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Lifetime milk production of Holstein cattle in the humid tropics compared to Holstein-Gyr and Holstein-Brahman crosses

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Abstract

Crossbred cattle are commonly used for milk production in the tropics, combining the potential benefits of pure breeds with the heterosis effects of the offspring. However, no comprehensive assessment of lifetime productivity for crossbred versus purebred cattle in low-altitude tropical environments has been carried out. The present study compares the lifetime productivity of purebred Holstein (HO, $n=17{,}269$), Gyr (GY4, $n=435$), and Brahman (BR4, $n=622$) with crossbreds Gyr × Holstein (GY × HO, $n=5521$) and Brahman×Holstein (BR × HO, $n=5429$) cows from dairy farms located in low and medium altitude tropical regions in Costa Rica. The production traits of interest were age at first calving (AFC), days open (DO), milk production per lactation (TMP), lactation length (LLEN), age at culling (ACUL), and number of lactations (NLAC). Estimates of heterosis were also calculated. The AFC for GY × HO crosses (33–34 months) was not significantly different ($p>.05$) from HO (33.8 months). For BR × HO crosses, a significant ($p<.05$) decrease in AFC (BR3HO1 35.6 months, BR2HO2 34.5 months, and BR1H03 33.3 months) was observed as the fraction of HO breed increased. Estimates of heterosis for AFC were favourable for both crosses, of a magnitude close to 3%. The DO for F1 crosses (GY2HO2 94 days; BR2HO2 96 days) was significantly ($p<.05$) lower than HO (123 days). Estimates of heterosis for DO were also favourable and above 15% for both crosses. The TMP and LLEN were higher for HO (TMP = 5003 kg; LLEN = 324 days) compared with GY × HO (TMP = 4428 to 4773 kg; LLEN = 298 to 312 days) and BR × HO (TMP = 3950 to 4761 kg; LLEN = 273 to 313 days) crosses. Heterosis for TMP was favourable but low for both crosses, with a magnitude below 3.0%. The NLAC for HO (4.6 lactations) was significantly ($p<.05$) lower than F1 (GY2HO2, 5.8 lactations; BR2HO2, 5.4 lactations). Heterosis for NLAC was above 6.0% for both crosses. Overall, estimates of lifetime income over feed costs per cow on average were USD 2637 (30.3%) and USD 734 (8.4%) higher in F1 GY × HO and BR × HO, respectively, compared to HO. In conclusion, crossbred animals, specifically those with Gyr and Brahman genetics, extend the productive lifespan, increasing economic returns.

KEYWORDS
crossbred, dairy cattle, heritability, heterosis, lifespan

1 | INTRODUCTION

The profitability of a dairy farm relies mainly on the ability of the cows to produce milk, use feed efficiently, and reproduce effectively (Sewalem et al., 2010). In temperate regions, milk production has been based mainly on zero-grazing production systems, using specialized dairy breeds such as Holstein and Jersey, well-known for their high yields of quality milk. However, selection for milk production per cow has resulted in a higher proportion of nutrient intake directed towards production at the expense of maintaining an adequate energy balance, thus negatively affecting animal health and fertility (Madalena, 2008). In contrast, under semi-intensive pasture-based production systems common in tropical and subtropical regions, the performance of specialized dairy cattle suffers from several adverse factors, such as high temperature and humidity, variability in diet composition, long walks on hilly roads, and increased exposure to pests and infectious diseases (Vargas-Leitón et al., 2023).

Inbreeding and decreased longevity due to the mating systems used in intensified dairy farm programmes are also major drawbacks of specialized dairy breeds (De Vries & Marcondes, 2020; Madalena, 2008). For instance, dairy cow longevity, a crucial economic trait increasing breeding value for production, determines the total milk yield over the lifetime of the dams (Hu et al., 2021). In temperate climates, like those found in the United States or Canada, zero-grazing systems yield three lactations on average before the animal is culled (Dallago et al., 2021). Similarly, the life expectancy of Holstein×Gyr crossbred cattle in Brazil has been estimated at between 4 and 5 years (Dallago et al., 2021). In contrast, in pasture-based systems in New Zealand and Ireland, the lifespan of dairy cows is calculated to be 4.5 lactations (Dallago et al., 2021; Kerslake et al., 2018). The optimal productive lifespan has been modelled for the fifth lactation and the highest annual profits for the sixth (De Vries, 2020; Horn et al., 2012). Consequently, the present short lifespan does not meet the economic criteria expected per cow, nor does it bear much relation to calf replacement policies.

In Costa Rica, specialized dairy production is based mainly on grazing systems, with variable use of supplementary feeds such as concentrates and agricultural by-products (Iñamagua-Uyaguari et al., 2016). Purebred Holstein cattle are found at low (0–800 m.a.s.l. and ≥24°C) and medium altitudes (801–1500 m.a.s.l and 18–23°C) (Vargas-Leitón et al., 2013). Under these conditions, calving-conception intervals are above 140 days (Vargas-Leitón & José Romero-Zúñiga, 2010). This is consistent with the estimated reduction of 0.4% in the pregnancy rate at first service observed during the last three decades for the Holstein cattle (Vargas-Leitón et al., 2023). Likewise, a decrease of 0.4 kg in daily milk yield for each 1% increase in the Temperature Humidity Index (THI) has been reported locally for Holsteins (Ruiz-Jaramillo et al., 2019). The use of specialized dairy breeds, even under high humidity and temperature conditions, has been driven principally by short-term economic goals based on the misconception that a reduction in health, fertility, and fitness is compensated by increased milk yield (Madalena, 2008). Milk production in the tropics is generally associated with crossbreeding strategies, which combine the potential benefit of breed with heterosis (Galukande et al., 2013; Madalena, 2008). Evidence from countries with tropical climates, such as Brazil, shows that crossbred cattle Holstein×Gyr are responsible for 80% of the total milk production (Silva et al., 2023).

Crossbreeding strategies for milk production in tropical regions have achieved variable degrees of success, depending on the specific breeds employed, as well as environmental factors and the level of management (Bunning et al., 2019; Galukande et al., 2013; Madalena, 2008). The crosses between *Bos taurus*×*Bos indicus* are becoming more popular in Costa Rica, with Holstein remaining the preferred dairy breed (La Roche Loaiza et al., 2019; Martínez et al., 2023). Among *Bos indicus* breeds, Brahman and Gyr are the most popular, introduced into the local stock mainly via artificial insemination and, more recently, embryo transfer (Canaza-Cayo et al., 2018; Castillo-Badilla et al., 2019; Martínez et al., 2023; Molina-Coto et al., 2020; Villanueva et al., 2023). While the rationale for crossbreeding seems evident, it is not always borne out by the actual performance of tropical and sub-tropical production systems. Despite the wide propagation of crossbreeding in the tropics, few studies have compared the efficiency of raising purebred animals with that of using crossbreeds, mainly because performance records are not readily accessible, scarce, or inaccurate (Galukande et al., 2013). Moreover, most of the available crossbreeding studies do not consider lifetime productivity, an essential indicator of the overall profitability of dairy cattle (Galukande et al., 2013).

The present study evaluates dairy cattle lifetime productivity and economics within specialized farms at low and medium altitudes in Costa Rica. We hypothesize that crossbred cows, specifically Holstein-Gyr or Holstein-Brahman crosses, perform better than purebred Holstein cows.

2 | MATERIALS AND METHODS

2.1 | Location and herd characteristics

A population-based, observational, retrospective, and longitudinal study was performed on farm-owned production records obtained from the Centro Regional de Informática para la Producción Animal Sostenible (CRIPAS) of the Escuela de Medicina Veterinaria at the Universidad Nacional de Costa Rica (Romero-Zúñiga et al., 2019; Sánchez-Hernández et al., 2020).

The cattle herds are in two altitudinal zones: low (0–800 m.a.s.l.) and medium (801–1500 m.a.s.l.). The predominant pastures in the low altitudes are *Cynodon nlemfuensis* (African star grass), *Paspalum* spp., and *Axonopus* spp., and in the high altitudes, *Lolium perenne* (ryegrass) and *Pennisetum clandestinum* (Kikuyu grass). Medium altitudes contain a mixture of grasses from both low and high altitudes.

Nutritional management on over 95% of the farms relies primarily on intensive rotational grazing and supplementation with commercial concentrate feed and mineral salts. Artificial insemination (AI) or natural mating (NM) is predominantly employed, with embryo transfer (ET) gaining popularity over the last decade. Immunization practices include vaccinations against brucellosis (Brucella abortus Strain RB51, administered at 3–8 months), clostridial polyvalent vaccine (biannually for the entire herd), leptospirosis polyvalent vaccine (biannually for the whole herd), and a polyvalent vaccine covering infectious bovine rhinotracheitis, bovine viral diarrhoea, bovine parainfluenza type 3, and bovine respiratory syncytial virus (administered to the entire herd, cows, and heifers before breeding). All farms have a milking parlour; cows are milked twice daily, and veterinary assistance is provided at least once a month.

2.2 | Data

The database comprises production, reproductive, and health-related information from over 2500 dairy herds nationwide. Data are collected daily primarily through the owners, digitized in the VAMPP Bovino 3.0 software weekly (Noordhuizen & Buurman, 1984), and centralized for analysis biannually. This information is stored and periodically sent to the industry, local cattle associations, and the School of Veterinary Medicine (Universidad Nacional). The recording and submission of information to the central database are voluntary; not all herds have data updated to the last year or comprehensive data on every type of event (Sánchez-Hernández et al., 2020).

2.3 | Inclusion criteria

For this study, a selection of records in the database was performed on specific criteria related to the production system, breed types, and essential information for both the herd and individual cows.

The criteria are outlined below:

Only data from specialized dairy herds located at low (0–800 m.a.s.l.) and medium (801–1500 m.a.s.l.) altitudes was used in this study. These are the zones where crossbreeding is more frequently practiced.

The breeds for this analysis were Holstein (HO, $n = 17{,}269$), Gyr (GY4, $n = 435$), and Brahman (BR4, $n = 622$) versus crossbreds Gyr × Holstein (GY × HO, $n = 5521$) and Brahman × Holstein (BR × HO, $n = 5429$). Breed composition in the VAMPP 3.0 software is assigned based on parental breeds. For this study, crossbred cattle were classified into six categories according to the expected breed proportion, as follows: ¾GY¼HO (GY3HO1), ½GY½HO (GY2HO2), ¼GY¾HO (GY1HO3), ¼BR¾HO (BR1HO3), ½BR½HO (BR2HO2), ¾BR¼HO (BR3HO1). Other breed composites, such as 5/8 and 7/8, or 1/8 and 3/8, were present in minor frequencies and were assigned to 3/4 and 1/4 categories, respectively. Some cows were reported as Girolando breed and added to the ¾ category.

Purebred Holstein cows included in the analysis were required to have crossbred herd mates. This criterion minimized bias introduced by management practices related mainly to purebred herds in low regions, such as free-stall barns. Only herd records for females born between 1995 and 2020 were included in the analysis. Cows included in the analysis must have at least a first calving date. A minimum of three cows for each herd/year/season of calving and five cows with information available per herd were also mandatory.

2.4 | Statistical analysis

For the statistical analysis, six traits of interest were chosen as representative indicators of the lifetime performance of cows and considered crucial for profitability in dairy production systems. Two traits were chosen as representative of reproduction performance: (1) Age at First Calving (AFC), defined as the months elapsed between birth and the first calving, and (2) Days Open (DO), measured as the days between calving and the conception date. Other two traits were selected as representative of production performance, namely: (3) Total Milk Production per Lactation (TMP), defined as the total amount of milk (kg) produced up to the last lactation day: and (4) Lactation Length (LLEN), obtained as the total number of days in milk per lactation. In addition, two traits were chosen as representative of longevity performance, namely: (5) Age at Culling (ACUL), calculated as the years elapsed between birth and the culling date: and (6) Number of Lactations (NLAC), defined as the total number of lactations from birth to the culling date (NLAC).

Descriptive statistics (mean, standard deviation) and graphical representations (histograms, boxplots) were utilized to identify and eliminate inconsistent or outlier values that might adversely impact regression models. Restriction intervals were established for the variables analysed in the study based on the observed distribution across the entire population. The applied restriction intervals were as follows: AFC between 20 and 60 months, DO between 30 and 500 days, TMP between 500 and 15,000 kg, LLEN between 200 and 600 days, ACUL between 1.7 and 18 years, and NLAC between 1 and 15. After database preparation, global and within-breed statistical parameters (mean ± S.E.M) were calculated.

A generalized linear mixed model (GLMM) (Gbur et al., 2012), using the PROC GLIMMIX procedure of SAS program (SAS Institute Inc., 2022), was used to compare breed performance on four of the variables mentioned above.

The model used in the present study is described below:

$$Y_{ijk} = \mu + BR_i + LA_j + hys_k + \varepsilon_{ijk} \qquad (1)$$

Y = Dependent variables (AFC, DO, TMP, and LLEN, as previously defined), μ = Population means, BR_i = Fixed effect linked to breed type (9 breed types: HO, GY, BR, GY3HO1, GY2HO2, GY1HO3, BR1HO3, BR2HO2, and BR3HO1), LA_j = Fixed effect linked to lactation × age at calving classes (15 LA) classes, combining lactation (1–≥5) and age (<=2–≥8 years). This effect was considered only for DO, TMP, and LLEN, hys_k = Random effect of *herd*×*year*×*season* of birth classes to account for similar environment/management conditions shared by cows in the same contemporary group. A minimum of 3 cows were required for each *hys*. If this minimum was not met, adjacent classes were joined until the required minimum was fulfilled, ε_{ijk} = Random residual error.

Appropriate probability distributions were selected for each dependent variable based on the observed dispersion in the histograms. Normal distributions were assumed for AFC, TMP, and LLEN, while a lognormal distribution was assumed for DO. An identity link function was applied to all models. In cases where the breed fixed effect showed statistical significance, the adjusted Least Squares Means (LSM) were pairwise compared using the Tukey-Kramer test (Daniel & Cross, 2019).

For variables ACUL and NLAC, a Cox proportional hazards model (Kleinbaum & Klein, 2012) was fitted using the *phreg* procedure from SAS (SAS Institute Inc., 2022). The model included a fixed effect for breed type and a random herd effect. Censoring for cows still alive was defined as the age (in years) at the time of the last reported event for the cow within the farm (for ACUL) or the previous lactation with available information (for NLAC). Survival probabilities within each breed were obtained based on age (1–18 years) or lactation number (1–15). Mean Survival Time (MST) for age in years (MST_years) or in number of lactations (MST_lac) were also estimated.

Finally, an estimate of heterosis (%H) was calculated for all traits under analysis, based on LSM (or MST) from previous models, according to the following formula (Bourdon, 2013):

$$\%\mathrm{H} = \left[\left(\mathrm{M_{F1}} - \mathrm{M_{PB}}\right) / \mathrm{M_{PB}}\right] \times 100 \quad (2)$$

where MF1=MF1 was approximated as LSM (or MST) for breed types GY2HO2 or BR2HO2. MPB=Average of LSM (or MST) for parental breeds (HO4 + BR4)/2, or (HO4 + GY4)/2.

The use of GY2HO2 and BR2HO2 as proxies of the F1 performance is supported by the fact that most of these cows within the database were reported with parental breeds H4 × GY4 or H4 × BR4.

2.5 | Economic analysis

An economic comparison was conducted based on an estimate of lifetime Income Over Feed Cost ($IOFC; Shonka-Martin et al., 2019), calculated for an average cow of the breed types HO4, GY2HO2, and BR2HO2. IOFC was calculated by subtracting feed costs from the actual milk income obtained during the productive lifespan of lactating cows.

For this calculation, we used the adjusted performance parameters (DO, TMP, LLEN, and MST_lac) from each breed type obtained from model (Bourdon, 2013).

Dry matter intake (DMI, kg) during lactation was estimated based on the following equation (NRC, 2001).

$$\mathrm{DMI} = \left(0.372 \times \mathrm{FCM} + 0.0968 \times \mathrm{BW}^{0.75}\right) \times \left(1 - e^{(-0.192 \times (\mathrm{WOL} + 3.67))}\right) \quad (3)$$

In this calculation, fat-corrected milk (FCM) and body weight (BW) for the week of lactation (WOL) were modelled under the assumption of an average lactation curve for the respective breed type. Real data on daily milk yield and milk components for the three breeds under comparison was used in this estimation. Mature body weight for the breed types under comparison was assumed as 575 kg at the beginning of lactation, based on local data obtained for the Holstein breed. No reliable data on mature body weight was available for crossbreds. Changes in body weight during lactation were based on NRC (2001), assuming a decrease in BW from the start up to the lactation peak, followed by a progressive BW increase up to the end of lactation.

The feeding strategy assumed for this study was based on the most common practices observed in local dairies, as described in a previous study using data from 104 dairy farms (Iñamagua-Uyaguari et al., 2016). Concentrate was fed according to a milk: concentrate ratio of 3.3, based on average data reported by the same study (Iñamagua-Uyaguari et al., 2016). Additionally, fixed amounts of forage and other industrial by-products were provided. Feed composition was also taken from the same study.

Cows were assumed to graze freely on pasture for the entire day. Pasture type and quality were assumed, as Iñamagua-Uyaguari et al. (2016). Dry matter intake from pasture was estimated as the difference between DMI estimated from the equation (Canaza-Cayo et al., 2018) and DMI supply from other feeds (concentrate, forage, and byproducts).

The cost of concentrate and supplements was based on current market prices. The cost of pasture considered only fertilization practices (Iñamagua-Uyaguari et al., 2016). Revenues from milk sales were estimated according to the current payment system applied by the largest dairy cooperative in the country, which is based on the portion of solids (fat, protein, and lactose) in milk.

3 | RESULTS

3.1 | Descriptive statistics

The final database included performance records from 513 herds, comprising 28,219 cows and 81,293 lactations (Table 1). The average number of lactations per cow in the final dataset was 2.9, and the average number of cows per herd was 55.0.

Descriptive statistics for all traits under analysis are presented in Table 2. There was considerable breed variation for all the analysed traits. The mean age at first calving (AFC) exceeded 32 months, and days open (DO) were over 120 days for all breed types. HO4 was the only breed type with total milk production (TMP) over 5000 kg, while most crossbreds ranged between 4000 and 5000 kg, with GY4 and BR4 below 4000 kg. Age at culling (ACUL) was consistently below 7 years, and the number of lactations (NLAC) was below 4 for all breeds. The range of variation was 8 months for AFC, 40.5 days for DO, 2139 kg for TMP, 60 days for lactation length (LLEN), 1.9 years for ACUL, and 1.5 lactations for NLAC. For all traits, the estimates for standard error of the mean (SEM) were generally low, especially for breed types with more performance records, such as HO4, GY2H2, and BR2H2. Conversely, the largest SEM tended to be associated with GY4 and BR4, the breed types with fewer performance records available.

3.2 | Comparison between breed types

For reproduction traits, age at first calving was higher ($p < .05$) for BR4 and GY4 compared to HO4 (Figure 1). For BR×HO crosses, a marked reduction in AFC was observed as the proportion of Holstein breed increased. The AFC for GY×HO crosses was between 33 and 34 months, not significantly different from HO ($p > .05$). The DO for HO4 was significantly higher ($p < .05$) than any other breed type. The best performance was observed for both F1 breed types, with estimates of DO under 100 days. The DO for BR2HO2 was also significantly lower ($p < .05$) than BR4, while the DO for GY2HO2 was lower, although not significantly different ($p > .05$) from GY4.

Estimates of heterosis were favourable for reproduction traits (Table 3). The AFC heterosis estimates for both crosses were similar, with an absolute magnitude close to 3% (Table 3). Estimates of heterosis for DO were high for both crosses, with an absolute magnitude above 15%.

Results obtained for production traits showed that TMP for HO4 was significantly higher ($p < .05$) than for all other breed types (Figure 2). TMP also increased as the Holstein fraction increased and tended to decrease significantly for purebred GY4 and BR4. A slight advantage of GY4 over BR4 was observed, although this was not statistically significant ($p > .05$).

For LLEN, a similar trend was observed (Figure 2). HO4 had significantly longer lactations than all other breed types ($p < .05$). Lower LLEN tended to be observed as the HO fraction decreased, although the 95% CI was long for GY4, BR4, and both GY3HO1 or BR3HO1, mainly due to the reduced number of records available for these categories. While the milk yield of HO4 was approximately 300 and 600 kg higher than GY2HO2 and BR2HO2, respectively, LLEN was also 26 and 32 days longer for HO4 than GY2HO2 and BR2HO2, respectively.

Estimates of heterosis for TMP were favourable but low for both crosses, with a magnitude below 3% (Table 3). Heterosis was negative for LLEN, with F1 cows consistently showing shorter lactations than HO4 (Table 3).

In relation to longevity traits, results from the Cox proportional hazards model showed similar differences between breed types, whether measured in years (MST_yr) or lactations (MST_lac) (Figure 3). An irregular result was obtained for G3HO1, which departed from the general trend. Apart from this group, MST_yr and MST_lac decreased as the Holstein fraction increased. MST_lac for

TABLE 1 After database preparation, the number of herds, cows, and lactations, global and per breed type.

Breed type[a]	Number of herds	Number of cows	Number of lactations
Global	*513*	*28,219*	*81,293*
GY4	103	435	1013
GY3HO1	72	266	569
GY2HO2	249	2964	7280
GY1HO3	184	1856	4278
HO4	454	17,269	52,433
BR1HO3	231	1693	5483
BR2HO2	360	2876	8248
BR3HO1	79	238	666
BR4	110	622	1323

[a]Breed types: GY4 = purebred Gyr, GY3HO1 = ¾Gyr¼ Holstein, GY2HO2 = ½Gyr½Holstein, GY1HO3 = ¼Gyr¾Holstein, HO4 = purebred Holstein, BR1HO3 = ¼Brahman¾Holstein, BR2HO2 = ½Brahman½Holstein, BR3HO1 = ¾Brahman¼Holstein, BR4 = purebred Brahman.

TABLE 2 Mean and standard error of the mean (SEM) for production, reproduction, and longevity traits[a] in purebred and crossbred cows from specialized dairy farms in the low and mid tropics of Costa Rica.

	AFC (months)		DO (days)		TMP (kilograms)		LLEN (days)		ACUL (years)		NLAC (*n*)	
Breed Type[b]	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
Global	*33.3*	*0.05*	*148*	*0.41*	*5305*	*11.1*	*324*	*0.45*	6.6	0.02	*3.7*	*0.02*
GY4	37.7	0.52	136	3.78	3834	191.9	286	7.4	6.5	0.26	3.3	0.21
GY3HO1	34.4	0.39	124	4.15	4421	108.1	302	5.4	5.1	0.19	2.5	0.16
GY2HO2	34.1	0.14	122	1.20	4770	30.5	297	1.3	5.6	0.08	2.8	0.07
GY1HO3	33.9	0.17	134	1.61	4736	39.5	311	1.7	5.2	0.08	2.6	0.07
HO4	32.4	0.06	158	0.52	5591	13.6	333	0.6	6.7	0.02	3.8	0.02
BR1HO3	32.4	0.17	146	1.47	4960	36.2	318	1.5	6.9	0.09	4.0	0.08
BR2HO2	35.5	0.21	123	1.14	4212	33.7	290	1.4	7.0	0.07	4.0	0.07
BR3HO1	35.8	0.69	126	4.03	3564	139.0	272	4.8	6.7	0.24	3.5	0.22
BR4	40.3	0.50	163	3.68	3452	126.5	281	5.4	6.5	0.14	3.0	0.11

[a]Traits: DO = days open, AFC = age at first calving (mo), ACUL = age at culling (yr), TMP = total milk production per lactation (kg), LLEN = lactation length (d), NLAC = Number of lactations.

[b]Breed types: GY4 = purebred Gyr, GY3HO1 = ¾Gyr¼ Holstein, GY2HO2 = ½Gyr½Holstein, GY1HO3 = ¼Gyr¾Holstein, HO4 = purebred Holstein, BR1HO3 = ¼Brahman¾Holstein, BR2HO2 = ½Brahman½Holstein, BR3HO1 = ¾Brahman¼Holstein, BR4 = purebred Brahman.

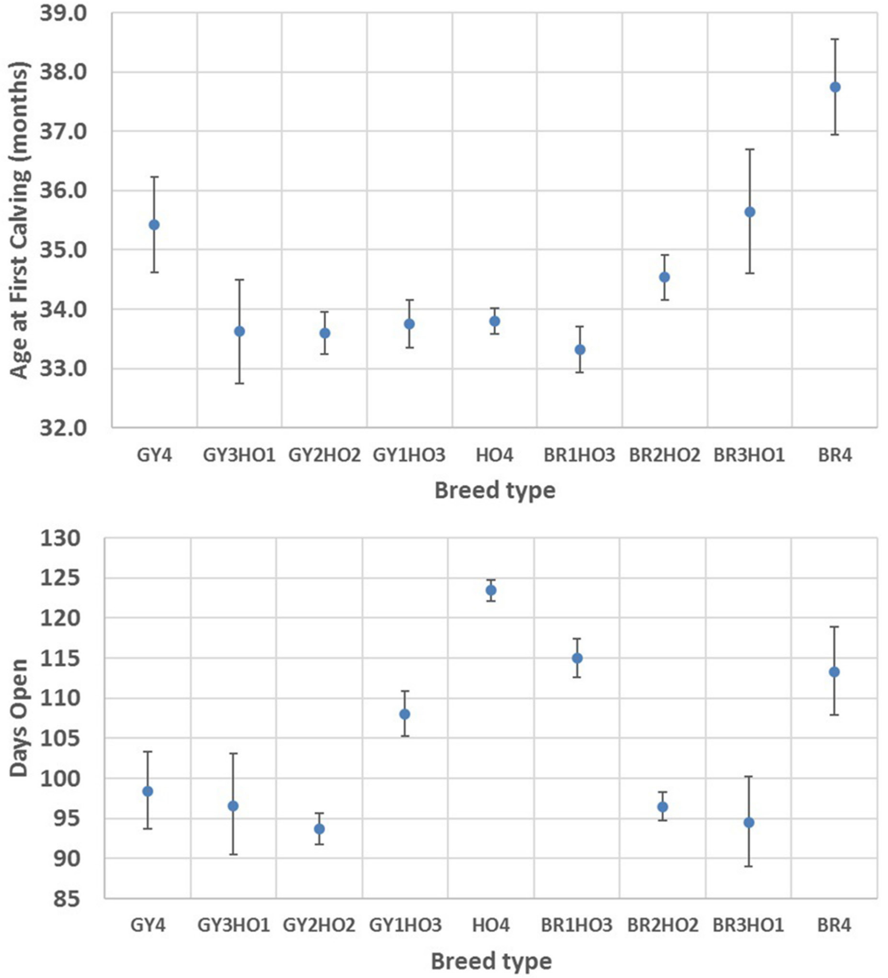

FIGURE 1 Least square means with 95% CI obtained by GLMM models for age at first calving (top panel) and days open (bottom panel) for purebred and crossbred cows from specialized dairy farms in the low and mid tropics of Costa Rica. Breed types: GY4 = purebred Gyr, GY3HO1 = ¾Gyr¼ Holstein, GY2HO2 = ½Gyr½Holstein, GY1HO3 = ¼Gyr¾Holstein, HO4 = purebred Holstein, BR1HO3 = ¼Brahman¾Holstein, BR2HO2 = ½Brahman½Holstein, BR3HO1 = ¾Brahman¼Holstein, BR4 = purebred Brahman.

TABLE 3 Estimates of heterosis (%H) for production, reproduction, and longevity traits in crossbred Holstein × Gyr and Holstein × Brahman cattle from low and mid tropics of Costa Rica.

		Holstein × Gyr			Holstein × Brahman		
Trait[a]	Units	Parent breeds average	F1	%H	Parent breeds average	F1	%H
AFC	months	34.6	33.6	−2.9	35.8	34.5	−3.4
DO	days	111	94	−15.5	118	97	−18.5
TMP	Kg	4579	4699	2.6	4361	4403	1.0
LLEN	days	305	298	−2.5	304	291	−4.3
MST_yr	years	8.3	8.5	3.0	7.9	8.2	3.9
MST_lac	lactations	5.5	5.8	6.9	4.8	5.4	12.6

[a]Traits: AFC = age at first calving, DO = days open, TMP = total milk production per lactation, LLEN = lactation length, MST_yr = mean survival time (age in years), MST_lac = mean survival time (lactations).

HO4 was significantly lower ($p < .05$) than for other breed types, except for G3HO1 and BR4. MST_lac for GY4 was higher ($p < .05$) than for other breed types, except for GY2HO2 and BR3HO1. MST_lac for GY2HO2 and BR2HO2 were higher and equal to those of parental breeds. Again, the 95% CI for GY4, BR3HO1, and BR4 was long, given the low number of records available for these categories.

Heterosis for longevity traits was favourable for both crosses (Table 3). Heterosis for MST_yr was 3% for the GY × HO cross and 3.9% for the BR × HO cross. Heterosis was higher for MST_lac, above 6% for both crosses.

3.3 | Lifetime income over feed cost analysis

Estimates of lifetime income over feed costs ($IOFC) per average cow were approximately USD 2637 (30.3%) and USD 734 (8.4%)

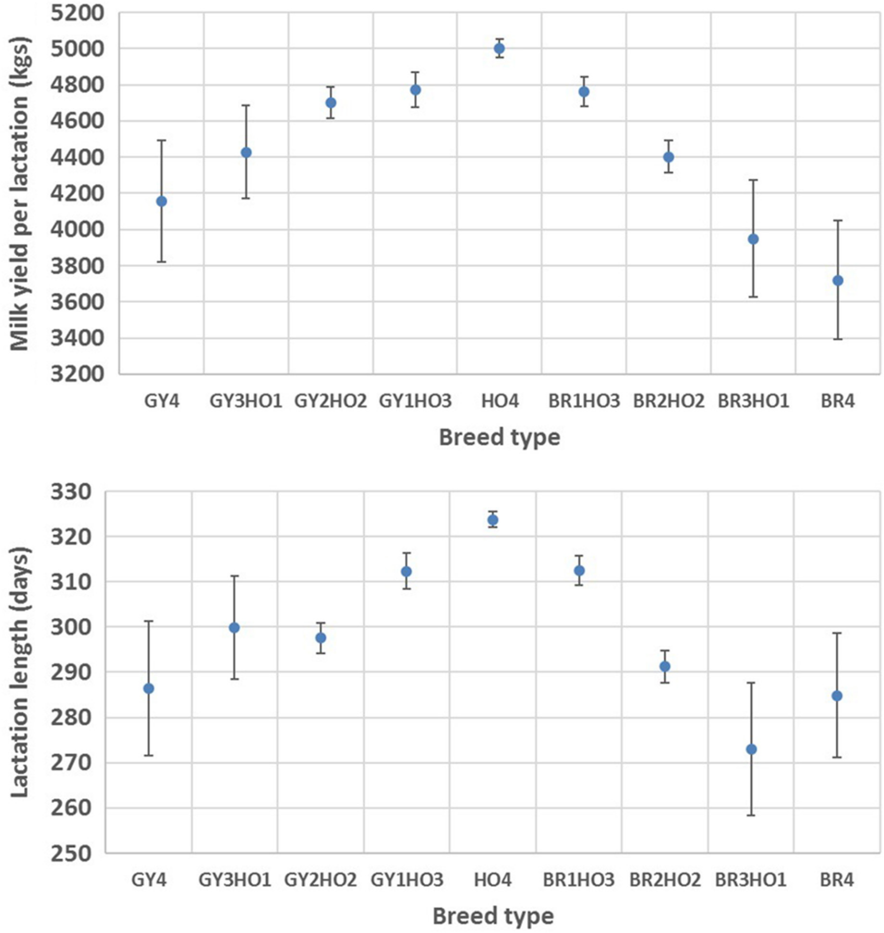

FIGURE 2 Least square means with 95% CI obtained by GLMM models for total milk yield per lactation (top panel) and lactation length (bottom panel) for purebred and crossbred cows from specialized dairy farms in the low and mid tropics of Costa Rica. Breed types: GY4 = purebred Gyr, GY3HO1 = ¾Gyr¼ Holstein, GY2HO2 = ½Gyr½Holstein, GY1HO3 = ¼Gyr¾Holstein, HO4 = purebred Holstein, BR1HO3 = ¼Brahman¾Holstein, BR2HO2 = ½Brahman½Holstein, BR3HO1 = ¾Brahman¼Holstein, BR4 = purebred Brahman.

higher in GY2HO2 and BR2HO2 compared to HO4 (Table 4). This difference was associated mainly with the higher mean survival time of the crossbred, which lasts on average 1.2 (GY2HO2) and 0.7 (BR2HO2) additional lactations compared to Holstein. The higher MST lac was, in turn, linked to the fewer days open, which were almost 1 month inferior in crossbred compared to Holstein. On the contrary, milk yield per lactation is 300 and 600 kg higher in Holstein than crossbred, but this is mainly due to almost one additional month in lactation length. In contrast, differences in daily milk yield among the three breed types were under 0.7 kg.

4 | DISCUSSION

The performance seen in this study in terms of production, reproduction, and longevity traits, is generally in the same range as reported in previous studies for the same breeds and crosses (Canaza-Cayo et al., 2018; Reis et al., 2020; Vieira et al., 2022). However, some important differences were observed, mainly related to production levels and the degree of heterosis.

An apparent breed effect on AFC was found, as demonstrated by the decrease in this parameter as the Holstein breed increases its participation, especially for the BR × HO crosses. Higher values of AFC were found for purebred Brahman and Gyr compared to Holstein. The heritability of AFC is generally reported as low, indicating that the management system greatly influences this trait and depends more on the breeders' decisions than on the animal's physiology (Vieira et al., 2022). However, there is substantial evidence that certain breeds, particularly *Bos taurus*, tend to have their first calving much earlier than *Bos indicus* (Galina & Arthur, 1989). In Colombia, for example, Grajales et al. (2006) found that Holstein crossbred animals reach puberty earlier than purebred Zebus. It is known that dual-purpose cattle, normally associated with crossbreeding practices, generally take longer to reach the trait AFC (Reis et al., 2020). Vieira et al. (2022) also found the lowest AFC means in cows with a greater proportion of Holstein, such as those belonging to the genetic groups pure Holstein (HO), 7/8HO1/8GYR, 5/8HO3/8GYR, 3/4HO1/4GYR, and 1/2HO1/2GYR, compared to 3/8HO5/8GYR, 1/4HO3/4GYR, and pure Gyr (GYR).

Heterosis for AFC in the present study was above 3% in both crosses, which means approximately one-month earlier AFC than the parental average. Vieira et al. (2022) reported higher heterosis estimates, around 10%, for HO × GY crosses, equivalent to 3 months earlier AFC than the parental average. These results reflect the positive impact of crossbreeding on this trait; nonetheless, there is controversy about whether crossbreed performance can be consistent after the first generation. When results are compared with subsequent generations, variability in performance must be expected (Fuerst & Sölkner, 1994; Plasse, 1983; Quenon et al., 2020). In our study, crossbred performance remained similar for all GY × HO

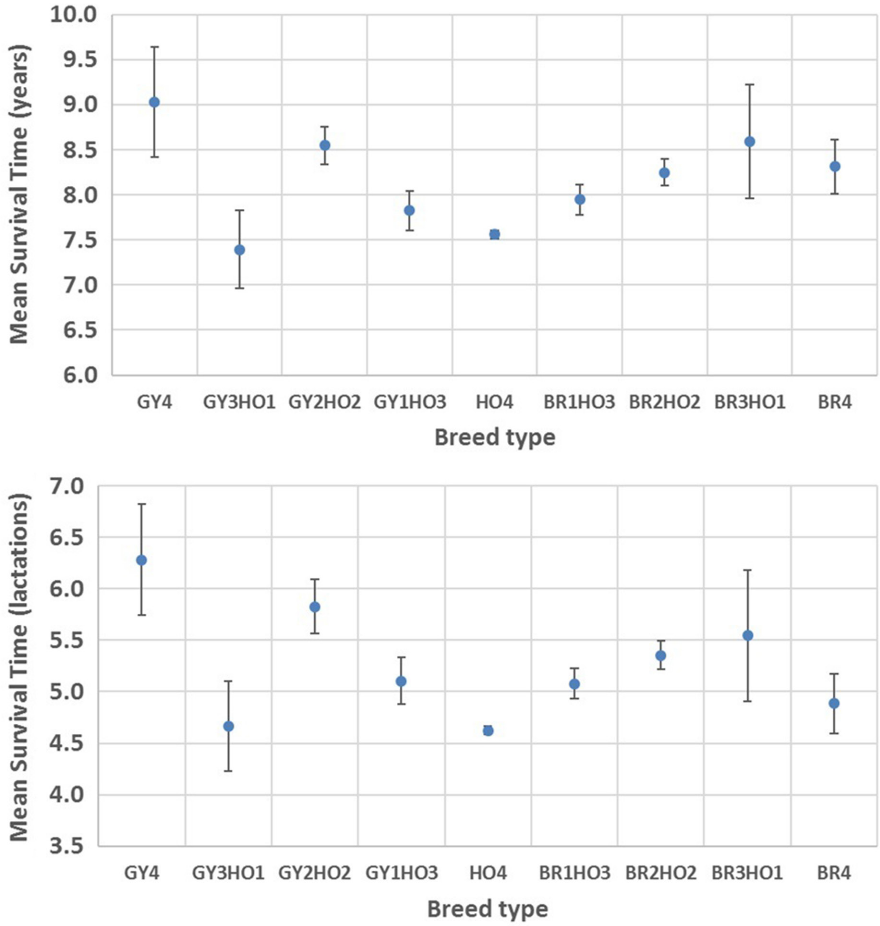

FIGURE 3 Mean survival time with 95% CI for age at culling (top panel) and predicted complete lactations (bottom panel) for purebred and crossbred cows from specialized dairy farms in the low and mid tropics of Costa Rica. Breed types: GY4 = purebred Gyr, GY3HO1 = ¾Gyr¼ Holstein, GY2HO2 = ½Gyr½Holstein, GY1HO3 = ¼Gyr¾Holstein, HO4 = purebred Holstein, BR1HO3 = ¼Brahman¾Holstein, BR2HO2 = ½Brahman½Holstein, BR3HO1 = ¾Brahman¼Holstein, BR4 = purebred Brahman.

crosses. At the same time, BR × HO showed a marked increase, in line with the proportion of the BR breed. Other studies have reported a decline in the performance of backcrosses as the Holstein fraction departed from 1/2 for categories higher and lower than the F1 (Quenon et al., 2020; Syrstad, 1989).

For days open, it was found that GY × HO crosses reduced their ability to become pregnant when they were closer to pure breed *Bos taurus*. A possible explanation is the interaction between milk production and environmental adaptation (Guanga et al., 2022). A similar pattern is observed in BR × HO animals, whereas in the purebred Brahman, longer DO was also seen. Effectively, there is ample information in the literature showing that Brahman cattle generally have long calving intervals (Cavani et al., 2015; Del Vecchio et al., 1988). Canaza-Cayo et al. (2018) found better reproductive performance in the genetic group 1/2HO:1/2GY, with a calving interval almost 1 month shorter than seen when applying different crossbreeding strategies. Similarly, the result from the present study points to the fact that days open increase with the proportion of Holstein in the genetic makeup. Our findings agree that DO benefits greatly from heterosis, which was above 15% in both cases, implying about 20 fewer days open in F1 cows compared to the parental average. Vieira et al. (2022) also reported a favourable, though much lower, heterosis effect for days open, with 6% (−9 days) and 10% (−13 days) for first and second lactation HO × GY cows, respectively.

Production traits show a marked breed effect and a reduced heterosis. There was a linear reduction in milk yield as the breed type approaches *Bos indicus* purebred animals. The same pattern is also apparent for lactation length. These results match those of Canaza-Cayo et al. (2018), demonstrating that crosses with a greater proportion of the Holstein breed had superior milk production. They also found higher milk yields in the genetic groups HO, 7/8HO, 3/4HO, and 1/2HO. Likewise, in a review, Castro and Marcondes (2022) highlighted that HO × GY cross produced less milk as the proportion of Holstein decreased. This trend, however, may vary according to the breed, management practices, and climatic conditions. An extensive review by Galukande et al. (2013), covering several crossbreeding studies in wet tropical climates, found that lactation milk yield and lactation length were, respectively, 2.4 and 1.2 times higher in 50% *Bos taurus* cattle than in the local stock.

Both crosses had low heterosis estimates for milk yield (<3%). F1 GY × HO was equivalent to 120 kg more milk per lactation than the parental average. A meta-analysis by Bunning et al. (2019) on 89 crossbreeding schemes using tropical cattle reported an average heterosis effect of 35% for production traits. Vieira et al. (2022) found a 20% heterosis for milk yield in F1 HO × GY, equivalent to 976 kg per lactation above the parental average. An important difference in their study was the lower production (<3000 kg) of the Gyr purebred. Our results were, on average, close to 3600 kg. The high production found in our research for *Bos indicus* breeds may

TABLE 4 Lifetime income over feed-cost (IOFC) average per cow for purebred Holstein (HO4) and crossbred Gyr×Holstein (GY2HO2) and Brahman×Holstein (BR2HO2) cows from specialized dairy farms in the low and mid tropics of Costa Rica.

Basal parameters		Units		Assumed value
Price per kg milk solids ($MSL)		USD		$6.05
Cost per kg concentrate ($CON)		USD		$0.67
Milk: Concentrate Ratio (MCRT) in lactation		Ratio		3.3
Concentrate per cow/day in dry period (CODD)		kg		2.0
Daily cost of other supplements ($SUP)[a]		USD		$1.56
Performance parameters (per breed)		***GY2HO2***	***HO4***	***BR2HO2***
Average days open (DO)	days	94	123	96
Average lactation length (LLEN)	days	298	324	291
Average dry period (DRYP)[b]	days	66	69	75
Average milk yield per lactation (TMP)	kg	4699	5002	4403
Average daily milk yield	kg	15.8	15.4	15.1
Average number of lactations (MST_lac)	*n*	5.83	4.63	5.35
Content of solids in milk (%MSL)	%	12.5	11.9	12.5
Lifetime performance (per breed)				
Lifetime milk production (LTMI)[c]	kg	27,395	23,159	23,556
Lifetime milk solids production (LTMS)[d]	kg	3424	2756	2945
Lifetime Income from milk sales (LTIN)[e]	USD	$20,718	$16,674	$17,814
Lifetime intake of concentrate (LTCO)[f]	kg	9068	7661	7946
Lifetime cost of concentrate ($LTCO)[g]	USD	$6075	$5133	$5324
Lifetime cost other supplements ($LTSU)[h]	USD	$3298	$2834	$3050
Lifetime $IOFC[i]	USD	$11,344	$8707	$9441

[a]This assumes an average daily dry matter intake of 16.5 kg (4.1–4.2 kg concentrate +1.47 kg by-products +1.51 kg forage +9.2–9.4 kg of pasture).
[b]DRYP = (DO +270)-LLEN.
[c]LTMI = TMP × MST_Lac.
[d]LTMS = LTMI×%MSL.
[e]LTIN = LTMS×$MSL.
[f]LTCO = LTMI/MCRT+MST_Lac×DRYP×CODD.
[g]$LTCO = LTCO×$CON.
[h]$LTSU = [MST_Lac× (LLEN+DRYP)] × $SUP.
[i]$IOFC = $LTIN-$LTCO-$LTSU.

be related to improved genetics for milk production in the lowland tropics. Another factor could be due to more favourable milk prices, permitting a greater use of concentrate in these systems.

Our results showed significant breed effects on longevity traits. The number of lactations at culling in the Holstein breed was lower than in hybrid animals, except for GY3HO1. These results indicate that Holstein is being culled much earlier than purebred Gyr, Brahman, and their Holstein crosses. The low number obtained for GY3HO1 could also be due to higher culling rates in predominantly *Bos indicus* cows. Crossbreeding studies on longevity or lifetime productivity are rare. One report on crossbreeding in tropical wet climatic zones by Galukande et al. (2013) found that crossbreds with 50% Bos taurus had a higher number of total lactations and lifetime milk yield than local breeds, which were mainly *Bos indicus*.

Our data also showed low and moderate heterosis effects for age at culling and the number of lactations. The higher heterosis obtained for MST_lac (>6%) results from the combination of lower AFC and DO for crossbred cattle compared to the parental average, indicating a more significant productive life. In contrast, a review by Bunning et al. (2019) estimated a 35% heterosis for longevity, although this was based solely on two studies and presented a large standard error (14%).

A simplified estimate of lifetime income over feed costs ($IOFC) was used to assess the aggregate economic benefit of crossbreeding combined over the six traits under analysis. Estimates of income over feed cost per average cow were 2637 USD (30.3%) higher in GY2HO2 and 734 USD (8.4%) in BR2HO2 compared to purebred Holstein. As explained previously, this difference is due mainly to an increase in productive lifetime. This suggests that crossbred animals, specifically those with Gyr and Brahman genetics, contribute to extending the productive lifespan and increasing economic returns.

Farmers face critical decision-making in choosing between purebred Holsteins, which yield rapid returns through significantly higher milk production, and hybrid animals, which exhibit a prolonged lifespan involving reduced milk production and replacement costs. The trade-off between quick returns and long-term sustainability becomes evident in our results, emphasizing the need for a sound approach to herd management and breeding strategies implemented at the farm level. The economic advantages observed in GY2HO2 and BR2HO2 challenge conventional wisdom's prioritization of maximum milk production. The extended mean survival times of crossbred animals represent an opportunity for farmers to optimize their herd composition by carefully considering both short-term and long-term economic and production goals. Decisions such as organizing a breeding programme with F1 animals have been known to be problematic but should be pondered. The estimated lifetime income over feed cost for GY2HO2 in our study supports, to some extent, the increased attention and promotion of this crossbred at the local and regional levels. In this sense, developing a breeding programme for the Girolando breed in Brazil (Silva et al., 2023) has been crucial for the relative success and dissemination of this breed type in Latin America.

Studies of this nature play a vital role in informing farmers about the possible advantages and disadvantages of using different management systems. The economic benefits associated with specific crossbreeding underscore the importance of considering not only immediate gains but also the long-term sustainability of the herd. As dairy farming practices continue to evolve, decision-making based on comprehensive studies remains essential for maximizing economic returns and ensuring the viability of dairy operations.

AUTHOR CONTRIBUTIONS

B. Vargas-Leitón: Database preparation, Formal analysis, Conceptualization, Writing – review and editing. J.J. Romero-Zúñiga: Database preparation, Formal analysis, Conceptualization, Writing – review and editing. J. Rojas: Database preparation, Writing – review and editing. C.S. Galina: Conceptualization, Writing – review and editing. J.F. Martínez: Conceptualization, Writing – review and editing, Funding. All authors have read and agreed to the published version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

None of the authors have any conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are available from the corresponding author upon reasonable request.

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