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Article

Additive and non-additive genetic effects for reproductive traits in a Holstein- Brown Swiss diallel in humid subtropical climate

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Abstract:

Crossbreeding allows taking advantage of additive genetic differences between breeds, they also allow making use of heterosis and complementarity. Therefore, it is necessary to generate information on the efficacy of crosses compared to pure breeds under the conditions of interest. The objective was to quantify the impact of additive and non-additive genetic effects for days to first estrus (DFE), days to first service (DFS), days open (DO), services per conception (SPC), calving interval (CI) and gestation length (GL). The productive and genealogical information of females from a diallel between Holstein (HO) and Brown Swiss (BS), a total of 148 cows of the breeds HO (n=43), BS (n=64) and their reciprocal crosses HO-BS (n=20) and BS-HO (n=21), was used. Contrasts were used to estimate individual heterosis and differences between direct genetic effects and between maternal genetic effects based on Dickerson models. The results showed that heterosis and differences between maternal effects were not significant (P>0.05) for any of the traits studied. Differences between direct genetic effects were only important (P<0.05) for SPC and GL. In conclusion, the heterosis generated by the crossbreeding between HO and BS did not influence the reproductive efficiency of females. Maternal effects were not different between HO and BS. Direct genetic effects for SPC and GL favored the BS breed.

Keywords: Bovine, Diallel crossbreeding, Direct genetic effect, Heterosis, Statistical models, Linear models, Reproductive parameters, Reproductive traits.

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Introduction

The selection of purebred animals allows improving traits of zootechnical importance, such as milk production in dairy cattle[1,2]. And precisely the high pressure of selection on this phenotype has generated antagonistic genetic correlations with longevity[3], udder health[4] and fertility[5]. Generating deteriorations[6,7,8] observable in a low general productive performance[9]. Establishing a system of crossbreeding between breeds is an alternative to solve this problem[10].

The purpose of crossbreeding between genetically distant individuals is to generate new combinations of genes that allow taking advantage of direct (average deviation caused by the direct effect of the genes of the purebred individual) and maternal (average deviation due to the effects of the dam's genes through the maternal environment) additive genetic differences between breeds, and mainly to use non-additive genetic effects due to dominance and epistasis, such as heterosis[10-14], which allows the average of hybrid offspring to be phenotypically superior to the average of contemporary parental pure breeds[15,16]. Individuals from crosses may have advantages over their parents if the traits of interest show positive or useful heterosis[17], which is reflected in better reproductive rates[18].

On the other hand, in the tropical conditions of Mexico the main interest is milk production, for this reason, crosses are made with Brown Swiss or Holstein cattle[19], but not among them. The crossbreeding of these breeds could allow preserving the dairy ability and improving the general reproductive indexes. Therefore, evaluating the phenotypic behavior of the hybrid progeny based on the environment and the productive conditions of interest will provide the necessary knowledge when deciding the mating strategies that will be used to maximize the estimators of the reproductive parameters. The objective of the present study was to quantify the additive and non-additive genetic effects on the reproductive efficiency of Holstein, Brown Swiss females and their reciprocal crosses in a subtropical environment.

Material and methods

Geographical conditions

The study was conducted at the "Las Margaritas" experimental site of the National Institute of Forestry, Agricultural and Livestock Research (INIFAP, for its acronym in Spanish), located in the municipality of Hueytamalco (latitude 19°, 20'N and longitude 97°, 20'W), in the northeastern sierra of the state of Puebla, Mexico, at 450 m asl. The climate is classified as humid subtropical Af(c)[20] and the average annual temperature is 20.8 °C, ranging from 15.3 (winter) to 24.2 °C (summer), and the average annual rainfall is 1,270 mm. The abundant rainy season occurs from July to October; drizzle with temperature drop occurs from November to February[21].

Herd characteristics

The information used was from reproductive and genealogical records of 148 Holstein (HO; n=43) and Brown Swiss (BS; n=64) cows and their reciprocal crosses HO-BS (n=20) and BS-HO (n=21), which were produced with 85 sires and 121 dams through artificial insemination and natural mating, and which were born between 1997 and 2006 and calved between 1998 and 2014.

Animals and reproductive management

Heifers weighing 350 kg or more and presenting no abnormalities in the reproductive tract after transrectal palpation were included. The detection of estrus was carried out from 0600 to 0700 h and from 1700 to 1800 h, with the help of a bull with a chin-ball marker. Females in estrus were inseminated with the conventional technique 12 h after visual detection of estrus. The diagnosis of gestation was made by transrectal palpation 45 d after the last service.

Health

The cows were vaccinated against clostridiosis, pasteurellosis (twice a year; March and September) and bovine paralytic rabies (September). Tests for the control of brucellosis and tuberculosis were also performed every 14 mo (free herd). To control ectoparasites (ticks and flies), immersion bath was performed every 14 to 30 d, depending on the degree of infestation and the ectoparasiticidal product used. Dried cows were dewormed one month before calving, in case the coproparasitoscopic diagnosis indicated it.

Feeding management

The cows were kept in an intensive rotational grazing system, mainly in African star grass (*Cynodon plectostachyus*) and pangola grass (*Digitaria decumbens*). The periods of occupation and rest of the paddocks were from 2 to 3 d and from 35 to 40 d respectively, depending on the season of year, with a stocking rate of 2.5 animal units per hectare per year. During the dry season (November to March), the cows received 20 to 30 kg/animal/d of chopped fresh fodder, mainly Japanese cane (*Saccharum sinense*) or sugarcane (*Saccharum officinarum*), added with a mixture of molasses (97 %) and urea (3 %) at a rate of two to three kilograms per animal per day. In addition, lactating cows received 3.5 kg/d of a commercial concentrated feed (16 % crude protein and 70 % total digestible nutrients) during milking, while dry cows were fed 2 kg/d of the same type of feed. Together, they were provided with a mixture of minerals and water *ad libitum*.

Milking management

The cows were separated from their calves on the third day postpartum, then classified and managed in three batches: 1) cows from calving to fifth month of lactation, 2) cows from the fifth month of lactation to drying and 3) dry cows. Milking of cows began on the fourth day after calving. They were milked twice a day (0600-0800 and 1400-1600 h) with a milking machine (Alfa Laval Agri, In-churn, United Kingdom). The cows were dry off at seven months of gestation or when their milk production was less than 2 kg per day. The averages of lactation length (days) and production per lactation (kg) were for BS: 323 ± 65 and 3190.55 ± 88, HO: 324 ± 69 and 3685.65 ± 1092, BS-HO: 323 ± 61 and 3887.29 ± 1058, and HO-BS 328 ± 59 and 3910.44 ± 1315, respectively.

Variables analyzed

The variables analyzed were: 1) days to first estrus (DFE), defined as the days that elapsed from the last calving to the first manifest estrus; 2) days to first service (DFS), defined as the days that elapsed from the last calving to the first service of artificial insemination or natural mating; 3) days open (DO), defined as the period between the last calving and the next conception; 4) services per conception (SPC), defined as the number of inseminations or natural mating necessary to achieve gestation; 5) calving interval (CI), defined as the days elapsed between two consecutive calvings and 6) gestation length (GL), defined as the days that elapse between conception and calving[22].

Data analysis

The MIXED procedure of the SAS[23] statistical package was used. The model included the fixed effects of year of calving (17 levels: 1998 to 2014), season of calving (three levels: November-February; March-June and July-October), number of calving (six levels: 1 to 6), the cows' breed group (four levels: HO, BS, HO-BS and BS-HO) and the random effect of the sire nested within the sire's breed. For the tests of fixed effects, the Satterthwaite approximation was used for the denominator degrees of freedom.

Estimation of heterosis

Contrasts were used to estimate individual heterosis and differences between direct genetic effects and between maternal genetic effects of Brown Swiss and Holstein based on the following models[24,25]:

$HO = \mu_n + g^i_{HO} + g^M_{HO} + g^N_{HO}$
$BS = \mu_n + g^i_{BS} + g^M_{BS} + g^N_{BS}$
$HOBS = \mu_n + ½(g^i_{HO} + g^i_{BS}) + g^M_{BS} + g^N_{BS} + h^i_{HOBS}$
$BSHO = \mu_n + ½(g^i_{BS} + g^i_{HO}) + g^M_{HO} + g^N_{HO} + h^i_{BSHO}$

Where HO and BS = Holstein and Brown Swiss; HOBS and BSHO = reciprocal crosses between HO and BS; μ_n = average of the pure breeds involved in the diallel cross; g^i_{HO} and g^i_{BS} = deviation due to the average direct effect of the individual's genes, which come from the HO or BS breed; g^M_{HO} and g^M_{BS} = deviation due to the average effects, through the maternal environment, due to genes of dams of the HO or BS breed; g^N_{HO} and g^N_{BS} = deviation due to average effects, through the maternal environment of HO or BS granddams, which may affect the maternal ability of their daughters; h^i_{BSHO} and h^i_{HOBS} = deviation due to the increase in average heterozygosity of the F1 crosses BS-HO and HO-BS. To estimate the differences between the direct genetic effects of HO and BS, the contrast (HO + HOBS - BS - BSHO) was used, while the differences between maternal genetic effects were estimated with the contrast BSHO - HOBS, assuming that $g^N_{HO} - g^N_{BS}$ was equal to zero. Individual heterosis was calculated by the contrast [HOBS + BSHO - HO - BS] / 2.

Results

Table 1 shows the significance levels for the fixed effects considered in the models for each trait analyzed.

Table 1: Levels of statistical significance of the fixed effects considered in the statistical model for analyzing reproductive traits

Effects	DFE	DFS	DO	SPC	CI	GL
Cow's breed group	0.298	0.216	0.738	0.008	0.364	<0.0001
Year of calving	0.001	0.001	0.003	0.079	0.019	0.233
Season of calving	0.737	0.859	0.286	0.192	0.050	0.214
Number of calving	0.739	0.770	0.338	0.781	-	0.560

DFE= days to first estrus, DFS= days to first service, DO= days open, SPC= services per conception, CI= calving interval, GL= gestation length.

The effect of the cow's breed group was significant for SPC (P=0.008) and GL (P=0.001). In the case of year of calving, it was significant for DFE (P=0.001), DFS (P=0.001), DO (0.003) and CI (P=0.019). The season and number of calving were not significant (P>0.05) for any of the traits studied, but they were still included in the model. The least square means and their standard errors for the traits studied are shown in Table 2.

Table 2: Least square means and standard errors for DFE, DFS, DO, SPC, CI and GL, of HO, BS cows and their reciprocal crosses (HO-BS, BS-HO)

Cow's breed group	DFE	DFS	DO	SPC	CI	GL
HOBS	97.81±7.18	97.65±7.03	118.78±7.39	1.70±0.12[ab]	405.83±6.67	281.22±1.00[ab]
BSHO	94.25±8.15	94.71±7.84	116.05±7.80	1.61±0.11[a]	406.55±7.11	283.65±1.08[a]
HO	88.79±6.95	89.19±6.84	124.47±7.41	1.88±0.12[b]	414.52±6.50	279.84±0.97[b]
BS	103.31±6.35	104.98±6.23	123.40±6.81	1.45±0.11[a]	417.74±5.82	287.29±0.88[c]

DFE= days to first estrus, DFS= days to first service, DO= days open, SPC= services per conception, CI= calving interval, GL= gestation length.

[a,b,c] Means with different literals within columns are different (P<0.05).

No differences (P>0.05) were found between the pure breeds and their reciprocal crosses in DFE, DFS, DO and CI. In the case of SPC, HO cows had significantly (P<0.05) higher number of SPC (1.88 ± 0.12) than the BS-HO (1.61 ± 0.11) and BS ones (1.45 ± 0.11), while HO-BS cows had an intermediate behavior (1.70 ± 0.12) to parent breeds (P>0.05). Regarding GL, the BS cows had significantly (P<0.05) longer gestations (283.65 ± 1.08) than the HO, BS-HO and HO-BS ones, and the HO-BS crosses had an intermediate behavior with respect to the breeds HO and BSHO (P>0.05). The estimate of heterosis, difference between direct genetic effects and difference between maternal genetic effects for the traits under study are shown in Table 3.

Table 3: Estimates of differences between direct genetic effects, difference between maternal genetic effects and heterosis for reproductive traits

Contrast	DFE	DFS	DO	SPC	CI	GL
Direct	-10.95±12.80	-12.86±12.45	3.79±11.54	0.52± 0.17**	-3.94 ±11.47	-10.24±1.68**
Maternal	3.56±10.30	2.94±9.96	2.72±9.05	0.09±0.13	-0.72±8.93	-2.43±1.34
Heterosis	-0.02±6.75	-0.90±6.55	-6.52±6.00	-0.01±0.09	-9.94±5.75	-0.95±0.87

DFE= days to first estrus, DFS= days to first service, DO= days open, SPC= services per conception, CI= calving interval, GL= gestation length.

*(P<0.05).

Direct genetic effects were important (*P*<0.05) for services per conception and gestation length. Heterosis and the difference between maternal genetic effects were not significant (*P*>0.05) for any of the traits studied.

Discussion

The effect of the cow's breed group was only significant for SPC and GL (*P*<0.01). A possible explanation for the effect of the cow's breed group on SPC and GL can be attributed to the fact that highly milk-producing cows tend to have a low conception rate(26). Decreased fertility in dairy cattle may have a pathological cause and be related to poor nutrition(27). Lack of adequate nutrition during the prepartum and early postpartum periods can lead to a reduction in levels of glucose, insulin, insulin-like growth factor 1 and a decrease in the frequency of LH pulses. At the same time, the levels of beta-hydroxybutyrate, non-esterified fatty acids and triacylglycerol can increase(28,29). Metabolic disorders predispose cows to gynecological disorders, thus reducing reproductive efficiency(28,29). On the other hand, it has been proven that some metabolites present in plasma are also found in the ovarian follicular microenvironment, and that the single profiles of these metabolites can affect the reproductive performance of dairy cattle at different physiological stages, such as heifers, primiparous and multiparous(30). It could also be attributed to differences in the genetic component resulting from the adaptability of pure breeds to tropical conditions(31). The origin of the phenomenon is unclear and is described as multifactorial.

The year of calving was significant for DFE, DFS, DO and CI (*P*<0.01). These results can be attributed to fluctuations in climatic conditions that influence the physiology of the animal through adverse or favorable environments(32,33); the season and number of calving were not significant (*P*>0.05) for any of the traits studied. These results partially agree with those obtained by Hundie *et al*(34) and Niraj *et al*(35), who also found no differences between seasons or the number of calvings(36). Contrary to this, in an evaluation of different breeds and crosses of cattle (Brahman, Indubrasil, BS, BS x Zebu) in southeastern Mexico, it was found that, during the first and second calving, there are longer periods (CI) due to the stress caused by lactation, which are erroneously attributed to postpartum management. It is possible that this stress caused by lactation is not so intolerable in the dairy breeds (HO and BS) used in the present study(37).

Regarding the least squares means, no differences (*P*>0.05) were found between the pure breeds and their reciprocal crosses in DFE, DFS, DO and CI. These results agree with those obtained by Blöttner *et al*(2), who found no difference in DO between HO and BS-HO. Contrary to this, when evaluating some reproductive traits of dairy cows in a rotational crossing system using three breeds (HO, Jersey and Montbeliarde) in the highlands of Mexico, HO cows had more DO and a longer CI than any of the crosses evaluated[38]. In another study, BS, HO-BS and BS-HO cows had significantly less DO[39,40] and the BS-HO cross a shorter CI than HO cows[39,40,41]. Similarly, in a study conducted with databases from the Canadian Dairy Network (CDN), they evaluated 128,376 reproductive records of 55,648 HO cows, pure and crossed with BS, Jersey, Norwegian Red and Swedish Red bulls, they found that differences in the number of services and in rates of no return significantly favor crossbred calves over the pure HO ones, therefore, hybrid animals will avoid the costs associated with a greater number of services per conception, will reduce the intervals between calvings and between lactations, which will result in a higher overall production[40]. In addition to the above, the results of the present study show that HO cows require a greater number of SPC (P<0.05) than the BS-HO and BS ones, while HO-BS cows had an intermediate behavior. These results partially agree with those of another study where BS and BS-HO cows had fewer SPC (2.92 and 2.96; respectively) than HO and HO-BS cows (3.54 and 3.37; respectively)[40]. Some authors even indicate that the BS breed and its F_1 crosseswith Holstein have better reproductive performance and greater adaptability to tropical conditions[42]. One of the possible causes of the reproductive inefficiency of the Holstein breed dates back to its historical selection focused on its high milk production[43,44]. The base method for its genetic improvement is the selection of individuals that exceed the productive merit for this trait[45], but the incorrect and widespread use of assisted reproductive technologies results in hundreds or thousands of calves from a single parent[46]. The strong pressure in the selection and the poor orientation of the use of reproductive tools have caused inbreeding problems of consanguinity, which are negatively reflected on reproductive traits[46,47]. Inbreeding generated by mating genetically related animals increases the frequencies of homozygous genes[48] and restricts heterozygosity[47,49], causing an increase in the frequency of harmful recessive alleles that manifest as less phenotypic variability[50,51].

Regarding other traits analyzed, Blöttner *et al*[2] found no differences in the number of SPC between BS-HO and HO in three consecutive lactations analyzed independently, on the contrary, in the present study the analysis was carried out considering six lactations together, it is possibly the explanation of why statistical differences were found between breed groups. It should be considered that the number of SPC may be influenced by the reproductive health status of the cows, the management, the type of feeding and the seminal quality of both the straws and the ejaculate during natural mating[52], however, these factors were not included in the model due to lack of availability and because all the animals were under the same climatic and management conditions. BS-HO cows had significantly longer gestations (P<0.05) (283.65) than the HO (279.84) and BS ones (287.29); HO-BS cows had an intermediate behavior (281.22). This result agrees with that obtained by Blöttner *et al*[2], who reported a longer gestation in BS-HO females (282 d) than in pure Holstein cows (280 d). Nevertheless, an important factor influencing GL is the sex of the calves[53], unfortunately these data were not available to be included in the statistical model.

Heterosis and the difference between maternal genetic effects were not significant (*P*>0.05) for any of the traits studied. Conversely, the results in the Mexican highlands where DO, CI and SPC were evaluated in a rotational crossbreeding with Holstein, Jersey, Montbeliarde and Swedish Red, found that crosses needed fewer SPC and showed shorther DO and CI than the HO ones, due to the effect of heterosis(38). This is consistent with results obtained in subtropical conditions in Egypt(42). Nonetheless, both studies do not mention the heterosis estimated in the traits analyzed. For example, in BS-HO crosses, 7 % heterosis is reported for DO (in Mediterranean conditions in the United States)(54), and 1.3, -1.0 and -8.4 % heterosis for CI, DO and SPC, respectively(40). On the other hand, in the southern region of Brazil, they evaluated crosses of Simmental cattle (SM) with Holstein (F1, ¾ Holstein x ¼ SM and ¾ SM x ¼ Holstein) and obtained shorter CI, DO and DFS in F1 and ¾ SM x ¼ Holstein cows(55). The authors mention that crossing HO with SM decreases body weight loss and guarantees a better postpartum energy balance that benefits the expression of reproductive traits(55,56). This effect is the result of complementarity between breeds, that is, combining the dairy ability of the HO with the reproductive ability of the SM cattle(57), despite the fact that both breeds are *Bos taurus*. The breeds are complementary to each other when they excel in different traits and the hybrid calf manifests a desirable performance for a greater number of phenotypes than pure breeds(57). The hybrid calf manifests superior phenotypic behavior if the parents contribute genes with dominant effect(18), the new combinations of different alleles at each locus (heterozygous)(13) will give rise to superior animals(58). However, for this to occur, it is necessary to use genetically divergent breeds(59,60). Then, the lack of significance (*P*>0.05) of the heterosis estimated in the crossbreeding of the breeds included in the diallel suggests little genetic divergence and similar gene frequencies between HO and BS for the traits evaluated, which translates into a scarce or null manifestation of heterosis(11); in this case, some authors recommend increasing the number of breeds involved in the crosses in order to increase heterozygosity(13,61). On the other hand, the differences between direct genetic effects were important (*P*<0.05) for SPC (0.52; with the HO breed exerting a greater effect) and GL (-10.24; with the effect of the BS breed predominating).

Conclusions and implications

The heterosis generated by the crossbreeding between HO and BS did not influence the reproductive efficiency of the females. The estimated heterosis suggests little genetic divergence between breeds for the traits evaluated. Maternal effects were no different between Holstein and Brown Swiss. Direct genetic effects favored the BS breed for SPC and GL. It is recommended to cross with genetically distant breeds to maximize the use of hybrid vigor, depending on the production objective and always considering a balance between productive and reproductive traits.

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Conflict of interest

The authors declare that they have no conflict of interest.

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