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Association between cow reproduction and calf growth traits and ELISA scores for paratuberculosis in a multibreed herd of beef cattle

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Abstract The objective of this research was to assess the association between 4 cow reproductive and weight traits, and 2 preweaning calf traits and ELISA scores for paratuberculosis (0 = negative, 1 = suspect, 2 = weak-positive, and 3 = positive) in a multibreed herd of cows ranging from 100% Angus (**A**) to 100% Brahman (**B**). Cow data were 624 gestation lengths (**GL**), 358 records of time open (**TO**), 605 calving intervals (**CI**), and 1240 weight changes from November to weaning in September (**WC**) from 502 purebred and crossbred cows. Calf data consisted of 956 birth weights (**BWT**), and 923 weaning weights adjusted to 205 d of age (**WW205**) from 956 purebred and crossbred calves. Traits were analyzed individually using multibreed mixed models that assumed homogeneity of variances across breed groups. Covariances among random effects were assumed to be zero. Fixed effects were year, age of cow, sex of calf, year × age of cow interaction (except WC), age of cow × sex of calf interaction (only for WC), and covariates for B fraction of sire and cow, heterosis of cow and calf, and ELISA score. Random effects were sire (except for TO and CI), dam, and residual. Regression estimates of cow and calf traits on ELISA scores indicated that lower cow fertility (longer TO), lower ability of cows to maintain weight (negative WC), lower calf BWT, and lower calf WW205 were associated with higher cow ELISA scores. Further research on the effects of subclinical paratuberculosis in beef cattle at regional and national levels seems advisable considering the large potential economic cost of this disease.

Keywords Beef, Cattle, Johne's disease, MAP, Multibreed, Paratuberculosis

Abbreviations

A	Angus

B	Brahman
BWT	birth weight
CI	calving interval
ELISA	Enzyme-linked immunosorbent assay
GL	gestation length
MAP	*Mycobacterium avium* subspecies *paratuberculosis*
TO	time open
WC	weight change of cow
WW205	weaning weight adjusted to 205 d of age

Introduction

Genetic evaluation of animals in beef cattle populations for reproduction and production traits is based on field records that are assumed to come from healthy animals. However, accurate identification of infected animals may be difficult for chronic infectious diseases with long subclinical stages such as paratuberculosis (caused by *Mycobacterium avium* subspecies *paratuberculosis*, **MAP**). Paratuberculosis, also known as Johne's disease, is a currently incurable disease that affects the intestinal tract of domestic (cattle, sheep, goats) and wild ruminants (bison, deer, elk, antelope) and has a worldwide distribution (Stabel, 1998; Lilenbaum et al., 2007). Its causing agent (MAP) has also been linked to Crohn's disease in humans; however, causation has not been established (Uzoigwe et al., 2007). Estimates of prevalence of MAP in cattle in several countries ranged from 1.6% to 18% (Lilenbaum et al., 2007), whereas

prevalence of MAP in beef cattle in several states of the US fluctuated between 3% and 9% (Thorne and Hardin, 1997; Roussel et al., 2005; Hill et al., 2003). The most recent estimate in Florida was 7.4% (Keller et al., 2004). Subclinical paratuberculosis was found to reduce milk, fat, and protein yields in US Holsteins (Lombard et al., 2005; Gonda et al., 2007; Raizman et al., 2007). Similar studies in beef cattle were unavailable. Thus, the objective of this research was to quantify the effect of subclinical paratuberculosis on 4 cow reproduction and weight traits and 2 calf preweaning growth traits using ELISA scores in a beef cattle herd of animals ranging from 100% Angus to 100% Brahman.

Materials and methods

ELISA for Paratuberculosis

A sample of blood was collected from the coccygeal vein of cows using a blood collection tube with a 3.8 cm 18 gauge needle. Blood samples were taken in late May from 2002 to 2006. Serum was separated, stored at -6.7 ºC, and subsequently evaluated by ELISA with a *Mycobacterium paratuberculosis* Antibody Test Kit from IDEXX Laboratories, Westbrook, Maine. The assay was conducted according to the manufacturer specifications. The specifications of the IDEXX kit indicated that its sensitivity (ability to detect infected animals) of the IDEXX kit was 50% and its specificity (ability to detect non-infected animals) was 99%.

The ELISA for paratuberculosis yields optical densities that are directly proportional to the amount of antibodies to MAP present in a serum sample. The ratio of the sample-to-positive optical densities corrected for the optical densities of the positive and negative controls (**S:P**; S =

optical density of the sample minus optical density of the negative control, and P = optical density of the positive control minus optical density of the negative control) was used to establish the presence or absence of antibodies to MAP in a serum sample. The ELISA S:P ratios were converted into 4 ELISA scores using the classification by Collins (2002): a) 0 = negative, for S:P ratios from zero to 0.09; serum antibodies to MAP: none detected; b) 1 = suspect, for S:P ratios from 0.10 to 0.24; serum antibodies to MAP: low level, but above normal background; c) 2 = weak positive, for S:P ratios from 0.25 to 0.39; serum antibodies to MAP: low levels, but at or above the standard cutoff ratio (S:P ratio = 0.25) for a positive test; and d) 3 = positive, for S:P ratios from 0.40 to 10.00; serum antibodies to MAP: moderate to high levels. These categories were created by Collins (2002) to help veterinary practitioners make decisions on cows in dairy herds infected with MAP. Collins (2002) defined these categories using S:P ratios and clinical information from MAP infected herds, and suggested recommendations for each category (ELISA score). Here, Collins' (2002) categories 3 and 4 were combined because of low representation of these ELISA scores in the multibreed herd.

Confirmation of paratuberculosis (clinical MAP infection) was accomplished by degree. Cows were monitored for change in body condition score and for elevated ELISA score. Cows that showed clinical signs or ELISA tests scores consistent with paratuberculosis were submitted to fecal culture (Merkal and Curran, 1974), blood or milk PCR (Buergelt and Williams, 2004) for detection of MAP. An ultimate confirmation of disease status was at slaughter or necropsy, based on postmortem signs, microscopic examination of tissues, and identification of MAP in postmortem tissues (Whitlock and Buergelt, 1996).

Animals and Data

Animals were from the multibreed beef cattle herd of the University of Florida. Established standards for their care and use were followed. Research protocols were approved by the University of Florida Institutional Animal Care and Use Committee (IACUC numbers A034 and D164). Animals in the multibreed herd have breed compositions that range from 100% Angus (**A**) to 100% Brahman (**B**). Animals (sires, dams, calves) are assigned to groups according to their breed composition as follows: breed group 1 = Angus : (1.0 to 0.80) A (0.0 to 0.20) B; breed group 2 = ¾ A ¼ B: (0.79 to 0.60) A (0.21 to 0.40) B; breed group 3 = Brangus: (0.625) A (0.375) B; breed group 4: ½ A ½ B: (0.59 to 0.40) A (0.41 to 0.60) B; breed group 5 = ¼ A ¾ B: (0.39 to 0.20) A (0.61 to 0.80) B; and breed group 6 = Brahman: (0.19 to 0.0) A (0.81 to 1.00) B. The mating design in this multibreed herd was diallel (Elzo and Wakeman, 1998). It involved mating sires and cows from 6 breed groups: A, ¾ A ¼ B, Brangus (5/8 A 3/8 B), ½ A ½ B, ¼ A ¾ B, and B. Sires from each breed group were mated to cows of all breed groups each year. Sires were used for 2 yr to create connectedness across years. Both artificial insemination and natural service sires were used. Cows were synchronized in March, artificially inseminated up to 2 times, and subsequently placed in a single-sire natural service group for 2 months. There were six natural service groups, one for each breed group of sire. Synchronization of cows consisted of an intra-vaginal progesterone device (CIDR, Pfizer Animal Health, Hamilton, New Zealand) for 7 d, followed by an injection of 5 ml of $PGF_{2\alpha}$ (LUTALYSE, Pfizer Animal Health, Hamilton, New Zealand) at CIDR removal. Calving season was from mid-December to mid-March.

Cow reproductive and weight data and calf preweaning growth data were collected from 2001 to 2006. Cow data included 624 gestation lengths (**GL**; time from conception to calving),

358 times open (**TO**; time from calving to conception), 605 calving intervals (**CI**; time between 2 consecutive calvings), and 1,240 weight changes from pre-calving time in late November to weaning in September (**WC**) from 502 cows (87 A, 91 ¾ A ¼ B, 58 Brangus, 125 ½ A ½ B, 67 ¼ A ¾ B, and 74 B). Table 1 shows numbers of cows by breed-group-of-maternal grandsire × breed-group-of-maternal granddam combination. Calf data were 956 birth weights (**BWT**), and 923 weaning weights adjusted to 205 d of age (**WW205**) from 956 calves (132 A, 204 ¾ A ¼ B, 101 Brangus, 256 ½ A ½ B, 120 ¼ A ¾ B, and 143 B). Table 2 presents the numbers of calves by breed-group-of-sire × breed-group-of-dam combination.

Feeding and Management

The cow-calf feeding and management of the multibreed herd was typical of a beef cattle commercial operation in Central Florida. In addition, this herd was under a paratuberculosis control program starting in 2002. Cows and calves were kept on bahiagrass (*Paspalum notatum*) pastures and had free access to a complete mineral supplement (Lakeland Animal Nutrition, Lakeland, FL). From mid-December to April cows were separated into 2 groups based on their ELISA score for paratuberculosis as part of the control strategy: 1) a low-risk group (negative and suspect), and 2) a high-risk (weak positive and positive). Supplementation during this period was the same for both groups: cottonseed meal (*Gossypium spp.*; 78% TDN and 44% CP), molasses (72% TDN and 4.5% CP), and both bahiagrass and bermudagrass *Cynodon dactylon*) hay (55% to 58% TDN and 7.5% to 12% CP). Cows also had access to ryegrass (*Lolium multiflorum*) pastures from January to mid-April. From mid-April to mid-June cows were placed in 6 separate pastures with a natural service sire (one sire per breed group and pasture). Between

mid-June and September, the 6 natural service groups were merged into 2 groups of cows and kept on bahiagrass pastures with supplementation of hay and molasses as needed. After weaning in September and until mid-December 4 groups were created: one group with first-calf heifers, and 3 groups of cows according to their BCS: 3 to 4, 5, and 6. Supplementation with cottonseed meal, molasses, and hay continued during this period.

Statistical Analysis

Traits were analyzed using mixed model procedures (Henderson, 1973, 1984) with multibreed models (Elzo and Famula, 1985; Elzo and Wakeman, 1998) that assumed equal variances and covariances for all breed groups (Koonawootrittriron et al., 2002). Although models differed by trait, all of them accounted for environmental, additive genetic, and intra-locus nonadditive genetic (heterosis) fixed effects, and random additive and residual effects. Fixed subclass effects present in the models for all traits were: 1) year (2001, 2002, 2003, 2004, 2005, and 2006 for GL, WC, BWT, and WW205; 2002, 2003, 2004, 2005, and 2006 for TO and CI), 2) age of cow (3 yr, 4 yr, and 5 yr and older cows), and 3) sex of calf (bull and heifer for GL, TO, CI, WC, and BWT; bull, heifer, and steer for WW205). Initial versions of these models included 2-way and 3-way interactions among year, age of cow, and sex of calf effects. Final models included only significant ($P < 0.05$) interactions. These interaction effects were: 1) year × age of cow for all traits except WC, and 2) age of cow × sex of calf, only for WC. Fixed linear covariates used by the models for all traits were: 1) B fraction of sire of calf (it measures sire additive genetic effects of B deviated from A), 2) B fraction of dam of calf (it measures cow additive genetic effects of B deviated from A), 3) heterosis of dam of calf as a linear function of her

heterozygosity (probability of intralocus interbreed interactions), 4) heterosis of the calf as a function of its heterozygosity, and 5) ELISA score for paratuberculosis. Interactions between B fraction of cow and ELISA scores, and between cow heterozygosity and ELISA scores were tested for all traits and found to be non-significant, thus they were excluded from the final models. Random effects common to all models were cow and residual. Random sire effects were included in the models for GL, BWT, and WW205. Random sire, cow, and residual effects were assumed to be uncorrelated, with mean zero, and common variance σ_s^2 for sire, σ_d^2 for dam, and σ_e^2 for residual effects.

Computations were conducted using the MIXED procedure of SAS (SAS, 2007). Estimates of variance components for sire, dam, and residual effects were computed using restricted maximum likelihood procedures (REML option in the MIXED procedure of SAS), and tested for difference from zero with a z-test.

Results and discussion

Year, age of cow, and sex of calf effects

Year effects were important (at least $P < 0.004$) for all traits except for CI ($P < 0.37$) and BWT ($P < 0.20$). Age of cow was important for all traits ($P < 0.001$), except for GL. Cows of all age groups lost weight between late November and September. Three-yr-old cows lost more weight (-25.2 ± 3.2 kg; $P < 0.001$) and had lighter calves at birth (-2.8 ± 0.8 kg; $P < 0.001$) than 5-yr-old and older cows. On the other hand, 4-yr-old cows lost less weight (15.8 ± 3.8 kg; $P < 0.001$) and had lighter calves at weaning (WW205 = -8.7 ± 4.3 kg; $P < 0.04$) than 5-yr-old and older cows.

Year × age of cow interaction was important for all traits except WC (from $P < 0.02$ for CI to $P < 0.001$ for GL and WW205). Sex of calf was relevant only for calf weight traits ($P < 0.04$ for BWT and $P < 0.001$ for WW205). Age of cow × sex of calf interaction was important only for WC ($P < 0.02$). Cows with male calves lost more weight between November and weaning than cows with female calves (-7.6 ± 2.8 kg; $P < 0.007$), perhaps due to larger nutritional demands from larger, faster growing male calves than from smaller female calves. Bulls were heavier than heifers at birth (2.4 ± 0.3 kg; $P < 0.001$) and at weaning (WW205 = 19.7 ± 3.0 kg; $P < 0.001$). Steers were heavier than heifers at weaning (WW205 = 12.1 ± 1.6 kg; $P < 0.001$).

Breed and heterosis effects

The regression of cow and calf traits on B fraction of sire was important for GL ($P < 0.001$), TO ($P < 0.03$), CI ($P < 0.05$), and BWT ($P < 0.001$), and non-significant for WC and WW205 (Table 3). Cows mated to sires of higher B percentages tended to have longer GL, shorter TO, longer CI, and heavier calf BWT than cows mated to sires of lower percentage B. On the other hand, the regression of cow and calf traits on B fraction of cow was only important for TO and BWT. Cows with higher B percentage tended to have shorter TO ($P < 0.02$), and their calves had lighter BWT ($P < 0.001$) than cows with lower B percentage. Longer GL and lighter BWT purebred and crossbred B cattle were expected based on previous research involving B and *Bos taurus* cattle (Plasse et al., 1968a,b; Reynolds et al., 1980; Sacco et al., 1990). Estrous synchronization combined with longer GL in cows with higher B percentage is likely to have contributed to their shorter TO than those cows with lower B fractions.

Heterosis of cow and heterosis of calf were important only for WW205 ($P < 0.001$ in both cases; Table 3). As expected, crossbred cows with higher levels of heterozygosity tended to have heavier calves at weaning than the mean weaning weight of calves from purebred cows. Similarly, crossbred calves with higher levels of heterozygosity tended to have heavier weaning weights than the mean of purebred calves. Estimates of cow and calf heterosis between A and B were comparable to those from earlier studies in subtropical Florida (Peacock et al., 1978; Elzo et al., 1990).

Sire and cow effects

Sire of calf genetic effects were in the models for GL, BWT, and WW205. Variation due to sire genetic effects was important for these traits. Estimates of sire variances were 3.2 ± 1.4 d^2 ($P < 0.01$) for GL, 2.2 ± 0.7 kg^2 ($P < 0.002$) for BWT, and 23.1 ± 10.6 kg^2 ($P < 0.02$) for WW205.

Cow effects were included in the models for all traits. Variation among cows was important only for calf weight traits (6.1 ± 1.2 kg^2; $P < 0.001$, for BWT, and 176.3 ± 27.3 kg^2; $P < 0.001$, for WW205), close to significance for GL (2.9 ± 2.0 d^2; $P < 0.07$) and WC (49.1 ± 33.7 kg^2; $P < 0.07$), and they could not be estimated for TO and CI because the REML iterations converged to the lower boundary (zero) in procedure MIXED of SAS.

ELISA Scores for Paratuberculosis effects

Estimates of regression of traits on ELISA scores for paratuberculosis (Table 3) were important for TO ($P < 0.001$), WC ($P < 0.02$), BWT ($P < 0.04$), and WW205 ($P < 0.01$), but not for GL and

CI. Cows with positive ELISA scores took longer time to conceive, lost weight between November and weaning in September, and gave birth to calves with lower birth weights, and their calves had lower weaning weights (Table 3).

Cows with positive ELISA scores took from one fourth (ELISA score 1) to three fourth (ELISA score 3) of an estrous cycle longer to conceive than cows with zero ELISA score. Longer TO in dairy cattle were attributed to an increased negative energy balance in the post-partum period in cows with subclinical paratuberculosis that slowed down the development of ovulatory follicles and prolonged the anestrous period (Johnson-Ifearulundu et al., 2000). This mechanism may help explain the longer TO estimated here for cows with positive ELISA scores. The negative regression estimate of WC on ELISA scores for paratuberculosis indicated that cows with positive ELISA score lost between 2.8 kg (ELISA score 1) and 8.4 kg (ELISA score 3) on the average during the 9 month period considered in WC. Thus, subclinical paratuberculosis appears to have negatively affected the energy balance of cows in this herd, which in turn may have affected their ability to produce viable follicles, delayed their return to estrous, and increased TO. Another negative consequence of the effect of subclinical paratuberculosis on TO is that cows with longer TO have a higher likelihood of calving out of season, thus increasing their chances of being culled, and lowering their stayability in the herd.

The negative effects of subclinical paratuberculosis on BWT were rather small. Calves from cows with non-zero ELISA scores were on the average from 0.4 kg (ELISA score 1) to 1.2 kg (ELISA score 3) lighter than cows with ELISA score zero. Although all cows were under the same nutritional environment, it appears that cows with subclinical paratuberculosis were less capable of absorbing nutrients (ELISA positive cows had negative WC), thus they were unable to provide the same level of nutrition to the fetus, and hence the lower BWT for cows with

positive ELISA score. Alternatively, cows with positive ELISA scores may have diverted nutrients for maintenance instead of supplying them to the fetus.

Calves from ELISA positive cows were, on the average, between 2.3 kg (ELISA score 1) and 6.9 kg (ELISA score 3) lighter at weaning than calves with zero ELISA score. During this same period, cows with positive ELISA score also lost weight. Thus, it may be hypothesized that the reduced ability of cows with subclinical paratuberculosis not only affected their ability to maintain weight, but it also lowered their ability to produce milk, which in turn led to lower calf weaning weights. Preweaning calf growth is heavily influenced by maternal milk. Subclinical paratuberculosis decreased milk production in dairy cattle (Lombard et al., 2005; Gonda et al., 2007; Raizman et al., 2007). Thus, it seems reasonable to speculate that MAP infected cows in this herd had lower milk yields and were less able to meet the nutritional needs of their progeny than uninfected cows.

The negligible estimate of regression of GL on ELISA score for paratuberculosis suggests that subclinical paratuberculosis effects during pregnancy in ELISA positive cows did not affect the capability of MAP infected cows to carry their calves to term, or trigger parturition at an earlier time. However, as discussed above, intrauterine growth of the calf appeared to have been negatively affected by MAP infection during this period. The lack of a measurable impact of subclinical paratuberculosis on CI may have been due to the estrous synchronization management in the herd. Estrous synchronization helped cows that calved later in the season to become pregnant sooner after calving (shorter TO) than cows that calved earlier in the season (longer TO). This may have reduced differences in CI (due to the combined effects of GL and TO) among MAP infected and uninfected cows, and rendered them non-significant.

Regressions of traits on the interaction between B fraction of cow and ELISA score, and on the interaction between cow heterozygosity and ELISA score were found to be non-significant for all traits. Thus, the magnitude of the effect of subclinical paratuberculosis on the traits considered here had no association with the B fraction of the cow. The greater immune response (higher production of antibodies) in high percentage B cows found here had apparently neither a positive nor a negative impact on their ability to perform. This may be an indication that B and high percentage B cows had a different immunological response to MAP than A and high percentage A cows. If this is true, then MAP control programs would need to consider the higher level of immune response in B and high percentage B cows when making culling decisions based on ELISA scores for paratuberculosis. Culling B and high percentage B cows with high ELISA scores may be counterproductive if their higher immunological response is an indication of resilience to a MAP infection. These aspects need to be addressed in future research.

Chronic diseases like paratuberculosis challenge the assumption that records used for genetic evaluation of beef cattle come from healthy animals. The apparent prevalence of paratuberculosis found in US beef cattle herds (3% to 8%; Thorne and Hardin, 1997; Hill et al., 2003; Keller et al., 2004; Roussel et al., 2005) suggests that records from animals from herds infected with MAP may be present in the datasets used for national genetic evaluations. Ignoring subclinical paratuberculosis or other chronic, subclinical disease conditions when present in the collected data will bias genetic evaluations. The significant negative effects of subclinical paratuberculosis on various cow and calf traits found here suggest that further research at regional and national levels is advisable. A voluntary herd monitoring system currently exists in the US (USDA, 2006). Information on paratuberculosis tests could be incorporated into the

whole herd reporting system used by beef cattle breed associations (BIF, 2002). Subclinical effects of paratuberculosis could be evaluated for all reproduction and production economically relevant traits to assess the full impact of subclinical stages of this disease. From a genetic evaluation perspective, aspects of interest would include identification of breed groups and individual animals that are more tolerant or resistant to paratuberculosis. Incorporation of paratuberculosis information into national beef cattle databases would facilitate monitoring and control efforts, selection of tolerant and resistant animals, and assessment of the economic impact of the disease over time.

Conclusion

Subclinical paratuberculosis, as indicated by ELISA scores, had a negative impact on cow reproduction and calf growth traits. Cows with positive ELISA scores conceived later, lost more weight while nursing their calves, and their calves had lower birth weights and weaning weights than cows with negative ELISA scores. Negative effects of subclinical paratuberculosis will likely bias genetic evaluations for growth traits as well as lower economic returns in beef cattle operations.

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412 **Table 1** Number of cows by breed group of maternal grandsire × breed group of maternal

413 granddam (BGMGD) combination

414

	Breed group of maternal grandsire[a]						
BGMGD[1]	Angus	¾ A ¼ B	Brangus	½ A ½ B	¼ A ¾ B	Brahman	Total
Angus	45	7	14	11	15	15	107
¾ A ¼ B	16	12	13	16	18	17	92
Brangus	12	3	31	5	6	6	63
½ A ½ B	25	13	19	10	15	19	101
¼ A ¾ B	15	11	6	9	12	13	66
Brahman	5	1	4	1	6	56	73
Total	118	47	87	52	72	126	502

[a]A = Angus, B = Brahman.

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417 **Table 2** Number of calves by breed group of sire × breed group of dam combination
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Breed group of dam[a]	Breed group of sire[a]						
	Angus	¾ A ¼ B	Brangus	½ A ½ B	¼ A ¾ B	Brahman	Total
Angus	76	19	26	16	20	28	185
¾ A ¼ B	40	22	31	23	32	27	175
Brangus	9	3	78	12	8	9	119
½ A ½ B	51	37	43	31	40	38	240
¼ A ¾ B	14	12	19	23	20	39	127
Brahman	2	0	3	0	5	100	110
Total	192	93	200	105	125	241	956

[a]A = Angus, B = Brahman.

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421 **Table 3** Least squares estimates of regression effects of traits on Brahman fraction of sire and
422 cow, heterozygosity of cow and calf, and cow ELISA scores for paratuberculosis
423

	Trait[b]					
Effect[a]	GL, d	TO, d	CI, d	WC, kg	BWT, kg	WW205, kg
B fraction of sire	12.2 ± 1.2	-8.0 ± 3.5	7.4 ± 3.8	-2.5 ± 3.3	5.1 ± 0.8	3.6 ± 3.0
P > |t|	< 0.001	0.03	0.05	0.45	< 0.001	0.22
B fraction of cow	2.1 ± 1.3	-13.3 ± 5.5	-4.8 ± 5.4	-0.7 ± 5.0	-4.0 ± 0.9	0.8 ± 4.3
P > |t|	0.12	0.02	0.38	0.90	< 0.001	0.85
H of cow	0.9 ± 1.5	4.0 ± 5.7	-1.2 ± 6.0	1.5 ± 5.6	0.7 ± 1.1	20.3 ± 4.9
P > |t|	0.53	0.48	0.84	0.79	0.53	< 0.001
H of calf	-3.0 ± 1.6	3.5 ± 6.6	2.3 ± 6.9	-8.6 ± 6.2	1.8 ± 1.1	14.5 ± 4.5
P > |t|	0.07	0.59	0.75	0.16	0.10	< 0.001
Cow ELISA score	-0.2 ± 0.4	4.8 ± 1.4	1.7 ± 1.6	-2.8 ± 1.2	-0.4 ± 0.2	-2.3 ± 0.9
P > |t|	0.66	0.001	0.29	0.02	0.04	0.01
No. records	580	358	605	931	953	921
No. sires	45	45	69	78	78	78
No. cows	312	185	252	363	373	362

424 [a]B = Brahman, H = heterosis measured as a function of heterozygosity (probability of intralocus
425 interbreed interactions).
426 [b]GL = gestation length; TO = time open; CI = calving interval; WC = weight change from late
427 November to September; BWT = birth weight; WW205 = weaning weight adjusted to 205 d.
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