Journal of Agricultural Science (2014), **152**, 497–503. © Cambridge University Press 2013
doi:10.1017/S0021859613000609

ANIMAL RESEARCH PAPER

Genetic parameters and non-genetic influences related to birth weight in farmed white-tailed deer

G. M. PARRA-BRACAMONTE[1]*, X. F. DE LA ROSA-REYNA[1], N. TREVIÑO-MARTÍNEZ[2], W. ARELLANO-VERA[1] AND V. MORENO-MEDINA[1]

[1] *Centro de Biotecnología Genómica – Instituto Politécnico Nacional, Boulevard del Maestro SN. Esq. Elías Piña, Col. Narciso Mendoza. C.P. 88710, Reynosa, Tamaulipas, México*
[2] *Asociación Nacional de Criadores de Cérvidos de México A.G. Canales No. 3841, Col. Centro C.P. 88000, Nuevo Laredo, Tamaulipas, México*

(*Received 8 January 2013; revised 25 June 2013; accepted 6 August 2013; first published online 4 September 2013*)

SUMMARY

Studying and understanding the sources of variation in early life traits in farmed deer are fundamental for management and/or breeding purposes. Data from a captive white-tailed deer population were analysed to identify non-genetic and genetic factors affecting the birth weight (BW) of fawns. The year, type of birth and sex were included in a fixed linear model to examine their significance. All of the examined non-genetic factors had a highly significant effect on BW ($P<0{\cdot}001$). The examined years showed variation attributed to food availability affecting the gestational conditions of does. Male fawns were 193 g heavier than female fawns at birth ($P<0{\cdot}001$), and singleton births were associated with a higher BW ($2{\cdot}97\pm0{\cdot}043$ kg) compared with twin ($-0{\cdot}261$ g) and triplet ($-0{\cdot}642$ g) fawning ($P<0{\cdot}001$). The best-fitting animal model was selected by comparing reduced and complete models. Based on the selected animal model, which included direct genetic and common maternal effects, genetic components and parameters were estimated. The direct heritability was found to be $0{\cdot}28\pm0{\cdot}126$, and a small but important contribution of common maternal environmental effects was identified ($c^2=0{\cdot}15\pm0{\cdot}062$). The results support the importance of certain environmental factors affecting BW and indicate the relevance of direct genetic and maternal environmental influences to sustained genetic changes in BW and positively correlated traits in farmed white-tailed deer populations.

INTRODUCTION

The white-tailed deer (*Odocoileus virginianus*) is the most important species involved in diversified livestock systems and wildlife hunting activities in northeast Mexico. As a natural consequence, in northern regions, wildlife hunting activities have become very attractive as an alternative source of income for cattle producers attempting to diversify their livestock systems. In the last decade, some ranchers have shifted from extensive to semi-extensive production systems, which include artificial insemination, fawn monitoring and nursing (mainly for breeding purposes) and the local dissemination of animals, which promotes sustainable reintroduction in response to extractive actions. The purpose of a semi-extensive system is to produce large numbers of trophy-quality animals to be released into natural conditions after weaning. According to the General Wildlife Law of Mexico (DOF 2000), diversified livestock systems as an assumed sustainable system, must have rules to prevent the hunting of females and young bucks within preserved areas, and genetic variability is maintained through the regular introduction of breeding males and germplasm from the appropriate subspecies into captive populations.

One advantage of these systems is the possibility of recording data and of eventually implementing breeding strategies for genetic improvement. Birth weight (BW), which is the first indicator of the productive life history of animals, is one of the easiest traits to record and serves as an implicit indicator of performance at older ages. Adverse conditions during the early stages of development affect growth and a variety

---

* To whom all correspondence should be addressed. Email: gparra@ipn.mx

of related traits, including metabolism, immunocompetence and subsequent sexual attractiveness in adulthood (Lindström 1999). In red deer, BW has been associated with total lifetime reproductive success in males (Kruuk *et al*. 1999), and some evidence link low BW with the probability of death or disease in later stages of life (Sieber *et al*. 2010).

Both genetic and environmental factors and their interactions promote early developmental traits in mammals. In white-tailed deer, there are a few studies focused on understanding environmental or non-genetic and genetic effects on various important traits (Williams *et al*. 1994; Schultz & Johnson 1995; Blaylock 2008; Monteith *et al*. 2009). For example, Monteith *et al*. (2009) identified the influence of the maternal and grandmaternal condition during gestation on the subsequent growth of offspring and noted the significance of nutrition during the gestation of white-tailed deer. Similarly, a few studies have analysed genetic variability and its effect on economic traits in deer (e.g. Williams *et al*. 1994).

The use of mixed models has been proposed as an unbiased way to analyse phenotypic data to isolate direct and maternal genetic variance components and explain how genes influence phenotypes (Kruuk & Hadfield 2007). Animal models involving mixed model equations have been extensively employed in genetic evaluations of commercial traits in cattle, beginning in the last century (e.g. Golden *et al*. 2009).

As key components of genetic change and/or evolution, genetic and non-genetic factors need to be distinguished. In natural populations, environmental effects may confound estimates of the effect of genetic variation on phenotypes. Combining long-term data on certain traits in wild populations subjected to breeding schemes in statistical models can effectively separate genetic and environmental components, and such information can then be used for management or breeding purposes (Kruuk & Hadfield 2007).

In the present study, was analysed the data available from a captive population of white-tailed deer to describe the main sources of non-genetic and genetic variation that affect BW.

MATERIALS AND METHODS

Data source

The analysis was performed using the production records from a hunting ranch in Nuevo Laredo, Tamaulipas, Mexico. This region is characterized as exhibiting a semi-arid climate with a mean annual of rainfall of 40 cm. The vegetation has been classified as Tamaulipan thorn scrub of the south Texas plain (Fulbright & Ortega-S 2006).

The database contained 765 BW records obtained from 2005 to 2011 and information on the genealogy of 1052 fawns, 64 bucks and 275 does. The transition to semi-extensive animal management began in 1999 with the construction of management pens and the confinement of native animals that were already present in the area. Natural mating was employed until 2005. Then, from 2006 to the present, assisted reproduction has been performed, first through intra-cervical insemination and later via laparoscopic insemination. Reproductive management is typically scheduled for the first week of December, and fawning begins approximately in the last week of June. The insemination success rate according the ranch owner is approximately 50%, and pregnancy is assured through the natural mating of non-pregnant does. Although no data on age could be obtained, age range of the does was estimated to be between 2·5 and 6 years.

Pregnant does were maintained in enclosed areas of 0·5 ha to monitor the gestational period and fawning. The feeding management procedures included natural grass and shrub grazing supplemented with a balanced pelleted commercial feed. Minerals and vitamins were provided, and water was available to the animals as all times. Birth weight was recorded 1 or 2 days after fawning using a mechanical spring weighing scale, verifying the birth type and doe identification. When necessary, paternity test verification was requested from DNA Solutions Inc. Laboratory, because most of the animals on the ranch are registered in the North American Deer Registry of the North American Deer Farmers Association (NADeFA) and the Texas Deer Association (TDA) in the USA.

Data analyses

The data were first analysed to identify the significant non-genetic factors affecting BW using the model $Y_{ijk} = \mu + S_i + A_j + T_k + \varepsilon_{ijk}$, where Y_{ijk} is the BW; μ is the overall mean; S_i is the ith effect of the sex of the fawn (male or female); A_j is the jth effect of the year (2005,…, 2011); T_k is the kth effect of birth type (single, twin or triple); and ε_{ijk} is the random error. Analyses were performed using the generalized linear model (GLM) procedure in SAS software (2001), and least-square means (LSM) were subsequently estimated and compared using the PDIFF method in the same software. First-degree interactions were excluded, as they had no significant effect on BW.

Variance component estimation

The original database was edited to fit an animal model in MTDFREML genetic evaluation software (Boldman *et al*. 1995). Several models were fitted, as follows:

$$y = X\beta + Zd + Wm + Mc + e,\ \mathrm{cov}_{dm} \neq 0$$
$$y = X\beta + Zd + Wm + e,\ \mathrm{cov}_{dm} \neq 0$$
$$y = X\beta + Zd + Wm + e,\ \mathrm{cov}_{dm} = 0$$
$$y = X\beta + Zd + Mc + e$$
$$y = X\beta + Zd + e,$$

where **y** is the phenotypic trait vector for BW; *X, Z, W* and *M* is known matrices of incidence related to their respective fixed (sex, year and type of birth type) and random (genetic and correlated effects) vectors; β is the vector of fixed effects; *d* is the vector of random direct additive effects; *m* is the vector of random maternal additive effects; cov_{dm} is the covariance between the direct and maternal genetic effects; **c** is the vector of random common maternal effects; and **e** is the vector of random residual effects. A likelihood ratio test (Sorensen 2004), was performed subsequently to determine the most suitable model for BW.

The best model selected included only direct genetic and common maternal effects ($P<0{\cdot}01$). The following variance components were estimated: direct genetic variance ($\sigma^2_{\rm d}$), common maternal variance ($\sigma^2_{\rm c}$), the variance of residual environmental effects ($\sigma^2_{\rm e}$) and phenotypic variance ($\sigma^2_{\rm p}$). From the variance components, the direct heritability (h^2), proportion of common maternal effects relative to phenotypic variance (c^2) and proportion of environmental effects relative to phenotypic variance (e^2) were estimated and discussed.

RESULTS

The overall mean BW was 2·7 kg. Three non-genetic factors were included in the analyses to examine their effect on the BW of white-tailed fawns. All three factors had a highly significant effect on the examined trait ($P<0{\cdot}001$). The LSM for these sources of variation are shown in Table 1. BW fluctuated in each evaluated year, but no pattern in this factor was identified. Birth type significantly affected BW, as BW was higher in single births compared with twin and triplet births (Table 1). Compared with the LSM obtained for single births of 2·97 ± 0·043 kg, the deviations for twin and triple fawning were −0·26 and −0·64 kg, respectively. Similarly, the sex of the white-tailed fawns corresponded to the observed BW dimorphism, as males were approximately 0·20 kg heavier than females at birth ($P<0{\cdot}001$). No interactions between the factors were identified.

Table 1. *Least-square means ± S.E. for birth weight (BW) in white-tailed deer by sex, year and birth type*

Source of variation	*P*-value	*n*	BW kg mean	± S.E.	*C*
Sex	< 0·001				
Male		380	2·76	0·037	a
Female		385	2·57	0·038	b
Year	< 0·001				
2005		131	3·09	0·057	a
2006		110	2·74	0·062	b
2007		106	2·65	0·065	bc
2008		52	2·41	0·086	c
2009		105	2·53	0·062	bc
2010		138	2·70	0·056	b
2011		123	2·54	0·057	bc
Birth type	< 0·001				
Single		209	2·97	0·043	a
Twin		489	2·71	0·028	b
Triplet		67	2·32	0·075	c

C, Within a factor, means without a common superscript are significantly different ($P<0{\cdot}001$).

The best model selected by likelihood ratio testing included random direct genetic effects and common environmental effects of does ($P<0{\cdot}01$). The variance components and genetic parameters are reported in Table 2. The direct genetic effects showed a moderate effect size (0·28 ± 0·126), and interestingly, the common maternal environmental effects also explained a proportion of the BW phenotype (0·15 ± 0·062). The residual variance explained more than half of the phenotypic variance in BW (Table 2).

DISCUSSION

Although there is theoretically an ideal BW in mammalian species, there is a strong genetic component accounting for the variation in this trait (Gardner *et al*. 2007). As BW extremes are associated with negative conditions (e.g., low BW with neonatal

Table 2. *Variance components and genetic parameters for the birth weight of captive white-tailed deer (*Odocoileus virginianus*)*

Variance components		Genetic parameters	
$\sigma^2{}_d$	0·10714	h^2	0·28 ± 0·126
$\sigma^2{}_c$	0·05914	c^2	0·15 ± 0·062
$\sigma^2{}_e$	0·21989	e^2	0·57 ± 0·093
$\sigma^2{}_p$	0·38618		

σ^2_{d}, direct genetic variance; σ^2_{c},maternal permanent variance; σ^2_{e}, environmental variance; σ^2_{p}, phenotypic variance; h^2, direct heritability; c^2,proportion of maternal environmental effects relative to phenotypic variance; e^2, environmental effects relative to phenotypic variance.

mortality and high BW with dystocia), understanding these and other factors such as environmental ones, will improve our ability to manage the main sources of variation related to white-tailed deer farming.

Non-genetic factors

Knowledge of factors affecting variation in BW is especially important given the positive relationships of this trait with neonatal and adult health (Lindström 1999; Lumma & Clutton-Brock 2002; Gardner *et al.* 2007), fertility and secondary sexual traits (Kruuk *et al.* 1999; Lindström 1999; Schmidt *et al.* 2001) and body mass in mature stages in white-tailed deer (Schultz & Johnson 1995) and, in larger ungulate species (e.g., cattle).

The year of birth had a significant effect on the analysed trait. This factor has been associated with BW variation and with climatic factors conditioning food availability (e.g. Schmidt *et al.* 2001). Some studies performed in northern latitudes have related BW variation to differences in spring climate favouring years with warm springs (Adams 2005; Nussey *et al.* 2005). Although the direct relationship of yearly variability with BW in natural populations is clear, in completely captive systems, less yearly variation would be expected. While in the present case, winter severity is not expected to be a determinant factor based on temperature extremes, precipitation is a key factor conditioning late winter and spring grass and shrub availability, and the observed differences may be attributed to the variation in this parameter affecting feed availability for the maintenance and gestational requirements of does.

Birth type (i.e., litter size) also had an important effect on BW, as expected, with a direct negative relationship being indicated between litter size and BW. This finding is in agreement with what has been reported in Roe deer (Andersen & Linnell 1997), sheep (Gardner *et al.* 2007), goats (Soundararajan & Sivakumar 2011) and, previously, in white-tailed deer (Blaylock 2008).

The sex of the fawns explained less of the variation in BW compared with the other factors. Proportionally, female fawns displayed a weight that was 93% of that in males at birth. This finding confirmed the sexual dimorphism observed in white-tailed deer for this trait (Sauer 1984). The mean values recorded in the present study were slightly lower than the BWs of captive male and female white-tailed deer recorded in Mississippi, although the pattern of divergence between the sexes was maintained, with BWs of 3·18 and 3·06 kg being found for males and females, respectively (Jacobson 1995). Blaylock (2008) reported same trend in wild white-tailed deer from Mississippi, although with lower means being obtained, observing an average female BW that was 88% of male birth mass. Physiologically, this trend may have a sex-specific origin in foetal growth because of the endocrine effects of androgens and anti-Mullerian hormone (Gardner *et al.* 2007).

Genetic effects

There are a few reports on genetic parameters estimates in deer species for BW compared with published studies performed in other domestic animals where have found that BW is moderately to highly heritable (Koots *et al.* 1994; Van Vleck *et al.* 2003; Hanford *et al.* 2005, 2006; Borg *et al.* 2009; Gowane *et al.* 2010; Shokrollahi & Baneh 2012). For example, for different breeds of sheep and beef cattle have been estimated direct heritabilities from 0·17 to 0·39 and 0·30 to 0·45, respectively.

Conversely, in white-tailed deer, what little evidence there is indicates that BW in deer species displays low heritability (Williams *et al.* 1994; Delgadillo *et al.* 2008; Ramírez-Valverde *et al.* 2011). Estimates of BW heritability conducted in a captive white-tailed deer population in Texas ranged from 0·00 to 0·17, depending on the method of estimation (Williams *et al.* 1994). Similarly, Delgadillo *et al.* (2008) reported direct heritabilities of 0·11–0·33, depending on the statistical model used for estimation, in a red deer population in Mexico.

Furthermore, in a recent analysis of a red deer population, Ramirez-Valverde *et al*. (2011) reported an h^2 of 0·00 under captive conditions based on using a model including only direct effects.

Here the h^2 estimated had moderate influence on BW, suggesting possibility for genetic change if used as selection criterion. Similarly, McManus & Hamilton (1991) estimated moderate heritabilities for BW in red deer from Scotland (0·27 ± 0·04). They explained that, although BW is not used as primary selection criterion, its utility may be important in case of calving difficulty occurrence or for indirect genetic change of positive correlated traits such as weaning weight and mature weights.

The estimated c^2 value suggested some influence (i.e., 15%) of common maternal effects on the BW phenotype. Hanford *et al*. (2005, 2006) reported lower estimates of this parameter ($c^2 = 0{\cdot}07$ and 0·10, respectively) in Polipay and Rambouillet sheep, but Gowane *et al*. (2010) reported similar permanent effects on BW in Malpura sheep. Even when reports define this effect as permanent for BW, it must be considered as a special case of a maternal effect due to common maternal effects on progeny (Kruuk & Hadfield 2007).

This important effect is mostly conditioned by different factors related to the mothering ability and capacity during the gestational period (Mrode 1996; Matika *et al*. 2003; Adams 2005; Nussey *et al*. 2005; Gardner *et al*. 2007; Räsänen & Kruuk 2007). The resemblance of progeny from the same doe could be because of maternal gestational conditions, which are closely tied to passive immunity, cytoplasmic inheritance, nutrition and maternal constraints on foetal growth (Bradford 1972; Cundiff 1972; Gardner *et al*. 2007).

Therefore, these common maternal effects can be explained further by the physiological nature of multiple fawning conditioned by both environmental variance and, to a certain degree, by the genetic basis of maternal ability. As discussed above, common effects may partly explain the effects of the maternal intrauterine environment (Matika *et al*. 2003). However, the genetic basis of maternal ability can be affected by ovulation rate (Bradford 1972), which is a trait that is subject to large genetic effects in some cases (Davis 2005), and by the cytoplasmic inheritance-influencing size because zygote development is impacted by the gamete size (Reinhold 2002; Van Vleck *et al*. 2003). Consequently, differences in maternal ability between fawns would cause environmental variance among families. Therefore, for BW in white-tailed deer, it would be very important to consider common maternal effects in determining whether selection is based on a doe's ability alone or on a combination of breeding parameters related to direct genetic effects and the performance of does from the same herd (Mrode 1996).

Determining the real genetic sources of variation also relies on the possibility of unravelling confounding environmental effects from direct genetic effects based on good data and effective statistical models (Kruuk & Hadfield 2007). As noted by Bijma (2006), data structure can act as a strong limiting factor in adjusting complex models and determining unbiased genetic estimators. Accordingly, the model analysed in the present study was assumed to exhibit some constraints, such as the failure to include certain doe-related factors (e.g., doe body condition and age). Were assumed these factors to have a minimum effect because of the regular management regime and age range under the captive conditions of the examined deer. However, the data analysis allowed the adjustment and selection of best-fitted model for all of the important genetic and correlated effects in the BW analysis, as suggested by Kruuk & Hadfield (2007).

Based on the present results, it can be concluded that sex, year and birth type are important sources of variation that are significantly related to BW in white-tailed fawns under farmed conditions, suggesting the need to pay attention to these factors in the management of white-tailed deer breeding farms. Additive direct genetic effects have a moderate influence on BW. However, maternal environmental effects displayed some importance as a source of variation in the BW of white-tailed fawns. Under the present study conditions, when changes in the breeding regime are considered, genetic evaluations including the examination of direct and environmental maternal effects might be taken into account to achieve sustained genetic progress in BW and positive correlated economic traits.

The authors would like to thank the Instituto Politécnico Nacional through SIP20090633-20100513 and SIP20110434 project financing, also to Asociación Nacional de Criadores de Cervidos de Mexico A.G. and the Treviño Martinez brothers from San Vicente Ranch for their genuine interest and support of this collaborative research.

REFERENCES

Adams, L. G. (2005). Effects of maternal characteristics and climatic variation on birth masses of Alaskan caribou. *Journal of Mammalogy* **86**, 506–513.

Andersen, R. & Linnell, J. D. C. (1997). Variation in maternal investment in a small cervid; the effects of cohort, sex, litter size and time of birth in roe deer (*Capreolus capreolus*) fawns. *Oecologia* **109**, 74–79.

Bijma, P. (2006). Estimating maternal genetic effects in livestock. *Journal of Animal Science* **84**, 800–806.

Blaylock, A. C. (2008). Effects of soil region, litter size, and gender on morphometric of white-tailed deer fawns. M.S. Thesis, Mississippi State University, Mississippi.

Boldman, K. G., Kriese, L. A., Van Vleck, L. D., Van Tassell, C. P. & Kachman, S. D. (1995). A manual for use of MTDFREML, A set of programs to obtain estimates of variances and covariances, Lincoln, Ne. United States Department of Agriculture, Agricultural Research Service. Clay Center. p. 120.

Borg, R. C., Notter, D. R. & Kott, R. W. (2009). Phenotypic and genetic associations between lamb growth traits and adult ewe body weights in western range sheep. *Journal of Animal Science* **87**, 3506–3514.

Bradford, G. E. (1972). The role of maternal effects in animal breeding: VII. Maternal effects in sheep. *Journal of Animal Science* **35**, 1324–1334.

Cundiff, L. V. (1972). The role of maternal effects in animal breeding: VIII. Comparative aspects of maternal effects. *Journal of Animal Science* **35**, 1335–1337.

Davis, G. H. (2005). Major genes affecting ovulation rate in sheep. *Genetic Selection Evolution* **37**, S11–S23.

Delgadillo, C. A. C., López, O. R., Montaldo, H. H., Berruecos, V. J. M., Luna, A. A. & Vásquez, P. C. G. (2008). Direct and maternal genetic variance components for growth traits in red deer (*Cervus elaphus scoticus*). *Veterinaria Mexico* **39**, 237–245.

Diario Oficial De La Federación, 2000. Ley General de Vida Silvestre. 3 de julio de 2000. p. 33.

Fulbright, T. E. & Ortega-S, J. A. (2006). *White-tailed Deer Habitat: Ecology and Management on Rangelands*. p. 256. Texas: A & M University Press.

Gardner, D. S., Buttery, P. J., Daniel, Z. & Symonds, M. E. (2007). Factors affecting birth weight in sheep: maternal environment. *Reproduction* **133**, 297–307.

Golden, B. L., Garrick, D. J. & Benyshek, L. L. (2009) Milestones in beef cattle genetic evaluation. *Journal of Animal Science* **87**, E3–E10.

Gowane, G. R., Chopra, A., Prakash, V. & Arora, A. L. (2010). Estimates of (co)variance components and genetic parameters for body weights and first greasy fleece weight in Malpura sheep. *Livestock Science* **131**, 94–101.

Hanford, K. J., Van Vleck, L. D. & Snowder, G. D. (2005). Estimates of genetic parameters and genetic change for reproduction, weight, and wool characteristics of Rambouillet sheep. *Small Ruminant Research* **57**, 175–186.

Hanford, K. J., Van Vleck, L. D. & Snowder, G. D. (2006). Estimates of genetic parameters and genetic trend for reproduction, weight, and wool characteristics of Polypay sheep. *Livestock Science* **102**, 72–82.

Jacobson, H. A. (1995). Age and quality relationship. In *Quality Whitetails, the Why and How of Quality Deer Management* (Eds K. V. Miller & R. L. Marchinton), pp. 103–111. USA: Stackpole Books.

Koots, K. R., Gibson, J. P. & Wilton, J. W. (1994). Analyses of published genetic parameter estimates for beef production traits. 1. Heritability. *Animal Breeding Abstracts* **62**, 309–338.

Kruuk, L. E. B. & Hadfield, J. D. (2007). How to separate genetic and environmental causes of similarity between relatives. *Journal of Evolutionary Biology* **20**, 1890–1903.

Kruuk, L. E. B., Clutton-Brock, T. H., Rose, K. E. & Guinness, F. E. (1999). Early determinants of lifetime reproductive success differ between the sexes in red deer. *Proceedings of Royal Society London Series B* **266**, 1655–1661.

Lindström, J. (1999). Early development and fitness in birds and mammals. *Trends in Ecology and Evolution* **14**, 343–348.

Lumma, V. & Clutton-Brock, T. (2002). Early development, survival and reproduction in humans. *Trends in Ecology and Evolution* **17**, 141–147.

Matika, O., Van Wyk, J. B., Erasmus, G. J. & Baker, R. L. (2003). Genetic parameter estimates in Sabi sheep. *Livestock Production Science* **79**, 17–28.

Mcmanus, C. M. & Hamilton, W. J. (1991). Estimation of genetic and phenotypic parameters for growth and reproductive traits for red deer on an upland farm. *Animal Production* **53**, 227–235.

Monteith, K. L., Schmitz, L. E., Jenks, J. A., Delger, J. A. & Bowyer, R. T. (2009). Growth of male white-tailed deer: consequences of maternal effects. *Journal of Mammalogy* **90**, 651–660.

Mrode, R. A. 1996. *Linear Models for the Prediction of Animal Breeding Values*, p. 187. Wallingford, UK: CAB International.

Nussey, D. H., Clutton-Brook, T. H., Albon, S. D., Pemberton, J. & Kruuk, L. E. B. (2005). Constraints on plastic responses to climate variation in red deer. *Biology Letters* **1**, 457–460.

Ramírez-Valverde, R., Sánchez-Cervantes, A., García-Muñiz, J. G., Núñez-Domínguez, R. & Lemus-Ramírez, V. (2011). Efectos ambientales y parámetros genéticos de variables de crecimiento para un rebaño de ciervo rojo (*Cervus elaphus*) en cautiverio. *Revista Mexicana de Ciencias Pecuarias* **2**, 319–330.

Räsänen, K. & Kruuk, L. E. B. (2007). Maternal effects and evolution at ecological time-scales. *Functional Ecology* **21**, 408–421.

Reinhold, K. (2002). Maternal effects and the evolution of behavioral and morphological characters: a literature review indicates the importance of extended maternal care. *Journal of Heredity* **93**, 400–405.

SAS. 2001. *SAS/STAT User's Guide (Release 8.20)*. Cary, NC: SAS Inst. Inc.

Sauer, P. R. (1984) Physiscal characteristics. In: *White-tailed Deer Ecology and Management* (Ed. L. K. Halls), pp. 73–90. Harrisburg, PA: Stackpole Books.

Sieber, V., Robert, N., Schybli, M., Sager, H., Miserez, R., Engels & Ryser-Degiorgis, M. (2010). Causes of mortality and diseases in farmed deer in Switzerland. *Veterinary Medicine International* **2010**, 1–8.

Schmidt, K. T., Stien, A., Albon, S. D. & Guinnes, F. E. (2001). Antler length of yearling red deer is determined by population density, weather and early life-history. *Oecologia* **127**, 191–197.

Schultz, S. R. & Johnson, M. K. (1995). Effects of birth date and body mass at birth on adult body mass of male white-tailed deer. *Journal of Mammalogy* **76**, 575–579.

Shokrollahi, B. & Baneh, H. (2012). (Co)variance components and genetic parameters for growth traits in Arabi sheep using different animal models. *Genetics and Molecular Research* **11**, 305–314.

Sorensen, D. 2004. An introductory overview of model comparison and related topics. *On short Course: Model Choice, Model Assessment, and Related Topics, from a Likelihood to Bayesian Perspective*, p. 48. Tjele, Denmark: Department of Genetics. Danish Institute of Agricultural Sciences.

Soundararajan, C. & Sivakumar, T. (2011). Factors affecting birth weight in Tellichery kids. *Tamil Nadu Journal of Veterinary and Animal Science* **7**, 60–63.

Van Vleck, L. D., Snowder, G. D., Hanford, K. J. (2003). Models with cytoplasmic effects for birth, weaning, and fleece weights, and litter size at birth for a population of Targhee sheep. *Journal of Animal Science* **81**, 61–67.

Williams, J. D., Krueger, W. F. & Harmel, D. H. (1994). Heritabilities for antler characteristics and body weight in yearling white-tailed deer. *Heredity* **73**, 78–83.