures of body fat and protein mass (change). Savietto et al. (2014) also documented inter-animal variation in the regression coefficients on the energy sink. This suggests heritable variation in individual animal energy conversion efficiencies; Savietto et al. (2014) did however caution that such variation could also be attributable to inter-animal variation in correlated contributors to differences in feed intake which were not included in the statistical model.

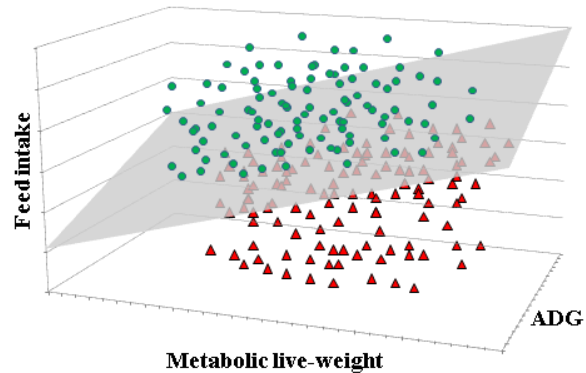


Figure 1. Two-dimensional plane of expected feed intake based on metabolic live-weight and average daily gain (ADG); circles represent animals eating more than expected and are therefore positive RFI (i.e., inefficient) while each triangle represents an individual animal that eats less than expected and is therefore negative RFI (i.e., efficient).

One of the properties of RFI is its independence from the independent variables (e.g., ADG) in the multiple regression model. Slow growing animals could, however, have good RFI values which may affect the acceptability by industry of the RFI concept. Berry and Crowley (2012) amalgamated RFI and residual gain (i.e., difference between actual growth rate and growth rate predicted from feed intake plus other energy sinks) to generate residual

intake and gain (RIG) which is correlated with both reduced feed intake and greater ADG. The likelihood of slower growing animals excelling in RIG is therefore less likely compared to animals ranked on RFI. Berry and Crowley (2012) showed that superior growing cattle ranked on RIG ate less to achieve a desired gain in weight compared to superior growing cattle ranked on either RFI or RG; a similar conclusion was reported in growing turkeys (Willems et al., 2013). Residual feed intake in mature lactating animals however is not necessarily a good measure of production efficiency due primarily to the inclusion of maintenance as an independent variable in the model. The requirement of mature animals is to produce more milk from less feed. Table 3 shows animals with very different FCE but identical RFI values.

Table 2. Milk output, feed intake, live-weight (Lwt) gain or loss¹ for three hypothetical mature animals as well as FCE and FCE_{adj} as defined in Table 1

Milk output (unit)	Feed intake (unit)	Lwt gain (kg)	Lwt loss (kg)	FCE	FCE _{adj}
30	15	0	0	2	2
30	15	2	0	2	2.26
30	15	0	2	2	1.67

¹Each unit live-weight gain costs 2 units feed equivalent while each kg in live-weight loss contributes 1.5 units feed equivalent

Not including live-weight in the RFI model to overcome this shortcoming is not recommended since the association between live-weight and energy intake will still be captured through covariances between live-weight and other independent variables such as BCS. If a residual type trait is preferred for use by producers it may be more appropriate to include (metabolic) live-weight in the regression model but add back the regression coefficient's times (metabolic) live-weight to the residual from the model. Of course then the residual will not be independent of (metabolic) live-weight which is one of the reported apparent advantages of RFI; this however may not be a requirement in lactating animals. Analogous to RG in growing animals, Coleman et al. (2010) defined residual solids production (RSP; Table 1) by regressing total solids production on DMI plus the energy sinks. RFI is independent of milk solids production and thus low yielding animals may rank highly on RFI; RSP is positively correlated with solids production, thus low yielding animals are less likely, on average, to rank highly on RSP but RSP is independent of DMI. Analogous to RIG defined in growing animals (Berry and Crowley, 2012) here we also propose residual intake and solids production (RISP; Table 1) which is RSP minus RFI (standardized to have equal variance if desired); RISP is still phenotypically independent of live-weight. High RISP ranking animals will, on average, eat less than their contemporaries but also milk more than their contemporaries. In the definition of RFI and RSP (and therefore RISP) we suggest including parity, stage of lactation and their interaction (to account for

different lactation profiles per parity) in the multiple regression model. Moreover, because the energy generated from a 1-kg loss in BW is less than the energy required for a 1-kg gain in BW, piece-wise regression should be fitted to body weight change in the multiple regression models to account for this. The advantages and disadvantages of the different feed efficiency measures have been discussed in more detail elsewhere (Berry and Crowley, 2013).

Table 3. Feed intake, milk output, live-weight (Lwt), FCE and RFI¹ of three hypothetical mature animals.

Feed intake	Milk output	Lwt	FCE	RFI
15	30	600	2	0
15	30	500	2	1
15	30	700	2	-1

¹RFI equation: $RFI = 36 + \text{Feed Intake} - (1.5 * \text{milk} + 0.01 * \text{LWT})$

Genetics of Feed Efficiency

A thorough meta-analysis of the variance components for feed efficiency traits in growing cattle and lactating cattle is presented by Berry and Crowley (2013). A summary of these heritability estimates for growing cattle and lactating cattle are in Table 4 and 5, respectively. Pooled heritability estimates from up to 45 different studies or populations of growing cattle varied from 0.23 (FCR) to 0.40 (feed intake) and were similar to those observed for other performance traits like ADG (0.31), live-weight (0.39) and feed intake (0.40). Moreover, considerable variation in heritability estimates existed across the populations investigated. This is not unexpected given the diversity in breeds and feeding systems contributing to the meta-analysis (Berry and Crowley, 2013). Heritability of feed efficiency traits in dairy cows was considerably lower with a mean heritability of 0.04 and 0.06 for RFI and FCR, respectively. The heritability (range in parenthesis) of gross feed efficiency (e.g., FCR) in growing poultry and pigs was 0.32 (0.11 to 0.67) and 0.26 (0.06 to 0.45), respectively (data not shown). Meta-analysis of the literature indicates a mean heritability (range in parenthesis) for RFI in growing poultry and pigs of 0.34 (0.21 to 0.49) and 0.24 (0.10 to 0.45), respectively (data not shown).

The phenotypic and genetic correlations between feed efficiency traits are less than unity (Berry and Crowley, 2013) implying that they are measuring different characteristics. Genetic correlations between feed efficiency traits and performance traits in cattle are discussed in detail elsewhere (Berry and Crowley, 2013). However because of the difficulty and expense of measuring feed intake, the datasets used to estimate genetic correlations are relatively small and precise genetic correlation estimates are generally not achievable. This is exacerbated for low heritability traits like fertility resulting in a large standard error of the estimated genetic correlation. More recent evidence suggests, nonetheless, that negative values for the traditional definition of RFI in growing animals is

Table 4. Number of studies (N), pooled heritability (pooled), minimum (min) and maximum (max) heritability estimates for average daily gain (ADG), weight (WT), feed intake (FI), residual feed intake (RFI), feed conversion ratio (FCR), residual gain (RG), kleiber ratio (KR), relative growth rate (RGR) and residual intake and gain (RIG) from a review of the literature in growing cattle (Berry and Crowley, 2013).

	ADG	WT	DMI	RFI	FCR	RG	KR	RGR	RIG
N	35	25	37	36	34	2	5	4	1
	0.31	0.39	0.40	0.33	0.23	0.28	0.35	0.26	0.36
Pooled (se)	(0.014)	(0.010)	(0.012)	(0.013)	(0.013)	(0.030)	(0.030)	(0.041)	(0.06)
Min	0.06	0.30	0.06	0.07	0.06	0.28	0.21	0.14	0.36
Max	0.65	0.88	0.70	0.62	0.46	0.62	0.52	0.33	0.36

associated with leaner growing animals (Berry and Crowley, 2013) and lactating cows (Pryce et al., 2014) which makes biological sense given the energy cost of fat relative to protein. Body fatness is well known to be associated with reproduction and health in mammals (Roche et al., 2009) and thus an unfavorable association between RFI and fertility (and possibly health) is not surprising.

Feed Intake or Efficiency in the Breeding Goal

There is much debate on whether to include feed intake itself in a breeding goal or to include RFI. Kennedy et al. (1993) showed that both scenarios, if undertaken correctly, are actually mathematically equivalent. The advantages and disadvantages of including either feed intake or RFI (i.e., feed intake independent of the energy sinks) in a breeding goal is summarized in Table 6. The conclusion is not obvious and is dependent on the several factors including the species, type of animal (i.e., growing or mature animals), and the end user (i.e., producers, breeders or sire analysts). One of the main advantages of providing estimated breeding values (EBVs) for DMI is that they are easy to explain and the concept is readily acceptable by producers (and scientists). The main disadvantages however of just presenting EBVs for DMI is that it is not easy to determine whether the animal is efficient or inefficient. For example an animal with a positive EBV for DMI may actually be more efficient than an animal with a negative EBV for DMI if the former animal is producing proportionally more.

The main disadvantage of presenting just EBVs for RFI is that RFI can be a difficult concept to understand and explain and, because of possible genetic antagonisms with other performance traits (mainly reproduction), selection pressure exerted on RFI over and above that in the breeding goal can have unfavorable repercussions. Of course antagonisms are also likely to exist between

reproduction/health and DMI but the concept of RFI may be construed to suggest it is independent of all performance traits. Nonetheless, RFI can also be made (genetically) independent of other traits such as reproductive performance. A compromise is to explicitly include DMI in the breeding goal as a trait but to have a stand-alone EBV for feed efficiency to identify efficient animals.

Depending on the definition of the feed efficiency variable, the reliability of the EBV could be low (at least in the short term) because EBVs for feed efficiency are likely to be genomic-based; because of the low reliability, EBVs may fluctuate wildly. Furthermore there may be confusion about the sign of the EBV to denote more efficient (i.e., negative RFI is more efficient). Simply altering the sign could cause even more confusion as the trait applied in the breeding program would be different to that applied in the scientific literature. Hence, categorizing animals into high, average, or low efficiency could aid in resolving these shortcomings. The EBV could also be standardized and presented like linear type traits in dairy cattle. An alternative is to put a monetary value on the efficiency index (e.g., feed cost saved); interpretation of the sign but more importantly the relative economic importance of differences in feed efficiency could be easily comprehensible.

Achieving High Accuracy of Selection on Feed Intake and Efficiency

Achieving high accuracy of selection for feed intake and efficiency is one of the main obstacles to the inclusion of these traits in breeding goals. Although Berry and Crowley (2013) recommended to use of selection index theory to predict genetic merit for feed intake in cattle from routinely measured performance traits (e.g., live-weight, growth rate, milk yield), such an approach captures little, if any, of the genetic variation in net feed efficiency. Several studies have attempted to explain differences among

Table 5. Number of studies/populations (N), pooled heritability (pooled), minimum (min) and maximum (max) heritability estimates for weight (WT), feed intake (FI), residual feed intake (RFI), feed conversion ratio (FCR) from a review of the literature in mature (lactating) cows (Berry and Crowley, 2013).

	WT	FI	RFI	FCR
N	10	7	11	7
Pooled (se)	0.63 (0.008)	0.06 (0.008)	0.04 (0.008)	0.06 (0.010)
Min	0.20	0.02	0.00	0.05
Max	0.72	0.28	0.38	0.32

Table 6. Reasons in favor and against including DMI or RFI in a breeding goal

DMI in the breeding goal	
For	Against
Easy to explain and understand	Cannot easily identify efficient animals
Economic value is relatively easy to calculate	May be misunderstood (positive EBV may be efficient)
Amenable to customised indexes	Correlated with performance
Economic value on other components reflect reality in the market place (e.g., fat:protein price ratio)	Independent culling levels may be harmful to overall gain
Good predictors available	Misinterpreted that negative EBV might imply poorer performing animals
Higher "reliability" through selection index theory	
May be less susceptible to genotype by environment interactions (GxE)	
RFI in the breeding goal	
For	Against
Economic value is relatively easy to calculate	Difficult to explain technically
Can "easily" slot in to current breeding goals	Low reliability (currently)
(Theoretically) uncorrelated with performance	Possibly more susceptible to GxE
Relatively simple message (if not caught up in details)	Selection index within a selection index
Could materialize in faster genetic gain for efficiency	Sensible to select on something we do not understand? (Never stopped us before!)
	Mixed messages from "pro" and "against" camps
	RFI in lactating animals (as currently defined) is not ideal
	EBVs may change as the RFI model changes
	Possibly correlated with fertility (so is DMI!)

animals in, for example, RFI. McParland et al. (2012) used the absorbance spectrum from mid-infrared spectroscopy analysis of bovine milk to predict feed intake and energy balance in lactating dairy cows; they reported that 58 and 64% of the variation in energy intake and between 22 to 48% of the variation in energy balance could be predicted from partial least squares analysis of the generated mid-infrared spectrum. Because energy balance and RFI are mathematically very similar traits (Saviotto et al., 2014), McParland et al. (2014) hypothesized that the milk MIR could also be used to predicted RFI; they reported a correlation of 0.59 between actual RFI and RFI predicted from milk infra-red spectroscopy. The genetic correlation between actual and predicted RFI was 0.78 (McParland et al., 2014).

Relatively small databases exist around the world for feed intake from either performance test stations, breeding nucleus herds, research experiments or even commercial units. In their own right, these datasets are usually too small to undertake accurate national genetic evaluations, in cattle at least. Collating datasets from different international sources and accounting for potential genotype-by-environment interactions, could be particularly useful to calculate EBVs for animals, especially where the global effective population size is low (e.g., Holstein dairy cattle). Moreover, genotypes available on these animals could be useful to derive genomic predictions. Berry et al. (2014) described, using real data from 10 different populations of Holstein-Friesian dairy animals, how

international data for feed intake could be combined; de Haas et al. (2014) proceeded to use these data in genomic predictions.

Genetic Gain Achievable in Net Feed Efficiency

Growing animals. The Irish terminal index for growing beef cattle was used as an example to illustrate, using selection index theory, the gains achievable for measuring actual feed intake. The terminal index includes direct calving difficulty, gestation length, calf mortality, docility, carcass weight, carcass conformation, carcass fat score as well as dry matter intake (DMI); individual animal DMI was measured until the year 2011 as a performance test but is now measured as a progeny test. Using the product of the economic value times the relative economic weight, the relative emphasis on DMI in the terminal index was 26%. Each bull was assumed to have 100 progeny calving traits and 85 carcass traits. Genetic gain in profit increased by 20% when feed intake information was available on the animal itself; an equivalent increase in gain was achieved with feed intake measured on 6 progeny. The heritability of DMI was 0.43; a genetic correlation of 0.24 exists in the selection index between carcass weight and feed intake. Assuming genetic gain of 0.22 index standard deviations annually, this equates to an improvement of €1.17 per animal annually attributable in part to an annual decline in feed intake of 0.04 kg/day despite carcass weight increasing by 2.2 kg/day. Terminal indexes and the

associated genetic parameters are likely to be relatively similar across different populations and species so therefore expected improvements in genetic gain for profit of ~20% is arguably expected in other populations.

Mature lactating animals. Gonzalez-Recio et al. (2014) evaluated the impact on genetic gain of including feed intake and efficiency in the Australian dairy cow breeding goal. They assumed genomic predictions for RFI in growing heifers (accuracy of 0.40) had a genetic correlation 0.67 with RFI in lactating dairy cows. Gonzalez-Recio et al. (2014) observed a 2.4% improvement in monetary returns when RFI in growing heifers (as a proxy for RFI in lactating cows) was included in the Australian dairy cow breeding goal. The relatively small increase was because gross feed efficiency was already (partly) accounted for in their breeding goal since milk production (positive weighting) and live-weight (negative weight) were already goal traits. A similar exercise was undertaken here for the Irish national dairy cow breeding goal, the economic breeding index (EBI). The EBI also includes a positive weight on fat and protein yield and negative weight on live-weight thereby accounting, in part, for differences in gross feed efficiency. Genetic parameters for growing bulls (i.e., sires) for feed intake information were assumed identical to those currently used in the Irish beef genetic evaluations, and, as with Gonzalez-Recio et al. (2014), a genetic correlation of 0.67 was assumed between RFI in a growing animal and mature lactating animal. Having an RFI record on the animal itself (i.e., single trait accuracy of 0.60) increased monetary genetic gain of the entire breeding goal by 1%. Having feed intake data on five lactating progeny (plus the sire itself) increased the monetary return by a further 4%; the feed intake information on the growing bull contributed 13% to this improvement.

Conclusions

A plethora of different definitions of efficiency, gross feed efficiency, and net feed efficiency exist in growing and mature animals; all traits investigated to date express heritable genetic variation most of which are

similar to other performance traits, the exception possibly being RFI in mature animals. Although there is much research in growing animals, there is a paucity of investigations on efficiency in mature animals. Whether or not to include feed intake or net feed efficiency in a breeding goal is dependent on many factors including the species, type of animal (growing or mature animals), and the end user (producers, breeders or sire analysts).

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