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Full Length Research Paper

Phenotypic and genetic parameter estimates for grasscutter production traits. 1. (Co) variance components and heritability

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The objectives of this work were to estimate genetic variation and heritability of traits in the *Thryonomys swinderianus*. The study was conducted at the grasscutter section of the Department of Animal Science Education, University of Education, Winneba, Ghana, from 2005 to 2010. Data were obtained from a random mating population and consisted of records of 502 kids born by 136 does and 40 sires over a period of 5 years. Data were analyzed by mixed model methodology using a full animal model and all known genetic relationships, in single trait analysis, using the MTDFREML programme. Body weight and growth rate showed the greatest additive genetic variation, with reproductive and survival traits, and feed intake showing relatively low additive genetic variation. Most traits had moderate maternal genetic variation. Body weight and growth rate had medium to high direct heritability (0.30-0.84). Medium direct heritability was obtained for feed intake (0.30) and feed efficiency (0.38). All reproductive traits, apart from those associated with weight, and survival traits had low direct heritability (0.02-0.06). Maternal heritability for most traits were low to high (0.13-0.99). Direct-maternal genetic correlations for traits was low negative to high negative (-0.01 to -0.95). Based on the results it was concluded that opportunity exists for fast genetic gains in the improvement of growth and body weight traits, whilst slow genetic progress may be made in reproductive and survival traits. It was also concluded that maternal effects are important in the grasscutter, and must be accounted for in breeding value estimations.

Keywords: Thryonomys swinderianus, cane rat, rodent, phenotypic and genetic parameters, domestication.

INTRODUCTION

Fruitless attempts were made in the past in Ghana to domesticate the grasscutter (*Thryonomys swinderianus*) (Asibey, 1966; 1974; Ntiamoah-Baidu,1998). One key factor that resulted in failure of grasscutter projects initiated before the 1990s was lack of improved breeding stock (Annor & Djang-Fordjour, 2006). The concern of farmers was availability of truly domesticated breeding stock. Initial breeding stocks of past projects were purchased from

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hunters (PARC, 1993). Farmers had no option but to resort to the process of domestication. However, high mortalities associated with domestication of wild animals deterred farmers from farming grasscutter (Adu, 1999).

Ghana and many sub-Saharan African countries are currently promoting grasscutter farming (Adu *et al.,* 2005; Mensah & Okeyo, 2006). The problem of acquiring truly domesticated breeding stock still confronts grasscutter farmers in the sub-region (Adu, 2005; Annor & Djang-Fordjour, 2006). Ghana started importing breeding stock from the Republic of Benin in the year 2000 (Alhassane *et al.,* 2004). Unfortunately, the Republic of Benin could not cope with Ghana's demand for breeding stock. Moreover, imported breeding stock were expensive and pedigree and genetic merits were unreliable (Adu, 2005).

A need for a national grasscutter breeding system as recommended by Adu (2002; 2005) and Annor & Djang-Fordjour (2006) is long overdue. The Ministry of Food and Agriculture has recognized this and grasscutter has been listed in the Ghana National Livestock Breeding Policy (MoFA, 2004) as one of the micro-livestock species to be developed. To facilitate breeding of highly prolific, docile and fast growing grasscutters, there is a need to know phenotypic and genotypic characteristics of the current population of captive grasscutters. Further, there is paucity of information in the literature on grasscutter phenotypic and genetic parameters. The only published work on genetic and phenotypic parameters of traits can be found in Yewadan (2000). The objectives of this work were to estimate genetic variation and heritability of traits in the grasscutter.

MATERIALS AND METHODS

The study was carried out at the grasscutter section of the Department of Animal Science Education, University of Education, Winneba, Mampong-Ashanti campus, Ghana from 2006 to 2010. Mampong-Ashanti lies in the transitional zone between the Guinea savanna zone of the north and the tropical rain forest of the south of Ghana. The climatic, vegetation and demographic characteristics of Mampong-Ashanti have been described by Ghana Districts (2006).

Essentially, Mampong-Ashanti lies between latitude 07^{o} 04' north and longitude 01^{o} 24' west with an altitude of 457m above sea level. Maximum and minimum annual temperatures recorded during the study period were 30.6^{o}C and 21.2^{o}C, respectively (MSD, 2010). Rainfall in the district is bimodal, occurring from April to July (main season) and August to November (minor season), and is about 1224mm per annum. The dry season occurs from December to March. The vegetation is transitional savanna woodland, and this is suitable for livestock rearing because most of the feed of herbivorous animals (grass) can be obtained from the wild. The common fodder species that are routinely fed to grasscutters, *Pennisetum purpureum* (elephant grass) and *Panicum maximum* (guinea grass) are readily available.

Data used for this study were obtained from a random mating population. This group was constituted in 2005 by randomly selecting and mating 48 does and 12 bucks from a base population of 100 breeding does and 25 bucks that were bought from 25 farmers in two out of the 7 grasscutter farming regions in Ghana. The breeding population was maintained at 48 does and 12 bucks. Replacement does and bucks were selected at random, and were also mated randomly. For each mating, each sire was allowed to mate 1-4 does. Data were collected from this population for a period of 5 years (2006-2010). Five hundred and two (502) records were collected from kids during this period. The kids were born by 136 does and 40 sires. Dams from this group gave birth up to the third parity. Table 1 shows characteristics of the traits measured.

Each kid record included animal (kid), sire and dam identification, sex, litter size at birth and weaning, parity of dam, season of mating and birth, year of birth, days from joining (pairing) to conception, age of dam at kidding, birth weight, weaning weight, 4-month weight, 6-month weight and 8-month weight, dam weight at birth and weaning, litter birth weight and weaning weight, pre- and post-weaning survival. Days of joining to conception was defined as the interval between first day of joining buck and doe, and day of conception. It was estimated backwards as the difference between days from joining to parturition and 150 days of gestation of the grasscutter. Dry matter feed intake of 199 animals (92 females and 107 males) aged 4-6 months that were randomly selected were also recorded.

Animals were housed singly and in groups, depending on the class (kid, young animal or adult) and physiological state (pregnant, dry or lactating), in either three-tier concrete or three-tier wooden cages. Cages were housed in cement house roofed with corrugated iron sheets. Concrete cages were used for mating animals. Pregnant animals stayed in concrete cages up to the last trimester of pregnancy when they were transferred into wooden cages. Each mating cage comprised 2 chambers with one serving as feeding and watering area, and the other being a resting area. Each chamber measured 70 cm x 69 cm x 50 cm. Wooden cages were used for suckling and growing of kids. There were two types of wooden cages i.e. family cage (housed doe and kids or many adults) and individual cages. Each family wooden cage measured 90 cm x 51 cm x 40 cm. Individual cage measured 60 cm x 50 cm x 40 cm. Wooden cages were partitioned by wire mesh. The sides and floor of the wooden cages were also covered with wire mesh. Wire mesh had a diameter of 2 mm, and was also used to line the exposed surfaces of wood to prevent gnawing by animals. The roof of each wooden cage was slanted and lined with felt to aid cleaning and drainage of liquid from stacks above.

Table 1. Distribution of data used for estimating parameters

Trait	Acronym	Number of Records	Means	Range	Standard Deviation
Birth weight, g	BWT	502	123.6	63.0-216.0	24.6
Weaning weight, g	WWT	441	535.6	270.3-1271.7	162.4
4-month weight, g	BWT4	413	954.9	487.8-2540.8	303.2
6-month weight, g	BWT6	392	1374.4	731.0-2894.8	342.9
8-month weight, g	BWT8	339	1690.1	946.1-3417.0	352.7
Pre-weaning daily gain, g/day	PWADG	441	6.9	2.2-18.3	2.4
Daily gain from 2-4 months, g/day	ADG4	413	7.0	1.2-26.3	3.4
Daily gain from 4-6 months, g/day	ADG6	392	6.8	0.1-25.2	4.0
Daily gain from 6-8 months, g/day	ADG8	339	6.2	0.1-25.3	3.8
Litter size at birth, number	LS	502	4.3	1.0-7.0	1.6
Litter size at weaning, number	LSW	492	3.8	1.0-7.0	1.6
Litter birth weight, g	LBWT	502	510.4	140.0-738.0	123.0
Litter weaning weight, g	LWWT	441	2107.6	370.0-3439.0	745.4
Days from joining to conception, days	DJC	502	20.8	1.0-58.0	14.2
Age of dam at birth, months	ADB	502	17.5	10.2-31.0	1.8
Lactation weight loss, g	LWTL	473	-359.3	-1560.0-536.0	322.3
Pre-weaning survival, %	PRS	492	88.8	20.0-100.0	24.3
Post-weaning survival, %	POWS	380	87.7	25.0-100.0	12.8
Feed intake, gDM/day	FI	199	108.2	67.8-135.6	7.9
Feed conversion ratio	FCR	199	14.4	5.7-44.6	5.5

Animals were fed on basal diet of elephant grass (*Pennisetum purpureum*) and a supplementary ration of concentrate that contained about 14% crude protein. Composition of the concentrate supplement was maize (44.0%), wheat bran (41.0%), Soybean (9.0%), Oyster shell (5.0%), common salt (0.5%) and vitamin-mineral-premix (0.5%). The animals were fed grass two times daily in the morning (8:00 hours GMT) and evening (17:00 hours GMT). Supplementary concentrate was fed in the afternoon at 14:00 hours GMT. Fresh grass was fed at a rate of about 200-1000g/head/day whilst concentrate was fed at 20-50g/head/day depending on the class (kid, young animal or adult) and physiological state (pregnant, dry or lactating) of the animal. Of the quantity of grass fed, about 30% was offered in the morning and 70% in the evening. Grass was harvested every three days and spread on the floor to wilt before being fed to animals. Water was offered *ad libitum.* Supplementary feed and water were provided in concrete troughs. Percentage dry matter of grass was 34.3, 89.9 and 92.5 for major rainy, minor rainy and dry seasons, respectively, whilst that of concentrate supplement was 87.2.

Cleaning of cages and grasscutter house was carried out daily. Feed and water troughs were also cleaned daily. Left-over feed was weighed and subtracted from amount offered to get daily feed intake. Routine de-worming was carried out by using Albendazole, 2.5% (Mobedco-Vet, Jordan). De-worming was carried out once in the minor rainy and dry seasons, and twice in the major rainy season.

Females were mated at 6 to 8 months of age when they weighed about 1.5 kg and above. Males were used for mating when they were 7 to 8 months old and weighed about 2.5 kg and above. Does were grouped into four and mated to one buck in concrete cages. Breeding bucks were separated from pregnant does after 40-60 days of paring or joining. Pregnant does in their last trimester were separated into family wooden cages.

All animals were identified at birth by metal ear tags (Hauptner, Germany). New born animals were weighed at birth (within 24 hours after birth), weaning, four, six and eight months of age. Litter size at birth and at weaning, doe weight at birth and at weaning were also recorded. Other records kept on the farm included flock health and individual health records, and income and expenditure records. All deaths were recorded and postmortem examination was carried out on dead animals. Kids were weaned at 60 days old. Weaner kids from one litter were kept together in one cage until they were 4 months old when females from the same litter were put together in one cage, whilst males were separated into individual cages. There is aggression and hostility towards each other, when

Table 2. Estimates of components for variance and covariance of traits**

Trait	σ^2_p	σ^2_g	σ^2_m	C^2	σ_{gm}	CV_g (%)	CV_m (%)
Birth weight	605.8	283.1	374.7	0.14	-138.2	13.6	15.7
Weaning weight	26380.0	14400.0	20220.0	0.04	-9380.0	22.4	26.5
Weight at 4 months	91960.0	43690.0	69970.0	0.01	-22530	21.9	27.7
Weight at 6 months	117590.0	78090.0	97850.0	0.10	-70490.0	20.3	22.8
Weight at 8 months	124430.0	105070.0	96050.0	0.08	-86060.0	19.2	18.3
Pre-weaning daily gain	5.7	1.7	4.5	0.18	-1.5	18.9	30.7
Post-weaning daily gain (2-4 months)	11.5	5.1	8.4	0.01	-2.2	32.3	41.4
Post-weaning daily gain (4-6 months)	16.0	6.2	2.1	0.69	-3.3	36.6	21.3
Post-weaning daily gain (6-8 months)	14.1	9.2	2.6	0.51	-4.4	48.9	26.0
Litter size at birth	2.5	0.1	2.5	0.03	-0.2	7.4	36.8
Litter size at weaning	2.5	0.1	2.5	0.00	-0.1	8.3	41.6
Litter birth weight	15140.0	7980.0	5130.0	0.00	-2030.0	17.5	14.0
Litter weaning weight	555620.0	307350.0	430440.0	0.00	-182180.0	26.3	31.1
Days from joining to conception	202.2	7.8	192.2	0.01	-0.4	13.4	66.7
Age of dam at birth	3.4	0.2	3.2	0.00	-0.1	2.6	10.2
Lactation weight loss	103880.0	64530.0	89880.0	0.00	-50530.0	70.7	83.4
Pre-weaning survival	589.4	35.4	651.4	0.00	-97.4	6.7	28.7
Pots-weaning survival	163.3	9.2	185.0	0.00	-30.9	3.5	15.5
Feed intake	61.9	23.6	8.2	0.66	-10.8	4.5	2.6
Feed conversion ratio	30.8	13.8	16.9	0.47	-14.5	25.8	28.6

*** σ^2_p = Phenotypic variance; σ^2_g = Direct additive genetic variance; σ^2_m = Maternal genetic variance; c^2 = proportion of phenotypic variance due to permanent effects of the dam; σ_{gm} = Covariance between direct and maternal genetic effects; CV_g = Direct genetic coefficient of variation; CV_m = Maternal genetic coefficient of variation*

sexually matured males are housed together (Annor *et al.*, 2009). Dry does were re-mated at about 2 weeks after weaning to allow for some rest resulting from stress of lactation.

Data were analyzed by mixed model methodology using a full animal model and all known genetic relationships, in single trait analysis, using the MTDFREML programme (Boldman *et al.*, 1995). Parameters estimated were phenotypic variance, direct additive and maternal genetic variances, covariance between direct and maternal effects, direct additive and maternal genetic coefficient of variation, proportion of phenotypic variance due to permanent effects of dam, direct and maternal heritability and direct-maternal genetic correlations of traits.

Single trait analysis was done according to the general mixed model:

$y = X\text{ß} + Z_ia + Z_jm + Z_kc + e$, where,

y = vector of observations; X = incidence matrix that associates ß with y; ß = vector of fixed effects, including litter size at birth, sex, parity of dam, year of birth, season of mating and season of birth; a = vector of breeding values for direct genetic effects; m = vector of breeding values for maternal genetic effects; c = vector of permanent environmental effects due to dam; Z_i, Z_j and Z_k = incidence matrices that associate a, m and c with y; and e = vector of random errors or residuals. Furthermore, with A, the numerator relationship matrix between animals, I_n, an identity matrix with order n, the number of dams and I, an identity matrix with order of the number of records, the co(variance) structure of random effects can be described as : $V(a) = \sigma^2_aA$, $V(m) = \sigma^2_mA$, $V(c) = \sigma^2_cI_n$, $V(e) = \sigma^2_eI$, where σ^2_a is the direct genetic variance, σ^2_m is the maternal genetic variance, σ^2_c is the maternal permanent environmental variance and σ^2_e is the residual variance. There were 572 animals in the pedigree that included the base animals for the analysis of all traits. Local convergence was considered to be met if the variance of the -2 log likelihoods in the simplex was less than 1×10^{-6}. After first convergence, restarts were made to find global convergence, with convergence declared when the values of -2 log likelihoods did not change to the second decimal. Heritability was categorized as low (< 0.30), medium (≥ 0.30-< 0.50) and high (≥ 0.50) (Rice *et al.*, 1970; Falconer and Mackay, 1996).

Genetic coefficient of variation was used as measure for ability of a trait to respond to selection and to determine

Table 3. Estimates of direct and maternal heritability, and genetic correlation of traits**

Trait	h^2_d	s.e. of h^2_d	h^2_m	s.e. of h^2_m	r_{dm}	s.e. of r_{dm}
Birth weight	0.47	0.149	0.62	0.115	-0.42	0.185
Weaning weight	0.55	0.123	0.76	0.103	-0.56	0.124
Weight at 4 months	0.48	0.039	0.76	0.063	-0.41	0.138
Weight at 6 months	0.66	0.185	0.83	0.108	-0.81	0.091
Weight at 8 months	0.84	0.179	0.77	0.049	-0.86	0.087
Pre-weaning daily gain	0.30	0.117	0.78	0.102	-0.55	0.169
Post-weaning daily gain (2-4 months)	0.45	0.126	0.73	0.100	-0.34	0.163
Post-weaning daily gain (4-6 months)	0.38	0.209	0.13	0.107	-0.92	0.180
Post-weaning daily gain (6-8 months)	0.65	0.260	0.19	0.137	-0.92	0.132
Litter size at birth	0.05	0.013	0.99	0.042	-0.40	0.186
Litter size at weaning	0.02	0.003	0.98	0.004	-0.39	0.135
Litter birth weight	0.53	0.111	0.34	0.074	-0.32	0.108
Litter weaning weight	0.55	0.001	0.77	0.109	-0.50	0.136
Days from joining to conception	0.04	0.009	0.95	0.033	-0.01	0.171
Age of dam at birth	0.07	0.015	0.95	0.037	-0.13	0.146
Lactation weight loss	0.62	0.122	0.87	0.114	-0.66	0.110
Pre-weaning survival	0.06	0.013	0.98	0.003	-0.64	0.084
Post-weaning survival	0.06	0.018	0.97	0.016	-0.75	0.103
Feed intake	0.38	0.366	0.13	0.198	-0.77	0.464
Feed conversion ratio	0.45	0.570	0.55	0.234	-0.95	0.273

*** h^2_d = Direct heritability; h^2_m = Maternal heritability; r_{dm} = Genetic correlation between direct and maternal effects; s.e. = Standard error*

genetic diversity of a trait in relative terms (Morris *et al.,* 1978; McLennan & Lewer, 2005). Coefficient of variation was computed as CV_x (%) = 100 x σ_x/μ, where σ_x is the standard deviation of the trait and μ is the estimated trait mean (Houle *et al.,* 1996). Coefficient of variation was classified as low (0-20%), medium (> 20-< 40%) and high (≥ 40%).

RESULTS

Estimates of components for variance and covariance of traits are presented in Table 2. Absolute values of phenotypic and, direct and maternal genetic variances were generally high for BWT, WWT, BWT4, BWT6, BWT8, LBWT, LWWT and LWTL. Next to these weight traits was PRS, followed by DJC, POWS, FI, FCR, ADG6, ADG8, ADG4 and PWADG. Age of dam at birth, LS and LSW had the lowest σ^2_p, σ^2_g and σ^2_m. The proportion of phenotypic variance due to permanent environmental effects of the dam (c^2) was essentially zero or nearly zero for all traits, with the exception of ADG6, ADG8, FI and FCR (Table 2). In these traits, the proportions of the phenotypic variance due to the permanent effect of the dam were large. The covariances between direct and maternal effects were negative.

The CV_g indicated that BWT, BWT8, PWADG, LS, LSW, LBWT, DJC, ADB, PRS, POWS and FI had low direct genetic diversity (variability). Weaning weight, BWT4, BWT6, ADG4, ADG6, LWWT and FCR had medium direct genetic diversity. Traits with the highest direct genetic diversity were ADG8 and LWTL. The maternal coefficient of variation followed a similar trend as the direct effects. However, there were some specific differences. Whereas the CV_m of PWADG and ADG4 were higher than their corresponding CV_g, the CV_m of ADG6 and ADG8 were lower than their corresponding CV_g. This trend was also observed in body weight traits. With the exception of LBWT and FI, CV_m of all reproductive and survival traits, and FCR were higher than their corresponding CV_g. Based on coefficient of variation, the maternal genetic variance of reproductive traits was generally higher than those of all other traits.

Estimates of heritability and genetic correlations between direct and maternal effects are presented in Table 3. Traits associated with size (body weight and growth rate) had medium (0.30 for PWADG) to high (0.84 for BWT8) h^2_d.

Maternal heritability of size traits were low (0.13 for ADG6) to high (0.83 for BWT6).

All reproductive traits, apart from those associated with weight, had low h^2_d, ranging from 0.02 for LSW to 0.07 for ADB. The h^2_m of reproductive traits were medium to high. Both PRS and POWS also had low h^2_d but very high h^2_m. FI and FCR had medium h^2_d. The h^2_m of FI and FCR were low and high, respectively. High standard errors associated with the heritability of FI and FCR reflect the relatively low number of records (Table 1) used for estimating variance components of the two traits.

Correlations between direct and maternal genetic effects (r_{dm}) were low negative to high negative (Table 3). The r_{dm} of size traits were medium (-0.34 for ADG4) to high (0.92 for ADG6 and ADG8). They were low (-0.01 for DJC) to high (-0.66 for LWTL) for reproductive traits, and high for survival traits, feed intake and feed efficiency.

DISCUSSION

Much of the differences in absolute values of phenotypic, and direct and maternal genetic variances are due to differing scales of each trait (Charlesworth, 1984; Houle, 1992). It is expected that a trait like litter size at birth that only has low values of 1-7 would have lower phenotypic and genetic variation than would a trait that might range from 946.1-3417.0 g (Table 1), such as 8-month weight. Both genetic variance and coefficient of variation are used as measures of diversity in domestic livestock (Morris *et al.,* 1978; McLennan & Lewer, 2005). There are two distinct reasons for making comparisons of genetic variation for quantitative characters. The first is to compare ability to respond to selection and the second is to make inferences about the forces that maintain genetic variability (diversity). The genetic coefficient of variation is appropriate for both purposes (Charlesworth, 1984; Houle, 1992). The coefficient of variation is a measure of relative comparison of variability or dispersion (Steel &Torrie, 1980; Gregory *et al.,* 1995). It does not depend on the unit scales, thus allowing comparison of experimental results involving different traits or variables. In this study, coefficient of variation was used as the final indicator of genetic variability (diversity) within a trait.

In general, growth rate showed the highest degree of additive genetic variation, followed by feed efficiency and body weight. Reproductive, survival and feed intake had relatively low additive genetic diversity. Reproductive traits that showed some degree of genetic diversity were lactation weight loss (high) and litter weaning weight (medium) (Table 2).

Estimates of phenotypic and genetic variances of traits in the grasscutter are scanty in the literature. However, results obtained in this work are similar to what generally pertains to other livestock species. Reports from cattle, sheep and goats have indicated that traits related to natural fitness (reproduction and survival) have low genetic variation whereas body weight and growth traits have medium to high genetic variation (Nicholas, 1987; Van Vleck *et al.,* 1987). Significant genetic variation has been reported for feed intake and feed efficiency for beef cattle (Archer *et al.,* 2002). Genetic variation in feed intake in this study is lower than reported in other species. The low additive genetic co-efficient of variation obtained for feed intake in this study is probably due to the low genetic standard deviation, relative to the mean value of the trait.

Genetic diversity, that is, the heritable variation within populations is usually acted upon by selection, be it natural or artificial. Differential survival of individuals in a particular population in each generation due to selection ultimately results in changes in gene frequencies, hence evolution of such populations. Genetic diversity therefore allows for evolution as well as artificial selective breeding to occur (Mensah & Okeyo, 2006). Additive genetic variance is variance of breeding values. Therefore, medium to high genetic diversity in body weight and growth traits, and feed efficiency will contribute to high response to artificial selection in these traits (Van Vleck *et al*; 1987; Nicholas, 1987; Blair, 1989). Reproductive traits (except those associated with size) and survival will be difficult to improve via artificial selection due to low genetic diversity (Van Vleck *et al;* 1987; Nicholas, 1987; Blair, 1989).

There have been no previous reports of maternal effects of traits in the grasscutter. A possible interpretation of zero or near zero permanent environmental effect of the dam on most traits is that the influence of non-permanent environmental factors is more important in these traits than permanent factors (Maria *et al.,* 1993). The large proportion of permanent environmental influence due to the dam observed in growth traits at the sexual matured stage of life, feed intake and feed efficiency indicates that the dam has great influence on these traits. These environmental influences (epigenetic effects) are possibly due to uterine capacity, feeding level at late gestation, and maternal behaviour of the dam (Maria *et al.,* 1993). The negative covariance between direct and maternal effects agrees with studies by Bryner *et al.* (1992) and Lee *et al.* (2000). Most traits in this study had medium maternal genetic variation (as indicated by their CV_m), with few having low or high values. Based on these results it was concluded that maternal effects account for a significant proportion of total phenotypic variance, which implies that maternal effects must be accounted for to obtain accurate breeding value estimates for these traits (Bryner *et al.,* 1992). However, the relatively high maternal genetic variance of growth traits at the pre-sexual stage (0-4 months), compared to the low values obtained at sexual maturity (4-8 months) indicates that maternal effects may be more important at the pre-sexual stage than at the sexual matured stage (Lee *et al.,* 2000). Similarly, high maternal genetic variance for reproductive and survival traits, and feed efficiency, compared to additive genetic variance gives an indication that maternal effects may be important in models for estimating breeding values of these traits.

Direct heritability values obtained in this study are similar to those reported by Yewadan (2000) who obtained medium to high (0.38-0.63) h^2_d for body weight traits and low (0.05-0.07) for LS in the grasscutter. Heritability results of this study are also similar to what is reported in other domestic livestock species. Koots *et al.* (1994) provided analysis and summary of published estimates of heritability for beef cattle production traits. Weighted mean direct heritability for growth and body weight traits were medium to high (0.22-0.79) and low (0.02-0.19) for reproductive traits. Koots *et al.* (1994) reported medium h^2_d for FI and FCR as 0.32 and 0.34, respectively, which are similar to 0.38 and 0.31, respectively obtained in this study. Their range of heritability for percentage mortality was low (0.10-0.15), and is close to low h^2_d of survival (0.06) obtained in this study.

The medium to high direct heritability in growth and body traits, FI, and FCR obtained in this study suggests that they are affected to a very large extent by additive genetic effects. With the exception of feed intake, the heritability results confirm the results of genetic variation of traits presented above. Reproductive and survival traits tend to have low heritability (Van Vleck *et al*; 1987; Nicholas, 1987; Blair, 1989). Natural selection of fitness traits (reproduction and survival) leads to loss of genetic variation, which results in low heritability (Hohenboken, 1985; Nicholas, 1987; Van Vleck *et al.,* 1987). Low heritability also suggests that factors other than additive genetic effects, which may or may not be subject to control by producers, account for substantial variation in these traits.

A broad range of heritability estimates of low to high (0.03-0.57) has been reported for litter weight in rabbits (Khalil *et al.,* 1987; Ferraz *et al.,* 1992; Rastogi *et al.,* 2000). The h^2_d estimates for litter weight in this work were high (0.53-0.55). This work observed a high h^2_d for lactation weight loss at weaning, and this is similar to high h^2_d of weight loss reported in the literature in pigs (Russo *et al.,* 2000) and in mice (Rikke *et al.,* 2006).

The medium to high direct heritability obtained for body weight and growth traits, litter weight, dam weight loss, feed intake and feed efficiency means that genetic selection will be effective in improving the performance levels of these traits (Hohenboken, 1985; Nicholas, 1987; Van Vleck *et al*., 1987).

Maternal heritability estimates for all traits were medium to high, with the exception of those for ADG6, ADG8 and FI, which were low. The results confirm the assertion made above that maternal effects have influence on most traits of the grasscutter. It is therefore necessary to account for maternal effects in breeding value estimation. Based on these results it was concluded that maternal effects affect growth of the grasscutter from birth to 4 months (pre-sexual mature stage) but this influence is reduced when the animal reaches sexual maturity. This is supported by the work of Meyer (2002). She analyzed large Australian beef field data sets and reported that maternal effects gradually decreased with increasing calf age, but were still important at 700 days.

The negative genetic correlation between direct and maternal effects indicates antagonistic effects (Bryner *et al.,* 1992; Lee *et al.,* 2000). Thus, as one effect increases, the other decreases. The high negative genetic correlation between direct and maternal effects has been observed in many studies (Diop, 1997; Lee and Pollak, 1997; Lee *et al.,* 2000). These authors suggested that negative estimates of direct-maternal genetic correlations for weaning weight were inflated when the effects of sire × year interaction were not included in the model. In this study sire x year interactions were not included in the model. Inclusion of a sire x year interaction term has been reported to reduce both direct heritability and direct-maternal correlation estimates (Lee *et al.,* 2000; Meyer, 2003). Lee *et al.* (2000) also concluded that a reason for why the estimate is so large and negative is not apparent although one reason may be that the pedigree structure might not be adequate for obtaining estimates of both direct and maternal heritabilities and the direct-maternal genetic correlation.

CONCLUSION

The findings in this study are in general agreement with reports in other farm livestock species. It was concluded that opportunity exists for fast genetic gains in the improvement of growth and body weight traits, whilst slow genetic progress may be made in reproductive and survival traits. Maternal effects are important in the grasscutter, and must be accounted for in breeding value estimations. The dam has permanent effect on growth at the sexual mature stage, feed intake and feed efficiency. The results could therefore be used to initiate grasscutter selection breeding programmes.

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