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Genetic parameters and factors influencing survival to twenty-four hours after birth in Danish meat sheep breeds

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ABSTRACT: In this study, influential factors and (co)variance components for survival to 24 h after birth were determined and estimated for Texel, Shropshire, and Oxford Down, the most common sheep breeds in Denmark. Data from 1992 to 2006 containing 138,813 survival records were extracted from the sheep recording database at the Danish Agricultural Advisory Service. Estimation of (co)variance components was carried out using univariate animal models, applying logistic link functions. The logistic functions were also used for estimation of fixed effects. Both direct and maternal additive genetic effects, as well as common litter effects, were included in the models. The mean survival to 24 h after birth was 92.5, 91.7, and 88.5% for Texel, Shropshire, and Oxford Down, respectively. There was a curvilinear relationship between survival to 24 h after birth and birth weight, with survival less for light and heavy lambs. Male lambs, as well as lambs from ewes in the first parity or with difficult lambing, had the least survival to 24 h after birth. Survival to 24 h after birth was greater in twin-born Texel and Shropshire lambs compared with singletons and vice versa in Oxford Down. Estimates of direct heritability were in the range from 0.05 to 0.07. Maternal heritability estimates were slightly greater (0.06 and 0.07) than direct heritabilities in Texel and Shropshire and less (0.04) in Oxford Down. The estimated genetic correlations between direct and maternal effects for survival to 24 h after birth were negative, which will make breeding for this trait more difficult. However, on the basis of estimated genetic parameters, it can be concluded that it is possible to improve survival to 24 h after birth in meat sheep breeds by accounting for both direct and maternal genetic effects in breeding programs.

Key words: genetic parameter, maternal effect, sheep, survival to twenty-four hours after birth

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INTRODUCTION

Texel, Shropshire, and Oxford Down are the most common sheep breeds in Denmark. Until now, the sheep breeding program in Denmark has mainly been based on genetic parameters obtained from the literature. In 2004 estimation of genetic parameters based on Danish data started and focused on growth, carcass traits, and litter size (Norberg et al., 2005; Maxa et al., 2007a,b). There is a need for estimating heritabilities and genetic correlations based on Danish data for other important traits involved in breeding programs.

Lamb survival is the crucial factor for sheep productivity, and as a complex trait, it is influenced by the ability of the lamb to survive and by the rearing ability of the lamb (Burfening, 1993). Of special importance under Danish production conditions is lamb survival to 24 h after birth. Therefore, this trait is included in the intensive registration system. Analysis of lamb survival at this stage is of interest because most deaths occur on d 1 after birth (Green and Morgan, 1993; Binns et al., 2002). The survival rates on d 1 after birth reported in the literature usually vary from about 90 to 96% (Morris et al., 2000; Sawalha et al., 2007; Riggio et al., 2008). Environmental and management conditions, as well as other systematic factors, such as litter size, age of ewe, and parity affect survival at a substantially important rate (Khalaf et al., 1979b; Petersson and Danell, 1985; Sawalha et al., 2007).

In several studies on the genetics of lamb survival, survival has been considered as a trait of the dam (Brash et al., 1994; Fogarty et al., 1994). Other studies analyzed lamb survival as a trait of the lamb, considering the effect of the offspring genotype more important than the effect of the genotype of the dam (Smith, 1977; Petersson and Danell, 1985; Gama et al., 1991b). Maternal effects on lamb survival were considered in

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Table 1. Proportion of observations on the original and the modified scale of lambing difficulty in Texel, Shropshire, and Oxford Down[1,2]

Lambing difficulty score	Texel		Shropshire		Oxford Down	
	Original	Modified	Original	Modified	Original	Modified
1	46,381 (76.44%)	57,508 (94.78%)	38,135 (84.36%)	42,792 (94.66%)	26,090 (86.73%)	28,736 (95.52%)
2	11,127 (18.34%)	3,166 (5.22%)	4,657 (10.30%)	2,415 (5.34%)	2,646 (8.80%)	1,347 (4.48%)
3	1,931 (3.18%)	—	1,287 (2.85%)	—	880 (2.93%)	—
4	1,212 (2.00%)	—	1,115 (2.47%)	—	453 (1.51%)	—
5	23 (0.04%)	—	13 (0.03%)	—	14 (0.05%)	—

[1]Original lambing difficulty score was recorded as 1 = easy lambing without assistance, 2 = easy lambing with assistance, 3 = difficult lambing without veterinary assistance, 4 = difficult lambing with veterinary assistance, and 5 = caesarean.

[2]Modified lambing difficulty score was assigned as 1 = easy lambing (originated from score 1 and 2 of original lambing difficulty score) and 2 = difficult lambing (originated from score 3, 4, and 5 of original lambing difficulty score).

later studies (Burfening, 1993; Hall et al., 1995; Morris et al., 2000).

The main objectives of this study were to estimate genetic parameters of lamb survival to 24 h after birth (**SB**), including both direct and maternal genetic effects, as well as to investigate the systematic and other factors affecting the mentioned trait in Danish populations of Texel, Shropshire, and Oxford Down.

MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained for this study because the data were obtained from an existing database (Danish Agriculture Advisory Service, Skejby).

Data

Field data on purebred Texel, Shropshire, and Oxford Down were collected from the beginning of 1992 to the end of 2006 by the Danish Agricultural Advisory Service. Pedigrees were traced back to 1962. The analyzed trait was SB, which was recorded within 24 h after birth. The value 0 was assigned for lambs born dead or dead within 24 h after birth and the value 1 for lambs still alive after 24 h. The exact time of mortality within 24 h was not recorded. Birth weight, litter size, and lambing difficulty were considered in the analyses of SB. Birth weight (kg) was defined as the BW of lamb measured at the latest 24 h after birth. Litter size of all lambs born was recorded on the day of lambing, and litters with more than 3 lambs were, due to low numbers, omitted. Lambing difficulty was recorded on a 5 grade scale as 1 = easy lambing without assistance, 2 = easy lambing with assistance, 3 = difficult lambing without veterinary assistance, 4 = difficult lambing with veterinary assistance, and 5 = cesarean. The frequency of observations in some of the groups was low; therefore, we merged the groups of easy lambing with and without assistance and assigned a new group 1 called easy lambing. Other observations were assigned to a group 2 called difficult lambing. The proportion of observations on the original and the modified scale of lambing difficulty are presented in Table 1. Almost all of the lambing occurred indoors in the period from January to May (98.5%), with most lambs born during March. For the statistical analysis 2 lambing seasons were created, 1 from October to March and the other from April to September. Animals belonging to a flock-year-season class with less than 6 animals were excluded. Lambs from ewes in first to fifth parity were included in the analyses. The characteristics of the data used in the analyses are presented in Table 2.

Statistical Analyses

Statistical analyses of lamb survival data were carried out by application of a linear logistic model with a binary response variable, which was modeled as a binomial random variable (y_i). The dependent variable (y_i) can take the value 1 with a probability of survival π_i or the value 0 with a probability of death $1 - \pi_i$ for observation i. The logistic model uses a link function $g(\pi_i)$ linking the expected value to the linear predictors η_i. The logit link function (McCullagh and Nelder, 1983) is defined by $ln\left[\frac{\pi_i}{1-\pi_i}\right] = \eta_i$, where π_i is the probability of lamb survival recorded within 24 h after birth.

The analysis of fixed effects was performed for each breed separately with a generalized linear model using the SAS GLIMMIX macro (Littell et al., 1999). The exception from separate analysis was done when the least squares means of SB by breed were calculated. Included fixed effects were sex, litter size, parity, lambing difficulty, lambing season, and year of birth. The effect of birth weight was considered as a covariate with a linear and a quadratic term. Only the significant interactions among the fixed effects were included in the final model. The summary of included effects for analyzed breeds is given in Table 3. Least squares means were estimated on the logit scale and then back-transformed to the original scale (probability) using the inverse link function $\pi = \exp(x\beta)/[1 + \exp(x\beta)]$, where x is the matrix of fixed effects and β is the vector of pa-

Table 2. Description of data used for analysis of survival to 24 h after birth in Texel, Shropshire, and Oxford Down

Item	Texel	Shropshire	Oxford Down
Animals in pedigree	85,880	63,052	50,445
Sires with offspring	1,803	1,217	841
Average No. offspring per sire	34	38	37
Average No. animals in fys[1]	35	29	30
Average No. sire per fys[1]	2.6	2.3	2.3
Average No. fys per sire	2.6	3.0	2.9
Survival to 24 h after birth			
No. of animals with records	61,953	46,159	30,701
Mean (SD), %	92.5 (26.4)	91.7 (27.6)	88.5 (31.9)
Birth weight			
No. of animals with records	56,377	41,033	26,597
Mean (SD), kg	4.5 (0.9)	4.2 (0.9)	4.4 (0.9)
Litter size			
No. of animals with records	61,948	46,149	30,670
Mean (SD)	1.7 (0.6)	1.7 (0.5)	2.0 (0.6)

[1]fys = flock-year-season class.

rameters of linear predictors, applying the LSMEANS statement. Significant differences between least squares means were tested using a *t*-test procedure by inclusion of the PDIFF option in the LSMEANS statement. Standard errors of least squares means were calculated as described by Littell et al. (1999).

A similar logistic linear model was fitted for estimation of (co)variance components, considering survival to 24 h after birth as a binomial trait. Estimation of (co) variance components was carried out with univariate animal models using REML and the ASREML package (Gilmour et al., 1998). Heritabilities were calculated using the variance of the logit link function, which implies a correction of the residual variance by factor $\pi^2/3$ (Southey et al., 2003). Estimates of total genetic variance (direct + maternal genetic variance + direct-maternal genetic covariance) and total heritability were calculated according to Morris et al. (2000). The ASREML package (Gilmour et al., 1998) was also used for calculation of SE of estimated genetic parameters. The following generalized linear model was used for estimation of (co)variance components:

$$\log\left(\frac{\pi_{ijklmnop}}{1-\pi_{ijklmnop}}\right) = \varphi + S_i + L_j + D_k + P_l + FYS_m + C_n + adir_o + amat_p,$$

where $\pi_{ijklmnop}$ = probability of lamb survival, φ = overall mean effect, S_i = fixed effect of sex, L_j = fixed effect of litter size, D_k = fixed effect of lambing difficulty, P_l = fixed effect of parity, FYS_m = fixed effect of flock-year-season class, C_n = random effect of common litter, $adir_o$ = random direct additive genetic effect of animal o, and $amat_p$ = random maternal additive genetic effect of animal p.

RESULTS AND DISCUSSION

Estimates of Fixed Effects and Covariates

In the first part of this study the effects on SB were determined with fixed logistic models, including interactions between different fixed effects. Significance levels of the fixed effects presented in Table 3 were determined

Table 3. Fixed effects used in analysis with level of significance for Texel, Shropshire, and Oxford Down

Item	Texel	Shropshire	Oxford Down
Birth weight—linear	<0.001	<0.001	<0.001
Birth weight—quadratic	<0.001	<0.001	<0.001
Sex	<0.001	<0.001	<0.001
Litter size	<0.001	0.233	<0.001
Lambing difficulty	0.001	0.185	0.241
Parity	0.077	0.003	0.008
Year of birth	<0.001	<0.001	<0.001
Season of birth	0.929	0.008	0.001
Birth weight × lambing difficulty	0.017	0.018	<0.001
Birth weight × parity	0.017	0.008	0.264
Lambing difficulty × litter size	<0.001	<0.001	0.066

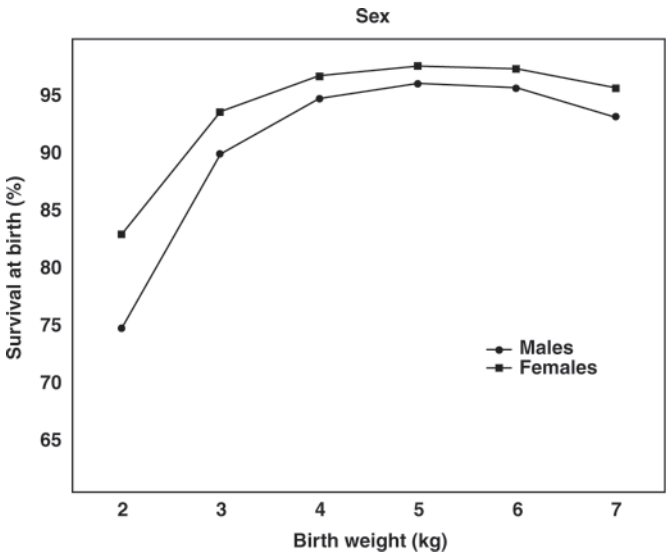

Figure 1. Least squares means of survival to 24 h after birth as a function of birth weight for different sexes in Texel.

using the F-test statistics. Furthermore, the estimated least squares means of SB in combination with the effects of sex, litter size, lambing difficulty, and parity are given in Table 4. The least squares means of SB by breed were 92.4, 88.3, and 91.6% for Texel, Shropshire, and Oxford Down, respectively. Survival to 24 h after birth differed significantly among the breeds.

Year of Birth, Season of Birth, and Sex. Year of birth had a significant effect on SB for all breeds. The effect of season of birth was not significant for Texel. The reason for that is unclear because there was no difference in lambing seasons among the breeds and all 3 breeds were kept under similar production systems. As expected from the results of previous studies, SB for all breeds was significantly affected by sex, with female lambs showing a greater SB compared with male lambs. Similar results for lamb survival at different ages from birth to weaning were found in different studies as well (Wiener and Hayter, 1975; Dalton et al., 1980; Burfening and Carpio, 1993; Southey et al., 2004). As mentioned by Petersson and Danell (1985), in all mammals, young males have greater risk of death compared with females. Even greater differences in survival between males and females, when adjusted to equal birth weight, were obtained by Smith (1977). In some studies, decreased survival in male lambs is explained by their greater average birth weight, which causes a greater risk of dystocia (Smith, 1977; Gama et al., 1991a). This explanation cannot be confirmed in this study as illustrated in Figure 1, where survival to 24 h after birth of both sexes at the same birth weight is compared. At older ages, differences in survival between sexes of lambs might also be affected by management practices. This is suggested in a study by Sawalha et al. (2007), where a much greater mortality rate in males is partially explained by their intensive management during the finishing period for slaughter.

Litter Size. Shropshire was the only breed in our study where litter size did not have a significant effect on SB. However, SB was significantly affected by the interaction of litter size and lambing difficulty in Texel and Shropshire. Survival to 24 h after birth of twinborn lambs was significantly greater compared with singletons and triplets in Texel. The same tendency, but without significant differences among litter sizes, was obtained for Shropshire. Everett-Hincks et al. (2005) and Sawalha et al. (2007) found similar results when analyzing mortality at birth in Coopworth and Scottish Blackface lambs. In general, several studies concluded that with increasing litter size, survival decreases, especially when management and environmental conditions are unfavorable (Hinch et al., 1983; Petersson and Danell, 1985; Riggio et al., 2005). Sawalha et al. (2007)

Table 4. Least squares means of survival to 24 h after birth (SE) with significance levels in superscript, by sex, litter size, lambing difficulty, and parity for Texel, Shropshire, and Oxford Down

Item	Texel	Shropshire	Oxford Down
Sex			
Males	94.8 (0.3)[a]	95.5 (0.3)[a]	94.9 (0.4)[a]
Females	97.1 (0.2)[b]	96.8 (0.2)[b]	96.2 (0.3)[b]
Litter size			
Singletons	96.2 (0.3)[a]	96.2 (0.3)[a]	96.7 (0.4)[a]
Twins	97.0 (0.2)[b]	96.7 (0.2)[a]	95.4 (0.4)[b]
Triplets	94.9 (0.6)[a]	95.9 (0.6)[a]	94.5 (0.5)[b]
Lambing difficulty			
Easy	98.6 (0.1)[a]	98.2 (0.1)[a]	98.0 (0.1)[a]
Difficult	89.6 (0.9)[b]	92.3 (0.8)[a]	90.7 (1.0)[a]
Parity			
1	95.4 (0.3)[a]	95.8 (0.3)[ac]	94.5 (0.4)[a]
2	96.8 (0.2)[a]	97.2 (0.2)[b]	95.8 (0.4)[b]
3	96.6 (0.3)[a]	96.5 (0.3)[a]	96.3 (0.4)[b]
4	95.7 (0.3)[a]	96.3 (0.4)[a]	95.7 (0.5)[b]
5	95.8 (0.3)[a]	95.1 (0.4)[c]	95.5 (0.4)[ab]

[a–c]Least squares means within variable and breed with different superscripts differ significantly ($P \leq 0.05$).

further reported that even though the single born lambs had greater mortality at birth, their postnatal survival later on was greater. The mean SB of triplets in our study was significantly less than that for twins in Texel. There was no significant difference of mean SB between twins and triplets in Oxford Down and Shropshire. Comparing SB in the 3 analyzed breeds, Oxford Down was the breed with greatest SB of singletons, but with the least SB of twins and triplets. Shropshire had the most balanced SB in the range from 95.9 to 96.7%.

Lambing Difficulty. The effect of lambing difficulty on SB was analyzed with a model including the interaction between birth weight and lambing difficulty and a model without interaction, which was computed additionally, without detailed results given in this paper. Including the interaction between birth weight and lambing difficulty in the model resulted in no significant effect of lambing difficulty on SB in Shropshire and Oxford Down. However, interactions between birth weight and lambing difficulty were significant for all breeds. Considering the model without the interaction resulted in significant effect of lambing difficulty on SB so that the difference between the means of levels of lambing difficulty was highly significant in all breeds. Only the effect of lambing difficulty was retained in the model for the variance component estimation. For lambs born without difficulties, SB ranged from 98.0 to 98.6%, and for lambs born with difficulties, SB ranged from 89.6 to 92.3%. This agrees with the results of Smith (1977), who analyzed preweaning survival in lambs. Smith (1977) found a greater mortality for lambs born with difficulty compared with lambs born without difficulty in Oxford Down, Suffolk, and other breeds. Only in the study of Smith (1977) was the effect of lambing difficulty on early lamb survival included, but there is a study conducted on calves that indicates greater survival at birth for calves with an easy calving in Hereford and Charolais cattle (Eriksson et al., 2004).

Parity. Parity had a significant effect on SB in Shropshire and Oxford Down. Survival to 24 h after birth was greatest in second parity for Texel and Shropshire and in third parity for Oxford Down. In general, SB observed in second and third parity was greater compared with SB in the first or later parities. As expected from results of previous studies on different sheep breeds (Purser and Young, 1959; Purser and Young, 1983), the least SB occurred in first parity for Texel and Oxford Down, probably as a result of lack of maternal experiences of ewes at that stage. Even though the least SB was estimated in later parities for Shropshire, these estimates are not significantly different from the estimate for first parity. Purser and Young (1959) noted that parity had a much greater effect on lamb survival than the effect of the age of ewe. In general, it is concluded in the literature that very young ewes have markedly greater lamb losses than older ewes and that increased parity within age class reduces lamb losses (Petersson and Danell, 1985; Riggio et al., 2005; Sawalha et al., 2007).

Birth Weight. Birth weight, in both linear and quadratic terms, had a significant effect on SB in all 3 breeds. The effect of lambing difficulty was fitted in models so that a part of the variation was removed. Therefore, this situation needs to be taken into account, especially when results related to birth weight are interpreted. There was a curvilinear relationship between SB and birth weight, as illustrated in Figures 1, 2, 3, and 4, for Texel. This breed was chosen to illustrate the results because it represents the major part of the sheep population in Denmark. The same curvilinear relationship was also found for the other breeds. For both sexes, decreased birth weight (<3 kg) was associated with reduced SB, which is especially remarkable in male lambs, as illustrated in Figure 1. The difference in SB between male and female lambs is much less when birth weight is above average. Low birth weight associated with increasing litter size resulted in reduced SB for Oxford Down compared with Texel (Figure 2) and Shropshire, where litters with twins with reduced birth weight had greater SB compared with singletons. This could suggest that reduced birth weight of twins was mainly due to their nutritional competition with their littermate during parity and, in fact, did not influence early survival to 24 h after birth. Reduced birth weight in singletons resulting in decreased SB adverts to unspecified problems during prenatal development, which decreased the chances of lambs surviving the first hours after birth. Ewe nutrition in pregnancy or pathological reasons could influence SB as well (Khalaf et al., 1979a,b). Survival to 24 h after birth of heavy twins (>6 kg) was greater than SB in heavy singletons in Texel and Shropshire. Reduced birth weight especially combined with difficult lambing decreased SB markedly in Texel (Figure 3) and Shropshire. A different situation appeared in Oxford Down where heavy lambs in combination with difficult lambing had the least SB. Considering the effect of birth weight on SB in relation to the number of parities, the least SB was associated with reduced birth weight, without any clear trend among the breeds and parities. On the other hand, this study concludes that heavy lambs in the first parity had the least SB in all analyzed breeds as illustrated in Figure 4 for Texel. In general, it can be concluded that lambs with birth weight around average tend to have greatest SB, which has been reported in other studies (Morris et al., 2000; Sawalha et al., 2007). Furthermore, deviations from average birth weight, especially toward a reduced birth weight, causes greater lamb loss (Petersson and Danell, 1985; Burfening and Carpio, 1993). Birth weight with greatest SB was slightly greater than the average birth weight for all breeds, which shows potential for improvement in both traits if they are positively correlated, and if the curvilinear relationship between birth weight and SB is taken into account. Furthermore, it is shown that SB of heavier lambs is greater compared with lambs with reduced birth weight, and therefore, the former are more likely to survive. This is in agreement with Morris et al. (2000) who mentioned that larger sized lambs have a good chance to survive once they get through the birth process.

In general, it can be concluded that lamb birth weight, litter size, sex, and parity are important factors in relation to lamb survivability, which is in agreement with most previous studies (Smith, 1977; Petersson and Danell, 1985; Southey et al., 2004). However, some of the main effects were not significant for some of the investigated breeds, but SB was significantly affected by their interaction. Therefore, all of the main effects were included in the model for estimation of genetic parameters. Although birth weight as a linear and quadratic covariate was highly significant, it was not possible to include it in the final model for genetic analyses of SB because of problems with convergence. Therefore, bivariate analyses of genetic parameters for the traits SB and birth weight will be conducted in a future study to verify the genetic association between these 2 traits.

Estimates of Variance Components and Genetic Parameters

Variance Components. Variance components and genetic parameters for SB are presented in Table 5. The direct additive genetic variances were similar for the 3 breeds, whereas a notable difference in maternal additive genetic variance was estimated, especially between Shropshire and Oxford Down. The total genetic variance was slightly greater in Oxford Down compared with Texel and Shropshire, mainly explained by the very low direct-maternal genetic covariance estimate in comparison to the other 2 breeds. Furthermore, less common litter variance was estimated for Oxford Down compared with the other breeds. However, total phenotypic variances were almost equal across the breeds.

Heritabilities. The direct heritabilities for SB ranged between 0.05 for Texel and 0.07 for Oxford Down. These estimates are in agreement with Sawalha et al. (2007), who focused on viability at birth in Scottish Blackface sheep using transformation to a normal liability scale, as described in Dempster and Lerner (1950). Decreased estimates of direct heritability, together with large SE using logit-transformation for survival up to 24 h of age in New Zealand sheep, were presented by Morris et al. (2000). Riggio et al. (2005) reported a much greater heritability for SB in Scottish Blackface (0.33), estimated with a sire model and using Probit transformation. Petersson and Danell (1985) estimated direct heritability for stillbirth to be in the range from 0.027 to 0.384 in different Swedish sheep breeds using the Dempster and Lerner (1950) transformation. The maternal effects on survival were not accounted for in the study of Petersson and Danell (1985), but the authors mentioned that maternal influence on survival was probably more important than the direct effect. Mortality within 24 h after birth of lambs of different breeds was analyzed by Gama et al. (1991b), who estimated direct heritabilities, converted to the liability scale, to be between 0.068 and 0.187.

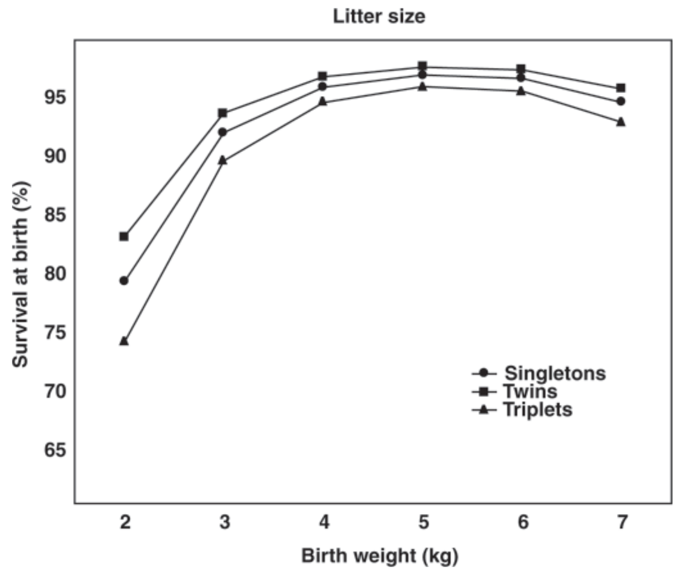

Figure 2. Least squares means of survival to 24 h after birth as a function of birth weight for different litter sizes in Texel.

In this study, maternal genetic effects had an important influence on SB. The maternal genetic effect on SB was larger than the direct genetic effect in Texel and Shropshire. Similar findings on contributions of direct and maternal genetic effects on survival at birth were reported by Morris et al. (2000) and Sawalha et al. (2007), as well as on survival from birth until later ages, especially weaning (Burfening, 1993; Matos et al., 2000; Southey et al., 2001). On the contrary, for Oxford Down the maternal heritability of SB was less than the direct heritability. Safari et al. (2005) reported underestimated direct and maternal heritabilities on the logit scale for survival between 5 and 8 d after lambing, using and comparing the estimates from the animal and the sire model. However, our estimates of direct, as well

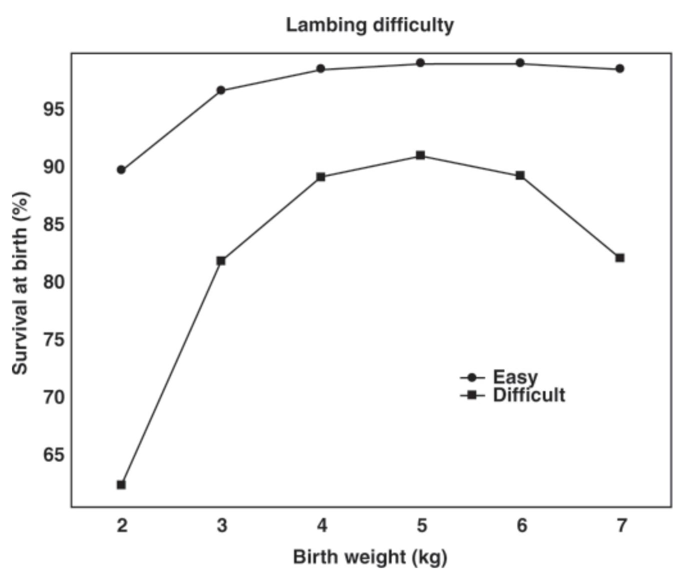

Figure 3. Least squares means of survival to 24 h after birth as a function of birth weight for lambing difficulty in Texel.

Table 5. Estimates of variance components and genetic parameters (SE) for survival to 24 h after birth for Texel, Shropshire, and Oxford Down

Item	Texel	Shropshire	Oxford Down
Variance component			
Direct additive genetic variance	0.23 (0.09)	0.24 (0.09)	0.30 (0.10)
Maternal additive genetic variance	0.26 (0.08)	0.31 (0.09)	0.18 (0.08)
Direct-maternal genetic covariance	−0.12 (0.08)	−0.22 (0.08)	−0.01 (0.09)
Common litter variance	0.64 (0.08)	0.72 (0.09)	0.50 (0.08)
Total genetic variance	0.36 (0.08)	0.33 (0.09)	0.47 (0.10)
Total phenotypic variance	4.29 (0.07)	4.34 (0.08)	4.27 (0.08)
Genetic parameter			
Direct heritability	0.05 (0.02)	0.06 (0.02)	0.07 (0.02)
Maternal heritability	0.06 (0.02)	0.07 (0.02)	0.04 (0.02)
Total heritability	0.08 (0.02)	0.08 (0.02)	0.11 (0.02)
Direct-maternal genetic correlations	−0.52 (0.22)	−0.79 (0.15)	−0.05 (0.33)

as maternal, heritabilities are in the usual range for fitness traits with, in general, low heritabilities. Identical estimates of total heritabilities (0.08) were obtained for Texel and Shropshire, whereas total heritability for Oxford Down was slightly greater (0.11). There are only few studies in the literature that focused on direct and maternal genetic effects for survival to 24 h after birth and reported direct, maternal, and total heritabilities as well. In comparison with these studies, our estimates of heritabilities for SB were within the reported range (Morris et al., 2000; Sawalha et al., 2007).

Genetic Correlations. The correlations between direct and maternal genetic effects for SB were negative for Texel and Shropshire and close to zero for Oxford Down. These estimates cause difficulties when genetic progress in lamb survival is the breeding objective. Everett-Hincks et al. (2005) suggested establishing separate selection lines for each trait and crossing these lines to obtain maximum benefit. As mentioned further in their study, the economics of this option is an important point that requires consideration. Meyer et al. (1993) mentioned environmental and management circumstances as inducing factors for large negative estimates of direct-maternal genetic correlations. Robinson (1996) used simulated data to explain the negative correlations between direct and maternal genetic effects and found that negative estimates may be obtained without a real genetic antagonism. The estimates of this study, especially for Texel and Shropshire, were similar to those presented by Morris et al. (2000) for survival from birth to 24 h of age using the same logit-transformation. On the contrary, Sawalha et al. (2007) found a positive direct-maternal genetic correlation. However, in both studies the estimates were subject to large SE. In the literature, estimates of genetic correlations between direct and maternal effects on survival at different ages vary considerably from being negative (Burfening, 1993; Southey et al., 2001; Everett-Hincks et al., 2005) to positive (Burfening, 1993; Matos et al., 2000). The results obtained in this study are among others supported by a large amount of data, and therefore, help to clarify the association between direct and maternal genetic effects on early lamb survival.

Conclusions

Analysis of factors affecting SB in Danish meat sheep breeds indicated a curvilinear relationship with birth weight. Optimum birth weight in relation to survival was slightly greater than average birth weight. Therefore, selection strategies resulting in increasing birth weight to the optimum should affect SB in a positive direction, which requires verification of genetic association between birth weight and SB in the analyzed breeds. The effect of lambing difficulty was always fitted in the models. For this reason, the results refer to a situation with little or no contribution remaining from this effect. Male lambs, lambs born with difficulties, as well as lambs born in the first parity, had the least SB. As illustrated in Texel and Shropshire, increasing litter size from singletons to twins does not necessarily cause a decrease in survival.

Estimates of genetic parameters showed the importance of both genes of the animal itself and of its dam for SB. The maternal genetic component was larger

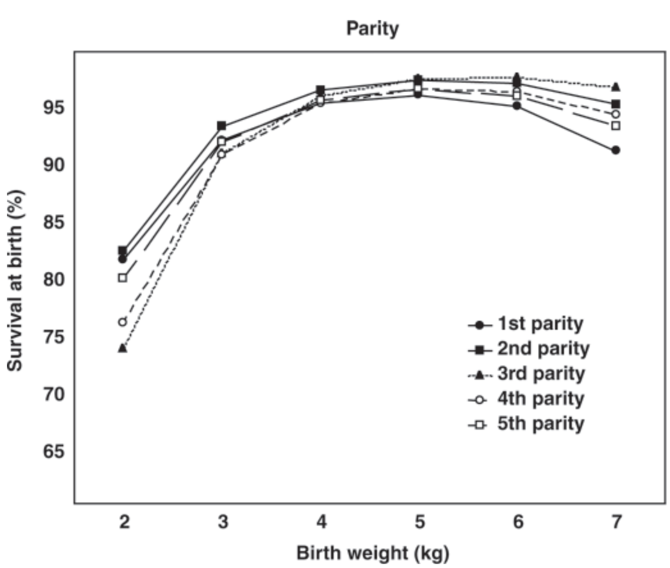

Figure 4. Least squares means of survival to 24 h after birth as a function of birth weight for different parities in Texel.

than the direct one in Texel and Shropshire and vice-versa in Oxford Down. Even though the estimates of heritabilities for survival traits are low, a possible improvement in the trait survival to 24 h after birth can be achieved by including both direct and maternal effects in animal breeding programs. Nevertheless, it is necessary to consider the negative direct-maternal genetic correlations obtained in this study when aiming for genetic progress in this trait.

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