MAPPING QTL FOR EARLY GROWTH AND MATERNAL PERFORMANCE IN SHEEP

H.W. Raadsma, E. Jonas, K.R. Zenger, C.A. Cavanagh, M.K. Lam and P.C. Thomson

ReproGen, Faculty of Veterinary Science, The University of Sydney, Camden, Australia

SUMMARY

This paper describes QTL for bodyweight, and growth rate between week 2 after birth up to 43 weeks of age, and maternal performance based on milk yield and milk energy content in Awassi-Merino backcross progeny. QTL were mapped using a population specific framework map with 50 QTL (LOD>2) mapped for body weight and growth rate, and six QTL for milk yield and milk energy content. The majority of QTL for bodyweight and growth showed a significant sex by QTL interaction with wethers showing stronger QTL effects than ewes. Fewer QTL were detected for body weight or growth in the period from 2 to 25 weeks (range 1-4 QTL) whereas for the period from 25-43 weeks and over the entire growth period a greater number of QTL were observed (range 5-8). Implementation of multiple QTL for early growth and maternal performance will be difficult in sheep with need for validation and tracking in each population.

INTRODUCTION

In sheep, growth rate and body mass represent economically important traits, which are under moderate genetic control and respond to directional selection. Furthermore in intensive lamb production, maternal performance is considered a major contributor to early growth of lambs. Despite extensive background information in terms of population specific genetic parameters, relatively few QTL studies have been reported for growth and maternal performance in sheep. In addition many QTL studies have been restricted to partial genome scans, limiting the discovery of and reports on new QTL. In this study we report on QTL for growth from birth till ten months of age, and milk production in ewes as one of the major traits for maternal performance.

MATERIALS AND METHODS

Animals. As described by Raadsma *et al.* (2009), animals from an Awassi x Merino backcross population were generated specifically for QTL mapping across a broad range of phenotypes. In brief, four Awassi (A) sires were crossed with medium and superfine Merino (M) ewes to produce 16 AM F1 families. Four F1 ram lambs were selected to represent each of the founder families, and these were backcrossed to superfine and medium Merino ewes, producing families with approximately 611, 202, 141, and 186 AMM backcross progeny respectively. Additionally 1391 double-backcross and intercross progeny were generated from all F1 sires by mating them to backcross females. Final family sizes were 987, 703, 274 and 567 for the four families. Results are specifically detailed for Family 1 in AMM backcross progeny only

Framework map for QTL mapping. A population specific framework genetic linkage map was constructed after screening a panel of 558 pre-selected polymorphic micro-satellite markers for a genome wide scan, of which a total of 204 markers were informative in the AMM flock using Carthagene software (http://www.inra.fr/bia/T/CartaGene/index.html) with a minimum significance of LOD > 2 for the next best map order (average LOD: 6.92). The average adjacent marker density across the genome was 22.2 cM and predicted genome coverage was approximately 95% for each chromosome.

Traits and Analyses. Non-fasted body-weight measurements were taken at weeks 2, 15, 25, 32, 37, and 43 for up to 510 backcross progeny (246 ewes and 264 wethers) of family 1. All sheep were weaned at 15 weeks of age, and maintained as separate sex cohorts on pasture. Growth rates were divided into four growth phases: week 2 to week 15 (GR 2-15), week 15 to week 25 (GR15-25), week 25 to week 37 (GR25-37), and week 37 to week 43 (GR37-43). In addition growth rate was analysed for each period adjusting for initial body weight at the start of the growth period (GR-adj). Lactation data were obtained from 590 ewes over different lactations. Ewes were milked once daily and milk yields recorded on average every 2-3 days. Total milk yield throughout the lactation was determined by fitting the Wood lactation curve model (Wood 1968) to the milk yield data and standardizing the milk yield till day 100 making adjustments for average age, parity, and milking frequency. Predicted energy take off through the milk was predicted from yield and composition analyses based on fat, protein and lactose composition recorded from weekly samples. From these ewes, genotypes of 170 ewes from family 1 were available among the group of animals with recorded body weight.

Genetic and statistical analyses. QTL-MLE was used as a maximum likelihood based approach specifically for half sib designs in non-inbred strains (Raadsma *et al.* 2009). A chromosome-wide threshold for statistical significance was calculated for each chromosome, based on a LOD score of 2. The model fitted to the phenotypes (y) had the form $y = \mu + \text{Sex} + \text{QTL} + \text{Sex.QTL} + \varepsilon$, where inclusion of the Sex.QTL interaction term facilitated sex-specific QTL to be fitted. A likelihood ratio test was used to assess statistical significance of the interaction term.

RESULTS

Average body weights and growth rates at the four growth phases are shown in Table I as well as the mean lactation performance of ewes milked. Significant sex effects were observed for all measures where applicable with ewes being smaller and showing lower growth rates.

Table 1. Average body weight at weeks 2, 15, 25, 37 and 43 (BWT, kg) with corresponding growth rate (GR, kg/week), and milk yield till day 100 (MY, L) with corresponding energy yield until day 100 (EY, MJ) for N progeny in the QTL mapping data set

Trait	BWT WK 2	BWT WK 15	BWT WK 25	BWT WK 37	BWT WK 43	GR WK 02-15	GR WK 15-25	GR WK 25-37	GR WK 37-43	MY day 100	EY day 100
N	514	406	409	385	385	385	400	382	382	156	139
Mean	6.22	11.52	17.31	19.24	29.07	4.69	5.79	2.14	9.79	73.30	326.9
SD	1.33	2.61	2.86	2.68	3.51	1.60	1.67	1.74	2.00	19.44	87.5
CV	0.21	0.23	0.17	0.14	0.12	0.34	0.29	0.81	0.20	0.27	0.27
Min	2.50	4.80	9.50	10.00	16.50	-0.40	-0.50	-4.00	0.00	26.04	136.2
Max	10.30	24.00	26.00	28.00	40.50	10.00	11.80	13.00	17.50	126.32	545.5

Average body weights at all sequential times showed positive growth. The period from pre weaning (week 2-15) showed similar growth to the period immediately post weaning (week 15-25), but the period between week 25 and 37 was characterised by relatively slow growth coinciding with the winter season, and a large number of lambs showing weight loss. The period of greatest growth was observed from week 37-43 coinciding with spring season and supplementary feeding late winder early spring. The lactation performance of the 170 genotyped ewes milked once a day showed an average (Wood model based) cumulative milk yield till day

100 of 73 L with a range of 26 to 126 L. The predicted energy output corresponding to the lactation was 328 MJ ranging from 136 to 545 MJ over the 100 day lactation period. The energy calculation was based on the milk yield and the milk composition which was on average 5.5% protein, 7.1% fat and 3.6% lactose.

Table 2 shows the QTL from the single QTL analyses for body weights at weeks 2, 15, 25, 37, and 43 and corresponding growth phases, as well as milk yield traits. Four chromosomes showed significant QTL (LOD>3) for body weight and growth on OAR 3, 11, 21 and 25. In addition chromosomes 1, 3, 5, 6, 7, 8, 9, 11, 12, 16, 19, 21, 23, 24, and 25 showed QTL with LOD >2. The majority of QTL for BWT and GR showed a significant sex by QTL interaction. Average QTL effect sizes were 0.35, 0.43, 0.58, 0.48 and 0.33 SD for BWT, and 0.60, 0.01, 0.14, 0.20 SD for growth rate in wethers, whereas corresponding QTL in ewes were 0.1, -0.06, 0.05, 0.13 and 0.08 SD for BWT and -0.01, -0.06, 0.17 and 0.23 SD for GR, respectively. Fewer QTL were detected for body weight or growth in the period from 2 to 25 weeks (range 1-4 QTL) whereas for the period from 25-43 weeks and over the entire growth period a greater number of QTL were observed (range 5-8). QTL for cumulative milk yield till day 100 were detected on OAR 2, 3, 20 and 25. Matching QTL for energy output were only detected for OAR 3 and 20 for corresponding locations to cumulative milk yield on the same chromosomes.

Table 2: Chromosomes (OAR) with significant QTL for bodyweight (BWT), growth (GR) and growth adjusted for starting body weight (GR adj), milk yield and milk energy. Location of QTL position (cM) indicated for each chromosome, QTL in italic suggest significance of LOD scores <1.75<LOD<2.0, whereas those in bold were LOD >3.0 Number (n) of significant QTL (LOD>2.0) for each trait shown in last column.

OAR	1	2	3	4	5	6	7	8	9	11	12	15	16	19	20	21	23	24	25	n
BW2	-	265	-	26	-	-	-	52	-	-	-	*79*	-	-	*99*	-	-	-	-	3
BW15	238	-	49	-	-	-	44	-	*146*	-	-	-	-	-	-	-	-	-	-	3
BW25	-	-	50	-	121	-	-	-	140	-	-	-	-	-	-	-	*25*	85	-	4
BW37	*111*	*265*	51	-	119	65	-	-	144	**58**	-	-	-	-	-	78	41	**87**	-	8
BW43	-	-	**47**	-	-	68	16	75	145	55	-	-	-	-	-	**25**	-	85	-	8
GR2-15	238	-	-	-	-	-	-	-	*146*	-	-	-	-	-	-	-	-	-	-	1
GR15-25	-	-	-	-	-	-	-	-	127	-	-	-	*20*	*20*	*60*	-	-	105	-	2
GR25-37	*310*	-	-	-	-	-	-	-	-	71	-	-	*120*	**60**	-	-	-	-	-	2
GR37-43	209	-	*139*	-	-	-	116	*81*	*154*	-	-	-	-	67	-	**58**	-	-	85	5
GR2-43	118	-	28	-	-	62	-	77	-	55	-	-	-	-	-	26	-	86	-	7
GR2-43 adj	357	-	-	-	-	43	-	-	-	56	104	-	98	-	-	19	-	91	-	7
Milk yield	-	214	96	-	-	-	-	-	-	-	-	-	-	-	-	52	-	-	105	4
Milk Energy	-	-	**94**	-	-	-	-	-	-	-	-	-	-	-	-	50	-	-	-	2

DISCUSSION AND CONCLUSIONS

In this study, we report 50 significant QTL across 17 chromosomes related to body weight and growth rate for animals up to 10 months of age as part of a subset of observations not reported in the study described by Raadsma *et al.* (2009). In addition we report on six QTL for maternal performance as expressed by milk yield and composition. The pattern of growth in this flock is consistent for sheep maintained on semi-improved pasture in a temperate Australian tablelands climate characterized by low pasture availability in the colder winter months, and abundant pasture growth in spring with a residual pasture carry over in summer and autumn. This was reflected in the growth curves seen here, with a period of arrested growth over winter, followed by a period of rapid, almost compensatory growth in spring. The sheep were weighed immediately off pasture so some of the fluctuations in body weight and growth rates may reflect gut content. Despite these limitations the overall growth as shown across multiple measurements could be estimated as shown over the period shortly after birth till 43 weeks. From this analysis, relatively few QTL were observed for body weight and growth pre weaning, whereas growth post weaning almost revealed twice as many QTL. This study had the advantage of positioning the QTL on a resource specific framework map and covers a full autosomal genome scan as distinct from the previous partial genome scans. The QTL on OAR 1, 2, 8, 20 support previous findings by others who report QTL for similar traits in sheep (Walling *et al.* 2004; McRae *et al.* 2005; Beraldi *et al.* 2007; Hadjipavlou and Bishop 2008). No QTL have previously been reported for milk energy content, but QTL for milk yield on OAR 3 reported in this study supports previous findings reported by Carta *et al.* (2003) and Barillet *et al.* (2005).

Consistent with the extensive genetic variation which has been reported for growth, body size and to a lesser extent maternal performance and milk production, the presence of QTL with relatively large effect were detected. The effects of the QTL detected in this study are relatively large (in the order of 0.4 to 0.7 phenotypic standard deviations) and originated predominantly from the larger-framed Awassi grandsire, as expected with the favourable allele for growth and body size. However, surprisingly for most traits, significant sex by QTL interactions were observed, with most QTL expressed in males but not females. No immediate or obvious explanation can be given for this, since the ewes and wethers were managed together for most of the period.

Utilization of multiple QTL for early growth and maternal performance would be difficult with at least 14 QTL of potential interest which would have to be mapped and tracked simultaneously in commercial populations. The problems of applying a multi QTL selection programme have been detailed by Boichard *et al.* (2006) for dairy cattle. A more amenable approach may be to combine high density marker information in genomic selection strategies.

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