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Genetic and phenotypic aspects of doe productivity in four breeds of rabbits

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SUMMARY

Data on 841 purebred Bauscat, White Flander, Giza White and Baladi Red litters provided estimates of genetic, phenotypic and environmental parameters for gestation length, litter size at birth and at weaning, mortality and sex ratio at weaning. A total of 170 daughters (paternal half-sisters) of 76 sires were available for the analysis. No important differences were detected among breeds for litter traits studied except litter size at weaning ($P < 0{\cdot}001$). Year of kindling affected ($P < 0{\cdot}001$) gestation length, litter size at birth and mortality percentage. No clear patterns of the effect of parity and month of kindling on litter traits were observed. The sire of the doe and doe within sire affected most of the traits studied. Estimates of heritability indicated that the sire's genetic contribution to litter traits are much higher during the pre-natal period than for the suckling period. Estimates of repeatability for litter traits studied were relatively low. Genetic and phenotypic correlations between gestation length and other litter traits were relatively low. Litter size traits were positively correlated both genetically and phenotypically. Estimates of genetic and phenotypic correlation between litter size traits and preweaning mortality were generally negative. Phenotypic and environmental correlations were generally very similar in size and sign. Predicted direct selection was shown to give greater improvement in litter size at birth than indirect selection through litter size at weaning.

INTRODUCTION

Doe productivity is a key factor affecting the efficiency and economy of the rabbit enterprise for both breeding stock and commercial production. Productivity per kindling is the usual basis for evaluating the genetic merit of animals in a unit including such traits as litter size at birth and at weaning.

Few studies have been published on the genetic analysis of doe productivity traits in rabbits. Reported estimates of heritability for litter size and preweaning mortality, computed from half-sib correlations, vary considerably, ranging from under 5 to 48% but with most estimates under 20% (Lampo & Broeck, 1975; Garcia *et al.* 1980; Randi & Scossiroli, 1980; Baselga, Blasco & Garcia, 1982; Lahiri & Mahajan, 1982; Lukefahr, 1982; Kadry & Afifi, 1984; Khalil & Afifi, 1986; Khalil, Owen & Afifi, 1987). Litter size traits appear to be highly positively intercorrelated both genetically and phenotypically (Afifi *et al.* 1980; Garcia *et al.* 1980; Lahiri & Mahajan, 1982; Khalil *et al.* 1987). Reported estimates of genetic and phenotypic correlations between litter size traits and preweaning mortality were negative and relatively moderate in magnitude (Rouvier, Poujardieu & Vrillon, 1973; Khalil *et al.* 1987). No information is available in the literature on the genetic analysis of gestation length and sex ratio in rabbits.

The main objectives of this study were: (1) to conduct a genetic evaluation of doe productivity traits in four pure breeds of rabbits; and (2) to assess the direct and correlated responses expected per generation from single-trait selection for these traits.

MATERIALS AND METHODS

Data for this study were collected from the rabbitry of the Dokki Experimental Station, Animal Production Research Institute, Ministry of Agriculture, Cairo, over 8 consecutive years of production (1971–2 to 1978–9). Records were analysed for 841 purebred litters of two foreign breeds (Bauscat and White Flander) and two native breeds (Giza White and Baladi Red). Only sires with at least two daughters (paternal half-sisters) were included in the analysis. Information was available on 170 daughters (does) by 76 sires for gestation length (days), litter size at birth and at weaning, within-litter preweaning mortality (percentage of dead rabbits in relation to total litter size at weaning (percentage of males relative to all males and females).

At the beginning of the breeding season (October), mating bucks within each breed were assigned at random to breeding females with the restriction of avoiding full-sib, half-sib and sire–daughter matings. Each doe was mated to only one buck during her productive life. Each doe was transferred to the buck's hutch to be mated and returned to her own hutch after being mated. Hand mating was exercised and each doe was palpated 10 days thereafter to determine pregnancy. Does that failed to conceive were returned to the same mating-buck to be remated, and were returned to the same buck every alternate day thereafter until a service was observed. Does were mated 7 days after each parturition. Weaning was practised at 35 days of age. Other details of the breeding plan and management and feeding procedures were described by Afifi & Emara (1986*a*).

Litter trait data were analysed by the least-squares and maximum likelihood program of Harvey (1977). Fixed effects considered in the analysis of the data were breed, year of kindling, parity and month of kindling. Sires within breed, and does within sires within breed, were considered to be random effects. The mean squares for sires within breed was used to test for significance of breed effects. The mean squares for does nested in sires and breed was used to test for significance of sires within breed. Significance of all other effects was tested using the remainder mean square. Percentages of preweaning mortality and sex ratio at weaning were subjected to arc-sin transformation before being analysed in order to make variances homogeneous.

Litter records were analysed genetically and phenotypically as doe traits. Accordingly, half-sib doe groups were utilized in estimating genetic, phenotypic and environmental variances and covariances by the paternal half-sib method (method III of Henderson, 1953). These estimates of genetic and phenotypic variances and covariances were used to compute heritabilities, repeatabilities and genetic, phenotypic and environmental correlations. Therefore, estimates of heritability (h^2_S) were obtained as:

$$h^2_S = 4\sigma^2_S/(\sigma^2_S + \sigma^2_{D:S} + \sigma^2_e),$$

where σ^2_S, $\sigma^2_{D:S}$ and σ^2_e are, respectively, components of variance for sires, does within sire and error (remainder). Repeatability estimates were computed from the ratio of sire and doe variance components to the sum of sire, doe within sire and the remainder variance components. Standard errors for heritability and repeatability estimates were calculated using an approximation formula as described by Swiger *et al.* (1964). Estimates of genetic (with standard errors), phenotypic and environmental correlations were obtained by computing techniques described by the LSML76 program of Harvey (1977). The predicted and correlated responses per generation from single-trait selection for litter traits studied were estimated according to Falconer (1981).

RESULTS AND DISCUSSION

Mean performance levels, their standard deviations and coefficients of variation (C.V.) for litter traits are shown in Table 1. Litter size at weaning showed higher C.V. than the corresponding trait at birth. Similarly, Lukefahr (1982) reported higher C.V. at weaning than at birth. Khalil *et al.* (1987) attributed the great variation in size within litter at weaning to differences in losses within litter that occurred during the suckling period.

Breed

Baladi Reds had the longest gestation and largest litter size at birth (Table 2). A positive association between ovulation rate and weight of the breed (Hulot & Matheron, 1979) may have accounted for this observation. At weaning, litter size and sex ratio were smaller in White Flander litters than in the other breeds. Baladi Red had longer gestation, largest litter size and sex ratio, and a low preweaning mortality. However, no significant differences were observed between breeds for litter traits except litter size at weaning ($P < 0{\cdot}001$). Evidence is available in the Egyptian studies on breed differences for litter size at weaning (El-Khishin *et al.* 1951; Afifi *et al.* 1976; Afifi, Abdella, El-Serafy & El-Sayaad, 1982; Afifi & Emara, 1986*a*).

Year of kindling

Gestation length, birth litter size and preweaning mortality varied significantly ($P < 0{\cdot}001$) from one

Table 1. *Means, standard deviations and coefficients of variation of unadjusted litter traits records*

Traits	*n*	Mean	S.D.	C.V.*(%)
Gestation length	841	31·3	1·0	3·0
Litter size at birth	841	6·5	2·1	31·9
Litter size at weaning	640	5·0	2·2	40·9
Preweaning mortality (%)†	841	40·0	—	—
Sex ratio at weaning†	640	48·8	—	—

* Coefficient of variation calculated as the residual standard deviation divided by the overall least-squares mean of the trait (Harvey, 1977).

† The arc-sin transformed values were retransformed to the original scale and consequently have no associated standard errors and C.V.%.

Table 2. *Least squares means, standard errors and tests of significance of factors affecting some litter traits in rabbits*

Independent variable	*n*	Gestation length (days)		Birth litter size (young)		Preweaning* mortality (%)		Weaning litter size (young)		Sex ratio* at weaning
		Mean	S.E.	Mean	S.E.	Mean	*n*	Mean	S.E.	Mean
Breed										
Bauscat	200	31·23	0·118	6·47	0·231	38·8	157	4·54	0·205	45·6
Giza White	343	31·21	0·098	6·44	0·187	41·0	253	4·83	0·164	48·8
White Flander	57	31·06	0·183	6·99	0·370	49·3	47	4·36	0·348	41·3
Baladi Red	241	31·28	0·120	7·03	0·230	36·0	183	5·65	0·193	51·6
Year of kindling										
1971	144	31·7	0·086	6·51	0·188	25·8	126	5·00	0·304	45·1
1972	87	31·7	0·105	6·31	0·231	27·5	67	5·00	0·408	38·7
1973	129	30·8	0·088	6·22	0·193	51·0	96	3·82	0·383	51·7
1974	190	31·3	0·074	6·64	0·161	36·6	148	5·24	0·293	52·4
1975	170	30·8	0·074	7·28	0·163	49·7	128	4·68	0·401	50·9
1976	33	32·3	0·171	7·63	0·375	63·8	19	5·33	0·745	57·1
1977	49	32·0	0·142	6·04	0·312	47·9	34	4·58	0·513	51·9
1978	39	31·1	0·159	5·71	0·348	54·9	24	4·78	0·527	50·2
Parity										
1st	203	31·24	0·114	6·53	0·232	40·6	151	5·04	0·265	48·2
2nd	191	31·40	0·105	7·09	0·212	38·4	146	5·20	0·233	43·3
3rd	151	31·16	0·109	6·53	0·220	36·9	120	4·70	0·240	46·0
4th	103	31·28	0·119	6·97	0·242	39·6	81	4·61	0·266	52·1
5th	69	30·93	0·139	6·94	0·285	24·2	55	4·91	0·323	43·2
⩾6th	124	31·15	0·133	6·33	0·273	50·0	87	4·58	0·320	48·1
Month of kindling										
October–November	217	31·45	0·107	6·05	0·216	47·7	169	3·89	0·232	47·6
December	81	30·84	0·136	6·72	0·279	35·5	63	4·25	0·327	45·5
January	105	31·70	0·124	6·63	0·253	60·1	67	4·85	0·319	41·8
February	161	31·54	0·108	7·11	0·219	34·2	126	5·50	0·236	49·3
March	101	30·50	0·124	7·39	0·252	27·1	82	5·25	0·281	47·7
April and May	176	31·14	0·107	6·49	0·216	43·7	133	5·30	0·238	49·5

* The values given are the retransformed estimates and consequently have no associated standard errors.

year of kindling to another while weaning litter size and sex ratio did not (Table 2). Similar results were obtained in the Egyptian studies (Afifi & Emara, 1985, 1986*b*; Khalil *et al.* 1987).

Parity

Parity was a minor source of variation affecting litter traits (Table 2) except gestation length and litter size at birth ($P < 0.05$ or $P < 0.01$). Significant parity effects on birth litter size were detected by Rollins *et al.* (1963), Randi (1982), Afifi, Galal & Kadry (1982) and Afifi, Abdella, El-Serafy & El-Sayaad (1982). However, insignificant and inconsistent parity effects on gestation length, litter size and weaning, preweaning mortality and sex ratio were observed by some Egyptian investigators (El-Tawil *et al.* 1971; Afifi, Galal & Kadry, 1982; Kadry & Afifi, 1982; Afifi & Emara, 1985, 1986*a,b*). These results indicate that the pattern of change in gestation length and/or litter size at birth, due to parity effects, may be the result of changes in physiological efficiency of does which occurs with advance in parity. This may be related to effects on ovulation rates, implantation sites, embryonic mortality rates, viability of foetus and to differences in the intra-uterine environment during gestation length.

Month of kindling

All litter traits studied, except sex ratio at weaning, varied considerably ($P < 0{\cdot}001$ or $P < 0{\cdot}01$) from one month of kindling to another, but no consistent pattern was observed (Table 2). In terms of litter size traits and preweaning mortality the February and March-born litters are favoured over litters kindled in other months. Month-of-kindling differences were evident in different Egyptian studies for gestation length (Afifi & Emara, 1985), litter size (Khalil *et al.* 1987) and preweaning mortality (Khalil & Afifi, 1986; Khalil *et al.* 1987). The insignificant month-of-kindling effects on sex ratio at weaning (Table 2) were confirmed by results of other Egyptian studies (Kadry & Afifi, 1982; Afifi & In relation to the Egyptian enviro tions, most studies attributed the sigr in litter size and/or preweaning r kindling dates to changes in the availa fodder and its nutritive value anc conditions (especially ambient temper

Random effects

Differences among sires within bre significant source of variation for all t sex ratio at weaning (Table 3). Simi Egyptian studies (Khalil & Afifi, 1986; 1987) reported important sire effects on of Giza White rabbits. Accordingly, impr litter traits of rabbits could be made by s sires based on their daughters' performa

The significant differences obtained in length and litter size due to doe effects (Ta be attributed to differences in ovulation pre-implantation viability (Rouvier, 197 may also be due to the maternal effects de by the number of mature, fertilized and est ova and the environment a doe provides for l and the genes she transmits to her offspring as due to differences in milk production du

Table 3. *Estimates of random components of variance* (σ^2) *and proportion of variation* (V %) *for some traits of four purebred rabbits*

	Sire within breed			Doe within sire within breed			Remainder		
Traits	D.F.	σ^2_s	V%	D.F.	$\sigma^2_{D:S}$	V%	D.F.	σ^2_e	V%
Gestation length (days)	76	0·11	11·3	170	0·06	6·2	581	0·80	82·
Litter size at birth	76	0·33	7·7	170	0·41	9·6	581	3·55	82·
Litter size at weaning	70	0·11	2·5	151	0·18	4·2	405	4·05	93·
Preweaning mortality (%)	76	38·56	3·6	170	20·86	2·0	581	1004·19	94·4
Sex ratio at weaning	70	10·58	2·7	151	*	0·0	405	375·46	97·3

* Negative estimate of variance component set to zero.

Table 4. *Estimates of heritability and repeatabilities and their standard errors (in italics on diagonal)*, genet correlations and their standard errors (below diagonal) and phenotypic and environmental correlations (abo diagonal)† for litter traits*

Traits ...	X1	X2	X3	X4	X5
Gestation length (X1)	*0·45 ± 0·134* *(0·17 ± 0·037)*	−0·06 (−0·11)	−0·01 (0·01)	0·04 (−0·03)	0·001 (0·12)
Litter size at birth (X2)	0·03 ± 0·23	*0·31 ± 0·116* *(0·17 ± 0·037)*	0·59 (0·64)	0·03 (−0·08)	0·084 (−0·02)
Litter size at weaning (X3)	−0·09 ± 0·45	0·27 ± 0·50	*0·10 ± 0·113* *(0·06 ± 0·038)*	−0·59 (−0·62)	0·065 (0·12)
Preweaning mortality (X4)	0·22 ± 0·24	0·14 ± 0·33	−0·6 ± 0·77	*0·15 ± 0·095* *(0·00 ± 0·030)*	−0·11 (−0·20)
Sex ratio at weaning (X5)	−0·49 ± 0·46	0·71 ± 0·56	−0·41 ± 0·68	0·95 ± 0·58	*0·11 ± 0·114* *(0·03 ± 0·035)*

* Repeatabilities are given in parentheses underneath the heritabilities.

† Environmental correlations are given in parentheses adjacent to the phenotypic correlations.

Table 5. *Heritability estimates* (h^2_s) *from literature cited for some litter traits in rabbits*

Reference	Birth litter size	Weaning litter size	Preweaning mortality
Rollins *et al.* (1963)	0·03	—	0·12
Lampo & Broeck (1975)	0·02	—	—
Randi & Scossiroli (1980)	—	0·03	—
Lahiri & Mahajan (1982)	0·11	0·14	—
Kadry & Afifi (1984)	0·48	0·32	—
Khalil *et al.* (1987)	0·25	0·27	0·36
Current study	0·31	0·10	0·15
Mean	0·21	0·17	0·21

suckling period (Randi & Scossiroli, 1980). In conclusion, evidence from the literature (Rouvier *et al.* 1973; Randi & Scossiroli, 1980; Khalil & Afifi, 1986) and other suggested interpretations here indicate that litter size and other preweaning litter traits are a female trait and should be improved through the selection of a doe based on her own or her dam's performance, as well as through selection of sires on progeny test as indicated above.

Variance components and heritability estimates

Estimates of heritability of litter traits (Table 4) indicate that the genetic contribution of the sire of the doe to litter traits is higher during the prenatal period than during the suckling period. Also the higher estimate of heritability for litter size at birth as compared with that at weaning suggests that selection for litter size at birth will tend to give greater improvement in this trait than selection at weaning. The heritability estimate of 0·455 obtained for gestation length (Table 4) indicates a relatively large sire's genetic component which is consistent with the relatively low levels of variation due to the other, environmental, factors examined in this and previous studies (El-Khishin *et al.* 1951; Afifi & Emara, 1985).

Estimates of heritability (based on the paternal half-sib method), summarized from several comprehensive studies involving litter size and preweaning mortality traits, are presented in Table 5 for comparison with estimates in Table 4. Estimates for this study were in reasonable agreement with the average of those reported from other studies. No literature estimates of heritability for gestation length and sex ratio at weaning were found.

Estimates of repeatability for litter traits were low in magnitude (Table 4). These estimates are in general agreement with the corresponding estimates reported in the literature (Rouvier *et al.* 1973; Lukefahr, 1982; Khalil & Afifi, 1986). However, the low repeatability estimates for these traits indicated again that assessment of several records is required before selecting does for such litter traits.

Genetic, phenotypic and environmental correlations

Estimates of correlations between litter traits are presented in Table 4. The implications of these correlations are discussed without regard to statistical significance to provide an interpretation of potential biological implications. Also, estimates of correlations involving sex ratio are not sensibly discussed because of lack of precision. Phenotypic and environmental correlations were generally very nearly equal in size and similar in sign (Table 4).

All correlation estimates between gestation length and other litter traits were generally low (Table 4). However, slightly larger litters at birth and at weaning and higher preweaning mortality could be expected from longer gestations since the young rabbits would have more time to develop and gain weight. There are no reports in the literature regarding the relationships between gestation length and the other litter traits.

The correlations between litter size at birth and at weaning were positive and moderate or high and indicate that selection for litter size at birth would

Table 6. *Estimates of genetic* (r_G) *and phenotypic* (r_p) *correlations between some of the litter traits as cited in the literature*

	r_G	r_p
Litter size at birth and litter size at weaning		
Garcia *et al.* (1980)	0·51	—
Afifi *et al.* (1980)	—	0·87
Lahiri & Mahajan (1982)	0·71	0·63
Lukefahr (1982)	—	0·78
Khalil *et al.* (1987)	0·43	0·49
Litter size at birth and preweaning mortality		
Rouvier *et al.* (1973)	—	0·34
Khalil *et al.* (1987)	0·20	0·14
Litter size at weaning and preweaning mortality		
Rouvier *et al.* (1973)	—	−0·36
Khalil *et al.* (1987)	−1·10	−0·59

Table 7. *Direct (on diagonal) and correlated (off diagonal) response* expected per generation from single-trait selection*

Criterion of selection	Item†	Expected genetic change in trait X1	X2	X3	X4
Gestation length, days (X1)	*a*	0·22	0·01	−0·02	0·93
	b	100·0	3·0	−20·0	39·2
	c	0·70	0·15	−0·4	2·3
Litter size at birth, young (X2)	*a*	0·01	0·33	0·05	0·49
	b	2·3	100·0	50·0	20·7
	c	0·02	4·9	1·0	1·2
Litter size at weaning, young (X3)	*a*	−0·01	0·05	0·10	−1·11
	b	−4·51	15·2	100·0	−46·8
	c	−0·03	0·8	2·1	−2·8
Preweaning mortality, % (X4)	*a*	0·03	0·03	−0·07	2·37
	b	13·6	9·1	−70·0	100·0
	c	0·09	0·4	−1·4	5·9

* Selection intensity equals 1·0 standard deviation, on female side; no selection on male side; † where *a* = response in actual units of measurements, *b* = response as a percentage of direct response, *c* = response (*a*) per generation as expressed as a percentage of the overall mean of the trait.

improve litter size at weaning as a correlated trait. However, the correlation estimates in the present study are generally lower than those reported by other workers as shown in Table 6.

The correlation estimates between litter size at birth and preweaning mortality were low. However, highly negative genetic, phenotypic and environmental correlations were found between litter size at weaning and preweaning mortality (Table 4). These results are in agreement with those reported by other authors (Table 6).

Prediction of response to selection

The expected genetic gains resulting from one phenotypic standard deviation of selection pressure directed at different criteria of selection are presented in Table 7. For example, if one standard deviation of selection pressure is applied directly to litter size at birth, one can expect a genetic increase in litter size at birth of 0·33 young per litter in the population, a correlated gain of only 0·05 young in litter size at weaning and a correlated increase of 0·49% in preweaning mortality per generation. Similarly, with one standard deviation of selection pressure applied directly to litter size at weaning, one can expect a correlated gain of 0·05 young per litter in litter size at birth, a 15·2% decrease as compared with the direct selection on litter size at birth. The difference is due mainly to the low positive genetic correlation (0·27) between litter size at birth and the corresponding trait at weaning, the higher heritability for litter size at birth than for litter size at weaning and due to the very low heritability for litter size at weaning (0·10).

Estimates given in Table 7 indicate that the theoretical maximum rate of direct genetic progress in rabbit stocks selected solely for litter size at birth and for litter size at weaning are 4·9 and 2·1% per generation, respectively. Also, the decrease in percentage of preweaning mortality per generation will be 5·9% over that due to direct selection for this trait. Therefore, the expected direct selection gave greater improvement in litter size and preweaning litter mortality than indirect selection.

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