

The estimation of live weight based on linear traits in indigenous Tswana goats at various ages in Botswana

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Accepted: 9 September 2011 / Published online: 2 October 2011
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Abstract The objective of this study was to determine the usefulness of some linear body measurements in predicting live weight in indigenous Tswana goats at various ages. Data for this study were obtained from 2,783 goats sampled from six agricultural regions of Botswana except for Tsabong and Ghanzi districts. Fifteen farmers keeping goats were randomly selected from each district and records taken on a random sample of 4–12 animals per farm depending on the 1999 Botswana Government average district flock size. Body measurements recorded were heart girth, height at withers, body length, shoulder width, and live weight. Information on age of each animal was estimated from dentition; flock size and sex of the animal were also recorded for each farm. Regression analysis using stepwise selection method in Statistical Analysis System was used to determine prediction equations for live weight with heart girth, height at withers, body length, and shoulder width as independent variables for male and female goats of different ages. In all models, heart girth contributed most in explaining variation in body weight as shown by high partial R^2 which ranged from 0.48 for female mature to 0.80 for mature male goats. Using mean square error, R^2 , and Mallows' $C(p)$, the best prediction

equations were for female and male kids ($R^2=0.83$ and 0.82 , respectively) and mature male goats ($R^2=0.82$). The poorest model was for mature female goats with $R^2=0.57$. Live body weight could be estimated with accuracy from linear body measurements in Tswana goats which are unique for each sex and age. More research is required to explore using these models to develop measuring tapes for use by resource poor farmers who keep indigenous Tswana goats.

Keywords Linear traits · Live weight · Mallow's $C(p)$ · Multiple regression · Tswana goats

Introduction

Goat rearing is an important agricultural activity in Botswana (Oladele and Monkhei 2008). The indigenous Tswana goats constitute (77%) of the 1.6 million national goat population. The majority (89%) of the 79, 341 goat holdings distributed across the country keep these goats (Central Statistics Office 2006). Characterization of this breed has been limited hence it is not fully exploited and conserved (Nsoso et al. 2004). Traditionally, as elsewhere in the tropics, goats are an important resource providing nutrition (meat and milk), income, employment, and food security to poor farmers (Nsoso et al. 2004; Khan et al. 2006; Moacén-ud-Din et al. 2006; Ojedapo et al. 2007; Kunene et al. 2009). Often farmers need to know the body weight of their animals for management reasons such as feeding, determination of dosages of various drugs, and most importantly for marketing (Slippers et al. 2000; Otoikhian et al. 2008). A good estimate of body weight is also important for studying the growth pattern of goats and selection for breeding purposes (Slippers et al. 2000). However, due to unavailability of scales, farmers in rural

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areas use visual assessment skills to determine body weight. This method of estimating body weight often has errors such as using the same estimate for more than one breed of a particular species and being deceived by the body structure of the animal (Otoikhian et al. 2008). Such difficulties can be overcome by developing simple, yet reasonably accurate methods to predict body weight such as the use of prediction equations based on linear body measurements using easily obtainable and cheaply available metric tape rule (Slippers et al. 2000; Adeyinka and Mohammed 2006a; Moaen-ud-Din et al. 2006; de Villiers et al. 2009). Fajemilehin and Salako (2008) studied West African Dwarf goat body measurements characteristics and concluded that body weights could be predicted accurately from heart girth, body length and wither height among other variables. Therefore, the objective of this study was to determine the usefulness of some linear body measurements as independent variables in predicting live weight of indigenous Tswana goats at various ages.

Materials and methods

The data used in this study were described in detail by Nsoso et al. (2004). Briefly, the study area covered representative areas of six agricultural regions that spanned the whole of Botswana except for Tsabong and Ghanzi districts. A total of 2,783 goats were sampled. In each district, a total of 15 farmers keeping goats were randomly selected and records were taken on a random sample of 4–12 animals per farm depending on the Botswana Government (1999) average district flock size. Body length, heart girth, height at withers, and shoulder width were recorded. In addition, age of each animal (estimated by dentition), flock size, and sex of the animal were recorded.

For this study, sex was characterized as females and males. Four age sub-classes were used following Katongole et al. (1996), namely: 0–12 (kids), 13–24 (grower), 25–36 (mature), and 37 months and older goats (old). The Procedure General Linear Model in Statistical Analysis System (SAS 2001–2003) was used initially to analyse the data by fitting the model below to identify the factors significantly affecting performance:

$$Y_{ijk} = \mu + \alpha_i + \beta_j + \alpha\beta_{ij} + e_{ijk} \quad (\text{Model1})$$

where:

$$\begin{aligned} Y_{ijk} &= \text{observed animal body weight} \\ \mu &= \text{general mean body weight} \\ \alpha_i &= i^{\text{th}} \text{ animal sex effect, } i = 1, 2 \\ \beta_j &= j^{\text{th}} \text{ animal age effect, } j = 1, 2, 3, 4 \\ \alpha\beta_{ij} &= ij^{\text{th}} \text{ sex and age interaction effect} \\ e_{ijk} &= \text{random variation } \sim N(0, \sigma^2) \end{aligned}$$

Least squares means and their standard error are reported. The means were separated using the least significant difference. Having identified the important effects, stepwise regression analysis using the Procedure REG in SAS (2001–2003) was used to find a suitable model to predict live weight (dependent variable Y) using independent variables (X) body length, heart girth, height at withers, and shoulder width. The model below was fitted:

$$Y_{ij} = a + \sum b_i X_i + e_{ij} \quad (\text{Model2})$$

where: a = intercept

b_i = slopes rate of change in body weight with unit change in independent variable

X_i = independent variables – heart girth(hg), shoulder width(sw), body length(bl) and height at withers(hw)

Y_{ij} = dependent variable (weight)

e_{ij} = random variation $\sim N(0, \sigma^2)$

For regression analysis, all animals aged 25 months and above were categorized as mature since their average weights were similar. Hence, the models were determined for male and female goats and three age groups namely kids, growers, and mature animals. These models were tested for significance using F statistic, while each parameter estimate was tested using the t statistic. The importance of each variable was determined by assessing its contribution to the model using the partial R^2 , coefficient of determination R^2 , Mallows' $C(p)$ statistic, and mean square error (MSE).

Results

There was a significant interaction ($P < 0.05$) between age and sex of the animals indicating that live weight of Tswana goats varied depending on sex and age (Table 1). Body weight, body length, height at withers, and heart girth tended to be significantly higher as age increased. In terms of sex, although, these traits did not differ significantly ($P > 0.05$), they were generally higher in male than female goats at the same age (Table 1).

Based on the observed significant interaction between sex and age, multiple regression analysis with stepwise method of selecting independent variables was performed according to age and sex categories (Table 2).

In all the models, the first variable to enter was heart girth which had the highest partial R^2 values ranging from 0.48 to 0.80 in the final models and the largest F values (Table 2). Thus heart girth contributed most to explaining variation in live weight and was included in all regression equations. All models with heart girth alone had high $C(p)$ and MSE values (Table 2) confirming the inadequacy of

Table 1 Measurement parameters (mean±SE) of 2,783 indigenous Tswana goats from farms in various districts of Botswana, in relation to age and sex (male and female)

Measurement parameter	Age (months)							
	0–12		13–24		25–36		>37	
	Male	Female	Male	Female	Male	Female	Male	Female
Live weight (kg)	18.8±0.51a	18.0±0.52a	33.8±0.51b	33.2±0.32b	48.8±0.99d	41.1±0.29c	45.5±1.91cd	41.8±0.48c
Body length (cm)	47.9±0.47a	46.9±0.47a	59.2±0.46b	58.5±0.29b	65.6±0.91d	62.8±0.27c	57.7±1.75b	62.1±0.44c
Height at withers (cm)	53.2±0.67a	51.7±0.67a	64.7±0.66bc	63.5±0.42b	71.1±1.29d	65.2±0.38c	64.9±2.49bcd	65.1±0.62c
Heart girth (cm)	59.7±0.48a	58.8±0.48a	75.8±0.47b	75.5±0.30b	86.3±0.93d	80.5±0.27c	82.3±1.78cd	80.6±0.46c
Shoulder width (cm)	11.8±0.26a	11.1±0.27a	13.3±0.26b	13.3±0.17b	16.2±0.51d	14.3±0.15c	18.0±0.99d	14.6±0.25c
Sample size (N) ^a	278	273	281	699	74	843	20	315

Means within the same row followed by different letters (a–d) are different at $P < 0.05$

^aN is the sample size for each sub-class

such models. Generally, inclusion of other independent variables in the model improved the fit or adequacy of the models, precision, and the amount of variability explained by the fitted model R^2 .

The R^2 values increased with each additional independent variable included in the model (Table 2). The final regression models had R^2 values ranging from 0.57 to 0.83. The regression equations with the highest R^2 values were

Table 2 Stepwise multiple regression equations and their assessment criteria for estimating live weight using linear traits of 2,783 indigenous Tswana goats from farms in various districts of Botswana, in relation to age and sex

Category of Tswana goats ^a	Fitted stepwise multiple regression equations	Model assessment criteria				
		Partial R^2	Model R^2	$C(p)$	F value	MSE
Male kids	0.37HG–28.44	0.78	0.78	64.44	979.00*	16.65
	0.37HG+0.03BL–28.44	0.03	0.81	27.24	36.03*	14.77
	0.37HG+0.03BL+0.30HW–28.44	0.01	0.82	5.56	23.55*	13.65
	0.37HG+0.03BL+0.30HW+0.05SW–28.44	0.002	0.82	5.00	2.55 ^{ns}	13.57
Female kids	0.36HG–27.54	0.78	0.78	88.53	941.94*	14.04
	0.36HG+0.37HW–27.54	0.03	0.81	36.19	48.37*	11.94
	0.36HG+0.37HW+0.47SW–27.54	0.02	0.83	3.03	35.29*	10.59
Male grower	0.46HG–52.60	0.68	0.68	109.79	592.68*	33.29
	0.46HG+0.57HW–52.60	0.063	0.74	35.90	67.91*	26.89
	0.46HG+0.57HW+0.55SW–52.60	0.024	0.77	8.89	28.51*	24.49
	0.46HG+0.57HW+0.55SW+0.13BL–52.60	0.005	0.77	5.00	5.89*	24.06
Female grower	0.77HG–46.38	0.57	0.57	141.93	935.43*	24.20
	0.77HG+0.34BL–46.38	0.07	0.64	12.68	129.44*	20.43
	0.77HG+0.34BL+0.12SW–46.38	0.01	0.65	3.20	11.50*	20.12
Mature male	0.83HG–50.62	0.80	0.80	8.64	375.88*	41.19
	0.83HG+0.40HW–50.62	0.02	0.82	2.49	206.72*	38.21
Mature female	0.58HG–44.10	0.48	0.48	240.80	1062.00*	34.91
	0.58HG+0.21BL–44.10	0.05	0.53	108.69	122.89*	31.59
	0.58HG+0.21BL+0.38SW–44.10	0.02	0.55	51.84	56.51*	30.15
	0.58HG+0.21BL+0.38SW+0.30HW–44.10	0.02	0.57	5.00	48.84*	28.95

ns not significant at $P=0.05$ level of significance

* $P=0.05$ (the level of significance where P value was significant)

^aKids, grower, and mature goats are aged 0–12, 13–24, and 25 months and over, respectively

for female and male kids (0.83 and 0.82, respectively), mature male goats ($R^2=0.82$) followed by male growers with R^2 of 0.77. The model explaining the least variability in live weight was for mature female goats with $R^2=0.57$ (Table 2). The final regression models also had different MSE values ranging from 10.59 for female kids to 38.21 for mature male goats. The Mallows' $C(p)$ statistics were similar to the number of parameters in the models (Table 2).

Finally through the collective use of the partial R^2 , coefficient of determination, MSE, and Mallows' $C(p)$ statistics, the best live weight prediction models were for male and female kids and mature male goats (Table 2). The female kids model was $\text{Weight} = 0.36\text{HG} + 0.37\text{HW} + 0.47\text{SW} - 27.54$, with $R^2=0.83$, $C(p)=3.03$ and $\text{MSE}=10.59$; while for the male kids, it was $\text{Weight} = 0.37\text{HG} + 0.03\text{BL} + 0.3\text{HW} - 28.44$, $R^2=0.82$, $C(p)=5.56$, $\text{MSE}=13.65$ and, for mature male goats, $\text{Weight} = 0.83\text{HG} + 0.40\text{HW} - 50.62$, with $R^2=0.82$, $\text{MSE}=38.21$ and $C(p)=2.49$. The next best predictive model was for male growers, $\text{Weight} = 0.46\text{HG} + 0.57\text{HW} + 0.55\text{SW} + 0.13\text{BL} - 52.6$, $\text{MSE}=24.06$, $R^2=0.77$, and $C(p)=5.00$. The poor models in estimating live weight were for female growers $\text{Weight} = 0.77\text{HG} + 0.34\text{BL} + 0.12\text{SW} - 46.38$, with $\text{MSE}=20.12$, $R^2=0.65$ and $C(p)=3.20$ and mature female goats where $\text{Weight} = 0.58\text{HG} + 0.21\text{BL} + 0.38\text{SW} + 0.30\text{HW} - 44.10$, $\text{MSE}=28.95$, $R^2=0.57$ and $C(p)=5.00$ (Table 2).

Discussion

The significant increase in body weight and linear traits with age is consistent with the studies of Owen et al. (1977) and Katongole et al. (1996) who reported these trends in Tswana goats. Such trends represent growth and development of farm animals as suggested by Butterfield (1988), where weight and other measurements increase with age. Management, especially poor disease and parasite control and poor nutrition during seasons of limited grazing would also contribute to differences between age groups (Owen et al. 1977). More than 80% of Tswana sheep and goats is kept under traditional farming (Botswana Government 1999) characterized by inadequate nutrition for most part of the year and low veterinary care leading to poor productivity (Nsoso et al. 2001).

In using body linear measurements to predict body weight, heart girth entered the model first demonstrating its close correlation to body weight and importance in predicting body weight. This is in line with the findings of Slippers et al. (2000), Fajemilehin and Salako (2008), Sowande et al. (2010), and Cam et al. (2010) who concluded that the body weights of goats can be confidently predicted from heart girth measurements. de Villiers et al. (2009) developed a regression model to estimate live body

weight using heart girth measurements alone and concluded that a tape measure can be developed to assist livestock farmers in managing their goats better. Kunene et al. (2009) developed prediction equations for estimating body weight using heart girth and other linear body measurements and concluded that a table could be constructed for the farmers to estimate the live weight of their animals. In this study, although heart girth had high partial R^2 , models with heart girth alone had high $C(p)$ and MSE values and hence would suffer lack of fit in explaining the observed variability.

Inclusion of other independent variables improved the fit and adequacy of these models. These findings are in support of Moaeen-ud-Din et al. (2006) who found that the best multiple regression model for their study included height at withers, chest girth and body length as independent variables. Semakula et al. (2010), Otoikhian et al. (2008), and Adeyinka and Mohammed (2006b) also reported an improvement in predicting goat live weight by including other variables in the model.

The best model for each age group was determined by using four criteria namely partial R^2 , coefficient of determination R^2 , mean square error, and Mallows' $C(p)$ statistic. R^2 is less suitable as a single criterion in selecting a regression model because it can be increased by inclusion of more independent variables in the model. Through the use of the partial R^2 , only variables contributing significantly to explaining variability are retained in the model. To improve the precision of predicted values, regression equations with small MSE were selected (Draper and Smith 1998; Freund and Wilson 2003). Finally, Mallows' $C(p)$ statistic which is a measure of the goodness of fit of a model and a stopping rule in stepwise regression (Draper and Smith 1998) was used. Applying these criteria, the best prediction equations were for male and female kids with R^2 of 0.82 and 0.83, respectively. The model for mature male goats had a high R^2 and a high MSE, thus the model should be used with caution. The model for mature female goats was the poorest with R^2 of 0.57. This poor prediction could be partially explained by the omission of other important variables which may affect body weight such as pregnancy status and body condition score (Serin et al. 2010). Silva et al. (2006) and Tiexeira et al. (2008) used the same four criteria above and found best models to predict sheep and goat carcass composition, respectively. Tiexeira et al. (2008) found that body weight was the first variable admitted into prediction models of muscle, mesenteric fat, and total body fat and accounted for 82%, 67%, and 79% of the variation in tissue weights, respectively.

Conclusion

Linear body measurements such as heart girth, body length, height at withers, and shoulder width were valuable

independent variables in predicting live weight for indigenous Tswana goats. The best body weight prediction models were for male and female kids which had high R^2 values (0.82–0.83). The variables which contributed significantly were heart girth, height at withers, and shoulder width for females and heart girth, height at withers, and body length for male kids. These models had a good fit ($C(p)$ ranging from 3.03 to 5.05) and high precision of the estimates as shown by low MSE (10.59–13.65). Though the mature male goats model had a high R^2 (0.82), it had a high MSE (38.21). Finally, the model for estimating live weight in mature female goats was poor with a low R^2 (0.57). Multiple regression analysis provided the most precise estimates for live weights of the kids irrespective of sex compared to predictions for other age and sex categories while live weight estimates for mature male goats were the least precise. More research is required to use the multiple regression equations to develop a tape measure or table to assist farmers in managing their goats better.

Acknowledgments This research project was funded by both the SADC/FAO/UNDP Regional project on the management of farm animal genetic resources and the Botswana government. The collaborative project was conducted by the Departments of Agricultural research, Animal Health and Production, Botswana College of Agriculture, Botswana Agricultural Union and the Smallstock Breeders Association of Botswana. The heads and the staff of all the involved agencies are thus being sincerely acknowledged for their assistance and support. The following are particularly thanked for assisting with the data collection and entry Mr. M. Marumo, Mr. K. Kelemogile, and Ms. M. Rakereng (from the Department of Agric Research) and Mr. L. Malela (from Botswana College of Agriculture). The farmers who served as enumerators are also appreciated including those who permitted the team to assess of their flocks.

References

- Adeyinka, I. A. and Mohammed, I. D., 2006a. Relationship of liveweight and linear body measurement in two breeds of goat of northern Nigeria, *Journal of Animal and Veterinary Advances*, 5 (11), 891–893
- Adeyinka, I. A. and Mohammed, I. D., 2006b. Accuracy of body weight prediction in Nigerian Red Sokoto goats raised in north eastern Nigeria using linear body measurement, *Pakistani Journal of Biological Sciences*, 9(15), 2828–2830
- Botswana Government, 1999. Botswana Agricultural Survey Report 1995, (Department of Printing and Publishing Services, Gaborone)
- Butterfield, R.M., 1988. New concepts of sheep growth, (University of Sydney Press, Sydney)
- Cam, M.A., Olfaz, M., and Soydan, E., 2010. Possibilities of using morphometrics characteristics as a tool for body weight prediction in Turkish hair goats (Kilkeci), *Asian Journal of Animal and Veterinary Advances*, 5 (1), 52–59
- Central Statistics Office, 2006. 2006 Annual Agricultural Survey Report, (Department of Printing and Publishing Services, Gaborone)
- de Villiers, J. F., Gcumisa, S.T., Gumede, S. A., Thusi, S. P., Dugmore, T. J., Cole, M., du Toit, J. F., Vatta, A. F., and Stevens, C., 2009. Estimation of live body weight from heart girth measurement in KwaZulu-Natal goats, *Applied Animal Husbandry and Rural Development*, 1, 1–8
- Draper, N.R. and Smith, H., 1998. *Applied Regression Analysis* (Third Edition), (John Wiley and Sons, Inc., New York)
- Fajemilehin, O.K.S. and Salako, A.E., 2008. Body measurement characteristics of the West African Dwarf goat in deciduous forest zone of southwestern Nigeria, *African Journal of Biotechnology*, 7(14), 2521–2526
- Freund, R. J. and Wilson, W. J., 2003. *Statistical Methods* (Second Edition), (Academic Press, New York)
- Katongole, J.B.D., Sebolai, B., and Madimabe, M. J., 1996. Morphological characterization of Tswana goats. In S. H. B. Lebbie and E. Kagwini (eds), *Proceedings of the Third Biennial Small Ruminant Network UICC*, Kampala, Uganda, 43–47
- Khan, H., Muhammad, F., Ahmad, R., Nawaz, G., Zubair, R. and Zubair, M., 2006. Relationships of body weight with linear body measurements in goats, *Journal of Agricultural and Biological Science*, 1(3), 51–54
- Kunene, N. W., Nesamvuni, A. E., and Nsahlai, I. V., 2009. Determination of prediction equations for estimating body weight of Zulu (Nguni) sheep, *Small Ruminant Research*, 84, 41–46
- Moaeen-ud-Din, M., Ahmad, N., Iqbal, A., and Abdullah, M., 2006. Evaluation of different formulas for weight estimation in Beetal, Teddi and Crossbred (Beetal x Teddi) goats, *Journal of Animal and Plant Sciences*, 16, 3–4
- Nsoso, S.J., Machete, J.B., Molatole, M., Ndebele, R.T., Lebani, N.N., Chabo, R.G., Kalake, A.M., Jacyna, L., Segadimo, B.W., Mine, O.M., 2001. The impact of traditional management on seasonal internal parasite burdens and productivity of indigenous Tswana goats in southern Botswana, *Onderstepoort Journal of Veterinary Research*, 68, 101–104
- Nsoso, S. J., Podisi B., Otsogile E., Mokhutshwane B.S., and Ahmadu, B., 2004. Phenotypic characterization of indigenous Tswana goats and sheep breeds in Botswana: continuous traits, *Tropical Animal Health and Production*, 36(8), 789–800
- Ojedapo, L.O., Adedeji, T.A., Olayeni, T.B., Adedeji, O.S., Abdullah, A. R., and Ojebiyi, O.O., 2007. Influence of age and sex on body weight and some body linear measurements of extensively reared WAD goats in derived savannah zone of Nigeria, *Journal of Animal and Veterinary Advances*, 6(1), 114–117
- Oladele, O. I. and Monkhei, M., 2008. Gender ownership patterns of livestock in Botswana, *Livestock Research for Rural Development*, 20(10), <http://www.lrrd.org/lrrd20/10/olad20156.htm>
- Otoikhian, C. S. O., Otoikhian, A. M., Akporhwarho, O. P., Oyefia, V. E., and Isidahomen, C.E., 2008. Body measurement parameters as a function of assessing body weight in goats under on-farm research environment, *African Journal of General Agriculture*, 4 (3), 135–140
- Owen, J.E., Norman, G., Fisher, I.L., and Frost, R.A., 1977. Studies on the meat production characteristics of Botswana goats and sheep—part I: Sampling methods and materials, and measurements on the live animals, *Meat Science*, 1, 63–85
- Semakula, J., Mutetikka, D., Kugonza, R. D., and Mpairwe, D., 2010. Variability in body morphometric measurements and their application in predicting live body weight of Mubende and Small East African goat breeds in Uganda, *Middle-East Journal of Research*, 5(2), 98–105
- Serin, I., Serin, G., Yilmaz, M., Kiral, F., and Ceylan, A., 2010. The effects of body weight, body condition score, age, lactation, serum trygliceride, cholesterol and paraoxanase levels on pregnancy rate of saanen goats in breeding season, *Journal of Animal and Veterinary Advances*, 9, 1848–1851
- Silva, S. R., Afonso, J. J., Santos, V. A., Monteiro, A., Guedes, C. M., Azevedo, J. M. T., and Dias-da-Silva, A., 2006. In vivo estimation of sheep carcass composition using real-time ultra-

- sound with two probes of 5 and 7.5 MHz and image analysis, *Journal of Animal Science*, 84, 3433–3439
- Slippers, S.C., Letty, B. A., and de Villiers, J. F., 2000. Prediction of the body weight of Nguni goats, *South African Journal of Animal Science*, 30 (Supplement 1), 127–128
- Sowande, O., Oyewale, B. and Iyasere, O., 2010. Age- and sex-dependent regression models for predicting the live weight of West African Dwarf goat from body measurements, *Tropical Animal Health and Production*, 42(5), 969–975
- Statistical Analysis System (SAS), 2002–2003. *SAS Users Guide Version 9.1*, (SAS Institute Inc, North Carolina)
- Tiexeira, A., Joy, M., and Delfa, R., 2008. In-vivo estimation of goat carcass composition and body fat partition by real-time ultrasonography, *Journal of Animal Science*, 86, 2369–2376