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3 **Leptin concentrations in finishing beef steers and heifers and their association with dry**
4 **matter intake, average daily gain, feed efficiency, and body composition**

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9 **ABSTRACT:**

10 The objective of this experiment was to determine the association of circulating plasma leptin
11 concentrations with production and body composition measures of finishing beef steers and
12 heifers and to determine if multiple sampling time points improve the associations of plasma
13 leptin concentrations with production and body composition traits. Individual DMI and ADG
14 were determined for 84 d using steers and heifers ($n = 127$ steers and $n = 109$ heifers). Blood
15 was collected on day 0, day 42, and day 83 for determination of plasma leptin concentrations.
16 Leptin concentrations was greater in heifers than steers on day 0 ($P < 0.001$ for sex by day
17 interaction) and leptin concentrations increased in both sexes but was not different from each
18 other on day 83. Leptin concentrations at all three time points and the mean were shown to be
19 positively associated with DMI ($P \leq 0.006$) while the mean leptin concentration explaining 8.3 %
20 of the variance of DMI. Concentrations of leptin at day 42, day 83, and the mean of all three
21 time points were positively associated with ADG ($P \leq 0.011$). Mean leptin concentration was
22 negatively associated with G:F and positively associated with residual feed intake (RFI),
23 indicating that more efficient cattle had lower leptin concentrations. However, leptin
24 concentrations explained very little of the variation in RFI (≤ 3.2 % of the variance). Leptin
25 concentrations were positively associated with body fat measured by ultrasonography at the 12th-
26 rib and over the rump ($P < 0.001$), with the mean leptin concentration explaining 21.9 % and
27 12.7 % of the variance in 12th rib and rump fat thickness, respectively. The same trend was
28 observed with carcass composition where leptin concentrations were positively associated with
29 12th rib fat thickness, USDA calculated yield grade (YG), and marbling score ($P \leq 0.006$) and
30 mean leptin concentration explained 16.8, 18.2, and 4.6 % of the variance for 12th rib fat
31 thickness, YG, and marbling score, respectively. Given these and previous results, it appears

that leptin physiology could be a candidate for mechanisms that contribute to feed intake and feed efficiency variation in beef cattle.

Keywords: beef cattle, feed efficiency, feed intake, growth, leptin

1. Introduction

Leptin is a hormone produced in adipocytes (1) that acts through central neural pathways to reduce appetite and feed intake of animals including ruminants (2,3). Given the unique biology of leptin and its regulation of appetite, leptin is a potential candidate to be used as a biomarker for beef cattle production traits such as feed intake, growth, and feed efficiency. Previous work using genetically diverse finishing beef steers observed that circulating leptin concentrations are positively associated with DMI and residual feed intake (**RFI**) and negatively associated with ADG and G:F (4-6). In addition to associations with production measures, leptin has repeatedly been shown to be related to carcass composition (4,7,8). Along with predicting carcass quality, leptin could potentially be used as a biomarker to determine composition of growth in cattle.

While Foote et al. (2015) used a fairly large sample size, the experiment was limited to steers and used only one time point to measure leptin concentrations. The purpose of this experiment was to determine if measurements across the production period would improve the association of leptin with production traits and if the observed associations were consistent with finishing beef heifers while using a diverse set of cattle. It is hypothesized that plasma leptin concentrations will be positively associated with DMI, feed efficiency measures, and body fat, and negatively associated with ADG in finishing steers and heifers. It is also likely that leptin concentrations change over the feeding period and that multiple measures of leptin

concentrations would likely yield improved estimates of the associations of leptin with other traits.

2. Materials and methods

This experiment was reviewed and approved by the U.S. Meat Animal Research Center (USMARC) Institutional Animal Care and Use Committee (IACUC; approval number 5438-31000-0092-03).

2.1 Animals

Details of the animals and experimental procedures have been previously described (9). Briefly, calves ($n = 236$ total; $n = 127$ steers and $n = 109$ heifers) from composite breed cows mated to Angus, Charolais, Gelbvieh, Limousin, Red Angus, and Simmental bulls that were in use on industry ranches were born in a single calving season for this study. Both steers (Angus- [$n = 35$], Charolais- [$n = 8$], Gelbvieh- [$n = 21$], Limousin- [$n = 21$], Red Angus- [$n = 17$], and Simmental-sired [$n = 25$]) and heifers (Angus- [$n = 25$], Charolais- [$n = 6$], Gelbvieh- [$n = 30$], Limousin- [$n = 18$], Red Angus- [$n = 14$], and Simmental-sired [$n = 16$]) were used in the study. At the beginning of the study, heifers weighed 395 ± 3.5 kg and steers weighed 416 ± 3.5 kg. Mean age of cattle at the beginning of the study was 298 ± 0.4 d of age. Calves were housed in a facility with Calan-Broadbent electronic headgates (American Calan, Inc., Northwood, NH) to measure individual feed intake. The cattle were trained to use individual Calan headgates during the adaptation period (approximately 45 d). The steers were implanted (200 mg trenbolone acetate and 40 mg estradiol-17 β ; Revalor-XS, Merck Animal Health, Madison, NJ) 86 d before the start of the experiment. Heifers received a Revalor-H implant (140 mg trenbolone acetate and 14 mg estradiol-17 β ; Merck Animal Health) 86 d before the beginning of the study and a

Revalor-200 implant (200 mg trenbolone acetate and 20 mg estradiol-17 β ; Merck Animal Health) 57 d after the study began.

Cattle were placed on a diet that on a DM basis consisted of 67.75% dry-rolled corn, 20% wet distillers grains with solubles, 8% chopped alfalfa hay, and 4.25% supplement 7 d before the feed intake and growth trial began. The supplement contained monesin to supply 300 mg/animal daily. Feed bunks were evaluated visually each day of the experiment at approximately 0730 h to determine the quantity of feed to offer each animal. The bunk management approach was designed to allow for approximately 0.25 to 0.50 kg of feed remaining in each feed bunk at the time of evaluation. After the quantity of feed to be provided to each bunk was determined, a portion of the ration sufficient to supply the feed for all the pens was mixed in the feed truck (Roto-Mix IV 274-12B, Dodge City, KS, scale readability $\pm$ 0.09 kg) for approximately 5 min. Cattle were fed once daily throughout the experiment, starting at approximately 0800 h. Feed was subsampled daily and a weekly composite sample was made to determine feed DM. Orts were determined once per week. Total DMI was the sum of total DM fed minus total orts and values reported are average daily DMI (referred to as DMI for simplicity). Fractional DMI was calculated as g DMI/kg initial BW. Dry matter intake data was partitioned into the first 35 d, the last 35 d, and the entire 84 d to determine if leptin concentrations were more associated with shorter- or longer-term measures of DMI. The feeding study lasted 84 d and cattle were weighed on day 0, 1, 21, 42, 63, 83, and 84 of the experiment. A quadratic equation was used to regress BW on day of study and total BW gain was determined by solving the equation for 84 d on study. Average daily gain was calculated as total BW gain divided by days on study. The G:F was calculated as the quotient of ADG divided by DMI. Residual feed intake (**RFI**) was calculated as the residual obtained when observed DMI was regressed against ADG and

calculated metabolic BW at the midpoint of the experiment. Steers and heifers were treated as separate cohorts for the RFI calculation.

Following the end of the DMI and growth trial, cattle received the same ration fed ad libitum and remained in the same pens with Calan gates locked open until they were shipped for slaughter. Body composition was evaluated by ultrasound between day 93 and 97. Ultrasound images were collected by an Ultrasound Guidelines Council–certified field technician using a Classic Scanner 200 with an ASP-18 transducer (Classic Medical, Tequesta, FL). Body composition traits measured included: 1) subcutaneous fat thickness over the termination point of the *biceps femoris* in the rump (rump fat); 2) subcutaneous fat thickness at $\frac{3}{4}$ the lateral distance across the LM between the 12th and 13th ribs (12th rib fat thickness); 3) LM area between the 12th and 13th ribs (LM Area); and 4) percent intramuscular fat within the LM between the 12th and 13th ribs (Intramuscular fat; **IMF**). Cattle were slaughtered at a commercial processing facility 44 d after the completion of the DMI and ADG data collection period. Cattle were 426 ± 0.4 d of age at the time of slaughter. Chilled carcasses were evaluated by plant personnel with the beef carcass grading camera.

2.2 Sample collection, processing, and analyses

Blood (approximately 9 mL) was collected on day 0, 42, and 83 of the DMI and ADG measurement period prior to feeding, via jugular venipuncture into tubes containing EDTA (1.7 µg/mL of blood) and immediately placed on ice. Samples were then centrifuged at $3,000 \times g$ for 25 min at 4°C to obtain plasma. Plasma concentrations of leptin were determined in triplicate using RIA (10), but the original primary anti-serum was substituted with rabbit anti-ovine leptin primary anti-serum #7105. Leptin standards and pooled aliquots of bovine serum were linear

(log/logit transformation; $R^2 > 0.98$) and parallel over a leptin mass of 0.1 to 7.5 ng/tube and a serum volume of 25 to 200 μ L per tube. Intra- and inter-assay CV's were $< 5.0\%$.

2.3 Statistical analysis

All analyses used animal as the experimental unit and were performed in SAS 9.3 (SAS Inst. Inc., Cary, NC). Additionally, degrees of freedom for the error term were calculated using the Kenward-Roger's approximation in all models. Differences in concentration of leptin between steers and heifers on day 0, day 42, and day 83 were tested using a mixed model with breed, sex, day, and sex by day main effects and sire as a random variable. Day was included as a repeated measure using an autoregressive covariance structure.

To evaluate the association of leptin concentrations on day 0, day 42, day 83, or the mean leptin concentration with DMI, ADG, G:F, RFI, ultrasound body composition, and carcass traits, a mixed model multiple regression analysis was utilized. All models included breed and sex as fixed effects and sire as a random variable. The independent variables of interest were analyzed in separate models and included leptin concentration on day 0, day 42, day 83, or the mean of day 0, day 42, and day 83 values. Solutions $\pm$ SEM of the mixed model are presented. To determine the amount of variation explained by leptin concentrations in the models, a pseudo- R^2 was calculated using differences in residual covariance parameter when all fixed factors are included (full model) and excluded (intercept only) from the analyses. The sire random variable parameter was constrained to the value in the full model that included all fixed factors. The variation explained by leptin was then calculated as the difference between pseudo- R^2 with (full model) and without (full model excluding the leptin variable) the leptin variable in the respective models. Variables were considered significant when $P < 0.05$.

3. Results

Descriptive statistics of variables used in the models are presented in Table 1. There was a sex by day interaction ($P < 0.001$; Figure 1) for leptin concentration indicating that heifers had a greater leptin concentration on day 0 and day 42. By day 83, plasma leptin concentrations were not different between steers and heifers. For both sexes, leptin concentration increased from day 0 to 42, and from day 42 to day 83.

All measures of plasma leptin (day 0, day 42, day 83, and mean leptin concentration) were positively associated with 84 d DMI ($P \leq 0.006$; Table 2). Plasma leptin measured on day 83 explained the greatest percentage of the variance of DMI (10.56 %; Table 3) with a pseudo $R^2 = 0.48$. Day 0 leptin concentration was not associated with 84 d fractional DMI (DMI on a body weight basis; $P = 0.465$), but day 42 and day 83 plasma leptin concentrations were positively associated with the 84 d fractional DMI, with day 83 leptin concentration explaining the greatest amount of the variance for fractional DMI (7.88 %; pseudo $R^2 = 0.29$). The same trend was evident when DMI was broken into the first and last 35 d of the experiment. Specifically, all plasma leptin measures were positively associated with DMI ($P < 0.001$, except for day 0 leptin association with the last 35 d DMI $P = 0.070$) and day 83 plasma leptin concentration explained the greatest amount of the variance (9.21 and 10.46 % of the variance for the first 35 and last 35 d DMI).

Plasma leptin measured on day 0 was not associated with ADG ($P = 0.575$), but day 42 ($P = 0.006$), day 83 ($P < 0.001$), and mean plasma leptin ($P = 0.011$) were all positively associated with ADG. Day 83 leptin concentration explained the greatest amount of the variance (4.40 %; pseudo $R^2 = 0.49$). Day 0 and mean plasma leptin concentrations were negatively

associated with G:F ($P < 0.001$ and $P = 0.043$, for day 0 plasma leptin concentration and mean leptin concentration, respectively). Day 0 plasma leptin concentration accounted for 4.79 % of the variance in G:F (pseudo $R^2 = 0.21$) and mean leptin explained 1.27 % of the variance (pseudo $R^2 = 0.17$). Day 83 ($P = 0.004$) and mean ($P = 0.029$) plasma leptin concentrations were positively associated with RFI. Day 83 plasma leptin concentration explained 3.21 % and mean leptin concentration explained 1.00 % of the variance for RFI, which was basically all of the variance explained by the models (pseudo $R^2 = 0.02$ and 0.01 for day 83 and mean leptin models, respectively).

In this experiment, body composition was measured by ultrasound after the completion of the DMI and ADG data collection, as well as carcass composition at slaughter. All measures of leptin were positively associated with ultrasound 12th rib fat thickness and rump fat thickness ($P < 0.001$). For these two variables, mean leptin concentration explained the greatest amount of the variance (21.87 and 12.68 % for 12th rib fat and rump fat thickness, respectively). The same trend was observed with carcass fat thickness and YG, where all measures of leptin were positively associated with carcass fat thickness and YG ($P < 0.001$) and the mean leptin concentration explained the greatest amount of the variance (16.82 and 18.22 % for carcass fat thickness and YG, respectively). Similar to the fat thickness data, all measures of leptin concentrations were positively associated with ultrasound IMF and carcass marbling scores ($P \leq 0.006$). For both of these variables, mean leptin concentration explained the greatest amount of the variance (4.19 and 4.59 % for ultrasound IMF and carcass marbling score, respectively).

Leptin concentrations were not associated with ultrasound LM area ($P > 0.104$). However, day 42, day 83, and mean leptin concentrations were negatively associated with carcass LM area ($P < 0.030$). The pseudo R^2 for these models were fairly low (0.05 to 0.06) and

the leptin concentration measurements accounted for 1.99 to 2.34 % of the variance in carcass LM area.

4. Discussion

Results from this experiment suggest that plasma leptin concentrations increase over the finishing period in beef steers and heifers. Plasma leptin concentrations in heifers were greater at the beginning of this experiment than steers, which could indicate that heifers were fatter at initiation of the study than in steers. The concept that heifers reach a greater proportion of body fat at a lower BW has been previously characterized in the literature (11,12), but it is noteworthy that this is observable with plasma leptin concentrations, which are associated with body fatness (7,8).

Data presented here indicated that circulating leptin concentrations are positively associated with DMI in finishing beef cattle. These results agreed with a previous study that showed a positive association of leptin concentrations with feed intake when you exclude measures of body fatness (4). Additionally, in heifers fed a predominantly forage ration, leptin concentration were also positively associated with DMI (5). In this experiment, decreasing the amount of time of the DMI measurement period from 84 to 35 d did not greatly change the amount of the variance that leptin concentrations explained. Thus, perhaps this was an indication that 35 d is an adequate amount of time to measure DMI in finishing beef cattle or that leptin is a fairly robust indicator of DMI. Generally the leptin concentration at the end of the data collection period was a better indicator of DMI, according to a greater amount of the variance of DMI explained by d-83 leptin concentration compared to the earlier time points. Foote et al. (2015) observed an association of leptin with DMI when leptin was measured in the early to

middle parts of the DMI data collection period. Therefore, two or three time points across large data sets and diverse cattle will most likely be a more robust indicator of DMI than a single measurement. This can also depend on the sample size used in experiments, but with variables such as plasma leptin concentrations that significantly change over feeding periods and a sex effect on the change, it is likely that multiple measures of plasma leptin will provide better estimates than single time point measures.

Leptin has been shown to act centrally to decrease appetite in several species, including ruminants (2,3). The observation reported here and previously (4,13), a positive relationship of circulating leptin concentrations with DMI, are perhaps opposite of what would be expected of a hormone that acts as a satiety signal. Leptin is thought to act as a long-term regulator of DMI (2), and it would therefore be expected to decrease DMI when circulating concentrations are elevated. However, the positive association of plasma leptin concentrations with DMI is similar to rodent models of diet-induced obesity (14) and leptin resistance. In these rodents, circulating leptin concentrations increase over time by as much as 400 % (14). It is possible that beef cattle on a finishing ration become slightly leptin resistant; however there is not enough data available to determine this.

Leptin concentrations were generally positively associated with ADG, even though day 0 leptin was not associated with BW growth. These data are in contrast to Foote et al. (2015) where leptin concentrations were shown to be negatively associated with ADG in finishing beef steers, even though the amount of the variance explained was about the same in both studies (~ 2 %). The reason for the divergent results remains unclear. However, the main differences between the studies was that the present experiment included finishing steers and heifers, whereas, Foote et al. (2015) used only steers and it was a larger experiment ($n = 473$ versus $n =$

236 in the present experiment). Previous experiments have not observed significant correlations between leptin concentration and ADG (5,6,13).

Foote et al. (2015) observed that leptin concentrations explained more of the variance of G:F than any other variable excluding body composition measurements. In the current experiment, leptin on day 0 and the mean leptin concentrations were negatively associated with G:F, which is somewhat in agreement with previous data. It is not clear why the middle and end leptin measurements were not associated with G:F. This is also in agreement with observations of Kelly, et al. (5) that showed a positive relationship of leptin with feed conversion ratio, which is the inverse of G:F. It is promising that the relationship of leptin to G:F was consistent in three separate experiments. However, the lack of a relationship with the middle and end leptin concentrations in the present experiment indicated that there is likely value in multiple sample time points for future experiments of this size.

Another measure of feed efficiency often used is RFI. Data from the current experiment testing the association of plasma leptin concentrations and RFI are similar to previous research showing a slight positive association of leptin with RFI (4,6,13), which indicated that more efficient animals have lower leptin concentrations. The association of leptin concentration with RFI is consistent with the association of leptin with G:F, where both measures of feed efficiency indicate that more efficient cattle have lower circulating concentrations of leptin. However, Kelly, et al. (5) showed no correlation between leptin and RFI and no difference in leptin concentrations of cattle classed by RFI ranking.

One of the most studied aspects of leptin biology in cattle has been the association of leptin concentration with body composition. Numerous studies have shown that leptin

concentrations are a good indicator of body composition and carcass quality and composition (4,7,8). Perhaps as expected, plasma leptin concentrations explain a greater amount of the variance of body composition, especially fatness, the closer that the measurements of leptin and body composition are in time. This was seen as day 83 plasma leptin concentrations explained more of the variance in either ultrasound or carcass body fatness measures than the earlier leptin measurements. Similar to some of the other variables, the mean leptin concentration over the 3 time points in most cases explained a greater amount of the variance of body fatness measures than the individual time points. This could be an indication that long-term concentrations are more indicative of body composition than single time points. Given the large amount of the variance that leptin explains for both body composition measured shortly after the data collection period as well as carcass composition, it is possible that leptin could have utility in distinguishing the role of composition of growth in efficient conversion of nutrients to body tissues in addition to the utility in predicting carcass quality.

Data presented here indicate that leptin is associated with production traits and body composition of finishing beef steers and heifers. Results also indicate that in an experiment with a comparable sample size, an average of 3 measures of leptin across the feeding period is likely more reliable than a single measure of leptin concentration. Leptin appears to explain a significant amount of the variance of body composition measures and carcass composition as well as feed intake. Given that several independent studies have observed a relationship of leptin concentrations with production traits, this biological system warrants further investigation into the potential mechanisms by which leptin could contribute to feed intake and efficiency.

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321 **Table 1.** Descriptive statistics of variables used in the mixed model regression analysis
 322 of 236 individually fed finishing beef steers and heifers

Variable	Mean	SD	Minimum	Maximum
Leptin day 0 (ng/mL)	7.03	2.002	3.24	14.38
Leptin day 42 (ng/mL)	8.51	2.076	3.52	14.33
Leptin day 83 (ng/mL)	9.75	2.149	3.60	16.47
DMI (kg/d)	9.40	1.477	4.93	14.55
Fractional DMI (g·kg BW ⁻¹ ·d ⁻¹)	23.10	2.605	13.89	30.27
ADG (kg/d)	1.74	0.339	0.74	2.74
G:F (kg/kg)	0.184	0.0200	0.138	0.240
RFI ^a	0.00	0.634	-1.38	2.24
Ultrasound LM Area (cm ²)	92.7	8.71	70.3	118.7
Ultrasound 12 th Rib Fat Thickness (cm)	1.22	0.379	0.30	2.39
Ultrasound Rump Fat Thickness (cm)	1.08	0.316	0.23	2.16
Ultrasound Intramuscular Fat (%)	3.73	1.004	2.29	8.78
HCW (kg)	385	41.5	287	502
LM area (cm ²)	89.7	8.79	66.5	111.6
12 th rib fat (cm)	1.25	0.517	0.20	2.74
YG ^b	3.01	0.930	1.00	5.40
Marbling Score ^c	424	75.1	303	736

323 ^aRFI = Residual feed intake, calculated within sex group.

324 ^bYG = USDA calculated yield grade.

325 ^c200 = Practically Devoid⁰; 300 = Traces⁰; 400 = Slight⁰; 500 = Small⁰; 600 =
 326 Modest⁰; 700 = Moderate⁰; 800 = Slightly Abundant⁰; 900 = Moderately Abundant⁰;
 327 1000 = Abundant⁰.

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Table 2. Mixed model estimates for leptin concentrations on day-0, day-42, day-83, or the mean of all 3 measures associated with production, body composition, and carcass traits from 236 individually fed finishing beef steers and heifers

	Day 0 Leptin			Day 42 Leptin			Day 83 Leptin			Mean Leptin		
	Solution ^a	SEM ^b	P-Value	Solution ^a	SEM ^b	P-Value	Solution ^a	SEM ^b	P-Value	Solution ^a	SEM ^b	P-Value
84 d DMI (kg/d)	0.11	0.040	0.006	0.18	0.036	< 0.001	0.22	0.033	< 0.001	0.23	0.041	< 0.001
Fractional 84 d DMI (g · d ⁻¹ · kg BW ⁻¹)	-0.06	0.083	0.465	0.19	0.076	0.011	0.33	0.069	< 0.001	0.23	0.087	0.010
First 35 d DMI (kg/d)	0.14	0.040	< 0.001	0.18	0.036	< 0.001	0.20	0.033	< 0.001	0.23	0.041	< 0.001
Last 35 d DMI (kg/d)	0.08	0.046	0.070	0.18	0.041	< 0.001	0.25	0.037	< 0.001	0.23	0.047	< 0.001
ADG (kg/d)	-0.005	0.0094	0.575	0.024	0.0086	0.006	0.035	0.0080	< 0.001	0.025	0.0098	0.011
G:F (kg/kg)	-0.003	0.0006	< 0.001	-0.007	0.0006	0.252	-0.001	0.0006	0.525	-0.001	0.0007	0.043
RFT ^c	0.031	0.0212	0.143	0.029	0.0203	0.149	0.057	0.0199	0.004	0.051	0.0233	0.029
Ultrasound												
12th Rib Fat Thickness (cm)	0.08	0.012	< 0.001	0.07	0.011	< 0.001	0.07	0.010	< 0.001	0.10	0.012	< 0.001
Rump Fat (cm)	0.04	0.010	< 0.001	0.05	0.009	< 0.001	0.05	0.009	< 0.001	0.06	0.011	< 0.001
LM Area (cm ²)	0.50	0.317	0.115	0.32	0.295	0.281	0.46	0.280	0.104	0.55	0.34	0.106
IMF ^d (%)	0.09	0.031	0.003	0.09	0.028	0.002	0.08	0.027	0.002	0.11	0.032	< 0.001
Carcass												
12 th Rib Fat Thickness (cm)	0.09	0.016	< 0.001	0.09	0.015	< 0.001	0.09	0.014	< 0.001	0.11	0.016	< 0.001
LM Area, (cm ²)	-0.30	0.323	0.349	-0.69	0.299	0.021	-0.69	0.294	0.016	-0.75	0.341	0.030
YG ^e	0.14	0.026	< 0.001	0.17	0.023	< 0.001	0.16	0.022	< 0.001	0.21	0.026	< 0.001
Marbling Score	6.32	2.288	0.006	6.79	2.111	0.002	7.26	2.004	< 0.001	8.85	2.405	< 0.001

^aLeptin solution is the estimate from the fixed effect of leptin concentration (on either day 0, 42, 83, or the mean of the 3 measurements) effect in the respective mixed model analysis. Other factors included in the models were the fixed effect of breed and sex and the random effect of sire. All measures of leptin were analyzed in separate models.

^bStandard error of the mean for the solution of leptin concentration in the respective mixed model analysis ($n = 236$).

335 ^cRFI = Residual feed intake, calculated within sex group. Model for RFI did not include fixed effect of sex as RFI was calculated
336 within sex group.

337 ^dIMF = Intramuscular fat.

338 ^eYG = USDA calculated yield grade.

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Table 3. Percentage of the variance explained by leptin concentration and the pseudo- R^2 values for the mixed model analysis of the association of leptin concentration on day 0, day 42, day 83, or the mean of all three measures with production, body composition, and carcass composition traits from 236 individually fed finishing beef steers and heifers

	Day 0 Leptin		Day 42 Leptin		Day 83 Leptin		Mean Leptin	
	% Variance Explained ^a	Pseudo R^2	% Variance Explained ^a	Pseudo R^2	% Variance Explained ^a	Pseudo R^2	% Variance Explained ^a	Pseudo R^2
84 d DMI (kg/d)	2.03	0.39	7.15	0.43	10.56	0.48	8.25	0.45
Fractional 84 d DMI ($\text{g} \cdot \text{d}^{-1} \cdot \text{kg BW}^{-1}$)	< 0.01	0.21	2.30	0.23	7.88	0.29	2.32	0.23
First 35 d DMI (kg/d)	3.58	0.36	6.92	0.39	9.21	0.43	8.59	0.41
Last 35 d DMI (kg/d)	0.70	0.41	4.82	0.45	10.46	0.51	6.19	0.46
ADG (kg/d)	< 0.01	0.45	1.90	0.47	4.40	0.49	1.59	0.46
G:F (kg/kg)	4.79	0.21	< 0.01	0.16	< 0.01	0.16	1.27	0.17
RFI ^c	0.46	< 0.01	0.55	< 0.01	3.21	0.02	1.00	0.01
Ultrasound								
12th Rib Fat Thickness (cm)	15.23	0.26	16.22	0.27	17.60	0.29	21.87	0.32
Rump Fat (cm)	6.22	0.14	11.67	0.20	10.78	0.20	12.68	0.20
LM Area (cm ²)	0.53	0.07	0.02	0.07	0.68	0.08	0.62	0.08
IMF ^d (%)	2.79	0.11	3.48	0.12	3.08	0.12	4.19	0.13
Carcass								
12 th Rib Fat Thickness (cm)	12.04	0.26	12.63	0.26	13.79	0.29	16.82	0.31
LM Area, (cm ²)	0.08	0.03	2.25	0.05	2.34	0.06	1.99	0.05
YG ^e	10.03	0.34	16.41	0.40	15.14	0.41	18.22	0.42
Marbling Score	2.40	0.13	3.57	0.14	4.37	0.16	4.59	0.16

^aOther factors included in the models were the fixed effect of breed and sex and the random effect of sire, except for the RFI model where sex was excluded as RFI was calculated within sex group. All measures of leptin were analyzed in separate models.

345 ^bRFI = Residual feed intake, calculated within sex group.

346 ^cIMF = Intramuscular fat.

347 ^dYG = USDA calculated yield grade.

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351 **Figure Legends**

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354 **Figure 1.** Change in circulating leptin concentration in individually fed finishing beef steers and
355 heifers ($n = 236$). $P < 0.001$ for the sex by day interaction.

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360 Figure 1.

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