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Factors That Affect Energy Efficiency and Indirect Response of Selection for Efficiency on Related Traits

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1. Introduction

The breeding goal of most livestock operations is maximizing profitability, which is a function of input and output (Veerkamp & Emmans, 1995; Archer et al., 1999; Crews, 2005). In most livestock populations, selection programs have primarily focused on progressively improving means for output traits such as live weight gain, fertility, meat and milk yield (Archer et al., 1999; Sainz & Paulino, 2004; Crews, 2005). However, there has recently been a renewed interest in another component of profitability, namely the reduction of inputs or the increase in efficiency (Crews, 2005). Feed is one of the most important input components, and it represents more than one-half of the total costs in most livestock operations (Kennedy et al., 1993). In the dairy industry, feed cost represents about 40 to 50% of the total milk production cost and has increased substantially over the last few years (Garcia, 2009). Gibb & Macallister (1999) reported that the economic effect of a 5% improvement in feed efficiency is four times greater than a 5% improvement in average daily gain. Therefore, reducing production costs or increasing feed efficiency are the two most important ways to improve production efficiency and profitability. They also decrease environmental pollution and the carbon footprint (Capper et al., 2010). In order to gain the maximum benefits of genetic selection for energy efficiency, factors that influence energy efficiency and its indirect effects on other traits should be known. The most common measures of energy efficiency and their properties are reviewed in this chapter. It also deals with factors that practically affect energy efficiency. Furthermore, as there are very few reports on direct selection for energy efficiency in dairy cattle (Linn, 2006), the authors reviewed the indirect effect of selection for energy efficiency on other traits in beef cattle as well as in other species in addition to dairy cattle.

2. Energy efficiency traits

Researchers have proposed many measures of energy efficiency such as feed conversion ratio (FCR), gross energy efficiency (GEE), residual feed intake (RFI) (Koch et al., 1963; Archer et al., 1999; Crews, 2005) and life time efficiency (LTE) (Vandehaar, 1998; Vandehaar & St-Pierre, 2006). Their definition, applications and benefits are different.

FCR and GEE are the most common measures of efficiency in the literature. FCR is the ratio of input (e.g. feed) to output (e.g. weight gain or milk production) (Crews, 2005). In the dairy cow, the GEE is defined as the energy in the milk divided by the total energy intake (Veerkamp & Emmans, 1995). These approaches lead to only limited insight into efficiency of the entire production system (Crews, 2005). The problems of GEE and FCR have been discussed in numerous studies (Korver et al., 1991; Veerkamp & Emmans, 1995; Crews, 2005) and are mainly categorized in three groups. First, the energy intake has different partial efficiencies for maintenance, lactation, pregnancy and body tissue gain or loss, but the GEE and FCR do not distinguish between them (Veerkamp & Emmans, 1995). Secondly, FCR and GEE are well known to be phenotypically and genetically correlated with measures of growth, production and mature size. Therefore, selection of animals based on these measures may increase the maintenance requirements. Finally, changes in GEE and FCR can be the result of changes in either intake (numerator), yield (denominator) or both (Gunsett, 1984; Veerkamp & Emmans, 1995) and selection direction cannot be predicted very well. Then, selection for improvement of FCR (i.e. decreased FCR) and GEE would result in increased growth rate, mature size, and consequently mature maintenance requirements (Korver et al., 1991). It can be concluded that improving FCR and GEE by selection for increased growth rate do not necessarily improve net feed efficiency, because of drawbacks associated with increased maintenance requirements (Van der Werf, 2004; Crews, 2005).

Lifetime efficiency (LTE), another measure of energy efficiency, is defined as “the capture of feed energy in milk, conceptus, and body tissue divided by gross energy intake during the life of cow, starting at birth” (Vandehaar, 1998; Vandehaar & St-Pierre, 2006). This index attempts to summarize an animal’s entire life efficiency and is a good criterion to set up a long term vision. In order to compare the LTE in dairy cows, total milk production should be standardized for all factors such as housing, feeding, age at first calving and calving interval. The LTE mostly depends on the precalving interval and intercalving intervals. The Precalving Interval is defined as the period from birth to first parturition and Intercalving Intervals are the intervals between successive calvings (King, 2006). The main concerns related to LTE are: lots of information is required to calculate the LTE, it is applicable for the entire life, and it is influenced more by precalving and intercalving intervals.

To overcome the problems associated with FCR, GEE, LTE and other measures of energy efficiency, an alternative measure can be expressed as residual feed intake (RFI). RFI is a measure of feed utilization corrected for live weight and production, and it is often referred

to as net feed or energy efficiency (Koch et al., 1963; Korver et al., 1991; Luiting et al.,1992). The concept of RFI can be described as “the difference between the actual feed intake and that predicted on the basis of mean requirements for body weight maintenance and levels of production” (Koch et al., 1963); it is explained schematically in figure 1. RFI relies simply on partitioning feed energy intake into portions required for body maintenance, stage and levels of production, and a residual portion. This residual portion is related to the true metabolic efficiency of an animal and would be comparable across individuals (Crews, 2005). Variation in RFI probably reflects underlying biological efficiency after adjustment for energy deposition (Crews, 2005; Herd & Arthur, 2009). In a population, the mean RFI index over all individuals is zero and approximately half of all individuals have RFI values below or above the mean. The efficient animals have low RFI values; it implies they consume less feed without compromising their production (Crews, 2005). Indeed, RFI is a net feed efficiency measurement and it can be calculated at any time of an animal’s life.

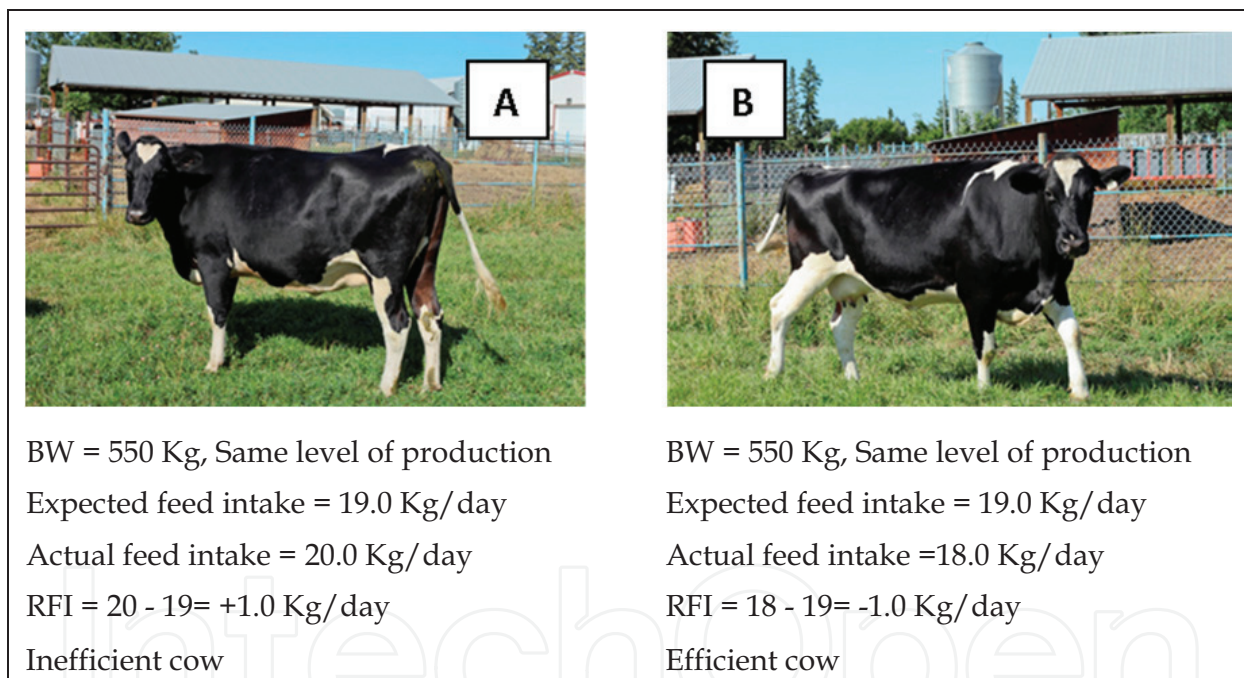


Figure 1. Schematic concept of residual feed intake (RFI). Two animals which have the same BW and ADG, are expected to consume the same amount of feed but in reality cow A consumes more than expected while cow B consumes less, so cow B is more efficient than A.

3. Factors affecting energy efficiency in dairy cattle

Several factors influence energy efficacy in dairy cattle. It is practically influenced by dry matter intake (DMI), production level, body tissue changes, age at first calving (AFC), and environmental factors (Vandehaar, 1998; Linn, 2006). Their approaches to affect the energy efficiency are different.

3.1. Dry matter intake and production

Dry matter intake (DMI) and production are the direct components of most energy efficiency traits. Dry matter intake (DMI) affects energy efficiency through energy transformation mechanisms from gross to net energy. The basic rule of most common efficiency measures, FCR and GEE, is increased production means increased efficiency, but the relationship between the marginal benefit of increased production and efficiency is not always linear.

DMI establishes the amount of nutrients available to an animal for maintenance and production. Inadequate intake of nutrients negatively affects production, efficient nutrient utilization and health status of the animal. Supplying nutrients in excess also increases feed costs and can result in excretion of nutrients into the environment (NRC, 2001; Collier et al., 2006). In dairy cows, the average DMI is 22.7 kg/d, and it ranges between 19.8 to 26 kg/d (Ordway et al., 2009; Vallimont et al., 2010). Heritability of DMI was reported from 0.16 to 0.48, and its genetic correlation with energy intake ranged from 0.8 to 0.9 (Veerkamp, 1998; Vallimont et al., 2010). Therefore, DMI and energy intake are genetically almost the same trait. However, the energy transformation mechanisms of DMI, which affect energy efficiency, involve digestion, fermentation and metabolic processes. Gross energy (GE) is the amount of released energy in heat combustion. Net energy (NE) is the energy which is directly used to support maintenance functions, including conversion to milk, conceptus growth and body tissue gain (NRC, 2001). Feedstuffs have energy in the gross form and it is converted to net energy in several steps (figure 2). Some amounts of the GE are indigestible and ultimately appear in feces; the remaining part is called digestible energy (DE). Some part of DE is lost due to gas production (mainly methane) and urinary energy (mainly urea) during the fermentation process. The remaining DE after deduction for gas and urinary production is called metabolizable energy (ME). Finally, converting the ME to net energy (NE) requires metabolic reactions, which produce heat that is termed the heat increment (NRC, 2001; Vandehaar & St-Pierre, 2006). Therefore, the accessible amount of NE from GE depends on the amount of losses in digestion, fermentation and metabolic processes. Practically, it depends on many factors, such as DMI levels, passage rate, and dietary fibre (especially, effective neutral detergent fiber, eNDF) level (NRC, 2001). Some studies have been conducted to determine the relationship between these factors and amount of nutrient losses in the different steps of the transformation mechanisms (Moe, 1981; Van Soest et al., 1992); they concluded there is an optimum point between them. For example, Vandehaar (1998) reviewed the literature and showed that the relationship between level of DMI and DE is not linear. When a dairy cow consumes DMI for its maintenance requirements, almost 80% of GE captured is in the form of DE. Furthermore, there is a reduction in digestibility as DMI increases (Vandehaar, 1998). Overall, NRC (2001) suggested that digestibility is depressed linearly at 4% per multiple of maintenance intake. It assumes that most of the cows consume 3 times their maintenance requirement, which is an optimum point of GEE. In addition, it has been shown that there is an optimum point of NDF level in terms of converting GE to DE, and it is reported to be between 25 to 30%. Amounts of NDF in the diet beyond this range will decrease energy intake. Higher levels of NDF fill the rumen,

whereas lower levels may cause some health problems (Eastridge, 2006; Vandehaar & St-Pierre, 2006). Finally, the portion of losses in the different steps of energy transformation shifts and it is dependent on DMI levels. At higher levels of DMI the losses into feces increase while the amounts of losses as heat increment are greater at lower levels of intake (Vandehaar & St-Pierre, 2006).

Although production is a fundamental component that determines efficiency, the relationship between marginal benefit of increased production and efficiency is not linear for all the time. During the past 18 years, the average milk production of Canadian Holstein cows has increased about 115 kg/cow/year and currently the average milk yield of a primarily Holstein herd is 9793 kg/cow/yr. The average rate of increase was 1.35% between 1991 and 2009 (DHI, 2009), and it likely will continue to increase. In addition, milk yield heritability is reported as 0.3 (Lee et al., 1992; VanRaden et al., 2009) and ranges between 0.16 to 0.5 (Veerkamp, 1998). This means that still there is still room to increase milk production by exploiting genetic selection. The genetic correlation between GEE and milk production in dairy cattle ranged from 0.88 to 0.95 (Pitchford, 2004). It confirms that selecting dairy cows for milk yield automatically improved GEE (Veerkamp & Emmans, 1995). Consequently, FCR (4% FCM/DM) has increased from 0.91 in 1991 to 1.2 in 2006, and a common goal is 1.5 (Eastridge, 2006). Korver (1991) concluded that the improved GEE and FCR mostly reflects the dilution of maintenance. Dilution of maintenance means that as cows consume more, a relatively small fraction of energy is used for maintenance and a larger portion is captured in milk. Although there is no evidence to suggest that the maintenance requirements depend on milk production and breed, cows with similar body weight and breed may vary for maintenance requirements by about 8 to 10% (NRC, 2001). These assumptions need further investigation. To set a vision for the future, Vandehaar (1998) modelled the optimum point of milk yield. He proposed that above 15000 kg/yr, the marginal increase in efficiency approaches zero. Therefore, the positive correlation between milk production and efficiency that has existed in the past may change in the future, when average milk production surpasses 15000 kg/yr/cow (Vandehaar, 1998).

DMI and milk yield are tightly linked as their genetic correlation is reported to be 0.5 (Vallimont et al., 2010) ranging from 0.46 to 0.84 (Veerkamp, 1998). Consequently, selection decisions which change milk yield and body weight (BW) also change DMI (Veerkamp & Emmans, 1995). Genetic selection mostly focuses on milk yield and it indirectly affects DMI. However, with increased milk production per animal, there is a limit to the increase in DMI because of rumen fill; therefore, the density of NE in dairy rations has been elevated as milk production increased in the last 30 years. For instance, the dietary NE density of dairy cattle rations has increased from 1.23 in 1980 to more than 1.6 Mcal/kg in 2006 (Eastridge, 2006). Thus, it can be inferred that some of the improved efficiency due to increased milk production is withdrawn by increasing the dietary energy concentration in terms of expenses. Furthermore, the linear relationship between milk production and efficiency may change in the future. Therefore, these concerns drive researchers to define net energy efficiency using concepts such as RFI, which is independent from production and maintenance in dairy cattle.

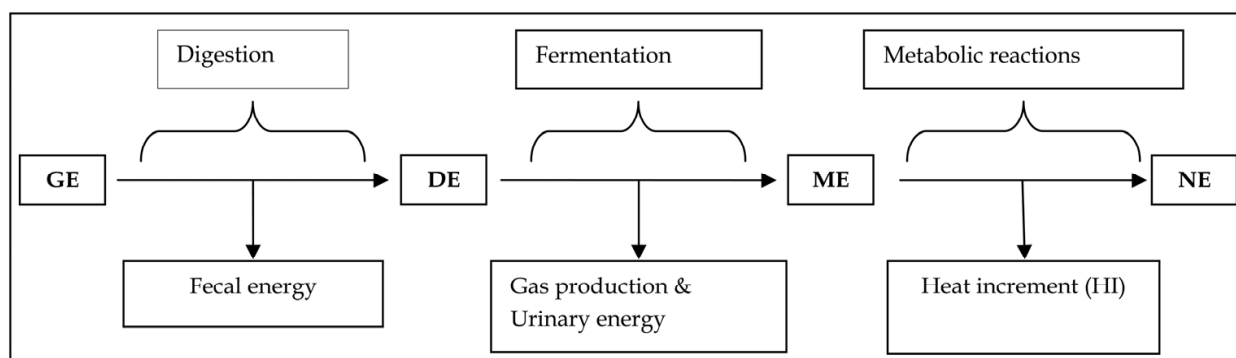


Figure 2. Energy transformation processes from gross energy (GE) to net energy (NE). The portion of lost energy in different steps is dependent on DMI level.

3.2. Body weight

Body weight influences energy efficiency through its relationship with milk production and digestive capacity. Heritability of body weight (BW) is reported to be in a range of 0.26 to 0.88 (Verrkamp, 1998). BW is genetically correlated with milk production. Although some researchers (Veerkamp, 1998; Vallimont et al., 2010) reported a negative correlation (range of -0.01 to -0.42), some other researchers reported positive correlations between BW and milk production (range of 0.05 to 0.45) (Veerkamp, 1998). This inconsistency in results could be due to mean differences of BW and milk production between populations under estimation. It can also be suggested that there is an optimum point of relationship between BW and milk production, and consequently energy efficiency. In order to illustrate this optimum relationship, Vandehaar (1998) modelled the relationship between body size, milk production and energy efficiency. He considered two possible relationships in which there were function of BW and digestive capacity (figure 3). In the first, he assumed that the digestive capacity of animals is not a function of BW and it is constant, the solid curve and dashed curve in figure 3. Therefore, increased BW increases the maintenance requirements and consequently decreases energy efficiency. In the second model, the digestive capacity was assumed to be a function of BW, so with increased BW digestive capacity will increase, and consequently a large cow would be efficient, dot-dashed curve and dashed curve in figure 3. In this case if a cow had a 200 kg greater BW (825 kg VS 625 kg), she should produce 60 kg/day more milk to become efficient. He concluded that the relationship between body size and efficiency depends on the relation between digestive capacities with body size (Vandehaar, 1998), and that there is an optimum point of relationship between BW and energy efficiency.

3.3. Body tissue changes

Body tissue changes increase energy efficiency by supporting milk production and tissue mobilization is a crucial factor in determining energy efficiency of dairy cattle. Although the conversion ratio of lost body reserves to milk production is less than that of regaining the

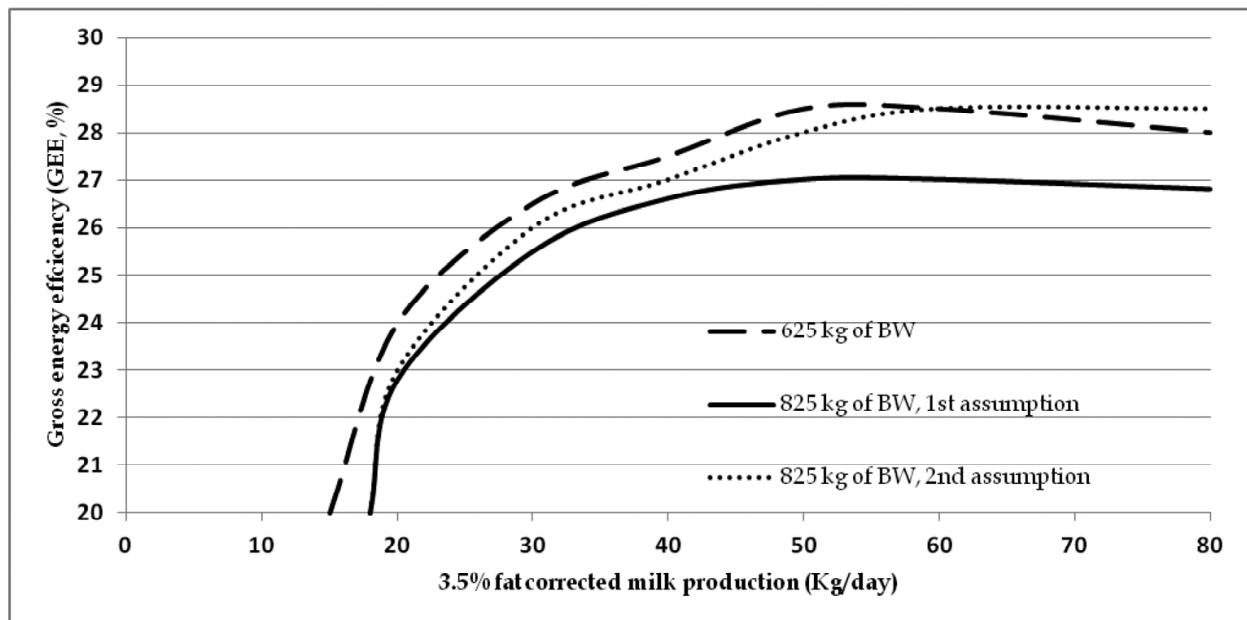


Figure 3. Adapted from Vandehaar (1998). He discussed the two possible relationships between digestive capacity and BW. In the first one, digestive capacity was not a function of BW while in the second, the digestive capacity was a function of BW.

reserves from feedstuffs, reasonable levels of losses still increase the energy efficiency. From an evolutionary point of view, mammals use their stored energy reserves to produce milk and support their young when their requirements exceed DMI consumed. In nature as the calf grows older, it gradually relies less on mothers' milk and the mother has an opportunity to regain energy resources for the next lactation (Bewley et al., 2008). Similarly, in the dairy industry, as the feed intake peak occurs later than the milk yield peak, dairy animals have a mechanism to use their body reserves to support milk production in early lactation and regain the body reserves in late lactation (Coffey et al., 2001; Bewley et al., 2008). In early lactation when energy intake is less than that used for milk, maintenance and activity, the cows are in a negative energy balance (NEB). Therefore, they sacrifice their body resources in this period to meet the requirements. Up to one-third of the total milk solids that are produced in early lactation, comes from body tissue reserves (Bewley et al., 2008). Practical measures of changes in energy resources include changes in BW and body condition score (BCS). BCS is a management technique used to appraise the body fat reserves in cattle (Coffey et al., 2001) and it is measured with either a 5 or a 9 point scale. The BCS represents 65, 55 and 66 percent of fat, protein and energy variation in dairy cattle, respectively (NRC, 2001). The ability to manage body reserves varies between animals, and they have a different pattern of BW and BCS changes during lactation and across lactations (Bewley et al., 2008). Heritability of changes in BW reportedly range from 0.1 to 0.27 (Verrkamp, 1998). Heritability estimates for BCS change depend on stage of lactation and range from 0.08 to

0.6 (Bewley et al., 2008). Negative and positive correlations have been reported between milk yield and BW changes (-0.41 to 0.45) (Verrkamp, 1998) and BCS changes (Bewley et al., 2008). One BCS unit (5 point scale) is equivalent to ~400 Mcal of ME and its conversion ratio to milk is estimated at 0.82. It is enough to produce an additional 8 kg milk/day in the first 60 days in milk (Vandehaar, 1998; Bewley et al., 2008). Therefore, losing one unit of BCS supports around 2000 kg of increased milk production over 305 days and it is expected to increase GEE from 25 to 26.5% in cows with a production of 8000 kg milk (Vandehaar, 1998). The lost energy reserves are replaced by cows in late lactation, and its replenishment conversion ratio is less (0.7) than that for loss (0.8) (Moe, 1981), but loss of BCS still increases efficiency (Vandehaar, 1998). Besides the increased efficiency, some researchers point out that side effects of losing energy reserves on other traits like reproduction and health should be considered (Vandehaar, 1998; Bewley et al., 2008). For example, cows restart reproduction activity after they pass the NEB period (Goff, 2006). Some of the metabolic diseases such as ketosis/fatty liver complex are highly correlated with NEB (Collier et al., 2006). Researchers proposed that there is a curvilinear relationship between BCS at calving and milk production; furthermore, maximum milk production is associated with 3.25 to 3.5 BCS at calving (Roche et al., 2007; Bewley et al., 2008). Indeed, during early lactation, a controlled loss of body condition of 0.5 to 1.0 units is associated with optimal milk production, health, and reproductive performance. Moreover, excessive BCS losses at calving predispose the animal to metabolic disorders such as ketosis and fatty liver (Spain, 1996; Bewley et al., 2008).

3.4. Age at first calving (AFC)

Age at first calving (AFC) is the period between birth and first calving. It represents a period when animals cost the farmer due to yardage expenses. Yardage expenses include costs related to housing, feeding and veterinary care, which represent 15 to 20% of animal expenditures toward the cost of milk production (Mayer et al., 2004). Breeding programs aim to have AFC at 22 to 24 months of age, and reducing the AFC can increase animal life time efficiency (LTE) (Mayer et al., 2004, Vandehaar & St-Pierre, 2006). Reduced AFC should not compromise weight at calving. The data suggest that the optimum weight for Holstein cows right after calving, is 570 kg. The results also showed that milk yield will be reduced about 70 kg for every 10 kg body weight below the optimum (Vandehaar & St-Pierre, 2006). Therefore, AFC can be reduced by a combination of increasing average daily gain and decreasing age at breeding (Mayer et al., 2004). Decreased AFC, and consequently yard cost, is associated with increased feed cost to support a rapid growth rate. Furthermore, if the optimum breeding weight is not achieved, there will be a negative effect on subsequent milk production (Vandehaar & St-Pierre, 2006). Indeed, the economic benefit of a decreased AFC is not well understood and there is a need for further investigation.

3.5. Environmental factors

Changes in environmental conditions (temperature and humidity) and photoperiod are called seasonal changes. Seasonal changes affect energy efficiency by altering hormone

signals and the target cell's responsiveness to hormonal stimulation (Collier et al., 2006). The thermoneutral zone is a range in which animals do not spend energy to maintain their normal body temperature. The upper critical range for dairy cattle is 25 to 26 °C and lower critical range depends on DIM and production level. The lower critical range is 2, -4 and -10 °C for an animal at maintenance or producing 10 kg or 20 kg of milk, respectively. Dairy cows in cold stress do not need to change their energy requirements due to high heat production but it has an effect on feed digestibility. Research has shown that there is a 2% reduction in digestibility for every 10 degree reduction in ambient temperature; this can possibly be attributed to the increase in passage rate of digesta (NRC, 2001). Therefore, cold stress does not affect energy efficiency significantly in dairy cattle; while, mild to severe heat stress increases the maintenance requirements from 0.7 to 2.4 %, respectively, and decreases DMI. Heat stress affects animal behaviour, metabolism and efficiency (NRC, 2001).

Photoperiod, another environmental factor, affects lactation, reproduction, production, growth and immune function. Most studies are done using short or long day photoperiod concept. Results demonstrated that the physiological basis of attainment of puberty is controlled by photoperiod rather than ambient temperature. Long photoperiod causes early puberty that is associated with rapid growth in calves, and greater mammary parenchyma (Collier et al., 2006). Long day photoperiod can affect energy efficiency by lowering AFC, and increases milk production, but it does not affect feeding behaviour. In addition, other temporary environmental factors such as milking frequency can also affect milk production and energy efficiency. Wall & McFadden (2007) concluded that milking 2 times more frequently than usual (4 vs 2 times/day) for a 3 week interval during early lactation significantly increases milk production.

4. Indirect effects of selection for energy efficiency on some related traits

To this point, factors that practically and directly affect energy efficiency in dairy cattle have been discussed; to maximize gain due to genetic selection for energy efficiency, its genetic base and indirect effects on other traits should also be known. Although reports on direct/indirect selection for efficiency in dairy cattle are scarce (Linn, 2006), many studies have been conducted to study its heritability and the direct/indirect effect that selecting animals based on efficiency traits has on other related traits in different species. The reviewed results showed that the weighted mean of 28 and 9 estimates of heritability in beef for FCR and GEE were reported as 0.32 ± 0.02 and 0.37 ± 0.05 , respectively (Koots et al., 1994). The weighted mean of 35 estimates of heritability for RFI in 7 species was reported 0.25 ± 0.02 (Pitchford, 2004). In order to point out the potential effect of selection for efficiency on other related traits, authors discussed this effect on reproduction, activities, organs, body composition, metabolites and health in beef cattle as well as other species in addition to dairy cattle (table 1).

Species	Reproduction	Activities	Organs	Chemical composition	Metabolites	Health
Dairy	Decrease daughter fertility	Data not available.	Data not available.	Data not available.	Data not available.	Increases the incidence of metabolic diseases (Wassmuth et al., 2000)
Beef	Decreases age at puberty, does not affect pregnancy rate (Shaffer et al., 2010). Did not affect bull performance (Wang et al., 2012).	Less feeding duration and less head-down time, (Durunna et al., 2010; Nkrumah et al., 2006; Kelly et al., 2010).	Did not affect tissues of gastro intestinal organs and internal organs (Richardson et al., 2001).	Less body fat (Richardson et al., 2001) more empty body water (Basarb et al., 2003).	Low plasma protein, blood concentration of urea and aspartate amino transfer (Herd & Arthur, 2009) high insulin, glucose and NEFA (Kelly et al., 2010).	Data not available.
Pig	Decreased litter size (Estany et al., 2002)	Less feeding time, less visits per day, less total time in feeder (Von Felde et al., 1996)				
Mice	Decreased litter size, ovulation rate (Nielsen et al., 1997)	Less activities (Hastings et al., 1997; Rau et al., 2000)	Larger livers, caeca, stomachs but smaller hearts (Hughes & Pitchford, 2004)	Fatter (Hughes & Pitchford, 2004)		Data not available.
Chicken	Increased fertility, hatchability, decreased mortality (Morrison et al., 1997). No losses in egg production (Bordas et al., 1992)	Less activities (Luiting & Urf, 1991)		Controversial results, increase or decrease fat traits (Liting & Urf, 1991)		

Table 1. Summary of indirect response of selection for energy efficiency on related traits in different species

4.1. Reproduction

Reproductive performance and milk production are two main entities in the profitability of dairy cattle industry (LeBlanc, 2010). Although milk production and energy efficiency have increased, the genetic trend of average daughter fertility in Canadian Holsteins has shown a 2% reduction over 14 years. It decreased from 101.9 in 1995 to 99.9 in 2009 (Van Doormaal, 2010). As a result, a selection objective to increase milk production seems to favour cows that genetically produce more milk, but consequently are prone to experience more negative

energy balance (NEB). It has been reported that the time of first estrus is closely related to NEB during the first 2 - 3 weeks after calving (Coffey et al., 2006) and “cows appear to resume reproductive activity only after the nadir of NEB has passed” (Veerkamp, 1998).

Some researchers studied the indirect effect of selection for energy efficiency on reproduction traits in beef, and other species. For example, Shaffer et al. (2010) allocated beef heifers into three groups based on their efficiency (low, medium and high RFI) and studied the indirect effects of selection for efficiency on reproduction performance. They reported a negative relationship between RFI and age at puberty. The efficient animals reached puberty later than inefficient animals but it did not affect pregnancy or conception rates. They also quantified this relationship and reported that each unit increase in RFI corresponds to a decrease of 7.5 days in age at puberty. Wang et al. (2012) studied the effect of RFI on bull's reproductive performance and fertility. They had 20 high RFI (inefficient) and 22 low RFI (efficient) beef bulls in a multi-sire breeding system on pasture and examined the association between RFI and semen quality traits (density, progressive motility and morphology), progeny per sire and some other related traits. They concluded that selection for RFI does not have a negative effect on reproductive performance and fertility in bulls bred in multi-sire groups on pasture.

In other species, Nielsen et al. (1997) divergently selected mice for energy efficiency, based on heat loss, over 15 generations. They had high efficient, low efficient and control groups, and each group had three replicates. Indirect effects of selection for energy efficiency on reproduction performance (litter size, ovulation rate, number of foetuses at 7 days of gestation and ovulation success) were measured. The results showed that the high efficient line (low heat loss) had 20% smaller litters at first parity in the 15th generation. The efficient line also had a 23% lower ovulation rate when measured at the second parity. However, the high efficiency line had a higher ovulation success rate (86%) than the low efficiency line (84%), but the differences were not significant (Nielsen et al., 1997). A report on pigs demonstrated that pigs with high litter size had a poorer efficiency compared to the control group (Estany et al., 2002). However, Morisson et al (1997) divergently selected hens for RFI over 18 generations and studied the effect of energy efficiency selection on reproduction and sperm characteristics. Contrary to mice and pigs, they found that a high efficient line of hens had only 6% unfertilised eggs compared with 30% in a low efficiency line. The early mortality rate in the inefficient line was twice that of the efficient line. Overall, the efficient line had a better hatchability performance (Morrisson et al., 1997). The better reproductive performance of efficient hens is supported by other researchers who selected hens for low RFI without losses in egg production (Bordas et al., 1992). It could be inferred that some species sacrifice litter size and maintain energy to better take care of the fetus. There is a need to study the associated effects of selection for energy efficiency and reproductive performance in dairy cattle.

4.2. Activity

Energy expenditure of feeding depends on feeding behaviour. In addition, results of studies in different species have shown that selection for efficiency had effects on animal's feeding

behaviour. Durunna et al (2010) conducted a 3 year study on 402 and 419 steers on two different diets (grower and finisher). They measured feed intake, feeding duration, head-down time and bunk visits using the Growsafe system. Their results showed that the efficient steers (Low RFI) exhibited less feeding duration, head down time, and bunk visits. In another study, efficient beef cattle (low RFI) had less feeding duration, but a higher feeding frequency (Nkrumah et al., 2006). These results are also supported by other researchers studying finishing heifers (Kelly et al., 2010) that showed efficient heifers had less feeding duration.

Some studies have been done on mice to determine the effect of selection for RFI on activity. Hastings et al (1997) found that high efficiency (low RFI) mice were 67% less active than the low efficiency mice. Furthermore, Rauw et al (2000) selected mice for high litter size at birth (S line) and showed that the S line had higher RFI (low efficiency). They reported that low efficiency mice, when compared with control group, had more locomotion activity, and they ran faster in two types of runaway tests. In hens, Luiting &Urff (1991) reported that high efficient layer hens were less active than the control group. However, efficient boars had a lower feeding rate, less feed intake per visit, fewer visits per day, and less total time in the feeder per day (Von Felde et al., 1996). Herd & Arthur (2009) concluded that the positive and high genetic correlation of feeding time per day and eating sessions per day with RFI indicates that there are some common genes controlling feeding behaviour and RFI.

4.3. Organs and body composition

Liver, the largest visceral organ, accounts for 17 to 31% of total body energy expenditures (Eisemann & Nienaber, 1990; Ortigues and Visseiche 1995). All of the visceral organs account for up to 40 to 50% of body energy expenditures in sheep and cattle (Perry et al., 1997). It was concluded that selection for efficiency may result in lower proportions of liver and visceral tissues (Pitchford, 2004). In female mice, the results contradicted this conclusion and the efficient mice (low RFI) had larger livers, caeca, intestines, and stomachs but smaller hearts (Hughes & Pitchford, 2004). In cattle divergently selected for RFI, the weight of highly activate tissues of gastrointestinal organs and internal organs were not significantly different. It was concluded that variation in ME intake and energy efficiency was due to metabolic processes rather than changes in body composition (Richardson et al., 2001).

Results of divergently selecting steers for RFI showed that there is a correlation between chemical composition and variation in RFI. Animals with low RFI had more whole-body chemical protein and less whole-body chemical fat (Richardson et al., 2001). Basarab et al (2003) also found that efficient steers had more empty body water but less empty body fat than low efficient steers. The divergently selected steers had almost the same amount of empty body protein. In another study, Shaffer et al (2010) grouped beef heifers of British breeds into low, medium and high RFI groups and found that efficient heifers (low RFI) had less lean meat area (cm²) per 100 kg of BW than inefficient (high RFI) heifers. In mice, the results have shown that the high efficiency lines had slightly lower post-weaning weight (0-12%), little differences in mature weight (0-30%) and were fatter (5-60% depending on the

age at measurement) than low efficiency lines. Luiting & Urff (1991) summarized reports of phenotypic and genetic correlations between RFI and body fat traits in chickens and found that they ranged from -0.4 to 0.45. Herd & Arthur (2009) concluded that the amount and direction of association between body composition and variation in energy efficiency in cattle depends on age and stage of maturity.

4.4. Metabolites and health

There are some reports on associations between efficiency and some metabolites, which are indicators of production, and health. For example, high concentrations of total plasma protein, blood concentrations of urea and aspartate amino transfer were reported in high RFI cattle (inefficient) compared to low RFI (efficient). These metabolites are an index of protein turnover and inefficient cattle had higher protein turnover rates compared to low efficient cattle (Herd & Arthur, 2009). In other research, Kelly et al (2010) divergently selected heifers based on RFI and found that inefficient animals had higher plasma urea, B-hydroxybutyrate, and leptin concentration and lower NEFA, plasma glucose and insulin than efficient animals. Higher levels of cortisol and red and white blood cells were reported in high RFI steers, which indicates that these animals (inefficient) may be more susceptible to stress (Richardson et al., 2004). In another report, a positive correlation between IGF-I, a growth metabolite, and RFI was reported in beef cattle (Moore et al., 2005). However, separation of RFI into post weaning and feedlot periods determined that there is a positive correlation of IGF-I with RFI during post weaning time while there is a negative correlation during the feedlot period (Herd & Arthur., 2009). Kelly et al (2010) concluded that some plasma analytes such as B-hydroxybutyrate may be potential indicators of net efficiency in beef cattle.

Overall, animals are efficient and profitable, if they are healthy. Rauw et al (1998) reviewed undesirable effects of selection for high efficiency in farm animals and concluded that selection had a negative correlation with health traits. Wassmuth et al (2000) used feed intake data of 7752 young dairy bulls (2203 Danish Red, 4527 Danish Friesian and 1022 Danish Jersey), and combined the feed intake data with recorded incidence of mastitis, retained placenta, metritis, sole of ulcer and ketosis data of 473,613 dairy cows in their early lactation to investigate the relationship between efficiency and diseases in dairy cattle. They defined efficiency as “the feed energy intake per kilogram live weight gain” in bulls. The size and direction of relationship depended on breed, but the overall energy efficiency was positively correlated with incidence of diseases. Currently, selection indices in dairy cattle favour animals with high milk production and consequently negative energy balance (NEB). NEB is generally related to poorer health status and fertility and it can have an indirect economic effect (Goff, 2006; Veerkamp, 1998).

Overall, the physiological basis of energy efficiency (RFI) has been reviewed by Herd & Arthur (2009). The results of Angus steers divergently selected for net feed efficiency (RFI) revealed that feeding pattern, metabolism including turn over and stress, body composition, digestibility, heat increment of fermentation, and activity accounted for 2, 37, 5, 10, 9 and 10

% of the variation in RFI, respectively, and the remaining variation was attributed to other unknown processes (Herd & Arthur, 2009).

5. Conclusion

It can be concluded that there is an optimum point for the factors (DMI, milk production, body weight, AFC and environment factors) that influence the energy efficiency, and their relationship with energy efficiency is not linear. Hence, increasing output traits does not necessarily increase net energy efficiency. Therefore, the measures of energy efficiency that represent net efficiency, like RFI, which is independent from maintenance and production, need to be considered to improve efficiency in dairy cattle. It is proven that RFI is a robust measure of the animals' energy efficiency because it is independent from animals' maintenance requirements and level of production. Genetic improvement on energy efficiency can be achieved through selection for RFI in the dairy industry since the heritability estimates for RFI are moderate for most species ($h^2 = 0.25$). Also, the traits are correlated and there are inconsistent results between species for indirect response of selection for energy efficiency on other related traits especially reproduction and health traits. Care should be taken when animals are selected for energy efficiency. Further research is required to define RFI in dairy cattle and to determine the indirect effects that selecting for efficiency may exert on other related traits, especially those related to reproduction and health.

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