

Mitochondrial DNA Polymorphism, Maternal Lineage and Correlations with Postnatal Growth of Japanese Black Beef Cattle to Yearling Age

A. E. O. Malau-Aduli*, A. Nishimura-Abe¹, T. Niibayashi², Y. Yasuda¹, T. Kojima², S. Abe¹, K. Oshima²
K. Hasegawa¹ and M. Komatsu^{2,3}

³ Department of Animal Breeding and Reproduction, National Institute of Livestock and Grassland Science
Tsukuba, Ibaraki 305-0901, Japan

ABSTRACT : Mitochondrial DNA haplotypes from the displacement-loop (D-loop) region (436 bp) were genotyped and sequenced in Japanese Black beef cattle raised in the same herd. Correlation coefficients between mitochondrial DNA haplotypes, maternal lineage, birth weight, preweaning average daily gain, weaning weight, post weaning average daily gain and yearling weight were computed. The objective was to study the relationship between maternal and postnatal growth traits and to investigate if postnatal growth of calves to yearling age could be accurately predicted from mitochondrial DNA haplotypes. Results of the phylogenetic analysis revealed 17 maternal lineages and four mitochondrial DNA haplotypes. There were strong, positive and highly significant ($p < 0.001$) correlations among maternal traits ranging from 0.52 to 0.98. Similarly, among postnatal growth traits, most of the correlations were also strong, positive and highly significant ($p < 0.001$); the highest correlation of 0.94 was between preweaning average daily gain and weaning weight. However, correlations between mitochondrial DNA haplotypes and postnatal growth traits were very low, mostly negative and non-significant ($p > 0.05$) ranging from -0.05 to 0.1. Prediction of postnatal growth from mitochondrial DNA yielded very low R^2 values ranging from 0.002 to 0.019. It was concluded that mitochondrial DNA polymorphism has no significant association with postnatal growth from birth to yearling age, and by implication, nuclear rather than cytoplasmic DNA, accounts for most of the genetic variation observed in postnatal growth of Japanese Black cattle. Therefore, mitochondrial DNA genotyping at an early age has no bearing on the accurate prediction of the future growth performance of calves. (*Asian-Aust. J. Anim. Sci.* 2004, Vol 17, No. 11 : 1484-1490)

Key Words : Mitochondrial DNA, Maternal Lineage, Japanese Black Cattle, Postnatal Growth, Correlations

INTRODUCTION

Bovine mitochondria contain a 16,338 nucleotide closed loop of DNA coding for 13 translated genes, 22 tRNA and 2 rRNA and are inherited exclusively through the maternal line, providing a genetic mechanism for cytoplasmic inheritance (Gibson et al., 1997). Some studies have suggested that maternal lineage effects influence growth, reproductive and production traits of livestock; in dairy cattle particularly, extensive mitochondrial DNA (mtDNA) diversity has been found (Boettcher et al., 1996a,b) and such differences in mtDNA have been significantly associated with milk yield traits in which 2-10% of the variation could be explained by maternal lineage effects (Ron et al., 1992; Schutz et al., 1993; Schutz et al., 1994). By contrast, mtDNA diversity has been less commonly reported in beef cattle and no significant effects on milk

yield or preweaning growth traits have been found in Brangus (Rohrer et al., 1994) and Hereford (Tess et al., 1987; Tess and Robison 1990; Tess and MacNeil 1994) breeds. However, Sutarno et al. (2002) found a significant association between mitochondrial DNA haplotypes and calving rate in purebred Hereford and composite multi-breed beef cattle.

The non-coding D-loop (displacement loop) region is the site of transcriptional and replicational control (Anderson et al., 1982). In Japanese Black cattle, Mannen et al. (1998a,b) reported significant mtDNA variation in the D-loop region in which an association between mtDNA haplotypes and two carcass traits (beef marbling score and longissimus muscle area) was found. More recently, Mannen et al. (2003) identified the mtDNA substitutions related to meat quality. However, there are no published reports of the correlations between mtDNA haplotypes and postnatal growth and average daily gain to yearling age in Japanese Black cattle. Furthermore, it has not yet been established if postnatal growth in this breed of cattle can be accurately predicted early enough by genotyping the mtDNA of calves. Therefore, our objectives in this study were to answer the following questions:

i) Are mtDNA haplotypes and maternal lineage significant sources of variation affecting birth weight, weaning weight, yearling weight, preweaning and postweaning average daily gains in Japanese Black cattle?

* Corresponding Author: A. E. O. Malau-Aduli. School of Agricultural Science, University of Tasmania, Private Bag 54 Hobart, Tasmania 7001, Australia. Tel: +61-3-6226-2717, Fax: +61-3-6226-2642, E-mail: Aduli.MalauAduli@utas.edu.au

¹ Shimane Prefectural Institute of Animal Industry, Izumo, Shimane, Japan.

² Department of Livestock and Grassland Science, National Agricultural Research Center for Western Region, Oda, Shimane 694-0013, Japan.

Received November 21, 2003; Accepted June 9, 2004

ii) What is the relationship between these postnatal growth traits with mtDNA haplotypes and maternal lineage?

iii) How accurately can postnatal growth be predicted from mtDNA haplotypes in Japanese Black cattle?

MATERIALS AND METHODS

Animals and management

Mitochondrial DNA extracted from one hundred and twenty nine progeny of five Japanese Black sires produced by artificial insemination at the Department of Livestock and Grassland Science, National Agricultural Research Centre for Western Region (WeNARC), Oda, Shimane Prefecture, Japan, were selectively genotyped and sequenced for this study. Sires 1 and 2 were selected for average daily gain while Sires 3, 4 and 5 belonged to the beef marbling score line. Routine management of the animals involved recording of weight at birth and monthly thereafter, until 18 months of age. Calves were allowed to suckle their dams in addition to being fed 1.5 kg/day/head of concentrate and 1 kg/day/head of corn silage until 6 months of age when they were weaned. After weaning, they were moved to the grower's barn and still raised on concentrates (37% corn grain, 39% rice bran, 17% soybean meal, 7% minerals) and corn silage until 10 months of age. Between 10 and 18 months of age, they were moved to another barn and fed intensively. The proportions of the ration on dry matter basis were: 61% corn grain, 34% soybean and corn gluten meal, 2% bran and 3% mineral. For every 20 kg bag, this ration provided an estimated 21% crude protein, 3.5% crude fat, 5% crude fibre, 7% ash, 0.6% calcium, 0.40% phosphate and a total digestible nutrient of 77%. From 18 to 24 months of age, breeding females were returned to the calving barn while steers were moved to the fattening barn and raised primarily on "Mosa meal" a specially formulated fattening ration containing 77% corn and rye grain, 10.5% wheat and rice bran, 9% soybean oil meal and 3.5% mineral supplement. At all ages, routine veterinary vaccinations and health checks were observed.

Extraction of genomic DNA

Following the method of Sambrook et al. (1989) and described in detail elsewhere (Malau-Aduli et al., 2003), genomic DNA was extracted and prepared from blood leucocytes and sperm.

PCR, primers and sequencing of the D-loop region of mtDNA

The D-loop region (436 bp) of mtDNA was amplified in PCR buffer solution containing 10 ng of genomic DNA derived from leucocytes as a template, 250 pmol of each dNTP, 10 pmol of each primer and 1 U of Taq DNA polymerase (Amplify Taq gold) in a volume of 20 µl. The

PCR reaction was as follows: 1 cycle of denaturation at 95°C for 30 sec, annealing at 53°C for 45 sec and extension at 72°C for 45 sec. The following primers were used: Forward primer, 5'-gccatacacagaccacaga-3' (position: 15, 921-15,940 of the mtDNA sequence, accession no. V00654, Anderson et al., 1982) and reverse primer, 5'-ttttattt ggggatgctt-3' (position: 59-78). PCR products were extracted by Micron YM-100 (Millipore, Bedford, MA) and sequenced bidirectionally using ABI Prism BigDye™ Terminator Cycle Sequencing Ready Reaction kit (PE Biosystems Japan Ltd., Tokyo, Japan).

Phylogenetic analysis of mtDNA

A phylogenetic tree was constructed using the nucleotide sequences of the mitochondrial displacement loop in order to classify the haplotypes into groups of mtDNA types (Mannen et al., 1998a,b, 2003) and maternal lineages in Japanese Black cattle. This was accomplished by the unweighted pair-group method with arithmetic means (UPGMA) using the Molecular Evolutionary Genetics Analysis (MEGA) software package (Kumar et al., 2001) utilising the Tamura-Nei distance function (Tamura and Nei, 1993).

Postnatal growth traits analyzed

Half-sib offspring of the five sires born between 1997 and 2002 were evaluated for postnatal growth traits. Birth weight (BWT), weaning weight (WT6) and yearling weight (WT12) were measured in kg, while preweaning average daily gain (PREWADG) and postweaning average daily gain (POSTADG) were computed in kg/day.

Statistical analysis

The mixed linear model procedure of PROC MIXED (SAS 2000) was utilized to statistically analyze the data. Sire and dam effects were fitted as random variables in the model which included the fixed effects of mtDNA haplotype group, maternal lineage, mtDNA haplotypes nested within maternal lineage, dam's parity, sex, season and year of birth, while age was fitted as a covariate. Sires were coded from 1 to 5, mtDNA haplotype groups were 1, 11, 73 and "new" and sex was coded as 1 and 2 to represent male and female respectively. Season of birth was coded as winter (December-February), spring (March-May), summer (June-August) and autumn (September-November). Year of birth was between 1997 and 2002, while parity ranged from 1 to 9. The complete model used for the statistical analysis is shown below:

$$Y_{ijklmnopq} = \mu + \text{SIRE}_i + \text{DAM}_j + \text{mtDNA}_k + \text{ML}_l + \text{mtDNA (ML)}_{kl} + \text{P}_m + \text{SEX}_n + \text{S}_o + \text{Y}_p + b_1(x_{ijklmnopq} - \bar{x})^2 + e_{ijklmnopq}$$

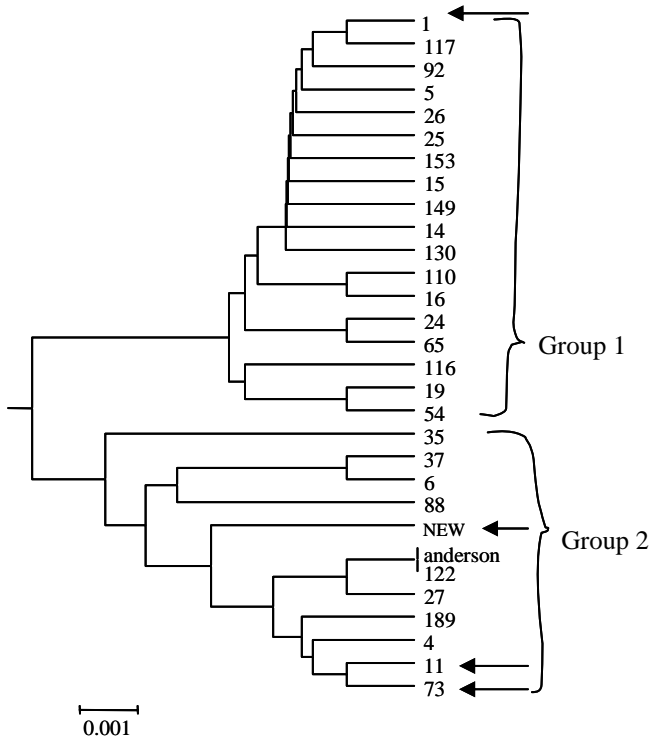


Figure 1. Phylogenetic tree showing the classification of the 17 maternal lineages, 4 mtDNA haplotypes (arrows) and relationship between the nucleotide sequences of the mtDNA displacement loop of Japanese Black cattle herd at WeNARC Oda, Shimane Prefecture, Japan.

Where, $Y_{ijklmnopq}$ = observation for a trait
 μ = the overall mean,
 $SIRE_i$ = random effect of the i^{th} sire ($i=1, 5$),
 DAM_j = random effect of the j^{th} dam ($j=1, 36$),
 $mtDNA_k$ = fixed effect of the k^{th} mtDNA haplotype ($j=1, 4$),
 ML_l = fixed effect of the l^{th} maternal lineage ($k=1, 17$),
 $mtDNA (ML)_{kl}$ = fixed effect of mtDNA nested within ML
 P_m = fixed effect of the m^{th} parity ($i=1, 9$),
 SEX_n = fixed effect of the n^{th} sex ($j=1, 2$),
 S_o = fixed effect of the o^{th} season of birth ($k=1, 4$),
 Y_p = fixed effect of the p^{th} year of birth ($l=1, 6$),
 b_1 = partial linear regression coefficient for age
 $x_{ijklmnopq}$ = age fitted as a covariate,
 $e_{ijklmnopq}$ = random error associated with each record with a mean of 0 and variance².

Primary interactions were initially included in the model but later dropped either because they were non-significant or means were inestimable due to empty cells or confounding. Least squares means and standard errors were estimated and the comparison of means for significant differences at $p < 0.05$ and $p < 0.01$ levels was carried out using the contrast option of Tukey. Correlations within and between maternal and growth traits were computed using PROC CORR (SAS 2000). Simple and multiple regression

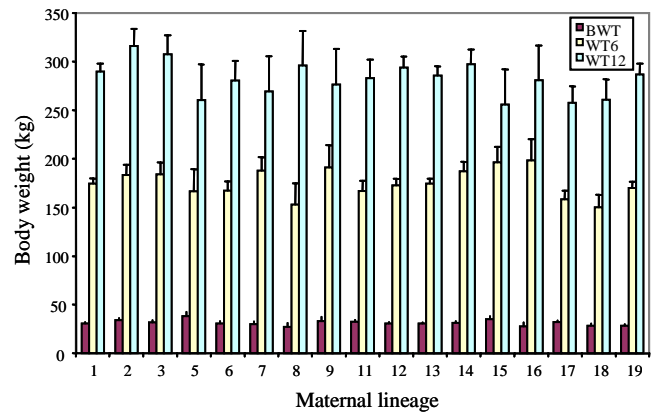


Figure 2. Effect of maternal lineage on body weights (LSM±SE) at birth (BWT), weaning (WT6) and yearling age (WT12) in Japanese Black cattle.

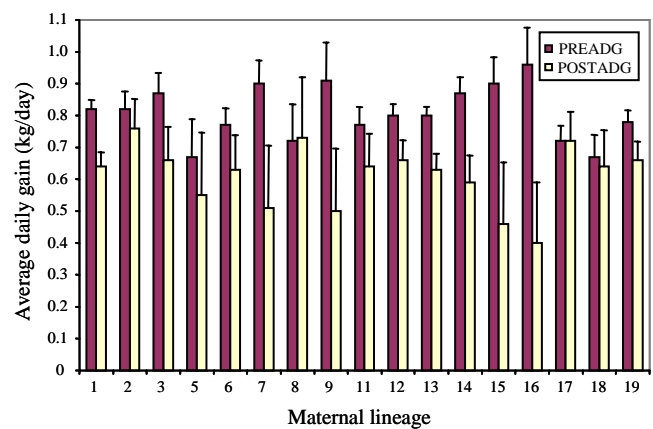


Figure 3. Effect of maternal lineage on preweaning (PREADG) and postweaning (POSTADG) average daily gain (LSM±SE) in Japanese Black cattle.

equations to predict growth traits from mtDNA haplotypes were fitted using PROC REG (SAS 2000) and the coefficient of determination (R^2) computed to establish the level of prediction accuracy.

RESULTS

Mitochondrial DNA (mtDNA) haplotypes from the displacement-loop (D-loop) region (436 bp) were genotyped and sequenced utilizing blood samples and phenotypic records of Japanese Black cattle to compute correlation coefficients (r) between mitochondrial DNA (mtDNA) haplotypes, maternal lineage (ML), birth weight (BWT), preweaning average daily gain (PREADG), weaning weight (WT6), post weaning average daily gain (POSTADG) and yearling weight (WT12). The objective was to study the relationship between maternal and postnatal growth traits and to investigate if postnatal growth of calves to yearling age could be accurately predicted from mtDNA genotype at an early age. Mixed linear models procedure was utilised to adjust for genetic and non-genetic

effects on postnatal growth traits. Simple and multiple linear regressions were fitted to predict postnatal growth traits from mtDNA haplotypes and the coefficients of determination (R^2) were computed. Results of the phylogenetic analysis are presented in Figure 1.

Phylogenetic analysis

There were 17 maternal lineages and four mitochondrial DNA haplotype classifications-1, 11, 73 and a hitherto unreported one tagged as NEW (indicated by arrows) identified in the WeNARC herd of Japanese Black cattle in Shimane Prefecture. There were two major haplotype groups: Group 1 and Group 2 (Figure 1).

Effect of maternal lineage on postnatal growth and

average daily gain

Figure 2 shows that the highest average birth weight (BWT) of 38.3 ± 4.4 kg was obtained in maternal lineage (ML) 5, while the lowest BWT of 27.1 ± 4.3 kg was recorded in ML 8. ML 16 had the highest weaning weight (WT6) of 198.4 ± 22.1 kg while the lowest WT6 value of 150.2 ± 13.1 kg was recorded in ML 18 (Figure 2). Yearling weight (WT12) was highest in ML 2 (316.2 ± 17.4 kg) and lowest in ML 15 (255.9 ± 36.2 kg). ML 16 also recorded the highest preweaning average daily (PREADG) value of 0.96 ± 0.11 kg/day and ML 5 and 18 the lowest PREADG of 0.67 ± 0.10 kg/day each (Figure 3). The highest postweaning average daily gain (POSTADG) of 0.76 ± 0.09 kg/day was obtained in ML 2 and the lowest POSTADG of 0.39 ± 0.19 kg/day was recorded in ML 16 (Figure 3). Overall, only between 2

Table 1. Body weights at birth (BWT), weaning (WT6) and yearling (WT12) age (kg), pre- (PREADG) and post- (POSTADG) weaning average daily gains (kg/day) in Japanese Black cattle (Least squares means \pm SE) as influenced by genetic and non-genetic factors

Factor	N	BWT	WT6	WT12	PREADG	POSTADG
mtDNA haplotype						
1	47	30.9 \pm 0.98	176.1 \pm 5.08 ^a	286.2 \pm 7.37	0.82 \pm 0.03	0.61 \pm 0.04
11	38	31.1 \pm 0.89	175.3 \pm 4.60 ^a	294.5 \pm 7.62	0.80 \pm 0.02	0.66 \pm 0.04
73	21	29.2 \pm 1.17	168.0 \pm 6.08 ^b	285.9 \pm 9.56	0.78 \pm 0.03	0.65 \pm 0.05
NEW	23	30.8 \pm 1.18	166.0 \pm 6.12 ^b	282.4 \pm 10.04	0.76 \pm 0.03	0.68 \pm 0.05
Sire						
1	38	33.1 \pm 1.09 ^a	159.3 \pm 5.66 ^b	293.3 \pm 8.50 ^a	0.71 \pm 0.03 ^b	0.73 \pm 0.04 ^a
2	36	35.2 \pm 1.32 ^a	167.4 \pm 6.88 ^b	289.7 \pm 10.72 ^a	0.73 \pm 0.04 ^b	0.67 \pm 0.06 ^a
3	19	26.5 \pm 1.59 ^b	176.9 \pm 8.24 ^a	280.0 \pm 12.69 ^b	0.84 \pm 0.04 ^a	0.57 \pm 0.07 ^b
4	17	29.2 \pm 1.32 ^b	173.1 \pm 6.85 ^a	282.7 \pm 10.13 ^b	0.81 \pm 0.04 ^a	0.61 \pm 0.05 ^b
5	19	28.6 \pm 1.37 ^b	179.0 \pm 7.14 ^a	281.8 \pm 10.20 ^b	0.86 \pm 0.04 ^a	0.60 \pm 0.06 ^b
Dam's parity						
1	30	23.9 \pm 2.47 ^d	143.0 \pm 4.52 ^d	264.4 \pm 8.33 ^c	0.67 \pm 0.02 ^b	0.62 \pm 0.04
2	35	30.9 \pm 0.84 ^b	176.3 \pm 5.79 ^b	285.7 \pm 7.66 ^b	0.81 \pm 0.02 ^a	0.63 \pm 0.04
3	17	32.7 \pm 1.07 ^a	176.6 \pm 4.39 ^b	297.2 \pm 9.26 ^a	0.85 \pm 0.03 ^a	0.66 \pm 0.05
4	16	30.1 \pm 1.17 ^b	179.4 \pm 6.01 ^b	295.6 \pm 9.64 ^a	0.83 \pm 0.03 ^a	0.66 \pm 0.05
5	18	33.2 \pm 1.11 ^a	183.7 \pm 5.55 ^a	288.2 \pm 9.1 ^b	0.80 \pm 0.03 ^a	0.64 \pm 0.05
6	7	33.6 \pm 1.60 ^a	189.8 \pm 8.32 ^a	297.7 \pm 16.19 ^a	0.89 \pm 0.04 ^a	0.62 \pm 0.08
7	3	28.2 \pm 0.87 ^c	170.6 \pm 12.84 ^c	287.7 \pm 20.22 ^b	0.79 \pm 0.07 ^a	0.65 \pm 0.10
8	1	28.4 \pm 4.25 ^c	164.2 \pm 22.09 ^c	267.6 \pm 21.20 ^c	0.76 \pm 0.12 ^a	0.63 \pm 0.07
9	2	33.5 \pm 3.00 ^a	158.3 \pm 15.55 ^c	281.6 \pm 24.66 ^b	0.72 \pm 0.08 ^b	0.70 \pm 0.13
Sex						
Male	72	32.2 \pm 0.86 ^a	177.8 \pm 4.48 ^a	297.0 \pm 6.38 ^a	0.82 \pm 0.02 ^a	0.67 \pm 0.03
Female	57	28.8 \pm 0.91 ^b	164.9 \pm 4.70 ^b	277.6 \pm 7.58 ^b	0.76 \pm 0.02 ^b	0.63 \pm 0.04
Season of birth						
Spring	31	30.9 \pm 1.07	173.7 \pm 5.7 ^a	282.4 \pm 3.0	0.80 \pm 0.02	0.60 \pm 0.04
Summer	33	31.9 \pm 1.06	173.5 \pm 5.7 ^a	291.1 \pm 8.48	0.80 \pm 0.03	0.67 \pm 0.04
Autumn	37	28.5 \pm 0.91	170.3 \pm 4.78 ^a	289.1 \pm 8.11	0.80 \pm 0.03	0.68 \pm 0.04
Winter	28	30.7 \pm 1.14	167.7 \pm 5.92 ^b	286.3 \pm 9.46	0.77 \pm 0.03	0.65 \pm 0.05
Year of birth						
1997	4	33.1 \pm 2.42	189.0 \pm 12.58 ^a	308.3 \pm 19.19 ^a	0.89 \pm 0.07	0.67 \pm 0.10 ^b
1998	33	32.0 \pm 1.27	164.8 \pm 6.2 ^b	299.5 \pm 9.35 ^b	0.75 \pm 0.03	0.75 \pm 0.05 ^a
1999	16	31.2 \pm 1.36	168.1 \pm 7.09 ^b	277.2 \pm 10.32 ^d	0.76 \pm 0.04	0.61 \pm 0.05 ^b
2000	35	29.1 \pm 1.04	166.2 \pm 5.40 ^b	274.9 \pm 9.65 ^d	0.77 \pm 0.03	0.62 \pm 0.05 ^b
2001	26	28.4 \pm 1.29	169.6 \pm 6.68 ^b	280.3 \pm 10.70 ^c	0.79 \pm 0.04	0.64 \pm 0.06 ^b
2002	15	29.3 \pm 1.58	170.3 \pm 8.21 ^b	283.4 \pm 16.39 ^c	0.78 \pm 0.04	0.61 \pm 0.09 ^b

Column means within each factor and variable bearing different superscripts are significantly different ($p < 0.01$).

and 5% of the variation in postnatal growth traits was explained by differences in maternal lineage.

Effect of mtDNA haplotype and other genetic and non-genetic sources of variation on postnatal growth

Table 1 shows that of all the postnatal growth traits analyzed, mtDNA haplotype was a highly significant source of variation ($p < 0.01$) in WT6 only, in which mtDNA haplotypes 1 and 11 had higher weaning weights than haplotypes 73 and NEW. On the other hand, highly significant differences ($p < 0.01$) attributable to sire effect were observed in all postnatal growth traits. Sires 1 and 2 on one hand, recorded the highest BWT, WT12 and POSTADG, while Sires 3, 4 and 5 had the highest WT6 and PREADG on the other (Table 1). Significant differences due to dam's parity and sex effects were also noticeable in all postnatal growth traits except POSTADG. Dams calving for the first time had calves with the lowest BWT, WT6, WT12 and PREADG, while 5th and 6th parity born calves recorded the highest weights and gains (Table 1). Season of birth did not influence postnatal growth traits except WT6, in which winter born calves had the lowest weight at weaning compared to their counterparts born in autumn, spring and summer (Table 1). Year of birth was also not a significant source of variation for differences in BWT and PREADG, but WT6, WT12 and POSTADG were significantly influenced (Table 1).

Relationship between mtDNA and postnatal growth traits

Correlation coefficients (r) among maternal traits were strong, positive and highly significant ($p < 0.01$, 0.001) ranging from a minimum of 0.52 between maternal lineage (ML) and Subgroup 2 haplotype (Subgroup 2), to a maximum of 0.98 between Subgroup 3 (Subgroup 3) and Subgroup 2 haplotypes (Table 2). Similarly, the correlations among postnatal growth traits were mostly positive and significant ($p < 0.05$, $p < 0.01$, $p < 0.001$), the highest r of 0.94 was obtained between weaning weight (WT6) and preweaning average daily gain (PREADG). Postweaning

average daily gain (POSTADG) was also significantly ($p < 0.001$) and positively correlated ($r = 0.70$) with yearling weight (WT12). However, there were some significantly negative correlations between WT6 and POSTADG ($r = -0.30$) and between PREADG and POSTADG ($r = -0.29$). Most importantly, the correlations between mtDNA haplotypes and postnatal growth traits were very low, mostly negative and non-significant ($p > 0.05$) ranging from -0.05 to 0.10 (Table 2).

Prediction of postnatal growth from mtDNA haplotypes using simple and multiple linear regression

Utilisation of only mitochondrial DNA haplotypes to predict the postnatal growth traits of Japanese Black cattle at birth, weaning and yearling age yielded very low coefficient of determination (R^2) values ranging from a minimum of 0.0021 for BWT to a maximum of 0.0193 for WT6 (Table 3). The inclusion of additional information of ML, Subgroup 3 and Subgroup 2 haplotypes in multiple regressions did not lead to any appreciable improvement in the R^2 values of predicting postnatal growth (Table 3).

DISCUSSION

A potential cause of maternal lineage effects is variation in maternally inherited mitochondrial DNA (Sutarno et al., 2002). Studies relating dairy performance to mitochondrial nucleotide variation across maternal lineages found significant associations, but did not provide an independent test of mitochondrial haplotype effects (Gibson et al., 1997). Therefore in our study, we carried out a phylogenetic analysis of maternal lineages and also independently tested the effects of mitochondrial DNA haplotypes and other non-genetic sources of variation, on the postnatal growth of Japanese Black cattle to yearling age. Since the displacement (D)-loop region of mitochondrial DNA does not code for any gene product and is the site of transcriptional and replicational control (Anderson et al., 1982), variations of this region can be used as genetic markers for the remaining regions of mtDNA because no

Table 2. Correlation coefficients between mitochondrial DNA (mtDNA), maternal lineage (ML), Group 2 (SGrp2) and Group 3 (SGrp3) haplotypes and postnatal growth traits of Japanese Black cattle¹

	mtDNA	ML	SGrp3	SGrp2	BWT	WT6	WT12	PREADG	POSTADG
mtDNA		0.56***	0.73***	0.62**	-0.10	-0.13	-0.05	-0.12	0.10
ML	0.56***		0.53***	0.52***	-0.05	-0.09	-0.10	-0.12	0.02
SGrp3	0.73***	0.53***		0.98***	-0.09	-0.08	0.05	-0.08	0.13
SGrp2	0.62***	0.52***	0.98***		-0.07	-0.07	0.07	-0.07	0.12
BWT	-0.10	-0.05	-0.09	-0.07		0.38***	0.23*	0.15	0.10
WT6	-0.13	-0.09	-0.08	-0.07	0.38***		0.30**	0.94***	-0.30**
WT12	-0.05	-0.10	0.05	0.07	0.23*	0.30**		0.28**	0.70***
PREADG	-0.12	-0.12	-0.08	-0.07	0.15	0.94***	0.28**		0.29**
POSTADG	0.10	0.02	0.13	0.12	0.10	-0.30**	0.70***	-0.29**	

¹ * $p < 0.05$. ** $p < 0.01$. *** $p < 0.001$.

BWT: birth weight. WT6: weaning weight. WT12: yearling weight.

PREADG: pre-weaning average daily gain. POSTADG: post-weaning average daily gain.

Table 3. Prediction of postnatal growth of Japanese Black cattle from mitochondrial DNA haplotypes using simple and multiple linear regressions

Dependent variable (Y)	Intercept (a)	b ₁ (mtDNA)	b ₂ (ML)	b ₃ (SGrp3)	b ₄ (SGrp2)	R ²
BWT	32.6530	-0.0063	-	-	-	0.0021
BWT	31.5400	-0.0046	-0.0269	-0.3450	1.4610	0.0037
WT6	173.0881	-0.0766	-	-	-	0.0193
WT6	174.3885	-0.1363	-0.2108	4.1895	-6.1633	0.0335
WT12	293.6071	-0.0464	-	-	-	0.0030
WT12	271.5943	-0.0498	-0.8058	-4.0596	26.0661	0.0373
PREADG	0.7814	-0.0003	-	-	-	0.0120
PREADG	0.8056	-0.0004	-0.0024	0.0201	-0.0356	0.0299
POSTADG	0.6715	0.0005	-	-	-	0.1040
POSTADG	0.6600	0.0002	-0.0021	0.0159	-0.0049	0.0206

mtDNA: mitochondrial DNA. ML: maternal lineage.

SGrp2: Group 2 haplotype. SGrp3: Group 3 haplotype.

R²: coefficient of determination. b₁, b₂, b₃, b₄: regression coefficients.

recombination would occur (Mannen et al., 1998). Therefore, animals having the same mitochondrial types classified by D-loop sequence variations would have the same or similar gene products in the coding regions influencing some traits. The existence of mitochondrial DNA variation in Japanese Black cattle demonstrated by Mannen et al. (1998) was confirmed in this study in which 17 maternal lineages and 4 mitochondrial DNA haplotypes were found (Figure 1). An interesting addition was the discovery of a hitherto unreported haplotype peculiar to the WeNARC herd of Japanese Black cattle referred to here simply as "NEW". Even though this study demonstrated some variation in postnatal growth traits due to the effect of maternal lineage (Figures 2 and 3), only between 2 and 5% of the variation in postnatal growth traits was explained by differences in maternal lineage. The significant variation in weaning weight due to mitochondrial DNA haplotype (Table 1) indicates the important role that mothering ability of dams plays in nurturing their calves to weaning. The trend of the influence of other genetic and non-genetic factors influencing growth observed in this study is generally comparable with reports in other breeds (Paschal et al., 1995; Herring et al., 1996; Baik et al., 2003; Casas and Cundiff, 2003; Lee and Kim, 2004).

The positive and significant correlations obtained between mitochondrial DNA, maternal lineage and Subgroups 2 and 3 haplotypes implied a strong, complementary association among these traits. This observation conformed to the expected trend since all the four traits were derivatives of cytoplasmic inheritance from the maternal line. Similarly, among postnatal growth traits, the strong, positive correlations indicated that on the basis of early data on preweaning average daily gain, selection decision on the future weaning weight of Japanese Black cattle calves could be made with some certainty because the two traits had a strong association in which weaning weight also increased as preweaning average daily gain increased.

The same trend could also be said of the association between postweaning average daily gain and yearling weight. It was anticipated that the early selection of Japanese Black cattle on the basis of higher preweaning average daily gain performance above their contemporaries would also lead to high postweaning average daily gain. On the contrary, our results clearly demonstrated that there were antagonisms as indicated by the negative correlations between preweaning and postweaning daily gains on one hand, and between weaning weight and postweaning daily gain, on the other. The genetic implication is that a selection for one of these traits would lead to a simultaneous decrease in the other. The fact that correlations between mitochondrial DNA, maternal lineage, Subgroups 2 and 3 haplotypes and postnatal growth traits were mostly negative and non-significant, is a clear evidence that maternal and postnatal growth traits are generally not strongly associated with each other, and at best, antagonistic. Our findings with Japanese Black cattle in this study agree with the report of Gibson et al. (1997) who found no association between cytoplasmic effects and growth traits in Hereford beef cattle. Furthermore, no significant effects of mitochondrial DNA on milk yield or preweaning growth traits have been found in Brangus (Rohrer et al., 1994) and Hereford (Tess et al., 1987; Tess and Robison 1990; Tess and MacNeil 1994) breeds of beef cattle. It was probably mainly as a result of the non-significant association between maternal and postnatal growth traits that led to the very low coefficients of determination (R²) values from the predictions using simple and multiple regression. The low R² implied that only a small amount of the variation (0 to 2% in this study) was accounted for by the independent variable (mitochondrial DNA). Therefore, the accuracy of prediction was very low, imprecise and unreliable. The inclusion of maternal lineage, Subgroups 2 and 3 haplotype information did not lead to any appreciable improvement in prediction accuracy. This observation is broadly consistent with 0 to

5% of variation in performance due to cytoplasmic effects, with the evidence pointing to the low end of this range (Gibson et al., 1997). It was concluded that mitochondrial DNA polymorphism has no significant association with postnatal growth from birth to yearling age, and by implication, nuclear rather than cytoplasmic DNA, is most likely responsible for genetic variation observed in postnatal growth of Japanese Black cattle. Therefore, mitochondrial DNA genotyping at an early age has no bearing on the accurate prediction of the future growth performance of calves.

ACKNOWLEDGEMENT

The authors are grateful to the Japan Society for the Promotion of Science for awarding a Post-Doctoral Research Fellowship in Bovine Genome Scanning for QTL to Dr. A. E. O. Malau-Aduli. The experimental and laboratory aspects of this research were carried out when the senior author was at the National Agricultural Research Centre for Western Region (WeNARC) Oda, Shimane Prefecture, Japan. The authors would like to extend their appreciation to the Director, WeNARC, Oda.

REFERENCES

- Anderson, S., A. R. deBruijn, A. R. Coulson, I. C. Eperon, F. Sanger and I. G. Young. 1982. Complete sequence of bovine mitochondrial DNA. *J. Mol. Biol.* 156:683-717.
- Baik, D. H., M. A. Hoque, G. H. Park, H. K. Park, K. S. Shim and Y. H. Chung. 2003. Heritabilities and genetic correlations and sire and environmental effects on meat production potential of Hanwoo cattle. *Asian-Aust. J. Anim. Sci.* 16:1-5.
- Boettcher, P. J., A. E. Freeman, S. D. Johnston, R. K. Smith, D. C. Beitz and B. T. McDaniel. 1996a. Relationships between polymorphism for mitochondrial deoxyribonucleic acid and yield traits of Holstein cows. *J. Dairy Sci.* 79:647-654.
- Boettcher, P. J., D. W. B. Steverink, D. C. Beitz, A. E. Freeman and B. T. McDaniel. 1996b. Multiple herd evaluation of the effects of maternal lineage in yield traits of Holstein cattle. *J. Dairy Sci.* 79:655-662.
- Casas, E. and L. V. Cundiff. 2003. Maternal grandsire, granddam and sire breed effects on growth and carcass traits of crossbred cattle. *J. Anim. Sci.* 81:904-911.
- Gibson, J. P., A. E. Freeman and P. J. Boettcher. 1997. Cytoplasmic and mitochondrial inheritance of economic traits in cattle. *Livestock Prod. Sci.* 47:115-124.
- Herring, A. D., J. O. Sanders, R. E. Knutson and D. K. Lunt. 1996. Evaluation of F1 calves sired by Brahman, Boran and Tuli bulls for birth, growth, size and carcass characteristics. *J. Anim. Sci.* 74:955-964.
- Kumar, S., K. Tamura, I. Jakobsen and M. Nei. 2001. *Molecular Evolutionary Genetics Analysis*. Version 2.1. Pennsylvania State University, University Park, PA, USA.
- Lee, D. H. and H. C. Kim. 2004. Genetic relationship between ultrasonic and carcass measurements for meat qualities in Korean steers. *Asian-Aust. J. Anim. Sci.* 17:6-12.
- Malau-Aduli, A. E. O., T. Niibayashi, T. Kojima, K. Oshima, Y. Mizoguchi, Y. Sugimoto and M. Komatsu. 2003. Microsatellite DNA marker mapping of bovine chromosome one for QTL affecting birth weight and preweaning growth in Japanese Black cattle (Wagyu). In: (Ed. Linda Highgate). 50 years of DNA. *Proc. Assoc. Advance. Anim. Breed. Genet. Melbourne, Australia* 15:14-17.
- Mannen, H., S. Tsuji, R. T. Loftus and D. G. Bradley. 1998a. Mitochondrial DNA variation and evolution of Japanese Black cattle (*Bos taurus*). *Genetics* 150:1169-1175.
- Mannen, H., T. Kojima, K. Oyama, F. Mukai, T. Ishida and S. Tsuji. 1998b. Effect of mitochondrial DNA variation on carcass traits of Japanese Black cattle. *J. Anim. Sci.* 76:36-41.
- Mannen, H., M. Morimoto, K. Oyama, F. Mukai and S. Tsuji. 2003. Identification of mitochondrial DNA substitutions related to meat quality in Japanese Black cattle. *J. Anim. Sci.* 81:68-73.
- Paschal, J. C., J. O. Sanders, J. L. Kerr, D. K. Lunt and A. D. Herring. 1995. Postweaning and feedlot growth and carcass characteristics of Angus-, Gray Brahman-, Gir-, Indu-Brazil-, Nellore- and Red Brahman-sired F₁ calves. *J. Anim. Sci.* 73:373-380.
- Rohrer, G. A., J. F. Taylor, J. O. Sanders and R. M. Thallman. 1994. Evaluation of line and breed cytoplasm effects on performance of purebred Brangus cattle. *J. Anim. Sci.* 72:2798-2803.
- Ron, M., I. Genis, E. Ezra, O. Yoffe, J. I. Weller and M. Shani. 1992. Mitochondrial DNA polymorphism and determination of effects on economic traits in dairy cattle. *Anim. Biotechnol.* 3:201-219.
- Sambrook, J., E. F. Fritsch and T. Maniatis. 1989. *Molecular cloning. A laboratory manual*. 2nd edn. Cold Spring Harbor Laboratory Press, New York, USA.
- SAS. 2000. *Statistical Analysis System*, SAS Institute Inc., Cary, North Carolina, USA.
- Schutz, M. M., A. E. Freeman, G. L. Lindberg and D. C. Beitz. 1993. Effects of maternal lineages grouped by mitochondrial genotypes on milk yield and composition. *J. Dairy Sci.* 76:621-629.
- Schutz, M. M., A. E. Freeman, G. L. Lindberg, C. M. Koehler and D. C. Beitz. 1994. The effect of mitochondrial DNA on milk production and health of dairy cattle. *Livestock Prod. Sci.* 37:283-295.
- Sutarno, A., J. M. Cummins, J. Greeff and A. J. Lymbery. 2002. Mitochondrial DNA polymorphisms and fertility in beef cattle. *Theriogenology* 57:1603-1610.
- Tamura, K. and M. Nei. 1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Mol. Biol. Evol.* 10:512-526.
- Tess, M. W., C. Reodecha and O. W. Robison. 1987. Cytoplasmic genetic effects on preweaning growth and milk yield in Hereford cattle. *J. Anim. Sci.* 65:675-684.
- Tess, M. W. and O. W. Robison. 1990. Evaluation of cytoplasmic genetic effects in beef cattle using an animal model. *J. Anim. Sci.* 68:1899-1909.
- Tess, M. W. and M. D. MacNeil. 1994. Evaluation of cytoplasmic genetic effects in Miles City Line-1 Hereford cattle. *J. Anim. Sci.* 72:851-856.