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Characteristics of developmental changes in the kinetics of glucose and urea in Japanese Black calves: Comparison with Holstein calves¹

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ABSTRACT: The current study was conducted to clarify the characteristics of glucose and urea kinetics in male Japanese Black calves, using a glucose and urea dilution method with stable isotopes, at preweaning (3 wk of age) and postweaning (13 and 26 wk of age) stages, in comparison with the kinetics of glucose and urea in male Holstein calves. Six Japanese Black and 6 Holstein calves were arranged in a 2 (breed) × 3 (stage) factorial block design. These 12 suckling calves were fed only whole milk, offered concentrate and orchardgrass hay after 3 wk of age, and weaned at 6 wk of age. Under steady-state conditions, glucose challenges (1.0 mg/kg of BW; [U-¹³C]D-glucose) and urea challenges (both 2.2 mg/kg of BW; [¹³C]urea and [¹⁵N₂]urea) were performed at the 3 stages examined. There were no significant differences in plasma glucose concentrations between Japanese Black and Holstein calves at any stage, but the glucose concentrations at 3 wk of age were greater ($P < 0.05$) than those at 13 wk of age in both breeds. The glucose pool size in Japanese Black calves was smaller ($P < 0.05$) than that in Holstein calves at all stages. Within each breed, there were no significant differences between the glucose pool sizes

at 3 and 13 wk of age, but the glucose pool size was larger ($P < 0.05$) at 26 wk of age. Moreover, Japanese Black calves had greater glucose irreversible loss rates ($P < 0.01$) than Holstein calves at 3 wk of age, and the glucose irreversible loss rates were less ($P < 0.05$) on and after 13 wk of age in both breeds. Japanese Black calves had greater plasma urea N concentrations ($P < 0.05$) than Holstein calves at all stages, and in both breeds, the urea N concentrations increased ($P < 0.05$) with age. The urea pool size was smaller ($P < 0.01$) in Japanese Black calves than in Holstein calves at all stages, and in both breeds, the urea pool size increased ($P < 0.05$) with age. In comparison with Holstein calves, Japanese Black calves had greater urea irreversible loss rates ($P < 0.05$) on and after 13 wk of age and greater urea recycling rates ($P < 0.05$) at 26 wk of age. In addition, in both breeds, urea irreversible loss rates and urea recycling rates increased ($P < 0.05$) with age. We conclude that Japanese Black calves have partially different glucose and urea kinetics from Holstein calves and that the kinetics of these metabolites in both Japanese Black and Holstein calves are strongly influenced by weaning.

Key words: breed, glucose kinetics, irreversible loss rate, Japanese Black calf, recycling rate, urea kinetics

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INTRODUCTION

Suckling ruminants fed only milk have digestive tracts functioning in a manner similar to those of mo-

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nogastric mammals. Thereafter, as they gradually begin to consume roughage, the rumen develops accompanied by substantial morphological changes. The development of the rumen has a great influence on glucose and urea metabolism in ruminants. On and after this transitional phase, most dietary carbohydrate in the rumen is fermented into VFA by the microorganisms, resulting in little glucose entering the intestinal tract (Bensadoun et al., 1962; Otchere et al., 1974). To counteract the lack of dietary glucose absorption, a rise in gluconeogenic function in the liver compensates for the lack of glucose that is essential for maintenance and growth in ruminants. In addition, N metabolism, in particular, the ruminant-specific N recycling system, is significantly affected when the ruminants begin to have microbial protein synthesis and more dietary N sources.

Japanese Black cattle (beef breed) have lower GH concentrations (Shingu et al., 2001), greater insulin concentrations (Matsuzaki et al., 1997; Shingu et al., 2001), and larger average muscle-to-bone ratios (Zem-bayashi, 1987) than Holstein cattle (dairy breed). Thus, the differences in the secretions of metabolic hormones and breed-specific morphological changes might be closely related. Based on those relationships, it can be speculated that differences in the kinetics of glucose and urea metabolism might exist between these breeds. So far, age-related changes in glucose and urea kinetics have been reported in Holstein calves (Hayashi et al., 2006), although the differences in glucose and urea kinetics between dairy and beef cattle and the age-related changes in the beef breed remain incompletely understood.

The aim of the current study was to clarify the characteristics of glucose and urea kinetics in Japanese Black calves in comparison with Holstein calves at preweaning and postweaning stages.

MATERIALS AND METHODS

All experimental procedures were approved by the Animal Care Committee of the National Agricultural Research Center for Tohoku Region, according to the Guide for the Care and Use of Experimental Animals (Consortium, 1988).

General Animal Management

Male Japanese Black ($n = 6$) and male Holstein calves ($n = 6$) at 3 wk of age (preweaning stage) and 13 and 26 wk of age (postweaning stage) were used in the current study. The calves were fed colostrum for 3 d after birth and thereafter were offered whole milk (10.0% of BW daily, as-fed basis) and weaned at 6 wk of age. The daily amounts of the milk offered to the calves met the requirements for maintenance and growth. In addition to the milk feeding, after 3 wk of age, commercial concentrate (79.2% TDN and 20.1% CP, DM basis; Snow Bland Seed Co. Ltd., Sapporo, Japan) and orchardgrass hay (48.0% TDN and 14.5% CP, DM basis) were offered

to the calves to meet the requirements for an ADG of 0.60 kg, according to the Japanese Feeding Standard (2000). All calves were housed in individual pens with 3.5 m² of floor space and free access to water.

Experimental Design

To investigate the change in glucose and urea kinetics accompanied with breed differences and advancing age, glucose and urea dilution experiments using stable isotopes were performed in Japanese Black and Holstein calves at 3, 13, and 26 wk of age. To maintain the concentrations of glucose and urea as close to steady state as possible, the feeding protocol was adopted by partially modifying the methods of Hayashi et al. (2006). From 10 d of age, the calves were offered a quarter of their milk at 6-h intervals (0430, 1030, 1630, and 2230) for 12 d. At the preweaning stage, the single injection of glucose and urea into the jugular vein was conducted at 18 and 21 d of age, respectively. Thereafter, from 12 d before reaching 13 and 26 wk of age, one-twelfth of the daily amount of concentrate (1.55% of BW daily, as-fed basis) at 2-h intervals was supplied using an automatic feeder (basal point amount of orchardgrass: 1030). One-half of the daily amount of orchardgrass hay (1.65% of BW daily, as-fed basis) was offered at 1030, and the remaining one-half was offered at 2230. The daily amounts of the offered orchardgrass hay and concentrate met the requirements for an ADG of 0.60 kg (Japanese Feeding Standard, 2000). At the postweaning stage, single injections of glucose and urea into a jugular vein were conducted at d 9 and 12 from the beginning of the regulated feeding pattern, respectively. All calves were weighed on 1015 at d 1 from the beginning of the regulated feeding pattern to adjust the amounts of diets and at d 8 and 11 to calculate the injected volumes of stable isotope-labeled glucose and urea. Moreover, the diet residues were measured on 1025 every day.

On 0845 of the challenge day, 1 indwelling needle that was 75 mm long was inserted into the right jugular vein of each calf for blood collection, and a second was inserted into the left jugular vein for injection of labeled glucose or urea solutions, to prevent contamination of loaded stable isotopes in blood samples. In the glucose injection experiment, 8-mL blood samples were collected at 0 (1030), 7.5, 15, 30, 45, 60, 90, 120, 150, 180, 240, 300, and 360 min after injection of [U-¹³C]D-glucose (1.0 mg/kg of BW, ¹³C: 98.2 atom %; Chlorella Industry Co. Ltd., Tokyo, Japan) dissolved in physiological saline. In the urea injection experiment, blood samples (15 mL) were collected at 0 (1030), 15, 30, 60, 120, 180, 240, 300, 360, 480, and 600 min after injection of [¹³C]urea (2.2 mg/kg of BW, ¹³C: 99 atom %; Cambridge Isotope Laboratories Inc., Andover, MA) and [¹⁵N₂]urea (2.2 mg/kg of BW, ¹⁵N: 99.6 atom %; Shoko Co. Ltd., Tokyo, Japan) dissolved in physiological saline. Blood samples were immediately chilled on ice and centrifuged at 1,600 × *g* at 4°C for 25 min. After centrifuga-

tion, plasma was harvested and stored at -30°C until analysis.

Sample Analysis

Plasma glucose and urea N concentrations were determined using commercially available colorimetric kits: Glucose 2-HA and UN-HA (Wako Pure Chemical Industries Ltd., Osaka, Japan), respectively, using a Hitachi 7070 autoanalyzer (Hitachi Ltd., Tokyo, Japan). The measurement of the enrichment of $[\text{U-}^{13}\text{C}]\text{D}$ -glucose was performed using a method described by Sano et al. (1996) using a GLC-mass spectrometric system (M-2000, Hitachi Ltd.). Urea fractions for measurement of $[\text{U-}^{13}\text{C}]\text{urea}$ and $[\text{U-}^{15}\text{N}_2]\text{urea}$ enrichment were separated from plasma samples through a series of chemical operations, as described by Hayashi et al. (2006), and the isotopic enrichment of $[\text{U-}^{13}\text{C}]\text{urea}$ and $[\text{U-}^{15}\text{N}_2]\text{urea}$ was measured using a mass spectrometer, EA/IR-MS (DELTA plus, Finnigan MAT, ThermoQuest, San Jose, CA).

Calculations

Glucose pool size and irreversible loss rates were calculated from the dilution curve of ^{13}C atom percentage excess in plasma after injection of the isotopes using the method described by White et al. (1969). In addition, urea pool size, irreversible loss rates, and recycling rates were calculated from the dilution curve of ^{13}C and ^{15}N atom percentage excess in plasma after injection of the isotopes using the method described by Nolan and Leng (1974).

Statistical Analysis

Data were analyzed using the GLM procedure (repeated measures method; SAS Inst. Inc., Cary, NC). Differences were considered significant at $P < 0.05$.

The statistical model was:

$$Y_{ijk} = \mu + \alpha_i + \gamma_{ij} + \beta_k + \alpha\beta_{ik} + \varepsilon_{ijk},$$

where Y_{ijk} = the data; μ = the overall mean; α_i = the effects due to breed; γ_{ij} = the effects due to individual calf (repeated treatment); β_k = the effects due to stage; $\alpha\beta_{ik}$ = the effects due to interaction between breed and stage; and ε_{ijk} = the residuals.

The significance of differences among means of the respective items measured was determined using Duncan's multiple range test.

RESULTS

BW and Diet Residue

Average BW of Japanese Black and Holstein calves were 36.4 vs. 57.8 ($P < 0.001$), 61.3 vs. 104.7 ($P < 0.001$), and 138.5 vs. 178.3 kg ($P < 0.01$) at 3, 13, and 26 wk of age, respectively. Throughout each experimental pe-

riod, diet residues of whole milk (preweaning stage) and concentrates and orchardgrass hay (postweaning stage) were zero in both breeds.

Glucose Kinetics

Experimental data for glucose kinetics are shown in Table 1. There was no significant difference in plasma glucose concentrations between Japanese Black and Holstein calves at any stage, but the concentrations were greater ($P < 0.05$) at 3 wk of age than at 13 wk of age in both breeds. Japanese Black calves had a smaller glucose pool size ($P < 0.05$) than Holstein calves at all stages. In addition, the glucose pool size at 3 wk of age was similar to that at 13 wk of age, but after 13 wk of age, the glucose pool size increased ($P < 0.05$). In terms of glucose pool size per kilogram of BW, there was no significant difference in the means between Japanese Black and Holstein calves (0.56 vs. 0.51 at 3 wk, 0.30 vs. 0.29 at 13 wk, and 0.29 vs. 0.28 at 26 wk of age, g/kg of BW). The values decreased ($P < 0.05$) after 3 wk of age in both breeds. Japanese Black calves had greater glucose irreversible loss rates ($P < 0.01$) than Holstein calves only at 3 wk of age, and the glucose irreversible loss rates decreased ($P < 0.05$) on and after 13 wk of age in both breeds.

Urea Kinetics

Experimental data for urea kinetics are shown in Table 2. Japanese Black calves had greater plasma urea N concentrations ($P < 0.05$) than Holstein calves at all stages, and in both breeds, the urea N concentrations increased ($P < 0.05$) with age. Urea pool size in Japanese Black calves was smaller ($P < 0.01$) than that in Holstein calves at the respective stages, and the urea pool size in both breeds increased ($P < 0.05$) with age. Japanese Black calves had greater urea irreversible loss rates ($P < 0.05$) on and after 13 wk of age and greater urea recycling rates ($P < 0.05$) at 26 wk of age than Holstein calves. In addition, in both breeds, urea irreversible loss rates and urea recycling rates increased ($P < 0.05$) with age.

DISCUSSION

In the current study, there were no significant differences in plasma glucose concentrations between Japanese Black and Holstein calves at either pre- or postweaning stages, but Japanese Black calves had a smaller glucose pool size than Holstein calves at all stages. In addition, there were no significant breed differences in glucose irreversible loss rates at the postweaning stage, although these rates were significantly greater in Japanese Black calves than in Holstein calves at the preweaning stage. These findings indicate that Japanese Black calves have greater blood glucose availability than Holstein calves at the preweaning stage. During the period when only milk was offered

Table 1. Plasma glucose kinetics in Japanese Black and Holstein calves at 3, 13, and 26 wk of age¹

Item	Age ²			Pooled SE	Significance ³		
	3 wk	13 wk	26 wk		B	S	B × S
Glucose concentration, mg/dL							
Japanese Black calves	91.2 ^a	81.3 ^b	87.9 ^a	1.86	NS	***	NS
Holstein calves	88.0 ^a	81.1 ^b	84.2 ^{ab}				
Glucose pool size, g							
Japanese Black calves	20.66 ^{***}	18.68 ^{***}	39.56 ^{b*}	1.28	**	***	NS
Holstein calves	29.25 ^a	30.07 ^a	48.94 ^b				
Glucose irreversible loss rate, mg·(kg of BW) ⁻¹ ·min ⁻¹							
Japanese Black calves	17.58 ^{***}	9.06 ^b	9.30 ^b	0.58	**	***	***
Holstein calves	12.34 ^a	8.68 ^b	8.73 ^b				

^{a,b}Means with different superscripts in the same row are significantly different ($P < 0.05$).

¹Japanese Black calves, $n = 6$; Holstein calves, $n = 6$.

²For age, * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$, in comparison with the corresponding values in Holstein calves.

³B = breed, S = stage; ** $P < 0.01$, *** $P < 0.001$, and NS = not significant ($P > 0.05$).

to the calves, the sources of glucose supply are limited to absorption of glucose in milk and blood lactic acid-derived glucose synthesis in the liver, gluconeogenesis (Cori, 1931). At the preweaning stage, considering that constant amounts of daily milk per BW were given to all calves, it is strongly possible that the greater glucose availability in Japanese Black calves is attributed to a greater rate of gluconeogenesis from lactic acid via the Cori cycle than that in Holstein calves. However, because the comparative research on the gluconeogenic enzymes in the liver of suckling dairy and beef breeds are not performed in detail, no further information is available on the greater rate of gluconeogenesis in Japanese Black calves. On the other hand, at the postweaning stage, glucose irreversible loss rates and glucose recycling rates decrease greatly in Holstein calves (Hayashi et al., 2006), indicating that the system of glucose

recycling in Japanese Black calves might also barely exist after weaning.

At the preweaning stage, plasma glucose concentrations in Holstein calves in the current study were less than those in Holstein calves as reported by Hayashi et al. (2006). It is likely that the primary cause is differences in the amounts of milk offered. Hayashi et al. (2006) gave 680 g of DM daily to all Holstein calves, but we offered 10.0% of BW daily to the calves. Irrespective of breed, glucose pool size increased after 13 wk of age, but the glucose pool size per kilogram of BW decreased considerably after weaning. In addition, glucose irreversible loss rates were greater at the preweaning than at the postweaning stage. In Holstein calves, the glucose pool size increases with age, and glucose irreversible loss rates are greater at the preweaning than at the postweaning stage (Hayashi et al., 2006).

Table 2. Plasma urea kinetics in Japanese Black and Holstein calves at 3, 13, and 26 wk of age¹

Item	Age ²			Pooled SE	Significance ³		
	3 wk	13 wk	26 wk		B	S	B × S
Urea N concentration, mg of N/dL							
Japanese Black calves	4.89 ^{a*}	5.92 ^{ab*}	6.50 ^{b*}	0.25	*	***	NS
Holstein calves	4.23 ^a	4.76 ^{ab}	5.48 ^b				
Urea pool size, g of N							
Japanese Black calves	0.68 ^{a***}	1.26 ^{b***}	2.45 ^{c**}	0.14	***	***	NS
Holstein calves	0.97 ^a	1.82 ^b	3.72 ^c				
Urea irreversible loss rate, mg of N·(kg of BW) ⁻¹ ·min ⁻¹							
¹³ C-Urea							
Japanese Black calves	0.267 ^a	0.457 ^{b**}	0.575 ^{b*}	0.036	***	***	NS
Holstein calves	0.225 ^a	0.317 ^b	0.384 ^c				
¹⁵ N-Urea							
Japanese Black calves	0.171 ^a	0.333 ^{b***}	0.332 ^{b*}	0.012	**	***	NS
Holstein calves	0.150 ^a	0.265 ^b	0.261 ^b				
Urea recycling rate, mg of N·(kg of BW) ⁻¹ ·min ⁻¹							
Japanese Black calves	0.097 ^a	0.125 ^{ab}	0.243 ^{b*}	0.033	**	*	NS
Holstein calves	0.074 ^a	0.052 ^{ab}	0.123 ^b				

^{a-c}Means with different superscripts in the same row are significantly different ($P < 0.05$).

¹Japanese Black calves, $n = 6$; Holstein calves, $n = 6$.

²For age, * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$, in comparison with the corresponding values in Holstein calves.

³B = breed, S = stage; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, and NS = not significant ($P > 0.05$).

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In sheep, glucose pool size per kilogram of BW and glucose turnover rates (irreversible loss rates) decrease considerably with age (Muramatsu et al., 1974). These reports are in accordance with the results in the current study. In suckling calves offered only milk, because glucose is almost entirely utilized as an energy source, glucose availability via the Cori cycle might be markedly enhanced in comparison with that in calves after weaning. In the pathway of the lactic acid-derived glucose synthesis, there are reversible enzyme-mediated reactions (the representative hepatic enzymes: glucose-6-phosphatase and fructose-1, 6-diphosphatase) and irreversible enzyme-mediated reactions (the representative hepatic enzymes: pyruvate carboxylase and phosphoenolpyruvate carboxykinase; Hanson, 1974). Recently, there has been evidence to support the speculation of greater glucose availability at the suckling stage in ruminants. In the liver of male Holstein calves during the period ranging from the pre- to post-weaning stages, the mRNA levels and activities of pyruvate carboxylase decrease with age, and the phosphoenolpyruvate carboxykinase activity at the suckling stage is greater than that at the postweaning stages (S. Haga, Tohoku University, Sendai, Japan, personal communication). The decreased mRNA levels and activities of hepatic enzymes for gluconeogenesis with age might be linked with the decreases in glucose irreversible loss rates after weaning.

Urea is an end-product of N metabolism in mammals. It is well-known that the urea metabolism of ruminants has unique characteristics as follows: 1) ammonia production from the degradation of protein by the rumen fermentation; 2) absorption of ammonia through the rumen wall and entrance into the portal circulation; 3) synthesis of urea from ammonia in the liver; 4) supply of urea from saliva and through the rumen wall to the rumen; 5) utilization of urea for the synthesis of rumen microbial proteins; and 6) absorption of the microbial proteins as AA N in the lower digestive tract. Thus, ruminants have a urea recycling system unlike monogastric mammals, and it is conceivable that the amounts of recycled urea are enhanced by intake of carbohydrates and N sources. The same might apply to the present results using Japanese Black and Holstein calves that plasma urea N concentrations increased with age in line with the intake of carbohydrates and N sources. This positive relationship between blood plasma urea N concentrations and intake of N sources or age is coincident with the reports in goats (Ide, 1975; Obara and Shimbayashi, 1980), Holstein heifers (Marini and Van Amburgh, 2003), Holstein calves (Hayashi et al., 2006), and Holstein and Japanese Black steers (Matsuzaki et al., 1997). In Holstein calves, urea pool size, urea irreversible loss rates, and urea recycling rates increase with age (Hayashi et al., 2006), and intraruminal infusion of urea induces increases in urea N pool size and irreversible loss rates in sheep (Obara and Dellow, 1994). Moreover, in male Holstein calves, the findings that the activities of the hepatic urea cycle

enzymes such as carbamyl phosphate synthetase, ornithine transcarbamylase, and argininosuccinate synthetase increase after weaning are just now emerging (M. Takashiro, Tohoku University, Sendai, Japan, personal communication). Therefore, the age-related changes in urea kinetics might be attributable to the enhancement of circulating urea due to substantial increases in the populations of microbials and intake of N sources with rumen function of calves developing and in the activities of the hepatic urea cycle enzymes.

Japanese Black steers have greater plasma urea N concentrations than Holstein steers (Matsuzaki et al., 1997). In the current study, in spite of a smaller urea pool size in Japanese Black calves than that in Holstein calves at all stages, Japanese Black calves showed greater plasma urea N concentrations and tended to have greater urea irreversible loss rates and urea recycling rates. It is unlikely that these findings in Japanese Black calves arose from the amounts of urea in the body, because constant amounts of rations per BW were given to both breeds. In general, Japanese Black cattle have larger average muscle-to-bone ratios (Zem-bayashi, 1987) and greater insulin concentrations in plasma (Matsuzaki et al., 1997; Shingu et al., 2001) than Holstein cattle, indicating that a stronger anabolic effect is exerted genetically in Japanese Black cattle. Allowing for the morphological and physiological traits and the present findings about urea kinetics of greater plasma urea N concentrations, irreversible loss rates, and recycling rates, Japanese Black cattle might enhance an availability of N sources in muscles and have a greater level of N diffusion into the digestive tract in comparison with Holstein cattle. In addition, the factors causing the breed differences in urea kinetics might be associated with the hepatic urea cycle enzymes. However, to date, because there is no information on profiles of urea cycle enzymes of Japanese Black cattle, further research on the cause of the greater rates of urea irreversible loss and recycle in the beef breed is required from viewpoints of hepatic urea cycle enzymes: carbamyl phosphate synthetase, ornithine transcarbamylase, and argininosuccinate synthetase.

In summary, the current study demonstrated that Japanese Black calves (beef type) have breed-specific glucose and urea kinetics at different growing stages in comparison with Holstein calves (dairy type) and that the kinetics of these metabolites in both Japanese Black and Holstein calves are strongly influenced by weaning.

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