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Relationships among Puberty, Muscle and Fat, and Liveweight Gain during Mating in Young Female Sheep

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Greater depths of muscle are associated with better reproductive performance in ewe lambs, but, in adult ewes, reproductive performance also seems to vary with liveweight gain during the mating period. Therefore, in a large field study with Merino ewe lambs, we tested whether the relationships among eye muscle depth (EMD), fat depth (FAT) and reproductive performance depend on liveweight gain during the mating period. We selected lambs with a wide range in phenotypic values for depths of eye muscle (EMD) and fat (FAT) and assigned them to dietary treatments designed to achieve low (LOW, $n = 244$) or high (HIGH, $n = 237$) rates of liveweight gain during a 28-day mating period. The LOW treatment maintained live weight, whereas the HIGH treatment gained 179 ± 3.8 g/day ($p < 0.001$). From those ewe lambs that attained puberty, first oestrus was detected at live weight 37.8 ± 0.2 kg and age 232 days. The proportion of ewes that attained puberty increased with EMD ($p < 0.01$). Ewes from the HIGH treatment were more fertile (pregnant ewes per 100 ewes exposed to rams) and had a higher reproductive rate (foetuses *in utero* per 100 ewes exposed to rams; $p < 0.001$) than those from the LOW treatment. Fertility and reproductive rate were positively correlated with weight gain during mating as well as live weight at the start of mating, FAT and EMD ($p < 0.05$ to <0.001). We conclude that faster growth, due to either extra nutrition during mating or higher phenotypic potential for fat and muscle, will increase reproductive performance in ewe lambs mated at 8 months of age.

Introduction

Ewe lambs usually achieve puberty when they attain 50–70% of their mature live weight (Hafez 1952; Dýrmundsson 1973), so environmental factors that influence the rate of growth both pre- and post-weaning are important determinants of the timing of sexual maturation (review: Foster et al. 1985). Similarly, genetic factors that influence growth will also affect the timing of puberty (Rosales Nieto et al. 2013a,b). However, the values for fertility (pregnant ewes per 100 ewes exposed to rams) and reproductive rate (foetuses *in utero* per 100 ewes exposed to rams) were markedly higher in one experiment (75% and 87%; Rosales Nieto et al. 2013a) than in the other (35% and 43%; Rosales Nieto et al. 2013b). Comparison of the data for live weight in these studies suggests that the reproductive outcomes were influenced by liveweight gain (LWG) during mating: 214 g/day (Rosales Nieto et al. 2013a) in contrast to only 40 g/day (Rosales Nieto et al. 2013b). LWG is an indirect measure of differences in metabolic balance, a factor known to affect reproductive success independently of changes in live weight (review: Scaramuzzi et al. 2006). These observations suggest that improving the nutrition of ewe lambs so that they gain more weight during mating will increase the reproductive benefits of genotypic strategies for advancing puberty, but this hypothesis needs to be tested within a single controlled experiment.

The outcome of mating at puberty might also be affected by variation in the rates of accumulation of muscle and fat because phenotypes for these factors are positively correlated with fertility and reproductive rate (Rosales Nieto et al. 2013a,b, 2014). It seems unlikely that differences in muscle and fat accumulation would influence the effects of hypothetical interactions between live weight and LWG during mating on reproductive performance.

Therefore, in a large field study with Merino ewe lambs, we tested whether the relationships among eye muscle depth (EMD), fat depth (FAT) and reproductive performance depend on liveweight gain during the mating period.

Materials and Methods

This work was carried out in accordance with the Australian Code of Practice for the Care and Use of Animals for Scientific Purposes and was approved by the Animal Ethics Committee of the Department of Agriculture and Food, Western Australia.

Experimental location and animals

The Merino ewe lambs (n = 481) were born at ‘Moojepin’ (33°69′S, 117°55′E), a commercial ram breeding farm near Katanning in Western Australia, during July–August 2010. Their mothers had been mated to sires with a wide range in ASBVs for growth and for depths of eye muscle and fat. The ewe lambs were weighed every week from 115 days before mating (25.3 ± 0.2 kg; range 15 to 40 kg; Day −115) to 60 days after the start of mating (Day 60), and these data were used to estimate live weight at puberty, the date of conception and LWG during mating. When the ewe lambs were on average 311 days old (range 289–318), ultrasound was used to measure the depths of the *longissimus dorsi* muscle and subcutaneous fat, at a point 45 mm from the midline over the twelfth rib (C-site). The range in EMD was 16–34 mm and the range in FAT was 1–8 mm.

Animal management and feeding

Ewe lambs were maintained in a 75-ha paddock with *ad libitum* access to clean water, oaten hay and sheep pellets. The pellets were based on barley, wheat and lupin grains, cereal straw and hay, canola meal, minerals and vitamins and had been formulated to provide 11.5 MJ of metabolizable energy per kg dry matter, 15% protein and minerals sufficient to meet requirements for maximum growth (Macco Feeds, Australia). A 'teasing period' began with the introduction of eight vasectomized Merino rams (MatingMark®; Hamilton, NZ, USA) to detect the onset of oestrus on November 26 (Day −115), when the ewe lambs were on average 135 days old (range 112–141 days) and weighed 25.3 ± 0.2 kg (range 15–40 kg). The rams were bearing marking harnesses with crayons that were changed every 2 weeks. Standing oestrus was detected by weekly scores of crayon marks, with score 1 being one narrow mark on the middle or the edge of the rump and score 3 being one large, wide mark across the rump (only scores 2 or 3 were accepted as indicating standing oestrus). The date and the age of the ewe lamb at the time of the first score 2–3 crayon mark was deemed to be age at first oestrus, and the live weight recorded closest to that date was deemed to be live weight at first oestrus.

The vasectomized rams were removed on March 22 (Day 0), when the ewe lambs aged on average 244 days (range 224–253 days). On Day 0, when the ewe lambs weighed 39.5 ± 0.3 kg (range 30–53 kg), they were allocated by birth type (single or twin) and sire to one of two dietary groups fed to achieve different target live weights by the end of mating. The LOW group (n = 244) received oaten hay *ad libitum* and 300 g of lupin grain per head three times per week; the HIGH group (n = 237) received the hay and lupin grain, plus sheep pellets *ad libitum*. For the 'mating period', the two dietary groups were subdivided into four groups of 54–75 animals, each placed in a separate 1-hectare paddock with access to clean water and the experimental diet. One experienced entire Merino ram bearing a marking harness was introduced into each of the eight subgroups, and crayon marks were recorded weekly. Crayons were changed bi-weekly. At the end of the mating period (Day 28), the rams were removed and all ewes were recombined.

The numbers of foetuses were determined by ultrasound scanning 50 days after removal of the entire rams, and the data were used to calculate fertility (pregnant ewes per 100 ewes exposed to rams) and reproductive rate (foetuses *in utero* per 100 ewes exposed to rams). On the day of lambing, the date, sex, birthweight and lamb survival were recorded. The date of conception was estimated to have occurred 150 days prior (Holst et al. 1986).

Statistical analysis

With the aid of SAS version 9.3 (SAS Institute Inc., Cary, NC, USA), liveweight data were analysed using linear mixed-model procedures allowing repetitive measures (PROC-MIXED) with fixed effects including dam age (2–5 years), birth–reared type (single–single or twin–twin) and dietary group (LOW or HIGH). FAT or EMD was included independently as covariates. Identification number of the ewe within the sire of the ewe lambs was used as a random effect.

Liveweight gains for each lamb, separated for the ‘teasing’ and ‘mating’ periods, were calculated using a random coefficient regression including a cubic smoothing spline for time, a process that is appropriate when the response is linear (TRANSREG). LWG data were analysed using the linear mixed-model procedures (PROC-MIXED). Fixed effects in the model were dam age, birth–rear type and dietary group. FAT and EMD were included independently as covariates. The sire of the ewe lamb was used as a random effect.

Live weight and age at first oestrus were analysed using mixed models (PROC-MIXED) and included the following fixed effects: dam age, birth–rear type and live weight at scanning and at the start of the ‘teasing period’. LWG during the ‘teasing period’, FAT and EMD were included independently as covariates. The sire of ewe lamb was used as a random effect.

Puberty, fertility and lambing data were analysed using the generalized linear mixed-model procedures with a binomial distribution and logit link function (PROC-GLIMMIX). Fixed effects were dam age, birth–rear type and dietary group for fertility and live weight at scanning or at the start of the ‘teasing’ period (for puberty) or the ‘mating period’ (for fertility). LWG (divided into ‘teasing period’ for puberty and ‘mating period’ for fertility), FAT and EMD were included independently as covariates. Sire of ewe lamb was used as a random effect. Data for reproductive rate were analysed using the generalized linear mixed-model procedures with a multinomial distribution and logit link function (PROC-GLIMMIX). The same fixed effects, covariates and random effects were used as for the analysis of fertility.

Birthweight of the progeny for the nutritional treatments was analysed using PROC-GLM. All 2-way interactions among the fixed effects were included in each model, and non-significant ($p > 0.05$) interactions were removed from the final model. The data for puberty, fertility and reproductive rate are presented as logit values and back-transformed percentages.

Results

Ewe live weight and liveweight gain

At the start of mating, ewe lambs born and reared as singles were heavier than ewe lambs born and reared as twins (41.4 vs 37.3 kg; $p < 0.001$), but birth type–rear type had no effect on LWG during mating ($p > 0.05$), so the data for singles and twins were combined (Fig. 1). The mean (±SEM) live weight of ewe lambs increased during the teasing period from 25.3 ± 0.2 kg at weaning on Day −115 to 39.5 ± 0.2 kg on Day 0 with an average LWG of 124 ± 1.2 g/day when they were allocated to dietary treatments at the start of mating. For the ‘mating period’, live weight remained relatively constant in the LOW group (39.2 ± 0.3 kg on Day 0–39.3 ± 0.3 kg on Day 28) but continued to increase in the HIGH group (39.7 ± 0.3 kg on Day 0–45.0 ± 0.3 kg on Day 28; $p < 0.001$). Thus, LWG during the ‘mating period’ was negligible for the LOW group (2 ± 4.2 g/day) and much greater for the HIGH group (179 ± 3.8 g/day; $p < 0.001$). Ewe lambs with higher values for EMD or FAT were consistently heavier and grew faster during the teasing and mating periods than ewe lambs with low values ($p < 0.001$).

Live weight and age at puberty

During the ‘teasing period’, 58% of the ewe lambs were marked with crayons at least once. A further 11% was marked during the ‘mating period’. The proportion of ewe lambs attaining puberty by Day 270 and the average age at first oestrus were not influenced by LWG during the ‘teasing period’ or the ‘mating period’ ($p > 0.05$; Table 1). At first oestrus, the average live weight was 37.8 ± 0.2 kg (range 25.2–51.5) and the average age was 233 days (range 177–281). The proportion attaining puberty by 270 days and the average age and live weight at first oestrus were all influenced by birth type–rear type ($p < 0.001$). More single-born and reared ewe lambs (72%) attained puberty by 270 days than twin-born and reared ewe lambs (8%; $p < 0.001$). Lambs born and reared as singles were on average younger (230 days) and heavier (37.6 kg) at first oestrus than those born and reared as twins (244 days and 34.5 kg).

The likelihood of achieving puberty by Day 270 was influenced by EMD ($p < 0.01$), but not by FAT ($p > 0.05$; Table 1). Ewe lambs with higher values for EMD ($p \leq 0.05$) and FAT ($p < 0.05$) were younger at first oestrus. When live weight at scanning was removed from the statistical model, the effects of FAT and EMD on age at first oestrus were no longer significant ($p > 0.05$; Table 1). Ewe lambs with higher values for EMD or FAT were heavier at first oestrus than ewe lambs with lower values for these traits ($p < 0.001$; Table 1).

Fertility and reproductive rate

Only 21% of all ewe lambs were identified as pregnant and the average reproductive rate was 25%. There was a significant effect of mating sire on reproductive performance ($p < 0.001$): the fertility rate was 2%, 5%, 7% and 15% in the ewe lambs that were single-sire-mated to the four sires within the LOW group; within the HIGH group, fertility was 18%, 33%, 38% and 60%.

A greater proportion of ewe lambs were pregnant at scanning in the HIGH group (38%; 90/237) than in the LOW group (7%; 18/244; $p < 0.001$). Ewe lambs that were heavier at the start of the mating period were more fertile than ewes that were light ($p < 0.001$) regardless of dietary treatment (Fig. 2). It was estimated that approximately 78% of ewe lambs from both nutritional treatments conceived during the first 15 days after introduction of the entire rams (14/18 for LOW; 70/90 for HIGH). The average age at conception was 264 days (range 256–280) for the LOW group and 260 days (range 225–280) for the HIGH group ($p > 0.05$). The average live weight at the estimated time of conception was 41.2 ± 1.0 kg for the LOW group and 43.0 ± 0.5 kg for the HIGH group ($p > 0.05$).

The fertility rate was improved with increases in LWG during mating ($p < 0.001$), EMD ($p < 0.001$) or FAT ($p < 0.01$; Table 1). The effect of EMD on fertility was still significant when live weight at scanning was retained in the statistical analysis ($p < 0.05$; Fig. 3), whereas the effects of the other variables only became significant when live weight was removed from the model.

In the LOW group, 89% (16/18) of the pregnant lambs were carrying a single foetus and 11% (2/18) were carrying twins, whereas in the HIGH group, 79% (71/90) were carrying a single and 21% (19/91) were carrying twins. Reproductive rate was influenced by diet (46% for HIGH; 8% for LOW; $p < 0.001$) but not by their birth–rear type ($p > 0.05$; data not shown). Reproductive rate was positively related to live weight at the start of mating, regardless of dietary group ($p < 0.001$). Each extra kilogram of live weight at the start of mating for ewe lambs from the LOW group was associated with 0.4 extra foetuses per 100 ewes mated, whereas each extra kilogram of live weight at the start of mating for ewe lambs from the HIGH group was associated with 3.4 extra foetuses per 100 ewes mated.

Reproductive rate increased with increases in LWG during mating, EMD and FAT (Table 1; $p < 0.001$). The effects on reproductive rate of EMD (Fig. 4) and FAT were still evident when live weight at scanning was retained in the statistical model (Table 1; $p < 0.05$). An extra one mm of eye muscle depth for ewe lambs in the LOW group was associated with 1.2 extra foetuses per 100 ewes mated, whereas an extra one mm of eye muscle for ewe lambs in the HIGH group was associated with an extra 5.5 extra foetuses per 100 ewes mated (Fig. 4).

Lambing

Of ewes identified as pregnant, only 81% lambed. Lambs were born to a greater proportion of pregnant ewes in the HIGH group (83%; 75/90) than in the LOW group (72%; 13/18) ($p < 0.05$). Of all lambs born, 93 survived and 10 were dead at birth. Of the surviving lambs, 74% (69) were single-born and 26% (24) were twin-born, and 53% (49) were female and 47% (44) were male.

The average birthweight did not differ ($p > 0.05$) between the LOW (5.2 ± 0.2 kg) and HIGH groups (5 ± 0.08 kg). Single-born lambs were heavier than twin-born lambs (5.2 ± 0.08 kg for single vs 4.8

± 0.12 kg for twin; $p < 0.001$). Ram lambs (5.3 ± 0.1) were heavier at birth than ewe lambs (4.7 ± 0.1) ($p < 0.001$).

Discussion

In this large field study using Merino ewe lambs that were approximately 8 months old and weighed 40 kg at the start of the mating period, we hypothesized that (i) improving nutrition to increase LWG during mating would improve fertility and reproductive rate; (ii) the effects of LWG on fertility and reproductive rate would be similar regardless of absolute live weight at the start of mating; and (iii) the response to nutrition during mating would depend on muscle and fat phenotype. The first hypothesis was clearly supported because reproductive performance improved several fold in response to better nutrition and thus greater LWG during mating, and the benefits for fertility and reproductive rate were additional to those resulting from extra live weight at the start of mating. These outcomes are consistent with those reported by Mulvaney et al. (2010) who found increases in fertility (63% vs 52%) and reproductive rate (86% vs 57%) when they fed Romney ewe lambs to gain more than 200 g/day, compared to maintaining weight during mating. Similar observations with two different breeds strengthen our conclusion that management of nutrition to ensure rapid gains in live weight during the mating period will help maximize the reproductive efficiency of 8-month-old ewe lambs. Moreover, we can now explain at least some of the contrasting results between our two previous experiments (Rosales Nieto et al. 2013a,b). Paganoni et al. (2014a,b) did not observe any differences in fertility or reproductive rate between Merino ewe lambs gaining 158 or 187 g/day during a 68-day mating period, but most of those differences in live weight occurred after conception. Supplementary feeding can impose prohibitive costs, so further work is needed to define the optimum combinations of live weight at mating and LWG during mating to enable development of cost-effective management guidelines.

Reproductive performance was positively related to live weight at the start of mating, regardless of the level of nutrition during the mating period, an observation that is consistent with our previous studies (Rosales Nieto et al. 2013a,b). Most ewe lambs conceived during the first 15–20 days after introduction of the rams so, based on a difference in growth rate of 180 g/day, the maximum difference in live weight at conception between the treatments could only be 3–4 kg and was estimated to be much less. An increase in live weight at the time of conception as a result of faster growth during mating could therefore only explain approximately 10–12% of the 38% difference in reproductive rate between the nutritional treatments, so most of the response was probably independent of change in absolute live weight at the time of conception.

Phenotypic differences in the depth of muscle and fat were strongly related to age and live weight at puberty, and to fertility and reproductive rate. However, unlike our previous studies (Rosales Nieto et al. 2013a,b), the relationships for EMD (fertility and reproductive rate) and FAT (reproductive rate) remained significant even when live weight was retained in the statistical model. After adjusting for correlated changes in live weight, an extra 1 mm of eye muscle depth at post-weaning age would increase fertility and reproductive rate by as much, if not more than, an extra 1 kg live weight at the start of mating. This relationship reflects the physiological links between muscle tissue and reproductive function in young female sheep (Rosales Nieto et al. 2014). For industry, it is important to note that promotion of muscle accumulation, and therefore meat production, might also promote early puberty and enhanced reproductive performance.

Overall, reproductive performance in the present study was lower than expected, even for the animals fed to grow rapidly during mating. A number of animal, environmental and management factors are likely to have contributed to this outcome. First, only 58% of the ewe lambs reached puberty when the entire rams were introduced and only 69% displayed oestrus by the end of the mating period, compared to 90–97% in previous studies (Rosales Nieto et al. 2013a,b; Paganoni et al. 2014a,b). All of these studies used the same genotype from the same original source. However, the ewe lambs in this study were 2–6 kg lighter when they reached puberty than in the other studies and, probably, and many of them might have failed to achieve the body weight that is critical for puberty (Hafez 1952; Dýrmundsson 1973). In any case, fertility is lower in the first cycle than in subsequent cycles (Hare and Bryant 1985), so the 28-day mating period in this experiment, which was shorter than we used previously (Rosales Nieto et al. 2013a,b), would have limited the opportunities to breed (Paganoni et al. 2014a,b).

In addition, the ram to ewe ratio in the current study was 1 : 54–1 : 75 which was at least double that used previously, and whilst this was within the recommendations provided by Kenyon et al. (2014) based on the work with cross-bred ewe lambs, this indicates that the ram to ewe ratio required may be much less for Merino ewe lambs. Finally, the ewe lambs were single-sire-mated as the research was undertaken on a commercial ram breeding property that required full pedigree records and more than half of the rams achieved less than 20% fertility. This study has not only highlighted the importance of nutritional management before and during mating and selection of animals with more potential for growth, fat and muscle, but it is also clear that husbandry practices associated with management of teasers, duration of mating and ram management are also important to improve reproductive performance of Merino ewe lambs mated at 8 months of age.

The lambing rate in the present study was within the range in early reports on ewe lambs with natural mating (Quirke 1981). Indeed, both lambing rate and fertility were more variable and lower for our ewe lambs than for mature ewes of the same genotype under the similar conditions (Paganoni et al. 2014a) perhaps due to early reproductive losses observed in ewe lambs. On the other hand, our observations for birthweights were unexpected. The weights of singles and twins, and of ram lambs and ewe lambs, were greater than those reported by Mullaney (1969) and, in fact, similar to those reported by Paganoni et al. (2014b) for Merino ewes aged 2–9 years. Paganoni et al. (2014b) reported that mature ewes (> 3 years old) produced heavier lambs than young ewes (< 2 years old) but, as shown in the present study, with good nutritional management, there need be no disadvantage in birthweight for lambs born to very young ewes.

We conclude that young ewes that grow faster, either because they are fed well during mating or because they have higher phenotypic potential for fat and muscle, will achieve higher fertility and reproductive rates without affecting birthweight of the progeny when mated at 8 months of age. Importantly, the data presented here and in our previous studies suggest that any programme that aims to improve meat production in sheep flocks is also likely to improve reproduction (Safari et al. 2008).

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Conflict of interest

None of the authors have any conflict of interest to declare.

Author contributions

M. Ferguson and A. Thompson designed the research. C. Rosales Nieto, G. Martin and A. Thompson drafted and revised the paper. C. Rosales Nieto, H. Thompson, J. Briegel and C. Macleay allocated rams and ewes to treatments and collected the data.

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Figure 1. Mean (±SEM) live weights of the Merino ewe lambs. Vasectomized rams (‘teasers’) were introduced on Day −115 and then removed on Day 0 (arrow) and replaced with entire rams. At the same time, the ewes were allocated to HIGH (○) or LOW diets (●) until the end of mating, after which they were recombined until lambing. Data from single and twin births types are combined

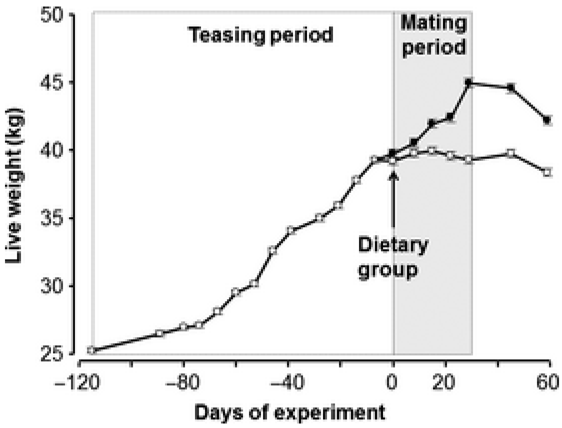

Figure 2. Relationships between live weight at the start of mating and fertility ($p < 0.001$), for the LOW dietary group (grey lines) and HIGH dietary group (black lines) in Merino ewe lambs mated at 8 months of age. Data from single and twin birth types are combined. The broken lines represent upper and lower 95% confidence limits

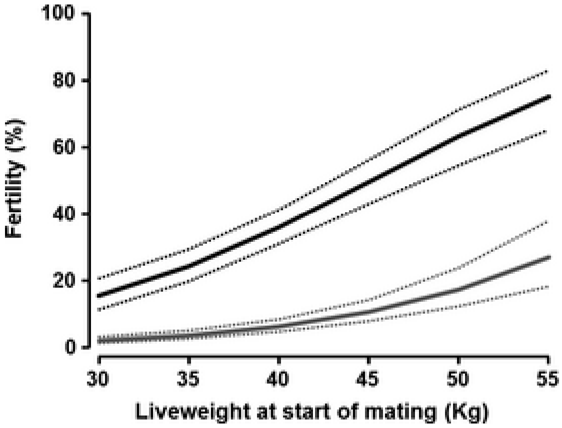

Figure 3. Relationships between phenotypic values for eye muscle depth (EMD) and fertility ($p < 0.05$) for the LOW dietary group (grey lines) and the HIGH dietary group (black lines) in Merino ewe lambs mated at 8 months of age. Live weight was retained in the analysis for eye muscle depth. Data from single and twin birth types are combined. The broken lines represent upper and lower 95% confidence limits

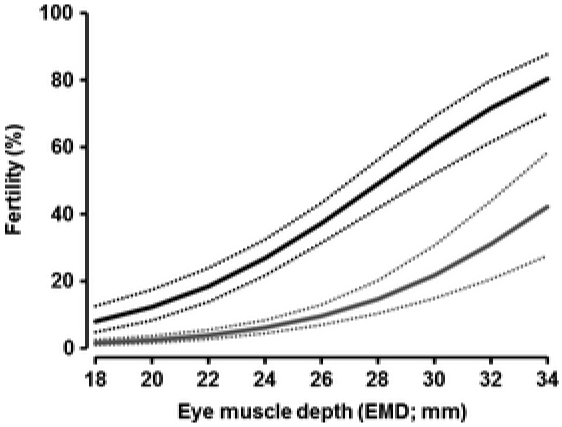

Figure 4. In Merino ewe lambs mated at 8 months of age, reproductive rate (foetuses in utero per 100 ewes exposed to rams) was related to the rate of muscle accumulation for both dietary groups ($p < 0.05$; LOW, grey lines; HIGH, black lines). Data from single and twin birth types are combined. Live weight was retained in the analysis for eye muscle depth. The broken lines represent upper and lower 95% confidence limits

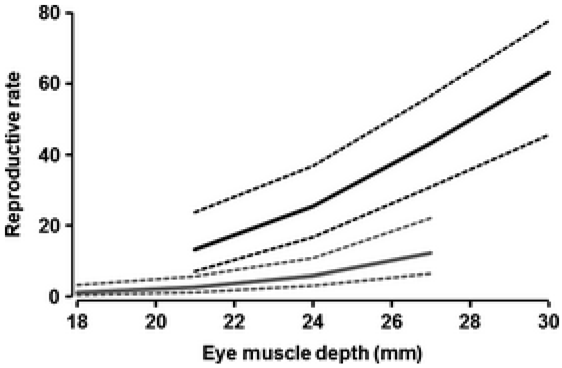

Table 1. Relationships for live weight (LW), liveweight gain (LWG; split into the teasing and mating periods), phenotype for eye muscle depth (EMD) and fatness (FAT), with measures of reproductive performance for Merino ewe lambs mated at 8 months of age. Information has been provided for analyses with and without live weight (LW) included in the statistical model. Puberty: first standing oestrus. Fertility: pregnant ewes per 100 ewes exposed to rams. Reproductive rate: foetuses *in utero* per 100 ewes exposed to rams

Variable	**Age at first oestrus**	**LW at first oestrus**	**Puberty**	**Fertility**	**Reproductive rate**
Live weight (at the start of mating)	na	na	na	***	***
LWG (during teasing)	ns	na	ns	na	na
LWG (during mating)	ns	na	ns	***	***
EMD	*	***	**	***	***
EMD (+ LW at scan)	ns	na	ns	*	*
FAT	*	***	ns	**	***
FAT (+ LW at scan)	ns	na	ns	ns	*

na, not applicable.

p -values: * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$; ns $p > 0.05$.