INTRODUCTION

Reproduction has been reported to be 5 times more important to commercial cattle producers than growth rate or milk production (Trenkle and Willham, 1977). Heifers that calve early in their first calving season tend to calve early throughout their lives and have greater lifetime calf production (Lesmeister et al., 1973). For optimum fertility during the first breeding season, heifers should have begun estrous cycles before beginning the breeding season because fertility at the first estrous cycle is less than for subsequent estrous cycles (Byerly et al., 1987). The influence of nutrition and growth rate on puberty in beef heifers has been studied by many researchers. Preweaning growth rate is inversely correlated with age at puberty in beef heifers (Wiltbank et al., 1966; Arije and Wiltbank, 1971, 1974). Postweaning growth rate is inversely correlated with age at puberty but can be influenced by plane of nutrition (Wiltbank et al., 1966; Arije and Wiltbank, 1974). The “target weight concept” involves a nutritional program where heifers are fed to grow at a rate that is predicted for them to be puberal at the beginning of the breeding season (Lamond, 1970). The onset of puberty appears to be controlled by the total amount of growth rather than the rate or time of the growth of the heifers with puberty and return to ovarian cyclicity after calving. Tropically adapted cattle (i.e., Santa Gertrudis and Brahman) selected for low residual feed intake had a lesser response of insulin to a glucose challenge than their less efficient herdmates. These studies indicate the possibility that animals with differing residual feed intake (efficiencies) may have differing intermediary metabolism and, therefore, differing rates of reaching puberty. Selection for low residual feed intake results in selection of leaner heifers that reach puberty at older ages. These leaner heifers calve later in their first and subsequent calving seasons. Selection for residual average daily gain has no negative influence on age at puberty or calving interval. Selection for residual ADG has a negative influence on age at first calving but not calving interval. There may be no acceptable method to improve feed efficiency without harming reproductive efficiency.

Key words: beef heifer, puberty, residual feed intake

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ABSTRACT: The influence of nutrition on puberty in beef heifers is complex and under neuroendocrine control. The stores of body fat in mammals are a determinant of the onset and maintenance of puberty. Body fat stores are greater in heifers with greater residual feed intake than in their more efficient herdmates. A 1 unit increase in residual feed intake resulted in a reduction of 7.54 d in age at puberty in Bos taurus beef heifers. However, Bos indicus-influenced heifers, which reach puberty at older ages, were not found to have sexual maturity influenced by selection for residual feed intake. The strong influence of body fat stores on return to estrus after calving does indicate that selection for leaner beef heifers could affect reproductive performance relative to puberty and postpartum rebreeding of first calf heifers. The influence of intermediary metabolism, through signals at the central nervous system, regulates the GnRH pulse generator, thereby influencing pituitary and ovarian function culminating...
MEASUREMENTS OF FEED EFFICIENCY

There are currently 3 methods in use for determining feed efficiency of beef heifers. Residual feed intake (RFI) is the residual from a regression model regressing feed intake on ADG and BW^{-0.75}. Residual average daily gain (RADG) is the residual from a regression model regressing ADG on feed intake and BW^{-0.75}. Feed conversion ratio is calculated as average feed intake divided by ADG. All of these measurements require individual feed intake information.

Feed conversion ratio has been the most used measurement in selection for feed efficiency in beef cattle. Feed conversion ratio does not account for maintenance requirements and can be affected by differences in patterns of growth and maturity (Archer et al., 1999). Use of feed conversion ratio for selection has resulted in increased BW gain and mature BW of females along with increased maintenance requirements in beef cows (Herd and Bishop, 2000). Increasing BW at maturity has resulted in increased age and BW at puberty in replacement heifers and reduced lifetime productivity of beef cows (Lesmeister et al., 1973). For these reasons the use of feed conversion ratio as a selection tool for selecting replacement heifers has fallen out of favor with researchers and should be discontinued by beef cattle breeders.

Residual feed intake allows for differences in maintenance requirement and is genetically independent from BW, BW gain, and mature size in beef cattle (Crews, 2005). Because selection for RFI is independent from growth traits and is a trait that relates to input, that is, feed consumption, it has become a favored selection tool for researchers and is being used by breeders of beef cattle in an attempt to decrease the input costs of feed consumed without altering growth performance.

Residual average daily gain is an alternative to RFI that places more emphasis on ADG and less on feed intake. This alternative selection method may be useful for improving both ADG and feed efficiency.

Influence of Selection for Residual Feed Intake on Body Composition

Body composition estimates have been reported to be useful in predicting BW at puberty in beef heifers (Brooks et al., 1985). The final regression equation predicting puberty included age, shoulder height, and estimates of body protein and fat with an $R^2$ of 0.87. Lower RFI, more efficient, yearling beef heifers have lower back and rump fat measures than their less efficient herdmates (Arthur et al., 2001; Basarab et al., 2003, 2011; Channon et al., 2004; Robinson and Oddy, 2004; Schenkel et al., 2004; Nkrumah et al., 2007; Lancaster et al., 2009a,b; Kelly et al., 2010; Shaffer et al., 2011). Low RFI heifers can have 2 to 5% less body fat than high RFI heifers (Basarab et al., 2011). To increase the proportion of fat in BW gain of growing beef cattle by 5%, energy intake must be increased by 1.16 Mcal/d (NRC, 1996). Heifers deposit more energy per unit of BW gain than steers and the difference increases at increased rates of BW gain (Lofgreen and Garrett, 1968). This difference between steers and heifers is probably due to differences in fat deposition. Selection for low RFI results in selection of heifers that are leaner and that will require them to be fed for a longer time to reach the degree of fatness required to reach puberty.

Influence of Selection for Residual Feed Intake on Puberty

The current system for testing beef cattle for RFI involves testing calves from 7 to 12 mo of age. This testing approach has resulted in selection of Bos taurus heifers that are older at puberty (Arthur et al., 2005; Basarab et al., 2007, 2011; Crowley et al., 2011; Shaffer et al., 2011). These heifers, which were selected for low RFI, had delayed puberty and conception. The delay in the onset of puberty has been related to the decrease in fat deposition in low RFI heifers. Shaffer et al. (2011) stated that “less efficient animals likely stored excess consumed energy as fat, which may have hastened maturity and initiated reproductive function at an earlier age.” Crowley et al. (2011) stated that “a delay in the onset of puberty in decreased RFI animals is biologically plausible because the partitioning of energy among animals differing in RFI may be altered with more energy in low RFI partitioned toward growth and away from...
other bodily functions, such as reproduction during that period.”

Brody (1945) suggested that puberty occurs at an inflection point of the growth curve corresponding to a shift in body composition away from lean accrual and toward fat deposition. In a study where individual feed intake and puberty were recorded with the heifers fed for 84 ± 6 d before puberty and for 90 ± 4 d after puberty, there was a correlation of 0.48 \((P < 0.001)\) between prepubertal and postpubertal RFI (Loyd et al., 2011). The conclusion from this report was that “physiological maturity should be considered when selecting cohorts of cattle for RFI evaluation.” The most common time for evaluating replacement heifers for RFI is after weaning at approximately 7 mo of age and before their first breeding season. Early maturing heifers from British and Continental breeds reach puberty during this period. From an RFI evaluation standpoint, the earlier maturing heifers are penalized due to their physiological age and the later maturing heifers tend to benefit from their relatively younger physiological age. This can result in selection of heifers that are later maturing from these relatively early maturing breeds of cattle. Later maturing breeds, such as the Brahman, may be less affected because few, if any, will reach puberty before the end of the RFI test period. Brahman heifers previously evaluated for RFI were evaluated for sexual maturity by exposing them continuously to fertile bulls after weaning and using calving age minus average gestation length for the breed, therefore age at conception could be calculated (Loyd et al., 2010; Table 1). The trend, although not significant statistically, follows the findings in British and Continental breeds of cattle where the most efficient heifers reached sexual maturity at an older age (Basarab et al., 2011; Crowley et al., 2011; Shafer, 2011). When RFI is adjusted for backfat thickness and feeding frequency, it is independent of fertility in replacement beef heifers (Basarab et al., 2011). This finding leads to the conclusion that differences exist in body composition and in intermediary metabolism between low and high RFI beef heifers.

**Residual Feed Intake and Energy Metabolism**

Insulin-like growth factor-I is a hormone related to growth and development. Concentrations of IGF-I have been positively correlated with RFI in beef cattle (Johnston et al., 2001; Moore et al., 2005). Subsequent reports failed to support these findings as no correlation between circulating concentrations of IGF-I and RFI in growing beef heifers was found (Lancaster et al., 2007; Caldwell, 2009; Kelly et al., 2010). These conflicting reports led to the conclusion that IGF-I concentrations are not predictive of RFI in beef cattle.

### Table 1. Age at first conception in Brahman heifers ranked by residual feed intake (RFI)

<table>
<thead>
<tr>
<th>RFI group</th>
<th>n</th>
<th>Age at conception, d</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Greater than 0.5 SD below the mean of contemporaries</td>
<td>49</td>
<td>731.0</td>
<td>35.6</td>
</tr>
<tr>
<td>Less than 0.5 SD below the mean of contemporaries</td>
<td>60</td>
<td>704.3</td>
<td>35.1</td>
</tr>
<tr>
<td>Less than 0.5 SD above the mean of contemporaries</td>
<td>66</td>
<td>700.3</td>
<td>34.5</td>
</tr>
<tr>
<td>Greater than 0.5 SD above the mean of contemporaries</td>
<td>68</td>
<td>698.0</td>
<td>34.4</td>
</tr>
</tbody>
</table>

1RFI \((P = 0.3885)\).
2Data are from R. D. Randel, unpublished data.

Greater circulating concentrations of insulin have been reported in high RFI steers at the end of the finishing phase (Richardson et al., 2004; Brown, 2005). High and low RFI Brahman yearling bulls and heifers were subjected to a glucose challenge and serial blood samples were collected to determine glucose and insulin concentrations (Shaffer, 2011). In those studies, glucose responses were similar after the glucose challenges (Fig. 1 and 2) in both heifers and bulls. The ability of low and high RFI yearling Brahman calves was similar in clearing glucose from circulation. High RFI heifers tended to have similar \((P = 0.6781)\) insulin response compared with low RFI heifers (Fig. 3). High RFI bulls had a greater \((P = 0.0271)\) insulin response compared with low RFI bulls (Fig. 4). Insulogenic index was greater in both high RFI heifers (Fig. 5) and bulls (Fig. 6).

These data indicate that inefficient Brahman yearling cattle are releasing more insulin in response to glucose and may be more sensitive to elevated circulating glucose than their more efficient herdmates. The conclusion from those reports is that selection for RFI can result in alterations in not only body composition but also intermediary metabolism. Both nutrient availability and

**Figure 1.** Serum glucose after a glucose challenge in Brahman heifers evaluated previously for residual feed intake (RFI). For statistical analysis, heifers were separated into those having negative (NEG) or positive (POS) RFI. Results are from Shafer (2011).
retained energy are important for replacement heifers to reach puberty and to continue estrous cyclic activity until conception occurs. The concept that ovarian function of beef heifers during acute submaintenance feeding is related to RFI was tested (Lents et al., 2011). In this study, heifers were evaluated for RFI and after they were estrous cycling, they were restricted to 40% of their maintenance energy requirements for 21 d. No relationship was found between luteal function during energy restriction and RFI of the heifers. Once estrous cycles begin there appeared to be little influence of RFI on the hypothalamic-pituitary-gonadal axis.

Influence of Selection for Residual Feed Intake on Return to Estrous Cycles as First Calf Heifers

Low RFI heifers have been reported to have a reduced conception rate from d 12 to 37 of the breeding season, pregnancy rate (76.84 vs. 86.32%; *P* = 0.092), and calving rate compared with high RFI heifers (Basarab et al., 2011). Arthur et al. (2005) selected heifers for RFI during the prepubertal period and found no differences in pregnancy or calving rates but did find that low RFI cows calved 5 d later (*P* = 0.07) than high RFI cows. Basarab et al. (2007) found that cows having low RFI progeny (the cows were not evaluated for RFI) calved 5 to 6 d later in the calving season (*P* < 0.001) than cows having less efficient progeny. All of these reports were from heifers that were British or Continental breeds. When evaluating Brahman first calf heifers, which have longer intervals from calving to first estrus, no differences were found in interval from first to the second calf due to selection for RFI (Table 2). Crowley et al. (2011) reported that there was no genetic correlation between RFI and calving interval. It appears that there is no difference in fertility of mature cows with low or high RFI. Basarab et al. (2011)

![Figure 2. Serum glucose after a glucose challenge in Brahman bulls evaluated previously for residual feed intake (RFI). For statistical analysis, bulls were separated into those having negative (NEG) or positive (POS) RFI. Results are from Shafer (2011).](image1)

![Figure 3. Serum insulin after a glucose challenge in Brahman heifers evaluated previously for residual feed intake (RFI). For statistical analysis, heifers were separated into those having negative (NEG) or positive (POS) RFI. Results are from Shafer (2011).](image2)

![Figure 4. Serum insulin after a glucose challenge in Brahman bulls evaluated previously for residual feed intake (RFI). For statistical analysis, bulls were separated into those having negative (NEG) or positive (POS) RFI. Results are from Shafer (2011).](image3)

![Figure 5. Insulinogenic index after a glucose challenge of Brahman heifers evaluated previously for residual feed intake (RFI). For statistical analysis, heifers were separated into those having negative (NEG) or positive (POS) RFI. Results are from Shafer (2011).](image4)
adjusted RFI of replacement beef heifers for backfat thickness and average feeding event frequency. This adjustment resulted in removal of the delay in calving for the low RFI heifers. Heifers must be selected in a manner that does not result in decreased body fat at younger ages for them to reach puberty early and for them to become early calvers as mature cows. The influence of later maturation of low RFI heifers results in calving later in the calving season than their high RFI herdmates.

Other Measurements for Feed Efficiency

Residual average daily gain has not been evaluated by as many researchers as RFI. Crowley et al. (2011) reports that there was a genetic correlation of 0.36 with age at puberty, which indicates that selection for RADG may have a negative influence on age at puberty in beef heifers. They also report that the genetic correlation with calving interval was –0.01 indicating that there should be no effect of RADG on calving interval. Days of age at conception of Brahman heifers evaluated for RADG were not different between high and low RADG groups (Table 3). Similarly interval from the first to the second calf was not different between high and low RADG groups (Table 4).

SUMMARY AND CONCLUSIONS

Selection of replacement heifers for low RFI results in selection of later maturing heifers. These later maturing heifers calve later in their first and subsequent calving seasons. These results occur when the heifers are evaluated themselves or when they are sired by low RFI bulls. Selection of replacement heifers using RADG may also have a negative influence on age at puberty but not calving interval. There may not be an acceptable method to improve feed efficiency without negatively affecting reproductive efficiency. The costs of late sexual maturity and delayed calving in subsequent calving seasons overcome gains in feed efficiency of the cow herd.

LITERATURE CITED


Table 2. Interval from the first to the second calf in Brahman heifers evaluated for residual feed intake (RFI)

<table>
<thead>
<tr>
<th>RFI group¹,²</th>
<th>n</th>
<th>Calving interval, d</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Greater than 0.5 SD below the mean of contemporaries</td>
<td>32</td>
<td>461.0</td>
<td>26.4</td>
</tr>
<tr>
<td>Less than 0.5 SD below the mean of contemporaries</td>
<td>41</td>
<td>455.9</td>
<td>23.4</td>
</tr>
<tr>
<td>Less than 0.5 SD above the mean of contemporaries</td>
<td>54</td>
<td>471.1</td>
<td>21.3</td>
</tr>
<tr>
<td>Greater than 0.5 SD above the mean of contemporaries</td>
<td>52</td>
<td>481.5</td>
<td>21.4</td>
</tr>
</tbody>
</table>

¹RFI (P = 0.7482).
²Data are from R. D. Randel, unpublished data.

Table 3. Age at first conception in Brahman heifers ranked by residual average daily gain (RADG)

<table>
<thead>
<tr>
<th>RADG group¹,²</th>
<th>n</th>
<th>Age at conception, d</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Greater than 0.5 SD above the mean of contemporaries</td>
<td>74</td>
<td>697.0</td>
<td>34.4</td>
</tr>
<tr>
<td>Less than 0.5 SD above the mean of contemporaries</td>
<td>51</td>
<td>714.9</td>
<td>35.9</td>
</tr>
<tr>
<td>Less than 0.5 SD below the mean of contemporaries</td>
<td>48</td>
<td>706.9</td>
<td>36.2</td>
</tr>
<tr>
<td>Greater than 0.5 SD below the mean of contemporaries</td>
<td>70</td>
<td>721.3</td>
<td>34.8</td>
</tr>
</tbody>
</table>

¹RADG (P = 0.5234).
²Data are from R. D. Randel, unpublished data.

Table 4. Interval from the first to the second calf in Brahman heifers evaluated for residual average daily gain (RADG)

<table>
<thead>
<tr>
<th>RADG group¹,²</th>
<th>n</th>
<th>Calving interval, d</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Greater than 0.5 SD above the mean of contemporaries</td>
<td>54</td>
<td>475.1</td>
<td>20.6</td>
</tr>
<tr>
<td>Less than 0.5 SD above the mean of contemporaries</td>
<td>42</td>
<td>461.3</td>
<td>22.9</td>
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<tr>
<td>Less than 0.5 SD below the mean of contemporaries</td>
<td>34</td>
<td>489.0</td>
<td>24.2</td>
</tr>
<tr>
<td>Greater than 0.5 SD below the mean of contemporaries</td>
<td>49</td>
<td>459.4</td>
<td>21.3</td>
</tr>
</tbody>
</table>

¹RADG (P = 0.6367).
²Data are from R. D. Randel, unpublished data.


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