HERITABILITY OF MILK PRODUCTION AND 21-DAY LITTER WEIGHT AND LITTER SIZE IN PUREBRED AND CROSSBRED RABBITS USING AN ANIMAL MODEL

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Abstract - Cumulative, 1 to 21 d milk production (MP), total 21 d litter weight (LW21) and litter size (LS21) records from Californian (CAL) and New Zealand White (NZW) purebred and CAL X NZW and NZW X CAL crossbred does were analyzed using an animal model to estimate heritability (h^2), and genetic effects attributable to direct and maternal breed additive and individual heterosis. Separate analyses were conducted involving first parity (n=71 does with records) vs multiple parity (1 through 8) data (n=83 does with 227 records). The first parity model consisted of fixed effects of diet, birth season of litter, and crossbreeding parameters as linear covariates, and random animal and residual effects. The multiple parity model consisted of additional fixed parity and random common effects. Analyses with or without LS21 in the models as a fixed effect were also conducted. Results yielded h^2 estimates of .14 and .11 for MP, .00 and .01 for LW21, and .00 and .00 for LS21, from first *vs* multiple parity models. When records were adjusted for litter size at 21 d, h^2 estimates increased to .23 and .27 for MP and .08 and .10 for LW21 from first *vs* multiple parity models. For MP and LW21, and for both models, the only significant crossbreeding parameter was the direct breed additive effect which favored NZW. However, individual heterosis for LS21 tended to be important (P<.10) across parities, unadjusted for litter size. These results bring into question the genetic basis of LW21 for MP selection.

INTRODUCTION

There is a paucity of reports on heritability of milk production (MP) in rabbits. PATRAS (1985) reported heritability of .31 for total milk yield in Champagne d'Argent does, whereas EL-MAGHAWRY *et al.* (1993) and AYYAT *et al.* (1995) recently reported heritabilities ranging from .09 to .26 for weekly and total milk yield records in NZW does. These limited studies suggest that MP is lowly to moderately heritable, as generally reported for other livestock species.

Despite the recognized economic importance of MP, its measurement is a tedious undertaking (e.g., weigh-suckle-weigh method) that usually requires cage or nest box design modifications. Conventionally, producers and researchers alike have used total 21-d litter weight (LW21) as a phenotypic reflection of a doe's milk producing ability, and also as selection criterion for improving this character. Earlier studies (LEBAS, 1969; DE BLAS and GALVEZ, 1973; NIEHAUS and KOCAK, 1973; LUKEFAHR *et al.*, 1983) confirmed phenotypic correlations close to unity between MP and LW21. Is LW21 a reliable genetic reflection of MP.

Our objective was to estimate heritability for MP and LW21, and also litter size at 21 d, according to parity class (first *vs* multiple), using an animal model that takes into account pedigree relationships between and within purebred and crossbred doe breed types. Since the data were based on a crossbreeding experiment, a second objective was to simultaneously compute direct and maternal breed additive and individual heterotic effects for the traits investigated.

MATERIAL AND METHODS

Population Background and Management

The data were taken from the dissertation of LUKEFAHR (1983), which involved a crossbreeding study conducted at Oregon State University (November, 1980 to February, 1982). Doe breed types were Californian (CAL) and New Zealand White (NZW) purebreds and CAL X NZW and NZW X CAL crossbred does. Purebred CAL and NZW sires and dams contributed both purebred and crossbred daughters to the experiment. Housing, diet, and doe management and culling aspects were previously documented by LUKEFAHR *et al.* (1983). A 14-d breeding schedule was practiced. A doe was randomly assigned for mating to a buck of either of three breeds: CAL, NZW or Flemish Giant. There was no crossfostering of kits at birth to equalize the litter size. A doe was removed from the experiment after one full year of reproduction (maximum of 8 litters).

Total 1 to 21 d milk production (MP) was measured using the weigh-suckle-weigh method involving 83 does rearing a total of 227 litters bearing 1,671 kits which survived to 21 d of age. Also, total 21 d litter weight (LW21, g) and litter size (LS21) were included for the purpose of comparing results from statistical, mixed-model analyses.

Statistical Analysis

Two data sets were analyzed: first parity (n=71 does) and multiple parity (1 through 8th parities). The multiple parity data set involved 83 does with 227 records. The rationale for the separate analyses (involving mostly the same does) was to determine if the ratios of additive genetic to phenotypic variances for MP, LW21 and LS21 were homogeneous between parity groups (e.g., first *vs* multiple). For the first parity data set, means (standard deviations) for MP, LW21 and LS21 were 3,018 g (730 g), 2,056 g (490 g), and 6.85 kits (2.08 kits), respectively. For the multiple parity data set, means (standard deviations) for MP, LW21 and LS21 were 3,527 g (997 g), 2,362 g (685 g), and 7.36 kits (2.45 kits), respectively.

The first parity model consisted of fixed effects of diet (2 classes), birth season of litter (4 classes), and crossbreeding parameters (direct and maternal breed additive and individual heterosis) as linear covariates, and random animal (71 does with records and 47 base animals) and residual effects. In addition, analyses with or without 21-d litter size with two classes (1 = less than 6 kits, 2 = 6 or more kits) as a fixed effect were conducted. Because of the more limited number of observations in the first parity data set, litter size at 21 d was grouped into two classes to avoid statistical confounding problems.

The multiple parity model consisted of fixed effects of diet (2 classes), birth season of litter (4 classes) and parity (3 classes: 1 = 1st, 2 = 2nd, and 3 = 3rd through 8th parities), and crossbreeding parameters (direct and maternal breed additive and individual heterosis) as linear covariates, and random animal (83 does and 44 base animals), permanent (i.e., non-additive genetic plus permanent environmental) and residual effects, and with or without LS21 as a linear covariate (2 through 11 kits). Sire breed of litter was not included in the models because previous analyses indicated this source to be non-significant for all traits studied.

Animal models with Restricted Maximum Likelihood (REML) procedures were employed using MTDFREML software by BOLDMAN *et al.* (1993). One feature of MTDFREML is that pedigree relationships (i.e., additive genetic) between and within purebred and crossbred doe breed types were taken into account. Random animal, permanent (multiple parity model) and residual effects were assumed to be uncorrelated and normally and independently distributed.

Doe breed type differences were assumed to be associated with direct and maternal breed additive, and individual heterotic effects. Recombination loss, linkage and maternal cytoplasmic effects were assumed not to be important. To estimate crossbreeding parameters in animal models by regression procedures (ARNOLD *et al.*, 1992; BITTANTE *et al.*, 1993), it was necessary to impose certain restrictions to remove linear dependencies in the design matrix. This was achieved by deviating direct and maternal breed additive coefficients for each doe breed type from those of the CAL breed. Since there were two doe breeds involved, this restriction ordinarily results in the overall least-squares mean (μ) being the mid-parent breed mean estimate. In MTDFREML, however, the simple mean is used rather than μ to provide solutions for model fixed effects. This is because no equation for μ is incorporated into the mixed-model equations.

RESULTS AND DISCUSSION

Heritability Estimates

Heritabilities for first and multiple parity MP were estimated at .14 and .11 (Table 1). The litter size adjustment, however, increased heritability estimates to .23 and .27, respectively. Hence, the ratio of additive genetic variance to phenotypic variance was fairly uniform between first and multiple parity groups. AYYAT *et al.* (1995) reported heritability of .04 for 1-4 wk total MP (adjusted for litter size at birth), however, 1st, 2nd and 3rd wk heritabilities ranged from .09 to .22, similar in magnitude to our estimates for 1-21 d MP. EL-MAGHAWRY *et al.* (1993) studying similar MP traits, obtained heritabilities ranging from .09 to .26. A heritability of .31 was reported by PATRAS (1985), although it could not be determined from the abstract report what parities, model effects, observation numbers, etc., were actually involved. Nonetheless, if multiple parity records were *involved, and a* litter size adjustment was made, the .31 estimate is consistent with our .27 estimate.

Table 1 : Variance component estimates for 1-21 d milk production (MP), 21-d total litter weight (LW21) and litter size (LS21)[a]

	First parity model			Multiple parity model			
Trait	σ_a^2	σ_ε^2	h^2	σ_a^2	σ_p^2	σ_ε^2	h^2
MP,kg^2	.0709	.4202	.14	.0854	.0000	.6771	.11
LW21,kg^2	.0002	.2106	.00	.0025	.0137	.3541	.01
LS21	.0000	4.3330	.00	.0000	.9608	4.2372	.00
MP,kg^{2,b}	.0712	.2370	.23	.1107	.0000	.2990	.27
LW21,kg^{2,b}	.0106	.1143	.08	.0163	.0121	.1293	.10

[a]Symbols for variances for first parity model: a = additive genetic, and ε = residual effects; and for multiple parity model: a = additive genetic, p = non-additive genetic plus permanent environmental, and ε = temporary environmental effects. [b]Adjusted for litter size at 21 d.

For LW21 and LS21, heritabilities near or at zero were obtained, for first or multiple parity groups, suggesting a lack of additive gene action. KHALIL *et al.* (1986) and BASELGA *et al.* (1992), found that litter size traits tend to be lowly heritable (h^2<.15). In this experiment, the phenotypic correlation between LW21 and LS21 was .80 (LUKEFAHR *et al.*, 1983). Interestingly, adjustment of LW21 for litter size only slightly increased heritability to .08 and .10 from analyses of first and multiple parity records. RANDI and SCOSSIROLI (1980) reported a LW21 heritability of .11, consistent with present estimates.

From multiple parity analyses, variances for permanent effects (non-additive genetic and[or] permanent environmental effects) were essentially zero for MP. More research is needed to determine whether permanent effects are absent for MP. It would appear that temporary environmental effects account for most of the variation. For LW21, the ratio of permanent effects to phenotypic variance was .04 and .08 (unadjusted *vs* adjusted for 21-d litter size), and for LS21 a ratio of .18 was obtained. The latter value is less, as expected, than the doe repeatability estimate of .23, as previously reported from the same experiment by LUKEFAHR *et al.* (1983).

Crossbreeding Parameter Estimates

Direct breed additive effects favored NZW over CAL for MP and LW21, and were significantly different from zero (P<.05 or P<.01), regardless of parity group or adjustment for litter size (Table 2). Overall, the magnitude of the direct breed additive effects was larger than the maternal breed additive or individual heterotic effects. The direct breed additive effect was not significant for LS21, however. Other reports involving crossbreeding parameter estimates for these same traits are not available for comparison.

Although the maternal breed additive coefficients were never significant for the traits investigated, an interesting pattern was observed. For MP and LW21, maternal breed additive coefficients were negative for first parity records, but positive for multiple parity records in models without adjustment for 21-d litter size. However, when data were statistically adjusted for litter size, maternal breed additive coefficients became consistently negative (favoring CAL maternity) and similar for both traits between parity groups. Direct and maternal breed influences on LS21 were quite small for first parity (.17 and -.12) and multiple parity (.14 and .20) results. Similarly, BRUN and ROUVIER (1988) reported non-significant direct and maternal breed effects for litter size at 28 d. A simple explanation for the discrepancy may that primiparous does have smaller litters, which, in turn, results in a decreased milk response. In first parities, total litter size at birth averaged 8.4 kits. In subsequent parities the average was 9.6 kits. The 21-d litter size adjustment effectively negated this influence of doe age and(or) parity on MP and LW21. In addition, the litter size adjustment markedly reduced maternal breed additive coefficients for MP between parity groups, suggesting that this genetic effect operates directly on litter size, and indirectly on MP through litter size. Of relevance, MCNITT and LUKEFAHR (1990), using regression techniques, predicted that 1-29 d milk output was maximized in CAL and NZW does when the number of kits suckling was 9.8 and 9.1, respectively.

Individual heterosis in CAL X NZW crossbred does was important (P<.10) only for LS21 for both parity models (Table 2). Crossbred does had a larger heterosis deviation in first *vs* multiple parity production (1.01 *vs* .77 kits), perhaps an indication of somewhat more advanced physiological maturity than purebred does at first breeding (154 d) as associated with the phenomenon of hybrid vigor. For first through eighth parity records, LUKEFAHR *et al.* (1983) reported heterosis percentage for LS21 of 15.4%, similar to our estimate of 10.9% obtained from the animal model analysis. From the same publication, heterosis percentages of 9.2 and 9.6 were reported for MP and LW21.

Crossbreeding parameter estimates can also be used to predict genetic performances of CAL and NZW purebred and crossbred does. For example, using multiple parity records, predicted doe MP for NZW, CAL, CAL♂ X NZW♀ and NZW♂ X CAL♀ breed types are 3,949, 3,105, 3,793 and 3,667 g, respectively.

Table 2 : Crossbreeding parameter estimates for 1-21 d milk production (MP), 21-d total litter weight (LW21) and litter size (LS21) traits as doe observations

Trait	g^{I}_{NZW}	g^{M}_{NZW}	h^{I}(%)	
First parity model				
MP,g	391±186*	-76±144	146±186	4.8
LW21,g	306±115*	-82±91	118±119	5.7
LS21	.17±.52	-.12±.41	1.01±.54†	14.7
MP,g[b]	311±152*	-4±116	82±149	2.7
LW21,g[b]	262± 92*	-38±72	74± 93	2.5
Multiple parity model				
MP,g	359±154*	63±116	203±146	5.8
LW21,g	257±93*	21±72	151±92	6.4
LS21	.14±.39	.20±.31	.77±.39†	10.5
MP,g[b] (β=277±18**)	351±133*	-7±99	-7±121	-.2
LW21,g[b] (β=213±12**)	261±73**	-46±56	-10±71	-.4

[a]Symbols for g^{I}_{NZW} and g^{M}_{NZW} = direct and maternal breed additive solutions for NZW (changing the coefficient sign yields solution for CAL) and h^{I} = individual heterosis solution for crossbred does.
[b]Adjusted for litter size at 21 d. For multiple parity model, regression coefficient (β) and SE are in parentheses.
†P<.10; *P<.05; **P<.01.

CONCLUSIONS

On the basis of the lower heritability estimates for LW21 than for MP, our results bring into question the reliability of LW21 as a basis for MP selection. Our data set was too small to accurately estimate the additive genetic correlation between LW21 and MP to further shed light on this issue. Alternatively, there is a need to identify more direct measurements of milk (e.g., a weekly measurement and[or] partial records) that have higher heritability and, further, are highly and favorably genetically correlated to total MP. On the subject of crossbreeding, favorable direct breed additive effects of the NZW were especially pronounced for MP and LW21. Direct breed maternal additive and individual heterosis were less important.

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