Estimation of genetic parameters for productive life, reproduction, and milk-production traits in US dairy goats

V. J. Castañeda-Bustos,* H. H. Montaldo,†¹ G. Torres-Hernández,* S. Pérez-Elizalde,* M. Valencia-Posadas,‡ O. Hernández-Mendo,* and L. Shepard§

*Colegio de Postgraduados, Campus Montecillo, Montecillo, Estado de México 56230, Mexico

†Departamento de Genética y Bioestadística, Facultad de Medicina Veterinaria y Zootecnia, Universidad Nacional Autónoma de México, Ciudad Universitaria, DF 04510, Mexico

‡División de Ciencias de la Vida, Campus Irapuato-Salamanca, Universidad de Guanajuato, Ex Hacienda El Copal, Irapuato, Guanajuato 36500, Mexico

§American Dairy Goat Association, Spindale, NC 28160

ABSTRACT

Heritabilities and correlations for milk yield (MY), fat yield (FY), protein yield (PY), combined fat and protein yield (FPY), fat percentage (F%), protein percentage (P%), age at first kidding (AFK), interval between the first and second kidding (KI), and real and functional productive life at 72 mo (FPL72) of 33,725 US dairy goats, were estimated using animal models. Productive life was defined as the total days in production until 72 mo of age (PL72) for goats having the opportunity to express the trait. Functional productive life was obtained by correcting PL72 for MY, FY, PY, and final type score (FS). Six selection indexes were used, including or excluding PL72, with 6 groups of different economic weights, to estimate the responses to selection considering MY, FY, PY, and PL72 as selection criteria. The main criteria that determined the culling of a goat from the herd were low FS, MY, and FY per lactation. Heritability estimates were 0.22, 0.17, 0.37, 0.37, 0.38, 0.39, 0.54, 0.64, 0.09, and 0.16 for PL72, FPL72, MY, FY, PY, FPY, F%, P%, KI, and AFK, respectively. Most genetic correlations between the evaluated traits and PL72 or FPL72 were positive, except for F% (−0.04 and −0.06, respectively), P% (−0.002 and −0.03, respectively), and AFK (−0.03 and −0.01, respectively). The highest genetic correlations were between FPL72 and MY (0.39) and between PL72 and MY (0.33). Most phenotypic correlations between the traits evaluated and FPL72 and PL72 were positive (>0.23 and >0.26, respectively), except for F% (−0.004 and −0.02, respectively), P% (−0.05 and −0.02), KI (−0.01 and −0.07), and AFK (−0.08 and −0.08). The direct selection for PL72 increased it by 102.28 d per generation. The use of MY, FY, PY, KI, or AFK as

selection criteria increased PL72 by 39.21, 27.33, 35.90, −8.28, or 2.77 d per generation, respectively. The inclusion of PL72 as selection criterion increased the expected response per generation from 0.15 to 17.35% in all selection indices studied.

Key words: productive life, heritability, genetic correlation, selection index

INTRODUCTION

Genetic evaluations for milk, fat, and protein yields in US goats have been calculated since 1983 in bucks and since 1984 in does. Genetic evaluations for these traits of US dairy goats have been calculated annually by the USDA Animal Improvement Programs Laboratory (Beltsville, MD) from records that are available through DHI programs and the American Dairy Goat Association (Spindale, NC; Wiggans and Hubbard, 2001).

For developing efficient selection programs, it is necessary to estimate genetic parameters (Weppert and Hayes, 2004). Some of the traits considered as potential selection criteria in dairy goats are milk, fat, and protein yields, type traits (Montaldo and Manfredi, 2002), reproductive traits (Torres-Vázquez et al., 2009; Montaldo et al., 2010), and longevity (Pérez-Razo et al., 2004). Longevity, despite being a little-studied trait not used so far in the genetic evaluation of goats, is of great economic importance, as it combines many traits associated with the permanence of an animal in the herd (Tsuruta et al., 2005). The increase in longevity allows a reduction in the number of replacement animals (Sewalem et al., 2007). It also allows a reduction in health care costs, especially those caused by mastitis (Rogers et al., 1998; Jensen et al., 1999), and an increase in the total milk production of the herd by increasing the proportion of mature animals with a greater production per lactation (Vollema et al., 2000).

Several definitions of longevity or productive life (PL) exist. Real PL is described in various ways, such

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¹Corresponding author: montaldo@unam.mx

as number of days from first calving to death or culling (VanRaden et al., 2006; Sewalem et al., 2007), total days in production (VanRaden and Klaaskate, 1993), stayability at different ages (Jakobsen et al., 2010) or at a specific number of calvings (Martinez et al., 2004), total months in production until a certain age (VanRaden et al., 2006), and number of lactations recorded (Pérez-Cabal et al., 2006). Functional PL (**FPL**) is defined as the ability to avoid involuntary culling caused by health or reproductive problems, and is obtained by including some covariates potentially used as voluntary culling criteria (e.g., milk, fat, and protein first-lactation production, and type traits) in the statistical models used to analyze PL (Dekkers, 1993; Mark, 2004).

Direct selection for longevity in the species used for milk production is not feasible, mainly because to obtain the information, the animal should be able to reach an advanced age or die, which would mean waiting too long and not being able to keep a herd with an age structure suitable for production or for selecting replacements. Trying to address this situation, several studies on cattle have been carried out to obtain early measures related to longevity, such as type traits (Martinez et al., 2004), functional traits, and milk-production traits (Tsuruta et al., 2005). Some of the countries that have used early measures as indirect predictors of longevity in cows are the United States (Short and Lawlor, 1992; Cruickshank et al., 2002), Canada (Sewalem et al., 2004, 2007), Japan (Hagiya et al., 2005), and Spain (Pérez et al., 1999).

Information about genetic parameters for longevity in goats and its relationship with milk production, reproductive, or conformation traits are scarce and limited to stayability estimates at a certain age or number of kiddings as a measure of PL (Pérez-Razo et al., 2004; Vicencio, 2009; Valencia-Posadas et al., 2010). Stayability merely indicates the presence or absence of the goat at a fixed age; therefore, it does not provide detailed quantitative information of the time during which a goat was productive. Thus, the aim of this study was to estimate the heritabilities and the genetic and phenotypic correlations between real PL and FPL at 72 mo, and milk-production and reproductive traits, using a quantitative definition of PL.

MATERIALS AND METHODS

Data

This study used data from the American Dairy Goat Association, processed by the USDA Animal Improvement Programs Laboratory, which contained information about milk (**MY**), fat (**FY**), and protein (**PY**) yields of Alpine, La Mancha, Nubian, Saanen, and

Toggenburg breeds. Yields were corrected to 305 d and mature equivalents. The records also included fat percentage (**F%**); protein percentage (**P%**); information of the sire, herd, birth, and kidding dates; and DIM production (15 to 305 d).

To estimate the parameters more precisely, we only used records from goats with consecutive information for ≥ 1 lactation, with a maximum of 10 lactations, and which remained in the same herd in all lactations. Records with information errors about date of birth and date of kidding were eliminated; herds with < 5 observations or < 2 breeds were also eliminated. The records containing information on FY but not on PY, or vice versa, were considered as missing observations. The final data file contained information on MY, FY, and PY of the first lactation for 33,725 goats born from 9,716 sires and 24,474 dams. Data of individuals without breed or identification information were eliminated from the original pedigree data set. The pedigree was subsequently ordered generationally and recoded using the software Pedigree Viewer 6.3 (Kinghorn and Kinghorn, 2009); the final file contained the complete information of 209,530 individuals from the breeds analyzed.

We calculated the age of the animals as the difference between the last date of kidding and the date of birth plus the last days in production recorded; we also calculated the age at first kidding (**AFK**), the interval between the first and second kidding (**KI**), and the PL at 48, 60, and 72 mo (**PL48**, **PL60**, and **PL72**, respectively), using the same criteria used for the genetic evaluation of longevity in dairy cows in the United States (VanRaden and Klaaskate, 1993); PL was obtained using information from the first to the tenth lactation. Records with KI < 168 or > 885 d (236 animals), and AFK < 271 or $> 1,140$ d (479 animals) were considered missing.

Productive life was defined as the total number of days in production recorded (VanRaden and Klaaskate, 1993) until the goat was 48, 60, and 72 mo of age. If the goat did not stay in the herd or did not have the opportunity to complete each period, data was considered as censored and was not included in the analysis. To obtain PL, we first determined if the animal had the opportunity to stay in the herd at 3 different ages (48, 60, and 72 mo), depending on the period of recording of the herd to which it belonged. This was calculated as last registration of the herd — date of birth ≥ 48 , 60, or 72 mo.

If the goat did not have the opportunity to stay in the herd at 48, 60, or 72 mo, the PL was defined as a missing value and was not included in the file for analysis. If the goat had the opportunity to stay in the herd, its PL was the sum of the DIM production

recorded (with a maximum of 305 d per lactation) until the corresponding age (48, 60, or 72 mo). Functional productive life at 48, 60, and 72 mo (**FPL72**) was PL corrected for milk-production traits (MY, FY, and PY) and final type score (**FS**).

In this study, we analyzed 10 traits: MY, FY, PY, combined fat and protein yield (**FPY**), F%, P%, KI, AFK, PL72, and FPL72.

Model

Four kidding seasons (**KS**) were defined: January to February ($n = 10,403$), March ($n = 9,308$), April ($n = 9,569$), and May to December ($n = 11,273$); and 4 birth seasons (**BS**): March ($n = 11,272$), April ($n = 12,090$), May to July ($n = 8,096$), and August to February ($n = 9,095$), to find a balance in the number of observations, given that, due to the reproductive seasonality of this species, kiddings and births were concentrated in certain months of the year, and due to distributions of kiddings and births being different, grouping of months for kidding season and birth season were very different between them. Twenty levels of BS-breed (**BSB**) and KS-breed (**KSB**) were obtained by combining KS or BS with breed (Alpine, La Mancha, Nubian, Saanen, and Toggenburg).

The traits were initially analyzed with single-trait animal models to estimate the phenotypic, additive genetic, and residual variances, using ASReml 3.0 software (Gilmour et al., 2009). The matrix representation of the model (Mrode, 2005) is

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{u} + \mathbf{e},$$

where $\mathbf{y}$ is the vector of observations of the traits studied; $\mathbf{X}$ is the incidence matrix of fixed effects for KSB or BSB; $\mathbf{b}$ is the vector of fixed effects of KSB or BSB; $\mathbf{Z}$ is the incidence matrix of the random effects of additive genetic effects of the animal, herd-year of kidding-breed (**HYKB**), or herd-year of birth-breed (**HYBB**) effects, and herd-sire (**HS**) effect; $\mathbf{u}$ is the vector of random effects of the additive genetic effects of the animal, HYKB, or HYBB and HS; and $\mathbf{e}$ is the vector of random error. Convergence of the analyses was assumed when the change in the restricted likelihood function was less than 0.002 and the change in the parameter estimates was less than 1% (Gilmour et al., 2009).

Considering that when the group subclass sizes are small, as in the current case, much information can be lost and, as a result, the compromise between accounting for bias and reducing prediction error variances should be found (Van Bebber et al., 1997). The HYKB and HYBB effects were considered as random

to avoid these losses (Chauhan, 1987). In the model used to obtain the genetic parameters for production traits (MY, FY, PY, FPY, F%, and P%) and KI, the effects considered were HYKB as random and KSB as fixed, whereas HYBB and BSB were fitted as random and fixed effect, respectively, for the AFK and PL. The effect of KSB was considered for production traits and KI because KS and breed modifies these traits, whereas BS and breed modifies AFK and PL. In the final data file ($n = 33,725$), only the levels with ≥ 5 observations for HYBB and HYKB were included, leaving, at the end of the edition, 3,255 and 1,809 levels, respectively. The random effect of HS was included in the models for all the traits analyzed.

Milk-production traits (MY, FY, and PY) and FS were included as covariates in the analysis models (Sewalem et al., 2004) to obtain estimates of genetic parameters of FPL at 48, 60, or 72 mo, and were excluded in the analysis models for PL48, PL60, and PL72. Regression coefficients for MY, PY, PY, and FS were obtained to know which factors were important for culling decisions in goats.

Genetic Parameters

Variance components and heritability were obtained using a single-trait animal model, whereas genetic ($\mathbf{r}_g$) and phenotypic ($\mathbf{r}_p$) correlations were obtained using bivariate analyses.

Heritability. For calculating the heritability within herd-breed, the total variance and the phenotypic variance were estimated as follows:

Total variance:

$$\hat{\sigma}_t^2 = \hat{\sigma}_a^2 + \hat{\sigma}_{\text{HYB}}^2 + \hat{\sigma}_{\text{HS}}^2 + \hat{\sigma}_e^2,$$

where $\hat{\sigma}_t^2$ = estimated total variance; $\hat{\sigma}_a^2$ = estimated additive genetic variance of the animal; $\hat{\sigma}_{\text{HYB}}^2$ = estimated HYKB or HYBB variance, according to the trait; $\hat{\sigma}_{\text{HS}}^2$ = estimated variance of the HS effect; and $\hat{\sigma}_e^2$ = estimated error variance.

Phenotypic variance:

$$\hat{\sigma}_p^2 = \hat{\sigma}_a^2 + \hat{\sigma}_{\text{HS}}^2 + \hat{\sigma}_e^2,$$

where $\hat{\sigma}_p^2$ = estimated phenotypic variance.

Having determined the variances (total and phenotypic), the heritability ($\hat{h}^2$) was estimated as follows:

$$\hat{h}^2 = \frac{\hat{\sigma}_a^2}{\hat{\sigma}_p^2}.$$

The ratio of $\hat{\sigma}_{\text{HYB}}^2$ with respect to $\hat{\sigma}_t^2$ (herd-year-breed ratio, **HYBR**) was calculated as follows:

$$\text{HYBR} = \frac{\hat{\sigma}_{\text{HYB}}^2}{\hat{\sigma}_t^2},$$

using variances obtained with a single-trait animal model to estimate the contribution of this effect. To estimate the contribution of the HS effect, we calculated the ratio of $\hat{\sigma}_{\text{HS}}^2$ with respect to $\hat{\sigma}_t^2$ (herd-sire ratio, **HSR**):

$$\text{HSR} = \frac{\hat{\sigma}_{\text{HS}}^2}{\hat{\sigma}_t^2},$$

using variances obtained using a single-trait animal model.

Genetic and Phenotypic Correlations. The bivariate analyses used to obtain r_g and r_p (Mrode, 2005) included the same effects included in the univariate models mentioned above. The analysis was performed using the software ASReml 3.0 (Gilmour et al., 2009). To test whether r_g and r_p were different from zero, we estimated their confidence intervals with a significance level of 95% using the software package for R psychometric (Fletcher, 2010).

Response to Selection

To estimate the responses to selection considering MY, FY, PY, and PL72 as selection criteria, we used 6 selection indices that included or excluded PL72. For the selection, we evaluated 6 groups with different relative economic weight. The economic weights for MY, FY, and PY were 0.01, 1.15, and 2.55, respectively (Wiggans and Hubbard, 2001), and remained the same in the 6 indices, whereas PL was assigned a different economic weight in each index (0.01, 0.03, 0.05, 0.07, 0.09, and 0.1), derived from the ratio of PL with respect to PY (0.02) used in cattle (Cole and VanRaden, 2010), to explore a range of values that could probably cover a relative value appropriate for goats. The responses to selection per generation were obtained from the average

of the results of the expected responses per generation in the selection indices for females and males, and assuming a selection intensity of 1.

In the case of the selection of females, it was assumed that a record existed for each one and 20 records of half-sisters. For males, 20 records of half-sisters and 10 records of daughters were assumed. In addition, it was assumed that 1 record of the dam existed for both sexes. The expected response to selection for each index was estimated using MTINDEX software (Van der Werf, 2007).

RESULTS

The descriptive statistics for the traits evaluated (PL72, MY, FY, PY, FPY, F%, P%, KI, and AFK) are shown in Table 1. The PL72 ranged from 32 to 1,560 d, with an average of 579.4 d. The averages (SD within parentheses) for milk-production traits were 1,043.1 (336.36), 37.1 (10.84), 30.5 (7.59), and 67.6 kg (17.70 kg). The averages for F% and P% were 3.8 (0.87) and 3.1% (0.47%), respectively.

With respect to the reproductive traits evaluated, the average (SD in parentheses) KI was 387.3 d (101.52 d) and the average AFK was 507.97 d (153.50 d). In the analysis model for FPL72, all regression coefficients of MY, PY, FY, and FS on PL72 were positive (66.12 ± 3.48 , 3.40 ± 6.61 , 20.44 ± 6.49 , and 3.06 ± 0.07 , respectively), and most of the covariates included (MY, FY, and FS) were significant ($P < 0.01$), except for PY ($P = 0.60$), showing that the probability that a goat is voluntarily culled from a herd increases when its MY, FY, or FS are low.

Genetic Parameters

The variances (total, phenotypic, and additive genetic), HYBR, HSR, and the estimates of heritability for the evaluated traits are shown in Table 2. The estimates of heritability were 0.22 ± 0.01 and 0.17 ± 0.01 for PL72 and FPL72, respectively. Milk-production and -composition traits had estimates of heritability of 0.37,

Table 1. Descriptive statistics for the traits analyzed in US goats

Trait	Abbreviation	n	Mean	SD	Minimum	Maximum	CV, %
Productive life at 72 mo, d	PL72	21,811	579.45	364.78	32.03	1,560.99	62.95
Milk yield, ¹ kg	MY	33,725	1,043.11	336.36	88.90	2,948.34	32.25
Fat yield, ¹ kg	FY	23,770	37.10	10.84	4.99	107.95	29.22
Protein yield, ¹ kg	PY	23,770	30.54	7.59	6.35	44.91	24.85
Combined fat and protein yield, ¹ kg	FPY	23,770	67.63	17.70	13.61	151.50	26.17
Fat percentage	F%	23,770	3.87	0.87	0.72	8.85	22.48
Protein percentage	P%	23,770	3.18	0.47	0.76	6.31	14.93
Kidding interval, d	KI	19,528	387.36	101.52	168.00	885.00	26.21
Age at first kidding, d	AFK	31,451	507.97	153.50	271.00	1,140.00	30.22

¹Yields corrected to 305 d and mature equivalent.

0.37, 0.38, 0.39, 0.54, and 0.64 for MY, FY, PY, FPY, F%, and P%, respectively. The estimates of heritability for KI and AFK were 0.09 ± 0.02 and 0.16 ± 0.01 , respectively. The highest variances of HSR with respect to total variance was for AFK (0.10). The variances of HSR were 0.04 for PL72, MY, PY, FPY, and F%, 0.05 for FPL72 and FY, 0.01 for P% and KI, and 0.10 for AFK. The highest variances of HYBR were for PY and FPY (0.44) and represented ratios, with respect to the total variance, of 0.07, 0.14, 0.40, 0.37, 0.44, 0.29, 0.19, 0.15, and 0.35 for PL72, FPL72, MY, FY, PY, FPY, F%, P%, KI, and AFK, respectively.

Genetic and Phenotypic Correlations

Preliminary analyses showed that PL72 had high r_g , with PL48 (0.96 ± 0.007) and PL60 (0.99 ± 0.001), indicating that similar results would be obtained with any of them from the viewpoint of selection. Considering that, by definition, PL72 is calculated at a higher age, it might better reflect the longevity of the goats, plus PL72 had higher heritability than PL48 and PL60 (0.22 compared with a value of 0.17 for PL48 and PL60), which is why, in this study, we decided to use only PL72. The r_g and r_p estimated between PL (PL72 and FPL72) and the reproductive and milk-production traits are shown in Table 3.

The r_g between PL72 and the milk-production and -composition traits were 0.33, 0.23, 0.30, 0.27, -0.04 , and -0.002 for MY, FY, PY, FPY, F%, and P%, respectively. The r_g between KI and PL72 was 0.11, and -0.03 between PL72 and AFK. The r_g between PL72 and production traits (MY, FY, PY, and FPY) and between PL72 and KI were significant ($P < 0.05$); similarly, the r_g between PL72 and F% and AFK were significant ($P < 0.05$), although, similar to the r_g between PL72 and P%, they were close to zero.

The r_p between milk-production traits and PL72 were 0.25, 0.23, 0.25, and 0.25 for MY, FY, PY, and FPY, respectively, and, similar to the r_g , all these r_p were significant ($P < 0.05$). The r_p between PL72 and F% and P% were -0.004 and -0.05 , respectively, whereas the r_p between PL72 and KI and AFK were -0.01 and -0.08 , respectively. Out of these, only the r_p between PL72 and P% and AFK were significant ($P < 0.05$).

The r_g between FPL72 and MY, FY, PY, and FPY were 0.39, 0.26, 0.29, and 0.28, respectively. The r_g of the milk-production traits with FPL72, similar to the r_g between KI and FPL72 (0.05), were all positive and significant ($P < 0.05$). On the other hand, the r_g between FPL72 and F%, P%, and AFK were negative and close to zero (-0.06 , -0.03 , and -0.01 , respectively), but significant ($P < 0.05$), except for the r_g between FPL72 and AFK.

Table 2. Total, phenotypic, and additive genetic variances, and heritabilities for the studied traits in US goats

Trait	$\hat{\sigma}_t^2$ ¹	$\hat{\sigma}_p^2$ ²	$\hat{\sigma}_a^2$	HYB ratio (HYBR) ³	$\hat{h}^2$ ⁴	HS ratio (HSR) ⁵
Productive life at 72 mo, d	130,710 $\pm$ 1,405.90	121,030 $\pm$ 1,305.80	27,505 $\pm$ 2,077.70	0.07 $\pm$ 0.007	0.22 $\pm$ 0.01	0.04 $\pm$ 0.008
Functional productive life at 72 mo, d	122,770 $\pm$ 1,460.00	104,980 $\pm$ 1,138.60	18,536 $\pm$ 1,803.90	0.14 $\pm$ 0.008	0.17 $\pm$ 0.01	0.05 $\pm$ 0.009
Milk yield, kg	98,654 $\pm$ 1,241.7	58,847 $\pm$ 557.55	22,108 $\pm$ 1,038.3	0.40 $\pm$ 0.007	0.37 $\pm$ 0.02	0.04 $\pm$ 0.007
Fat yield, kg	123,75 $\pm$ 1.55	77.43 $\pm$ 0.78	28.54 $\pm$ 1.52	0.37 $\pm$ 0.008	0.37 $\pm$ 0.02	0.05 $\pm$ 0.008
Protein yield, kg	86.55 $\pm$ 1.18	48.29 $\pm$ 0.48	18.52 $\pm$ 0.90	0.44 $\pm$ 0.008	0.38 $\pm$ 0.02	0.04 $\pm$ 0.008
Combined fat and protein yield, kg	456.01 $\pm$ 6.28	256.30 $\pm$ 2.63	100.76 $\pm$ 4.87	0.44 $\pm$ 0.008	0.39 $\pm$ 0.02	0.04 $\pm$ 0.008
Fat percentage	0.38 $\pm$ 0.004	0.26 $\pm$ 0.002	0.14 $\pm$ 0.005	0.29 $\pm$ 0.008	0.54 $\pm$ 0.02	0.04 $\pm$ 0.008
Protein percentage	0.11 $\pm$ 0.001	0.08 $\pm$ 0.001	0.05 $\pm$ 0.001	0.19 $\pm$ 0.008	0.64 $\pm$ 0.02	0.01 $\pm$ 0.008
Kidding interval, d	9,600.8 $\pm$ 105.99	8,179.7 $\pm$ 93.37	790.06 $\pm$ 147.60	0.15 $\pm$ 0.007	0.09 $\pm$ 0.02	0.01 $\pm$ 0.008
Age at first kidding, d	22,764 $\pm$ 276.74	14,851 $\pm$ 148.00	2,447.9 $\pm$ 250.30	0.35 $\pm$ 0.008	0.16 $\pm$ 0.01	0.10 $\pm$ 0.009

¹Total variance ($\hat{\sigma}_t^2$) = variance of HYB + additive genetic variance ($\hat{\sigma}_a^2$) + variance of herd-sire (HS) effect + residual variance (where HYB = herd-year of kidding-breed for milk yield, fat yield, protein yield, combined fat and protein yield, fat percentage, protein percentage and kidding interval; HYB = herd-year of birth-breed for productive life at 72 mo, functional productive life at 72 mo, and age at first kidding).

²Phenotypic variance ($\hat{\sigma}_p^2$) = $\hat{\sigma}_a^2$ + variance of HS effect + residual variance.

³Ratio of the variance of the HYB effect with respect to total variance (i.e., HYBR = variance of HYB/ $\hat{\sigma}_t^2$).

⁴Heritability ($\hat{h}^2$) = $\hat{\sigma}_a^2/\hat{\sigma}_p^2$.

⁵HSR = variance of HS/ $\hat{\sigma}_t^2$.

Table 3. Genetic and phenotypic correlations ($\pm$ SE) between production and reproductive traits with productive life and functional productive life at 72 mo in US goats

Trait ¹	Genetic correlation		Phenotypic correlation	
	PL72 ²	FPL72 ³	PL72	FPL72
MY	0.33 $\pm$ 0.04	0.39 $\pm$ 0.04	0.25 $\pm$ 0.008	0.29 $\pm$ 0.009
FY	0.23 $\pm$ 0.05	0.26 $\pm$ 0.05	0.23 $\pm$ 0.009	0.26 $\pm$ 0.01
PY	0.30 $\pm$ 0.05	0.29 $\pm$ 0.06	0.25 $\pm$ 0.009	0.29 $\pm$ 0.01
FPY	0.27 $\pm$ 0.05	0.28 $\pm$ 0.05	0.25 $\pm$ 0.009	0.29 $\pm$ 0.01
F%	-0.04 $\pm$ 0.04	-0.06 $\pm$ 0.05	-0.004 $\pm$ 0.01	-0.02 $\pm$ 0.01
P%	-0.002 $\pm$ 0.04	-0.03 $\pm$ 0.04	-0.05 $\pm$ 0.01	-0.02 $\pm$ 0.01
KI	0.11 $\pm$ 0.08	0.05 $\pm$ 0.09	-0.01 $\pm$ 0.01	-0.07 $\pm$ 0.01
AFK	-0.03 $\pm$ 0.06	-0.01 $\pm$ 0.07	-0.08 $\pm$ 0.008	-0.08 $\pm$ 0.009

¹MY = milk yield; FY = fat yield; PY = protein yield; FPY = combined fat and protein yield; F% = fat percentage; P% = protein percentage; KI = kidding interval; AFK = age at first kidding.

²PL72 = productive life at 72 mo.

³FPL72 = functional productive life at 72 mo.

As in the case of PL72, both the r_g and the r_p between the milk-production traits and FPL72 were all positive and significant ($P < 0.05$), with slightly higher values than those found in the r_p between the same traits and PL72. The r_p obtained were 0.29, 0.26, 0.29, and 0.29 between FPL72 and MY, FY, PY, and FPY, respectively. The r_p between FPL72 and milk components (F% and P%) were -0.02 in both cases and were not significant, whereas the r_p between KI and FPL72 (-0.07) and between AFK and FPL72 (-0.08) were significant ($P < 0.05$) in both cases (Table 3).

Response to Selection

The increase in PL72 per generation, selecting directly for this trait, was 102.28 d (Table 4), considering this value as 100% of the increase in PL72 by selection; the selection for the increase in MY, FY, PY, KI, or AFK achieved an increase in PL72 per generation of 39.21 d (38.33%), 27.33 d (26.72%), 35.90 d (35.10%),

-8.28 d (-8.10%), or 2.77 d (2.70%), respectively. The inclusion of PL72 as a selection criterion increased from 0.15 to 17.35% the expected response per generation in all selection indices studied (Table 5).

DISCUSSION

During the life of a goat and other species (i.e., dairy cows), the risk always exists that the animal is rejected for not meeting the requirements of the herd to which it belongs. According to the regression coefficients obtained from the model for the analysis of FPL72 (66.12 ± 3.48 , 20.44 ± 6.49 , and 3.06 ± 0.07 for MY, FY, and FS, respectively), if a goat has higher MY, FY, and FS, it will be at less risk of being culled from the herd. The importance of PY as culling criterion in cows (Sewalem et al., 2004) was not evident in this study, probably because, having a high correlation with MY (>0.90 ; Torres-Vázquez et al., 2009), it provides similar information in the model.

Table 4. Responses to selection for productive life at 72 mo in US goats

Selection type	Response to selection per generation, ¹ d			Increase in productive life, ² %
	Females	Males	Total ³	
Direct	95.19	109.37	102.28	100
Indirect ⁴				
MY	37.47	40.95	39.21	38.33
FY	26.12	28.54	27.33	26.72
PY	34.37	37.44	35.90	35.10
KI	-7.50	-9.07	-8.28	-8.10
AFK	2.55	2.99	2.77	2.70

¹Assuming 1 record for each goat, 1 record of the dam, and 20 records of half-sisters for selection of females; and 1 record of the dam, 20 records of half-sisters, and 10 records of daughters for the selection of males.

²Considering direct selection as 100% of the response to selection.

³Average response to selection of both sexes, assuming selection intensity = 1.

⁴Selecting to increase milk yield (MY), fat yield (FY), or protein yield (PY), or to decrease age at first kidding (AFK) or kidding interval (KI).

Table 5. Expected economic selection response¹ for some of the traits evaluated using different economic weights for real productive life in US goats

W_{PL} ²	Selection criterion ³	Selection response per generation, \$			Increase in selection response, ⁴ %
		Females ⁵	Males ⁶	Total ⁷	
0.01	With PL	12.62	13.79	13.20	0.15
	Without PL	12.60	13.76	13.18	
0.03	With PL	13.49	14.78	14.13	1.80
	Without PL	13.27	14.49	13.88	
0.05 ⁸	With PL	14.57	16.02	15.29	4.80
	Without PL	13.95	15.24	14.59	
0.07	With PL	15.81	17.45	16.63	8.62
	Without PL	14.63	15.99	15.31	
0.09	With PL	17.18	19.02	18.10	12.84
	Without PL	15.33	16.75	16.04	
0.11	With PL	18.65	20.71	19.68	17.35
	Without PL	16.03	17.52	16.77	

¹Response to selection for relative economic weights of milk yield, fat yield, protein yield, and productive life (PL) at 72 mo of 0.01, 1.15, 2.55, and weighted PL (W_{PL}), respectively.

²Relative economic weights assigned to PL in the selection index.

³Using or without using records for PL in the selection of females and males.

⁴Percentage increase in the response due to PL information in the selection index.

⁵Assuming 1 record of each animal, 1 record of the dam, and 20 records of half-sisters.

⁶Assuming 1 record of the dam, 20 records of half-sisters, and 10 records of daughters.

⁷Average genetic gain of both sexes (monetary units), assuming selection intensity = 1.

⁸Basal economic weight (Cole and VanRaden, 2010).

The averages of MY, FY, PY, and FPY, and their components (F% and P%) were within the range of values obtained in the same population (García-Peniche et al., 2012) and in Saanen goats in Mexico (Torres-Vázquez et al., 2009) for MY (1,026 to 1,095 kg), FY (33.5 to 38 kg), PY (28.05 to 32 kg), FPY (62.5 to 70 kg), F% (3.24 to 3.70%), and P% (2.72 to 3.10%). However, they were higher than those found by other authors for MY (683 to 1,008 kg), FY (24.05 to 30 kg), PY (25.3 to 30.75 kg), F% (3.16 to 3.52%), and P% (2.65 to 3.07%) in Alpine, Saanen, and Toggenburg goats in Mexico (Valencia Posadas et al., 2007a) and France (Rupp et al., 2011).

The KI average (387 d) was similar to that obtained in Alpine (384 d; García-Peniche et al., 2012), La Mancha, Nubian, Saanen, Toggenburg (379 d; Montaldo et al. 2010), and Oberhasli (369 d; García-Peniche et al., 2012) goats from the same population, but higher than the one obtained in Toggenburg goats raised in small production systems (287.91 d; Ahuya et al. 2009), and in Taggar (242.60 to 288.94 d; Bushara et al., 2010), Beetal, Beetal × Alpine, Beetal × Saanen (300–323 d; Shrestha and Fahmy, 2007), and Norwegian (367.4 d; Bagnicka et al., 2007) goats in countries such as Kenya, Sudan, Norway, and India.

The average AFK (507.97 d) coincided with that obtained in similar breeds (505.99 to 507 d; Torres-Vázquez et al., 2009; García-Peniche et al., 2012) and in Alpine × Beetal goats (495 d; Shrestha and Fahmy, 2007). Moreover, the average AFK found in the current

study was higher than the one mentioned for Norwegian goats (412.9 d; Bagnicka et al., 2007) and lower than that for Toggenburg goats (759.37 d; Ahuya et al. 2009).

The differences between the means obtained in the present study with respect to higher or lower means obtained by other authors for KI and AFK, are mainly attributed to differences in reproductive seasonality between the breeds and regions of the world (Montaldo et al., 2010) as well as to differences in management.

Genetic Parameters

Great variability exists in the literature with respect to the estimates of heritability of milk-production traits in goats (MY, FY, PY, and FPY), their components (F% and P%) and their reproductive traits (KI and AFK) due to estimation errors associated with the sample size, structure of the data, breed used, management conditions, and estimation methodology used (Moioli et al., 2007). In addition, it was observed in the present study that the HSR contributes significantly to the total variance of AFK, whereas HYBR makes a large contribution in the total variance of most of the traits evaluated; the largest contributions of HYBR were observed in the total variance of MY, FY, PY, FPY, and AFK, which is why both HYBR and HSR must be considered in the statistical models for estimating heritability.

Estimates of heritability for MY, FY, PY, and FPY (0.37 ± 0.02 , 0.37 ± 0.02 , 0.38 ± 0.02 , and 0.39 ± 0.02 , respectively) were within the range of the estimated values in other populations of dairy goats for MY (0.17 to 0.41; Valencia et al., 2007; Torres-Vázquez et al., 2009; Montaldo et al., 2010) and FY (0.19 to 0.40; Barillet, 2007; Leboeuf et al., 2008; Torres-Vázquez et al., 2009) as well as for PY (0.04 to 0.37) and FPY (0.16 to 0.36) in other populations (Valencia Posadas et al., 2007b) or in the same population (Torrero, 2010; García-Peniche et al., 2012) of dairy goats. Similarly, estimates of heritability for F% (0.54 ± 0.02) and P% (0.64 ± 0.02) were within the estimates for F% (0.26 to 0.62; Valencia Posadas et al., 2007b; Rupp et al., 2011) and P% (0.14 to 0.67; Moiola et al., 2007; Rupp et al., 2011) in other populations of dairy goats. The estimates of heritability obtained in the current study confirm the feasibility of improving the MY, FY, PY, FPY, F%, and P% of dairy goats by selection (Montaldo et al., 2010; García-Peniche et al., 2012).

The estimated heritability for KI (0.09 ± 0.02) was within the range of estimates of heritability for the same population of dairy goats (0 to 0.15 ± 0.006 to 0.09; Montaldo et al., 2010; García-Peniche et al., 2012). The estimated heritability of AFK (0.16 ± 0.01) was below the estimates in the same population (0.23 ± 0.01 ; García-Peniche et al., 2012) and in another dairy goat population (0.31 ± 0.09 ; Torres-Vázquez et al., 2009). Probably, the difference is due to the inclusion of the HS effect in the analysis models. Despite this, the heritability estimate obtained for AFK confirms that selection is a viable option for modifying this trait in dairy goats.

Compared with other species, the longevity of goats is a trait that is not commonly evaluated, which limits the information about PL to a single study by Torrero (2010) in goats of the same population. That study obtained a lower heritability estimate for stayability until the second lactation (0.13 ± 0.01) than the one obtained in the present study for PL72 (0.22 ± 0.01), and although the measurements used to describe the PL life in both studies are different, both estimates of heritability can be used as future references in the development of new selection indices for increasing the longevity of goats.

The estimated heritability for PL72 was also higher than the estimates for dairy cows, using the same definition of PL as in the present study (0.08; VanRaden and Klaaskate, 1993; USDA, 2007), or using other definitions of PL, such as time from first calving to culling (0.10 to 0.18; Caraviello et al., 2004; Tsuruta et al., 2005), stayability at different ages (0.001 to 0.15 ± 0.01 to 0.03; Martinez et al., 2004; Valencia Posadas et al., 2008), months in production until a certain age (0.01 to

0.07; VanRaden et al., 2006), and number of recorded lactations (0.10 ± 0.007 ; Pérez-Cabal et al., 2006). Similarly, the estimates of heritability for longevity found in other species were lower, as in the case of the estimates for longevity in sows (0.05 to 0.10; Serenius and Stalder, 2004; Fernández de Sevilla et al., 2008), and rabbits (0.15; Piles et al., 2006), and the estimates for longevity (0.02 to 0.06 ± 0.01 to 0.02; El-Saied et al., 2005) or stayability at different ages (0 to 0.13 ± 0.05 ; Hatcher et al., 2010) in sheep.

The estimated heritability of FPL72 obtained in this study (0.17 ± 0.01) was higher than what was estimated in sheep, for which FPL was defined as the months elapsed from one lactation to the next or to culling, corrected for milk production (0.11 ± 0.025 ; Riggio et al., 2009); it was slightly higher than the upper limit of the range obtained in dairy cows (0.06 to 0.14), for which FPL was defined as the days after the first calving to culling (0.06 to 0.14 ± 0.01 ; Sewalem et al., 2005; Samoré et al., 2010), or the number of lactations (0.10; Pérez-Cabal et al., 2006) corrected for milk production.

Although in most PL definitions used throughout time, some authors (i.e., VanRaden and Klaaskate, 1993; Serenius and Stalder, 2004; El-Saied et al., 2005) obtained low estimates of heritability of PL (real and functional) in sheep, rabbits, sows, and in some studies of dairy cows of different countries (i.e., Denmark, Canada, and the United States), the estimates of heritability obtained in the current study indicate that the response to selection for PL can be relatively higher in dairy goats than in the other species mentioned above, and that it is convenient to include PL as an additional criterion in selection indices to improve the genetic progress for longevity in goats.

The standard errors of heritability estimates in this study for milk-production and milk-components (0.02) traits, as for reproduction (0.01 to 0.02) and PL (0.01) traits, were within the range of the estimated values in the studies mentioned above for milk-production (0.001 to 0.07), milk-components (0.009 to 0.02), reproduction (0.006 to 0.09), and PL (0.007 to 0.07) traits, indicating that our estimation of parameters is reasonably accurate.

Genetic Correlations

In goats, the r_g estimated by Torrero (2010) between stayability until the second lactation and MY (0.12 ± 0.05), FY (0.44 ± 0.05), PY (0.53 ± 0.05), and FPY (0.52 ± 0.05) are the only references with respect to the estimation of r_g between PL and milk-production traits (MY, FY, PY, and FPY) in goats, and although the definition of the variable used as a measure of PL is not the same as the one used in the current study, it would

be risky to say that one or the other is more valuable for the development of this subject. Both the r_g found by Torrero (2010) and the ones obtained in the current study were positive and significant, indicating that it is possible to select indirectly for an increase in PL by selecting for milk-production traits in dairy goats.

The r_g estimated between PL72 and MY (0.33 ± 0.04) was higher than the r_g estimated in dairy cows (0.14 to 0.26; Cruickshank et al. 2002; Tsuruta et al., 2004). The r_g estimated between PL72 and FY (0.23 ± 0.05), and between PL72 and PY (0.30 ± 0.05), were within the ranges of the r_g estimated in dairy cows between PL and FY (0.08 to 0.32; Cruickshank et al. 2002; Tsuruta et al., 2005), and between PL and PY (0.22 to 0.35; Cruickshank et al. 2002; Tsuruta et al., 2004). With respect to the milk components, the r_g estimated between PL72 and F% (-0.04 ± 0.04), and between PL72 and P% (-0.002 ± 0.04), were similar to the r_g estimated in dairy cows between PL and F% (-0.08 ; Kaupé et al., 2007) and between PL and P% (0.01; Kaupé et al., 2007).

The r_g estimated between FPL72 and MY (0.39 ± 0.04) was higher than that obtained in cattle (0.22; Cruickshank et al., 2002), whereas the r_g estimated between FPL72 and FY (0.26 ± 0.05), and between FPL72 and PY (0.29 ± 0.06) were similar to those obtained in cattle between FPL and FY (0.25; Cruickshank et al., 2002) and between FPL and PY (0.25; Cruickshank et al., 2002). The r_g found between FPL72 and F% (-0.06 ± 0.05), and between FPL72 and P% (-0.03 ± 0.04), proved to be lower than the r_g obtained between FPL and F% (0.10 ± 0.11 ; Samoré et al., 2010) and between FPL and P% (0.09 ± 0.11 ; Samoré et al., 2010) in dairy cows.

The r_g between KI and PL72 (0.11 ± 0.08) estimated in the current study was significantly different from the values obtained in sows (-0.34 to -0.36 ; Serenius and Stalder, 2004), but similar to the r_g estimated in Holstein cattle (0.09; Pérez-Cabal and Alenda, 2003). The r_g between PL72 and the AFK obtained in the current study (-0.03 ± 0.06), taking into account that it had a large standard error, was similar to that estimated in cattle (-0.11 ; VanRaden and Klaaskate, 1993) using the same definition of PL as in the present study; however, it was lower than the r_g obtained in sheep (-0.35 ± 0.41 ; El-Saied et al., 2005) and sows (-0.28 ± 0.11 ; Serenius and Stalder, 2004), for which PL was defined as the days from first parturition to culling.

The r_g obtained between the milk-production traits (MY, FY, PY, and FPY) and PL72 (0.23–0.33), as with FPL72 (0.26 to 0.39), were higher than the r_g obtained between the milk components (F% and P%) and PL72 (-0.002 to -0.04) or FPL72 (-0.03 to -0.06), indicating that the indirect genetic improvement of FPL72

and PL72 would be more efficient using the milk-production traits (MY, FY, PY, and FPY) than using the information of the milk components (F% and P%). As with F% and P%, it is not advisable to use KI or AFK as selection criteria to achieve an increase in PL72 and FPL72 because, in addition to the r_g estimated with PL72 and FPL72 in the KI and the AFK having had high standard errors, the use of KI as indirect selection criterion would result in an 8.1% decrease in PL72 per generation, whereas if were to decide that the only criterion for selection is AFK, the days of PL72 would increase by only 2.70% per generation; thus, genetic progress would be slow. However, the optimal strategies for the use of both AFK and KI as indirect selection criteria of PL72 will depend on the economic values to be estimated for these traits.

It is necessary to carry out further research on the adverse relationships observed in this study between longevity and AFK, KI, F%, and P% in dairy goats as well as research the relationship that may exist with other reproductive and disease-resistance traits to obtain correct foundations to know whether these traits may be used in indirect selection for PL in dairy goats.

While waiting for the research on the longevity of goats to advance, the implementation of strategies such as introducing independent culling levels for MY and fat content (Kominakis et al., 2000), including reproductive traits in selection indices (Valencia Posadas et al., 2008) and improving the management of the animals (Montaldo et al., 2010), will lead to improvements in MY, which, in turn, could lead to an indirect increase in PL in goats, due to the genetic relationship between MY and PL, reflected in the values obtained in the present study. In addition to these strategies, the selection of cows with the lowest fat:protein ratio (Buttchereit et al., 2010) and the selection of female sheep with multiple lambings (Abdelqader et al., 2012) have shown that the PL can be increased directly in these species; however, these traits have not been evaluated in goats, so more research on this subject is needed to reach a conclusion about the role they play in selection, to design useful strategies for increasing PL in goats.

Phenotypic Correlations

The r_p estimated in this study between PL72 and MY (0.25), FY (0.23), PY (0.25), and FPY (0.25) were positive and significant ($P < 0.05$), similar to the r_p estimated in goats of the same population by Torrero (2010) between stayability to the second lactation and MY (0.15 ± 0.01), FY (0.64 ± 0.00), PY (0.56 ± 0.00), and FPY (0.66 ± 0.00), and they were within the r_p estimated in dairy cows between PL and FY (0.11 to 0.28; Cruickshank et al., 2002; Ajili et al., 2007) and

PY (0.17 to 0.29; Cruickshank et al., 2002; VanRaden et al., 2006). The r_p between PL72 and MY was similar to the r_p estimated in dairy cows between PL and MY (0.26; Cruickshank et al., 2002).

The estimated r_p between FPL72 and MY (0.29 ± 0.009), FY (0.26 ± 0.01), and PY (0.29 ± 0.01) were similar to those obtained in dairy cows between FPL and MY (0.23), FY (0.26), and PY (0.30), defining FPL as the days from birth to culling (Cruickshank et al., 2002), but when FPL was defined as the total days in production (Pérez-Cabal and Alenda, 2003), the r_p calculated in the current study were lower than the r_p estimated in that population of dairy cows between FPL and MY (0.49), FY (0.47), and PY (0.44).

The estimated r_p between KI and PL72 (-0.01 ± 0.01) was similar to that found in sows (-0.01 ; Serenius and Stalder, 2004) but lower than that calculated in cows (0.06; Ajili et al., 2007). In the case of FPL72, the r_p estimated between KI and FPL72 (-0.07 ± 0.01) was similar, in terms of its proximity to zero, to that calculated by Pérez-Cabal and Alenda (2003) in Holstein cattle (-0.04). The r_p between PL72 and AFK (-0.08 ± 0.008) was similar to that obtained in sheep (-0.08 ± 0.02 ; El-Saied et al., 2005) and sows (-0.05 ; Serenius and Stalder, 2004), whereas the r_p between FPL72 and AFK (-0.08 ± 0.009) was lower than that estimated in Landrace sows (-0.02 ; Serenius and Stalder, 2004).

The standard errors for r_g and r_p between PL72 and milk-production traits (0.04 to 0.06 and 0.008 to 0.01) were acceptable compared with the value for the parameter and were within the values mentioned for the authors of other studies mentioned above (0.05 and 0 to 0.01). However, in the case of the standard errors for r_g and r_p between PL72 and milk components (0.04 to 0.05 and 0.01), or reproduction traits (0.06 to 0.09 and 0.008 to 0.01), the standard errors were the same or larger than those for the parameter estimates, meaning that the values of these parameters were probably close to zero or that is necessary to investigate larger data sizes to obtain parameter estimates that are closer to their real values.

Response to Selection

As has been mentioned throughout this article, knowing the PL of a herd is an aspect of great importance, as it not only helps reduce replacement (Mark, 2004) or health (Rogers et al., 1998) costs, but also, as suggested by the results shown here, when information on PL is available and is included in an index, the selection response is maximized, achieving an increase in simultaneous genetic improvement per generation of 0.15 to 17.35% for MY, FY, PY, and PL72.

In addition to the inclusion of PL72 in a selection index, the indirect improvement using information of other economically important traits (MY, FY, PY, FPY, F%, P%, KI, and AFK) can be also a useful way to increase PL in goats, a goal that, according to the heritability and the r_g estimated in this study, is relatively easy to achieve, with an even greater response to selection per generation than in other species specialized in milk production.

In research conducted in dairy cows (i.e., Dürr et al., 1999; Cruickshank et al., 2002), the traits that turned out to be (as in the present study) the most relevant for indirect prediction of real and FPL were milk-production traits. The highest r_g in the current study was between MY and PL72 or FPL72, which suggests that using MY as selection criterion is the most viable option for indirect improvement in both FPL72 and PL72, being more effective than any of the other milk-production traits evaluated in this study. So, if the only selection criterion used were MY, an increase of 39.4% in the direct response of PL72 would be achieved.

In the present study, we showed some of the advantages gained by using information on PL72 and other traits of economic interest (MY, FY, PY, KI, and AFK) for the direct or indirect selection of PL72; however, the genetic improvement observed in the present study could be more efficient using information on FPL72, because, when removing the effects of voluntary culling (Dekkers, 1993; Mark, 2004), the goat that is able to stay in a herd, in addition to being a good producer, will also be less susceptible to diseases (i.e., mastitis) or reproductive problems (Vukasinovic et al., 1997; Neerhof et al., 2000).

CONCLUSIONS

The main criteria that determine the culling of a goat from the herd are low MY and FY per lactation, and a low FS. According to the estimates of heritability (0.22 and 0.17 for real and FPL, respectively), the genetic improvement of PL is an achievement that can be made possible by the inclusion of this trait in a selection index, as the improvement is more efficient when the effects of voluntary culling are removed using information on FPL or of other traits commonly evaluated in young goats. The indirect selection for real PL and FPL in dairy goats is more efficient when information on MY, FY, and PY traits is used than when information on reproductive traits, such as AFK or KI, is used. The inclusion of PL in a selection index involving MY, FY, and PY could increase the economic response to selection per generation (0.15 to 17.35%). However, it is necessary to carry out more research on the economic

value of the PL of dairy goats to obtain the maximum economic response to selection in this population.

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