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Effects of non-genetic factors on reproductive and survival traits of the grasscutter (*Thryonomys swinderianus*)

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This study was conducted at the grasscutter section of the University of Education, Winneba, Ghana, to estimate non-genetic effects on reproductive and survival traits. Data consisted of records on 136 does from 2006 to 2010. Litter size at weaning, litter weight and lactation weight loss all increased (P < 0.01) with increasing litter size at birth. Litter weight and lactation weight loss increased (P < 0.05) at weaning, whilst days of joining decreased (P < 0.01), with increasing years. Minor rainy season was found to be the most suitable mating season. Dams that kidded in dry season took fewer (P < 0.05) days to conceive than in other seasons. Nursing dams lost more (P < 0.05) weight in dry and minor rainy seasons than in major rainy season. Increasing parity led to decreasing (P < 0.05) pre-weaning survival of offspring. Post-weaning survival of offspring decreased (P < 0.01) with increasing years. Kids conceived in the minor rainy and dry seasons had significantly higher (P < 0.05) post-weaning survival rates than those conceived in the major rainy season. Post-weaning survival rates of kids born in the minor rainy season were lower (P < 0.05) than those born in other seasons. It was concluded that non-genetic factors influenced fitness traits and must therefore be considered when designing grasscutter breeding programmes.

Key words: Domestication, environmental factors, reproduction, rodent.

INTRODUCTION

Fitness traits measure survival and reproductive rates (Goddard, 2009). Heritability estimates are generally low for these traits, suggesting that response to artificial selection will be slower than that of growth traits (Hohenboken, 1985; Nicholas, 1987; van Vleck et al., 1987). For these reasons, some breeders normally do not include these traits in the breeding objective and selection index , or do not include them in the recording

scheme (Haile-Mariam et al., 2007). Therefore, these traits sometimes show a negative genetic trend in livestock populations, despite their importance to profitability (Goddard, 2009). This negative trend may also arise from inbreeding depression (Cassell et al., 2003; Wall et al., 2005). The most important recommendation to overcome this problem is to include fitness traits in the breeding objective, recording scheme and selection index (Goddard, 2009). The low heritability of fitness traits also suggests that environmental or non-genetic factors, which may or may not be controllable by producers, account for substantial variation in these traits (Annor et al., 2012a).

The influence of non-genetic factors on reproductive and survival performance of domestic livestock is very well documented in traditional livestock species reared in tropical environments e.g. cattle (Osei and Effah-Baah, 1989; Osei et al., 1991) and pigs (Darko and Buadu, 1998; Baffour-Awuah et al., 2005). There is however, scanty information in the literature about effects of non-genetic factors on fitness traits of the grasscutter.

The objective of this work was to estimate effects of non-genetic factors on reproductive and survival traits of the grasscutter.

MATERIALS AND METHODS

Location, animals and experimental protocol have been described in a companion paper (Annor et al., 2012c). Essentially, the study was carried out at the grasscutter section of the Department of Animal Science Education, University of Education, Winneba, Ghana, from 2006 to 2010. Mampong-Ashanti is located in the transitional zone between the Guinea savanna zone of the north and tropical rain forest of the south of Ghana. It lies between latitude 07° 04' north and longitude 01° 24' west with an altitude of 457 m above sea level. Maximum and minimum annual temperatures recorded during the study period were 30.6 and 21.2°C, respectively (MSD, 2010). Rainfall in the district is bimodal, occurring from April to July (major rainy season) and again August to November (minor rainy season), and is about 122 cm per annum. The dry season occurs from December to March. The vegetation is transitional savanna woodland. The common fodder species that are routinely fed to grasscutters, *Pennisetum purpureum* (elephant grass) and *Panicum maximum* (guinea grass) are readily available in this zone.

Data consisted of records of 136 does over a 5-year period (2006 - 2010). Dams gave birth up to their third parity. They were fed a basal diet of elephant grass (*P. purpureum*) and a supplementary ration of concentrate which contained 14% crude protein and 1845.6 kcal/kg ME. Composition of concentrate supplement was maize (44%), wheat bran (41%), soybean (9%), oyster shell (5%), common salt (0.5%) and vitamin-mineral-premix (0.5%). Dams were reared and housed in concrete (for mating) and wooden (birth to pre-weaning) cages placed in a large animal house. Animals were reared in wooden cages during the post-weaning period. Kids were weaned at 2 months of age. Animals were identified by metal ear tags at the pre-weaning stage (Hauptner, Germany). The following traits were recorded:

Reproduction

Litter size at birth (LS), litter size at weaning (LSW), litter birth weight (LBWT), litter weaning weight (LWWT), days from joining (introduction of male to female) to conception (DJC), age at first parturition (AFP) and lactation weight loss at weaning of dam (LWTL).

Survival

Survival was defined in two ways, as trait of dam and as trait of offspring: Pre-weaning survival as a trait of dam (PRS_d): Percentage of kids surviving from birth to weaning. Pre-weaning survival as a trait of offspring (PRS_o): Survival from birth to weaning = 1; died = 0. Post-weaning survival as a trait of dam ($POWS_d$): Percentage of kids surviving from weaning to maturity (8 months). Post-weaning survival as a trait of offspring ($POWS_d$): Survival from weaning to maturity = 1; died = 0.

Data on reproduction (except age at first parturition) and survival as a trait of dam were analyzed using Linear mixed models (LMM) with MIXED procedure of SAS (2008). Data on survival as a trait of offspring were analyzed using Generalized linear mixed models (GLMM) with GLIMMIX procedure of SAS (2008). Model used for both situations was:

$$y = X\beta + Zu + \varepsilon$$

Where, y represents vector of observations; X and Z are design, or regressor, matrices associated with fixed and random effects, respectively; β is a vector of fixed-effects (type of birth, parity of dam, year of birth, season of mating and season of birth) parameters; u represents the random effects (animal or dam) vector; and ε, is the vector of residuals.

Sex was included as a fixed effect in analysis of survival as trait of offspring. An account was made for repeatable observations of reproductive traits and survival as trait of dam in SAS analysis.

Data on age at first parturition were subjected to least squares analysis using Generalized linear models (GLM) Type III procedure of SAS (2008) on the following fixed models:

$$y = X\beta + \varepsilon$$

Where, y represents vector of observations, X is design, or regressor, matrix associated with fixed effects; β is a vector of fixed effects (type of birth, parity of dam, year of birth, season of mating and season of birth) parameters; and **ε**, is the vector of residuals.

All model equations included 2-way interactions of fixed effects. Three-way and higher level interactions were not considered important. Differences between means of significant effects were separated by the probability of difference (PDIFF) procedure of SAS (2008). The following coding was used for fixed factors:

Type of birth (litter size): Single = 1, twin = 2, triplet = 3, quadruplet = 4, quintuplet = 5, sextuplet = 6 and septuplet = 7;

Sex of kid: Females = 1 and males = 2.

Parity of dam: First birth = 1, second birth = 2 and third birth = 3.

Seasons: Major rains (April to July) = 1, minor rains (August to November) = 2 and dry season (December to March) = 3.

Year of birth: 2006, 2007, 2008, 2009 and 2010.

RESULTS AND DISCUSSION

Effect of non-genetic factors on reproductive traits

Least squares means of reproductive traits are shown in

Table 1. Least squares means and standard errors for the effect of fixed factors on LS, LSW, LBWT and LWWT.

Fixed factor	LS		LSW		LBWT		LWWT	
	No.[x]	Units	No.	Units	No.	g	No.	g
Type of birth[y]				< 0.0001		< 0.0001		< 0.0001
1	-	-	7	1.0 ± 0.35^a	8	158.5 ± 25.40^a	7	844.4 ± 231.00^a
2	-	-	7	1.4 ± 0.35^a	7	296.2 ± 27.11^b	7	1031.6 ± 231.00^{ab}
3	-	-	31	2.6 ± 0.16^b	33	390.2 ± 12.53^c	31	1482.8 ± 109.77^b
4	-	-	46	3.7 ± 0.14^c	47	505.4 ± 10.71^d	46	2143.1 ± 91.11^c
5	-	-	30	4.3 ± 0.17^d	32	566.0 ± 12.71^e	30	2153.9 ± 111.59^c
6	-	-	4	6.0 ± 0.47^e	4	673.2 ± 35.83^f	4	2988.1 ± 305.59^d
7	-	-	5	5.4 ± 0.42^e	5	710.7 ± 32.16^f	5	2295.4 ± 275.33^{cd}
Parity[y]		0.4438		0.4438		0.3036		0.1843
1	57	3.7 ± 0.17	56	3.3 ± 0.19	57	450.7 ± 18.62	56	1782.4 ± 101.73
2	61	4.0 ± 0.16	61	3.5 ± 0.18	61	489.3 ± 18.13	61	1884.5 ± 98.23
3	18	4.1 ± 0.31	16	3.6 ± 0.36	18	489.4 ± 33.12	16	2199.3 ± 194.40
Year of birth[y]		0.8718		< 0.001		0.0280		0.0202
2006	26	3.7 ± 0.26	26	3.0 ± 0.28^{ac}	26	429.2 ± 27.04^a	26	1503.1 ± 145.82^a
2007	31	4.0 ± 0.24	31	3.9 ± 0.25^b	31	462.6 ± 24.77^a	31	1833.3 ± 130.97^{ab}
2008	24	4.0 ± 0.27	24	3.6 ± 0.29^{bc}	24	520.8 ± 28.13^b	24	2023.0 ± 152.01^{bc}
2009	35	4.0 ± 0.22	35	3.6 ± 0.25^{bc}	35	509.5 ± 24.45^b	35	2200.3 ± 127.79^c
2010	20	3.7 ± 0.29	17	2.6 ± 0.34^a	20	427.0 ± 30.90^a	17	1702.7 ± 182.09^b
Mating season[y]		0.0329		0.4860		0.0496		0.0001
Major rains	51	3.7 ± 0.18^a	51	3.3 ± 0.20	51	453.2 ± 19.38^a	51	1728.5 ± 106.53^a
Minor rains	42	4.3 ± 0.20^b	42	3.7 ± 0.23	42	520.3 ± 21.61^b	42	2082.8 ± 119.56^b
Dry season	43	3.6 ± 0.19^a	40	3.4 ± 0.23	43	452.0 ± 21.11^a	40	1846.8 ± 120.10^a
Season of birth[y]		0.1842		0.1612		0.7870		0.5425
Major rains	37	3.8 ± 0.21	34	3.5 ± 0.25	37	460.2 ± 23.31	34	1874.1 ± 130.45
Minor rains	29	3.6 ± 0.24	29	3.0 ± 0.27	29	472.1 ± 26.37	29	1730.0 ± 147.94
Dry season	70	4.1 ± 0.16	70	3.6 ± 0.17	70	480.2 ± 17.13	70	1925.2 ± 93.79
Overall	136	3.9 ± 0.11	133	3.4 ± 0.13	136	473.2 ± 12.06	133	1888.2 ± 66.58

[x]Number of animals; [y]Probability value of test of main effects; [abc]Means in the same column and within the same effect, with different superscripts are significantly different; LS, Litter size at birth; LSW, litter size at weaning; LBWT, litter birth weight; LWWT, litter weaning weight.

Tables 1 and 2. Mean values of kidding interval and number of parturitions per doe per year were 8.2 months and 1.8, respectively. Mean litter size at birth (3.9) and litter size at weaning (3.4) fall within ranges from the literature, 3.8 to 4.8 and 2.4 to 3.9, respectively (Adu et al., 1999; Jori and Chardonnet, 2001; Adu, 2003; Ikpeze and Ebenebe, 2004c; Addo et al., 2007). Mean litter birth weight (473.2 g) and litter weaning weight (1888.2 g) are also within ranges, 289.2 to 798.0 g and 1038.4 to 2242.5 g, respectively (Schrage and Yewadan, 1999; Adu et al., 2000; Ikpeze and Ebenebe, 2004a; Ikpeze and Ebenebe, 2004b).

There is positive correlation between duration of male-female pairing (joining) and conception rates (Addo et al., 2003). Determination of optimal duration of pairing to achieve pregnancy is important for successful breeding.

Mean days of joining to conception of 21 days observed in this study is far below the common practice in Ghana where most farmers pair males and females for no less than 45 days (Greater Accra Grasscutter Farmers Association, personal communication). Breeding males prey on pregnant does if duration of pairing is too long. There is also a common practice where farmers leave breeding pairs together until parturition. This practice results in breeding males preying on male kids in the litter (Asibey, 1974; Addo et al., 2003).

This study provides evidence that the period for which farmers commonly pair males and females for breeding is too long. Addo et al. (2003) observed 80% sexual receptivity and 79.3% resultant pregnancies within the first 3 days of male-female pairing. Addo et al. (2007) reported a conception rate of 87.1% when males and

Table 2. Least squares means and standard errors for the effect of fixed factors on DJC, ADB and LWTL.

Fixed factor	DJC No.[x]	DJC Days	AFP No.	AFP Months	LWTL No.	LWTL g
Type of birth[y]		0.3988		0.1696		0.0006
1	8	22.0 ± 3.98	5	12.3 ± 0.33	7	122.7 ± 93.33[a]
2	7	29.3 ± 4.22	1	12.0 ± 0.71	7	-119.0 ± 93.33[ab]
3	33	20.1 ± 1.98	16	11.6 ± 0.19	31	-254.1 ± 45.08[b]
4	47	21.8 ± 1.70	23	11.8 ± 0.17	46	-267.7 ± 36.81[b]
5	32	20.1 ± 2.00	9	12.6 ± 0.30	30	-452.3 ± 45.08[c]
6	4	28.6 ± 5.57	1	11.6 ± 0.71	4	-360.0 ± 123.46[bc]
7	5	18.7 ± 5.05	2	12.1 ± 0.52	5	-588.0 ± 110.42[cd]
Parity[y]		0.5136				0.0558
1	57	22.1 ± 1.51	-	-	56	-251.4 ± 38.02
2	61	20.0 ± 1.47	-	-	61	-301.0 ± 36.38
3	18	22.7 ± 2.68	-	-	16	-317.0 ± 72.14
Year of birth[y]		0.0019		0.0461		0.0255
2006	26	18.8 ± 2.08[a]	18	11.6 ± 0.26[a]	26	-193.6 ± 55.13[a]
2007	31	28.2 ± 1.91[b]	9	12.0 ± 0.31[ab]	31	-227.7 ± 49.51[a]
2008	24	22.4 ± 2.17[a]	11	12.0 ± 0.28[ab]	24	-311.9 ± 58.77[b]
2009	35	19.1 ± 1.82[a]	16	12.4 ± 0.22[b]	35	-370.4 ± 47.27[b]
2010	20	14.5 ± 2.38[c]	3	12.0 ± 0.45[ab]	17	-389.8 ± 68.91[b]
Mating season[y]		0.0239		0.2107		0.0259
Major rains	51	24.6 ± 1.56[a]	23	12.3 ± 0.28	51	-272.6 ± 40.12[a]
Minor rains	42	17.9 ± 1.74[b]	19	12.0 ± 0.27	42	-355.6 ± 44.40[b]
Dry season	43	20.0 ± 1.70[c]	15	11.7 ± 0.27	40	-256.7 ± 44.97[a]
Season of birth[y]		0.0482		0.1445		0.0233
Major rains	37	20.1 ± 1.85[a]	14	12.3 ± 0.30	34	-220.9 ± 48.12[a]
Minor rains	29	23.6 ± 2.12[b]	12	12.2 ± 0.30	29	-313.9 ± 55.03[b]
Dry season	70	18.8 ± 1.39[c]	31	11.6 ± 0.22	70	-322.4 ± 34.02[b]
Overall	136	21.0 ± 0.98	57	11.9 ± 0.10	133	-293.7 ± 24.91

[x]Number of animals; [abc]Means in the same column and within the same effect, with different superscripts are significantly different; [y]Probability value of test of main effects; DJC, Days of joining to conception; AFP, age at first parturition; LWTL, lactation weight loss.

females were paired for 14 days, and recommended that mates be paired for 2 to 4 weeks for mating purposes. In this study, only 60.0% of females were pregnant at the mean 21 pairing days (3 weeks), with 75.0 and 91.2% of females pregnant at the end of the 4th and 5th week of pairing, respectively. It is therefore being suggested that mates (males and females) should be paired for a maximum of 5 weeks (35 days) for mating purposes. This recommendation is based on the optimum pregnancy rate of 90.0% reported for the grasscutter (Schrage and Yewadan, 1999; Addo et al., 2007), and an observation in this study that males begin preying on pregnant females after about 40 days of pairing. One suggestion for producers is to only retain replacement females from those that get pregnant early. For example, farmers may

keep replacements out of females that get pregnant in the first 21 days.

Mean age at first parturition of 11.9 months observed in this study is similar to 11.0 months reported by Schrage and Yewadan (1999). It is also close to 10 to 11 months calculated from data presented by Mensah and Okeyo (2006). Kidding around 11 to 12 months is ideal because age at first mating is around 6 to 7 months, and gestation is approximately 5 months (Schrage and Yewadan, 1999; Adu et al., 1999).

Mean lactation weight loss of dam (-293.7 g) was approximately 10% of the dam's body weight at birth, despite being given supplementary feed. A similar observation was made by Mattingly and Mcclure (1985) in cotton rats. They reported that even with ample food,

lactating cotton rats lost 11% of their body weight at weaning.

Mean kidding interval of 8.2 months obtained in the study is similar to 7.5 months reported by Adu et al. (1999). It is however longer than the 6.9 and 6 to 7 months reported by Schrage and Yewadan (1999) and Mensah and Okeyo (2006), respectively. Shorter kidding intervals are desirable to increase number of litters per doe per year. Kidding interval is variable and depends greatly on weaning period. Weaning age can be reduced to increase number of litters per doe per year. In this study, weaning was done at 2 months, but it could be reduced to about 1 month, which would reduce kidding interval to 7.2 months to improve upon number of litters per doe per year. This is supported by the work of Adu (2003). In his study of patterns of parturition and mortality in weaned grasscutters, he concluded that it is practical to wean kids at 4 weeks of age with proper post-weaning management. Based on the results of this study and experience from the field and in the literature farmers are advised to wean kids at the age of 2 months.

Litter size at weaning, litter birth weight, litter weaning weight and lactation weight loss all increased ($P < 0.01$) with increasing litter size at birth (Tables 1 and 2). However, kids of various litter size groups had similar ($P > 0.05$) days of joining to conception and age at first parturition, indicating that the effect of litter size on these two traits was not important. Litter size at birth explained 57.0, 72.8, 30.7 and 22.9% of the variation in litter size at weaning, litter birth weight, litter weaning weight and lactation weight loss, respectively.

As litter size at birth increases, litter size at weaning will increase due to a high positive genetic correlation between the two traits (Annor et al., 2012b). In mammals, litter weight is positively correlated with litter size (Millar, 1981). Therefore, if litter size at birth increases, litter birth weight and litter weaning weight will increase. Large litters consume more milk than small litters (Epstein, 1978); therefore, increasing litter size will also increase lactation weight loss. In some instances, dams of litter size of 6 to 7 became very emaciated during suckling, sometimes resulting in alopecia and death. Emaciated condition of nursing female reflected the physiological stress resulting from raising an extraordinary large litter over the pre-weaning period (Cameron, 1973). These results should stimulate experimental inquiry into role of nutrition as an ultimate factor in family size determination. There was no influence ($P > 0.05$) of parity on any reproductive trait. Parity was relatively not important in explaining variation in reproductive traits, possibly because of the few parity levels (1, 2 and 3) involved in the study or the few observations made for Parity 3, compared to Parity 1 and 2.

Year of birth had an effect ($P < 0.05$) on all reproductive traits, except, litter size at birth (Tables 1 and 2). Mean litter size at birth was similar in all years. There was no trend of the effect of year on reproductive traits. However,

litter weaning weight and lactation weight loss increased whilst days of joining to conception decreased with increasing years. Year of birth explained 3.7, 4.3 and 7.1% of the variation in litter weight at weaning, days of joining to conception and lactation weight loss, respectively.

It was observed by Addo et al. (2007) that increasing years of the dam had an effect of increasing weaning weight. In that study, increasing year by 1 unit increased weaning weight by 39.6 g. Observed increase in weight with increasing years led to recorded increases in litter birth weight and litter weaning weight with years. Days of joining to conception decreased with years because multiparous dams with bigger body size conceived earlier than primiparous dams with smaller body size. Increasing years has the effect of producing bigger dams and also bringing many multiparous dams into play. Lactation weight loss increased with increasing years because heavier offspring were produced with increasing years. The demand for milk from heavier offspring is higher than that of lighter ones (Epstein, 1978), therefore, physiological stress resulting from suckling from heavier offspring is also higher than that of lighter ones (Cameron, 1973; Vaughan et al., 2009).

Season of mating affected ($P < 0.05$) litter size at birth, litter birth weight ($P < 0.05$), litter weaning weight ($P < 0.01$), days of joining to conception ($P < 0.05$) and lactation weight loss ($P < 0.05$) but had little effect ($P > 0.05$) on litter size at weaning and age at first parturition. Mean litter size at weaning and age at first parturition of dams that conceived in all seasons were similar. However, dams that conceived in the minor rainy season had higher ($P < 0.05$) litter size at birth, litter birth weight ($P < 0.05$), litter weaning weight, lactation weight loss and fewer ($P < 0.05$) days of joining to conception than those conceiving in major rainy and dry seasons.

Mean litter size at birth, litter size at weaning, litter birth weight, litter weaning weight and age at first parturition did not differ ($P > 0.05$) between seasons of birth. However, dams that kidded in dry season took fewer ($P < 0.05$) days to conceive than those kidding in the other seasons. Dams that kidded in dry and minor rainy seasons lost more ($P < 0.05$) weight than those kidding in major rainy season.

The best reproductive performance of females was exhibited by those mated in the minor rainy season. Litter size at birth, litter birth weight and litter weaning weight were significantly higher for females mated in the minor rainy season than the other two seasons. Lactation weight loss at weaning was also higher for females mated in the minor rainy season. The shortest days of joining to conception was also observed in the minor rainy season. The minor rainy season, August to November, coincides with the natural breeding season of grasscutters in the wild, as the major rains had encouraged the growth of fresh vegetation with abundant food supply (GNA, 2009). The abundance of food

provides good nutrition, which is important for adequate and good ovulation (Bronson, 2009). This probably led to the highest litter size in dams mated in the minor rainy season. An increase in litter size at birth also led to an increase in litter weight at birth because in mammals litter weight is positively correlated with litter size (Millar, 1981).

Dams that were mated in the minor rainy season took the shortest days to get pregnant, probably because that is their natural breeding season. The minor rainy season is therefore the best breeding period for domesticated grasscutters, although the animals are known to breed throughout the year (Asibey, 1974; Adu, 2003; Addo et al., 2007). Lactation weight loss was highest among does mated in the minor rainy season because these females gave birth in the dry season, and produced the largest litters that also had the highest litter birth weight. Poor grass quality, in addition to increased litter size and litter birth weight, in the dry season adversely affected lactation weight loss. Despite providing supplementary feeding, the effect of season was still significant. This is relevant when it is recognized that feeding standards used to provide supplementary feed for nursing mothers were based on those of growing grasscutters.

Dams that gave birth in the dry season had the shortest days of joining to conception because they were mated in the minor rainy season which is the best or natural mating period (GNA, 2009). Dams that gave birth in the dry season also lost more weight than those that gave birth in the major rains because the former had the largest litter size at birth and highest litter birth weight, though the difference between the means of season of birth was not significant. It is concluded that farmers could mate their animals in any season of the year but should make sure to provide animals with adequate nutrition.

Effect of non-genetic factors on survival traits

Least squares means of survival traits are shown in Table 3. Post-weaning survival was higher than pre-weaning survival. There is wide variation in survival rates of grasscutter in the literature, most likely due to wide variations in environmental and management conditions. Both pre- and post-weaning survival rates range from 75 to 100% (Mensah, 2000; Adu, 2003; Ikpeze and Ebenebe, 2004b; Addo et al., 2007). Mean survival rates (as trait of dam and offspring) are higher than 75% observed in Nigeria (Ikpeze and Ebenebe, 2004c) and Benin (Mensah, 2000), respectively. They are however lower than 100% reported by Addo et al. (2007) in Ghana.

Pre- and post-weaning survival rates did not differ (P > 0.05) between litter sizes (Table 3). The results do not follow general observation in rodents that survival of kids decreases with increasing litter size (Cameron, 1973;

Myers and Master, 1983), probably because the husbandry was congenial for survival in this study. Both grass and concentrate supplement were provided to nursing dams to enable them provide sufficient milk for kids. Based on the present results it is suggested that it will be advantageous to select animals from larger litters at weaning, on account of their survival, for breeding.

Survival did not differ (P > 0.05) between the sexes. Thus, sex had no influence on pre- and post-weaning survival. There is little information in the literature on survival rates in the sexes. However, a study in wild birds also observed no differences in survival between the sexes (Fisher and Wiebe, 2006).

Year of birth had an effect (P < 0.05) on all survival traits (Table 3). Nevertheless, there was no trend of the effect of year on survival traits. However, post-weaning survival rate as a trait of offspring decreased with increasing years. Year of birth explained 2.7% of the variation in this trait. The reduction in post-weaning survival as the years progressed was attributed to an increase in population of animals with increasing years. The annual population growth rate of the study animals on the farm was 108.5%. Increase in population facilitates the spread of infectious diseases in grasscutter herds (Annor et al., 2009). This probably led to reduced survival. In domestic animals, survival depends not only on diseases and their characteristics but also on husbandry practices (Thrusfield, 2007). Animals may die from negligence of farm workers or from the absence of farm inputs. It is concluded that most year effects were due to variation in management practices, knowledge and/experience of the farmer and farm workers, and facilities available on the farm.

Season of mating affected (P < 0.01) post-weaning survival but had little effect (P > 0.05) on pre-weaning survival rates. Kids conceived in all seasons had similar pre-weaning survival rates. Kids conceived in minor rainy and dry seasons had higher (P < 0.01) post-weaning survival rates than those conceiving in major rainy season (Table 3). Mean pre-weaning survival rate as trait of dam and offspring did not differ (P > 0.05) between seasons of birth. Post-weaning survival rates of kids born in minor rainy season were lower (P < 0.05) than those born in other seasons.

Animals that were conceived in the major rainy season had significantly lower post-weaning survival rates than those conceived in other seasons. Post-weaning here refers to age of 2 to 8 months. Effect of season on survival is known to be mediated through quantity and quality of food available to rodents (Cittadino et al., 1994). Most dams that conceived in the major rainy season (April to July) gave birth and weaned kids in the minor rainy season (August to November). These weaned kids had to spend the first part (4 months) of their adult life (post-weaning) in the dry season (December to March) when grass quality was poor (Annor et al., 2012c). Poor nutrition is probably

Table 3. Least squares means and standard errors for the effect of fixed factors on survival traits.

Fixed factor	PRS$_d$		POWS$_d$		PRS$_O$		POWS$_O$	
	No.[x]	%	No.	%	No.	%	No.	%
Type of birth[y]		0.1534		0. 6236		0.1934		0.2514
1	8	99.9 ± 8.55	6	99.9 ± 11.58	8	97.6 ± 0.11	6	97.9 ± 0.12
2	7	99.9 ± 8.55	7	99.7 ± 10.70	14	97.2 ± 0.09	11	93.3 ± 0.11
3	33	85.9 ± 3.94	27	87.8 ± 5.46	96	79.1 ± 0.04	73	88.4 ± 0.06
4	47	93.3 ± 3.37	39	82.1 ± 4.63	179	87.3 ± 0.04	145	83.1 ± 0.05
5	32	86.29 ± 4.06	23	90.7 ± 5.91	157	81.9 ± 0.04	111	80.2 ± 0.06
6	4	71.4 ± 11.31	3	92.1 ± 16.36	24	91.5 ± 0.10	18	79.4 ± 0.13
7	5	77.2 ± 10.11	5	79.3 ± 12.67	24	77.6 ± 0.10	20	77.4 ± 0.12
Sex[y]						0.1633		0. 6630
Male	-	-	-	-	245	84.9 ± 0.04	187	83.9 ± 0.05
Female	-	-	-	-	257	81.5 ± 0.04	197	85.1 ± 0.04
Parity[y]		P = 0.3472		P = 0.5731		0.0444		0.4236
1	57	90.1 ± 3.07	47	86.7 ± 4.12	224	88.0± 0.04[a]	177	83.9 ± 0.05
2	61	89.4 ± 2.97	50	86.3 ± 4.04	203	86.7± 0.04[a]	160	80.9 ± 0.05
3	18	80.6 ± 5.75	13	85.5 ± 7.84	75	74.8± 0.06[b]	47	88.7 ± 0.07
Year of birth[y]		0.0058		0.0170		0.0098		0.0031
2006	26	81.8 ± 4.26[a]	25	92.2± 5.22[a]	79	78.9 ± 0.06[ab]	70	91.3± 0.07[a]
2007	31	96.8 ± 3.90[b]	31	98.1± 4.69[a]	117	91.3± 0.05[b]	116	99.9± 0.05[a]
2008	24	91.0 ± 4.44[b]	23	66.3± 5.45[b]	91	88.3± 0.05[b]	82	79.2± 0.06[b]
2009	35	93.5 ± 3.73[b]	24	87.6± 5.45[a]	148	88.4± 0.04[b]	94	75.1± 0.06[b]
2010	20	71.0 ± 5.27[a]	7	94.3± 9.87[a]	67	79.0± 0.07[a]	22	75.8± 0.10[b]
Mating season[y]		0. 6126		0.0112		0.2340		< 0.0001
Major rains	51	89.1 ± 3.24	36	74.3± 4.47[a]	188	80.8 ± 0.05	124	72.3± 0.07[a]
Minor rains	42	85.8 ± 3.61	35	92.4± 4.66[b]	165	78.4 ± 0.05	129	91.0± 0.06[b]
Dry season	43	90.9 ± 3.65	39	96.0± 4.28[b]	149	90.3 ± 0.05	131	99.9± 0.05[b]
Season of birth[y]		0.3456		0.0076		0.1177		0.0233
Major rains	37	92.6 ± 3.95	32	96.3± 4.69[a]	133	86.3 ± 0.06	111	85.5± 0.06[a]
Minor rains	29	83.9 ± 4.27	23	76.7± 5.53[b]	98	82.8 ± 0.06	68	73.7± 0.07[b]
Dry season	70	88.6 ± 2.77	55	90.5± 3.61[a]	271	90.5 ± 0.04	205	94.3± 0.05[a]
Overall	136	86.5 ± 2.26	110	87.4 ± 2.70	502	84.4±0.04	384	85.0±0.05

[x]Number of animals; [y]Probability value of test of main effects; [abc]Means in the same column and within the same effect, with different superscripts are significantly different; PRS$_d$, pre-weaning survival as trait of dam; POWS$_d$, post-weaning survival as trait of dam; PRS$_o$, pre-weaning survival as trait of offspring; POWS$_o$, post-weaning survival as trait of offspring.

responsible for the poor post-weaning survival of animals conceived in the major rainy season.

Post-weaning survival of animals born in the minor rainy season was significantly poorer than those born in other seasons. Kids born in the minor rainy season were weaned in the same season. Similar explanation given above also applies to this situation because these weaned kids had to spend the first part (4 months) of their adult life (post-weaning) in the dry season (December to March).

Interaction effects of fixed factors on traits

Interaction effects of type of birth with all other fixed factors on litter size at weaning, litter birth weight, litter weaning weight and post-weaning survival as a trait of offspring were important (Table 4). Year × season of mating interaction was important for litter size at birth, litter size at weaning, litter birth weight, litter weaning weight and days of joining to conception. Year × seasons and season of mating × season of birth interactions were

Table 4. Interaction effects of fixed factors on fitness traits.

Type of interaction	LS	LSW	LBWT	LWWT	DJC	AFP	LWTL	PRS$_d$	POWS$_d$	PRS$_o$	POWS$_d$
TOB*Sex	-	-	-	-	-	-	-	-	-	ns	ns
TOB*Parity	-	**	**	**	ns	-	ns	ns	ns	ns	**
TOB*YOB	-	**	**	*	ns	ns	ns	ns	ns	ns	**
TOB*SOM	-	**	**	**	ns	ns	ns	ns	ns	ns	**
TOB*SOB	-	**	**	**	ns	ns	ns	ns	ns	ns	*
Sex*Parity	-	-	-	-	-	-	-	-	-	ns	ns
Sex*YOB	-	-	-	-	-	-	-	-	-	ns	ns
Sex*SOM	-	-	-	-	-	-	-	-	-	ns	ns
Sex*SOB	-	-	-	-	-	-	-	-	-	ns	ns
Parity*YOB	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	*
Parity*SOM	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	ns
Parity*SOB	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	**
YOB*SOM	*	*	*	*	**	ns	ns	ns	ns	ns	ns
YOB*SOB	ns	ns	ns	ns	**	ns	ns	ns	*	**	*
SOM*SOB	ns	ns	ns	ns	**	ns	ns	ns	*	ns	ns

* = $P < 0.05$; ** = $P < 0.01$; LS, Litter size at birth; LSW, litter size at weaning; LBWT, litter birth weight; LWWT, litter weaning weight; DJC, days from joining to conception; AFP, age at first parturition; LWTL, lactation weight loss; PRS$_d$, pre-weaning survival as trait of dam; POWS$_d$, post-weaning survival as trait of dam; PRS$_o$, pre-weaning survival as trait of offspring; POWS$_o$, post-weaning survival as trait of offspring; TOB, type of birth; YOB, year of birth; SOM, season of mating; SOB, season of birth.

important for joining to conception. Year × season of birth and season of mating × season of birth interactions were important for post-weaning survival as a trait of dam.

The significant first order interactions observed in this study for both reproductive and survival traits indicate that the ranking of levels of the same factor do not hold when combined with sets of levels of two factors are considered. There are no previous studies on interactions of fixed factors in the grasscutter. However, studies in rodents and other farm animal species have confirmed the existence of some of the above interactions. Significant parity × season interactions on litter size and litter weight in rabbits were reported by Tuma et al. (2010). Chineke (2005) also reported significant interactions of parity × season on litter weight in rabbits. Significant year × season of birth interactions on litter size has been reported in pigs (Gaugler et al., 1984) and goats (Hamed et al., 2009). The importance of interactions of fixed factors has been recognized in farm animal genetic improvement and evaluation programmes (Diop, 1997; Lee and Pollak, 1997; Lee et al., 2000; Meyer, 2003).

Conclusion

The mean values of traits obtained in this study were compared favourably with similar studies conducted in sub-Saharan Africa on the grasscutter. In most cases, the study showed that non-genetic effects influenced reproductive and survival traits. It is important that the extent to which these environmental factors influence traits under study be evaluated for appropriate

adjustments to be made when estimating genetic values for a breeding programme in grasscutter. Interaction effects were important in the grasscutter and must be considered in genetic improvement and evaluation programmes. There is also a need to find the nutrient requirements for pregnant and lactating grasscutters.

Conflict of interests

The author(s) have not declared any conflict of interests.

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