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Current status of QTL and association studies in New Zealand cattle, sheep and deer

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ABSTRACT

In the last 15 years, a series of experiments has been carried out to search for quantitative trait loci (QTL) in New Zealand cattle, sheep and deer. A QTL represents the position on a chromosome where there is a statistically significant genetic effect on a measured trait. This paper reviews data published so far from these QTL trials and from various association studies. Although the measurement of traits (or 'phenotypes') and the sampling of tissue or fluid for DNA may be complete, the genotyping of DNA is still incomplete in most studies; further work may be expected as new DNA genotyping techniques and new genomic data become available, and as funds allow. In cattle, we describe the current status of research for carcass composition, meat quality, pubertal traits, milk yield and milk composition traits, and resistance to facial eczema and bloat. In sheep, we include QTL searches for disease traits (resistance to nematode parasites, facial eczema, ryegrass staggers, and footrot), muscling and carcass composition, reproductive traits, wool traits, and lamb survival. In deer, QTL searches have been carried out for live weights, seasonality and pubertal traits, using measurements from an interspecific hybrid. Generally, significant results have been followed further by fine-mapping and independent validation, before release to industry. Some of the mapping techniques will be described, with examples. So far, QTLs under study in New Zealand have led to the identification and use of gene-tests or marker-tests for meat tenderness and carcass composition in beef cattle, milk yield and composition traits in dairy cattle, and meat yield %, muscling and litter size genes in sheep.

Keywords: cattle; sheep; deer; QTL.

INTRODUCTION

In the last 15 years, a series of experiments has been carried out to search for quantitative trait loci (QTL) in New Zealand cattle, sheep and deer. This paper describes the trial design of these major animal experiments, established to search for DNA markers linked to production traits, and ultimately for the causal gene variants. A QTL represents the position on a chromosome where there is a statistically significant genetic effect on a measured trait. We describe the approximate size of each study, and its time period and the trait groups recorded. Given the research climate in which we find ourselves in New Zealand, many unpublished or unpatented findings are retained by the research groups involved, so we cannot expect to be complete in reporting and summarising results at this stage. We have endeavoured to cite the published QTL and genes, and those citations give more detail of the trial design and methodologies used.

RESULTS AND DISCUSSION

Cattle

Carcass composition and meat quality

Table 1 (#1) shows a double-backcross experiment with beef cattle, being managed by AgResearch in collaboration with the University of Adelaide. Six first-cross Jersey x Limousin sires were generated, and were used to breed backcrosses from both breeds of straight-bred dams. The offspring were phenotyped primarily for carcass composition and meat quality traits, but many additional traits were also recorded,

including facial eczema resistance and age at puberty (both described later). A Limousin-derived mutant myostatin allele ('F94L') was found to be segregating in all first-cross sires, and sire-derived effects on body composition traits were evaluated from this mutant allele compared with the wild-type allele (Sellick *et al.*, 2007), including possible pleiotropic effects on other traits such as meat tenderness (main results currently being prepared for publication).

From this backcross resource and other independent New Zealand Angus and Hereford cattle recorded, the calpain-1 gene (*CAPN1*) was confirmed with a major effect on meat tenderness (Page *et al.*, 2002), and the combined effects of *CAPN1* and calpastatin on meat tenderness were characterised at six stages during the meat-aging process (Morris *et al.*, 2006b).

Pubertal traits

Angus breeding lines have been selected by AgResearch over multiple generations since 1984/85 for 'Early' or 'Late' age at puberty in heifers (Morris *et al.*, 2006a). These lines are not replicated in any other domestic or international experiments. Bulls which were first-crosses between the lines were bred, and then used to generate over 400 backcross calves out of cows from the 'Early' and 'Late' age-at-puberty lines. Three analyses have been carried out using puberty phenotypes, the results of which are currently being prepared for publication. These analyses include: the confirmation of age-at-puberty QTL (identified in the Jersey x Limousin trial) by linkage analysis in the backcross calves of both sexes (Table 1, #2), validation of these QTL in an association study using pure selection-line animals, and thirdly an association study of candidate 'puberty' genes in the selection line animals. Pubertal QTLs are also part of experimental studies by LIC (described below). Resources are not yet available to undertake a genome scan of all the remaining chromosomes that failed to reveal QTL for pubertal traits in the Jersey x Limousin study. Thus any puberty alleles that differ between the divergent Angus selection lines, but which did not differ between the Jersey and Limousin breeds, are still to be identified.

Facial eczema

Facial eczema (FE) is caused by sporidesmin, a toxin produced by spores of the fungus, *Pithomyces chartarum*, which are found on many pastures in summer and autumn in the North Island of New Zealand. In susceptible ruminants, sporidesmin causes liver injury, with deleterious effects on production. Following the original

demonstration in sheep that resistance to FE is inherited (Campbell *et al.*, 1981), similar results have been reported in cattle (recently reviewed by Cullen *et al.*, 2006). Progeny testing of Friesian and Jersey sires for resistance has been carried out in the last four years, by sporidesmin-dosing young sons of sires (n = 572 sons, in 2002-04), and by phenotyping lactating daughters of sires following unintended FE challenge in commercial herds (n = 6300 cows, in the autumns of 2004-06). A total of 164 sires have been ranked by these methods, with each sire having a breeding value reliability of at least 0.70. Using DNA from the sires, cows and bull calves which were extreme for resistance or susceptibility to FE (known as the 'tails'), an association study has been carried out to confirm and fine-map QTL regions originally identified in the Jersey x Limousin trial (Table 1, #3). There are three promising chromosomal regions under study, and these are now being followed up by genotyping further microsatellites. Another option under consideration is to use the SNP chips available from Affymetrix™, to undertake a whole-genome scan and generate tens of thousands of SNP genotypes per animal. This technology is new and will require new statistical approaches to process the results, and an understanding of the relevant linkage disequilibrium (LD) for Friesian and Jersey sires in New Zealand.

For FE, Spelman *et al.* (2000) also describe survey data collected in 2- and 3-year-old daughters in 350 sire proving scheme herds following unintended natural FE challenge. The authors proposed an association study, using pooled DNA from 516 daughters scored as at least 'severely affected', compared with pooled DNA from unaffected herd-mates.

Milk yield and composition

The first New Zealand QTL project began in 1994 and was an international collaboration between the then New Zealand Dairy Board and groups in Holland and Belgium, using New Zealand and Dutch dairy cattle families (Spelman *et al.*, 1996, 2001). The 1996 report identified a significant QTL on chromosome 6 for milk protein % from five traits analysed (lactation milk yield, protein yield, fat yield, protein % and fat %). Subsequent findings published from these sire families included QTL for a series of 'Traits Other than Production' (Spelman *et al.*, 1999). Perhaps more importantly, the collaborators discovered the acylCoA:diacylglycerol acyltransferase (*DGAT1*) gene on chromosome 14 in the Dutch population (granddaughter design) and in the New Zealand population (daughter design) of Holstein-Friesians (Grisart *et al.*, 2002), and its effect was also

characterised subsequently in New Zealand Jerseys (Spelman *et al.*, 2002). The allele substitution effects were 120 to 130 L for lactation milk yield (both breeds), 2 to 3 kg for lactation protein yield (both breeds) and 3 kg (Jersey) and 6 kg (Holstein-Friesian) for lactation fat yield. In both breeds, the allele for increased fat yield also reduced milk and protein yields. Additional research with granddaughter and daughter designs from Holland and New Zealand, including both the New Zealand Holstein-Friesian and Jersey populations, then identified the growth hormone receptor (*GHR*) gene on chromosome 20 as the underlying cause of another major QTL for milk production (Blott *et al.*, 2003), with an SNP at amino-acid position 279 being postulated as the major cause. Adding one Y 'allele' at SNP F279Y increased lactation milk yield by 87 to 162 kg in the New Zealand populations. The authors suggested that the *GHR* and *DGAT1* mutations had additive effects on milk production traits.

An intensive dairy cow study, managed by LIC and Boviquest, has been underway with approximately 800 Friesian x Jersey cows born in 2000 and 2001 in New Zealand, using an F2 design with six F1 sires (Table 1, #4). The most recent public information appears to be from Bennett *et al.* (2005), who describe the continuing phenotyping of the F2 cows for milk production, health, reproductive, behavioural and food-conversion-efficiency traits at the research site in Hawera. The authors reported that 7 QTL for production had been identified (*DGAT1*, *GHR*, and genes for milk proteins: α_{S1}-casein, β-casein - also known as the A2 test, κ-casein, α-lactalbumin and β-lactoglobulin). Two other heifer calf crops have been bred ('Cohorts 3 and 4' in 2003 and 2004, daughters of the F2 cows), and samples/measurements from them are being used to confirm the genes identified in the F2 cows. Additionally, the authors described 'Outlier' trials for cow fertility and for milk protein yield, where DNA from industry animals with extreme phenotype has been sampled, and where respectively 6 and 2 QTLs have been identified. For puberty, McNaughton *et al.* (2005) reported five QTL for live weight at puberty (as a percentage of estimated mature weight) on chromosomes 5, 6, 7, 11 and 16.

Following all the above molecular gene search work carried out so far by LIC, there is now a move towards whole-genome SNP technology (Schaeffer, 2006), with tens of thousands of SNP genotypes being completed per animal (sire), to increase the rate of annual genetic gain in various dairy industries, including the New Zealand one.

A milk composition trial was established by AgResearch in 2000/01 (Table 1, #5), collecting milk samples from the daughters of 11 Holstein-Friesian sires widely-used in New Zealand (average = 373 daughters per sire; samples from 21 herds), and this has led to the identification of genetic differences in the fatty acid composition of milkfat. The composition is associated with a SNP in the fatty acid synthase gene (*FASN*), and subsequent work in milk from randomly sampled Friesian and Jersey cows from independent dairy herds has confirmed the presence and direction of the effect (Morris *et al.*, 2007). However, according to the phenotypes recorded in the Jersey x Limousin beef trial, this *FASN* gene appears to have an effect opposite in sign in adipose fat from that in milkfat (Morris *et al.*, 2007).

Bloat

Two breeding lines of Friesian x Jersey cross cattle were available at Ruakura for generating a genomic resource to study resistance/susceptibility to pasture bloat. For 30 years from 1972/73, the lines were divergently selected for differences in susceptibility (estimates of heritability and repeatability for single-record bloat score being 0.19 ± 0.04 and 0.44 ± 0.02, respectively, with a divergence between lines of 1.20 phenotypic standard deviations: Morris *et al.*, 1997). The lines were used to generate first-cross sires and then backcrosses (1996-2002 calf crops) from selection-line dams. The backcrosses were phenotyped for bloat susceptibility, with DNA collected and stored for future analysis (Table 1, #6). Discovery of the dominance relationship for the bloat phenotype, in crosses and the first crop of backcrosses between the two selection lines, led to our breeding all subsequent backcrosses by using matings to susceptible-line cows only; gene(s) for high-bloat susceptibility appear to be recessive to those for low-bloat susceptibility.

To supplement animals/DNA samples from the research herd environment, described above, a second DNA resource for studying bloat genetics in dairy cattle has been collected by AgResearch. In the spring seasons of 2001-03 working with industry herds, a total of 795 samples for DNA have been collected from cows, all of which were said to have died of bloat. This resource, along with DNA samples from control animals, should provide an independent test of any association found between DNA and bloat phenotype.

Sheep
Nematode parasites

Crawford (2001) reviewed early experimental QTL studies from New Zealand and overseas in sheep, and his summary included detail of

experiments by AgResearch on QTL for host resistance to nematode parasites. Table 1 (# 7) shows the experimental flocks bred to provide resources for phenotyping and DNA sampling for parasite-related traits, mainly faecal egg count (FEC) *in vivo* and gastro-intestinal parasite burden (determined *post mortem*). The experimental flocks are currently being augmented through access to industry flocks, by collecting DNA from approx. 1000 sires which are being progeny-tested for FEC. This latter trial is the traditional 'daughter' design of the dairy industry (Weller *et al*., 1990) although, in the case of sheep parasites, FEC data are collected from sons and/or daughters, and LD rather than linkage is used for analysis. From the number of research teams worldwide (New Zealand, Australia, France, Kenya, UK, USA) cited by Crawford (2001) as working on 'parasite-resistance' QTL in sheep, and the paucity of published results since then, it is clear that the subject area is proving difficult.

Using the outcross resource #7 (Table 1), Paterson *et al*. (2001) described a QTL on ovine chromosome 3q, for which a strong candidate gene is interferon gamma, but it has not been possible to fully substantiate this gene in subsequent work. Crawford *et al.* (2006) reviewed four international studies, all with paternal half-sib pedigrees, two of which were only partially published; the other two identified 0 and 4 chromosomes (numbers 2, 3, 14 and 20) with QTL for parasite-related traits at the genome-wide level of significance. The Crawford *et al.* (2006) publication presented results from the AgResearch outcross study on host resistance (Table 1, #7), with data from 5 large paternal half-sib families They showed evidence for 6 QTL with genome-wide significance from genotyping the 'tails', but confirmation was only obtained for the two at one position on chromosome 8 (telomeric end) from genotyping all animals. For sheep carrying the favourable allele at the chromosome 8 QTL, the size of the effect was estimated to be a 2.3-fold reduction in adult *Trichostrongylus spp.* worms and late stage larvae in the abomasum and small intestine. With only one QTL locus identified from the study, the authors concluded that a more attractive experimental design for future discovery work with host resistance to parasites is to use LD or allelic association studies to search for further relevant chromosomes and genes. They suggested that the simplest explanation for the small number of genes identified so far is that many genes of small effect are involved, for this quite highly heritable trait. Other complementary approaches include microarray studies to determine differences between lines of sheep selected for resistance or susceptibility to nematodes; Diez-Tascon *et al.* (2005) have demonstrated that AgResearch's resistant and susceptible FEC-selection lines of Perendales differ in pathways associated with 1). development of an acquired immune response and 2). structure of intestinal smooth muscle.

Facial eczema

Early DNA studies on FE resistance in sheep, using outcross pedigrees from AgResearch's Romney FE selection lines (Table 1, #8), implicated catalase as one of the enzymes associated with detoxification (Phua *et al*., 1999). Two other enzymes shown to differ in activity between the resistant and susceptible lines of sheep are superoxide dismutase and glutathione peroxidase (Hohenboken *et al*., 2004). All three enzymes have antioxidant roles, and are capable of scavenging reactive oxygen species. Transferrin alleles also appear to be associated with FE resistance (Morris *et al*., 1988).

From the same outcross pedigrees of Romney FE selection lines noted above, an ATP-binding cassette transporter gene (*ABCG2*) has recently been identified with involvement in FE resistance. An intronic SNP marker on the gene showed significantly different allelic frequencies between the selection lines (Duncan *et al*., 2007). The *ABCG2* gene lies on ovine chromosome 6, in a region already identified as providing weak evidence for an FE QTL. This xenobiotic transporter gene was originally implicated as a candidate from its sequence homology with a yeast protein, *PDR5* (*pleiotropic drug resistance protein-5*, or *STS1*) which had been found to modulate the sporidesmin sensitivity of yeast, *Saccharomyces cerevisiae* (Bissinger & Kuchler, 1994). Further resistance genes of sheep remain to be identified from the three resources of data and DNA already collected (Table 1, #8).

Ryegrass staggers

Ryegrass Staggers (RGS) is predominantly a summer/autumn metabolic disorder in ruminants, caused by ingestion of the lolitrem-B toxin from endophyte-infected perennial ryegrass, and it is common in New Zealand. It causes neuromuscular in-coordination in susceptible animals under stress, *e.g.* when mustered by sheep dogs. It is of welfare concern, and it is costly to farmers because it severely compromises grazing management. In sheep, resistance to clinical RGS is heritable (Amyes *et al*., 2002), and divergent lines have been bred for resistance or susceptibility to RGS. Using 3 F1 sires, backcrosses and outcrosses have been generated from these breeding lines (Table 1, #9), phenotyped for RGS resistance, with tissue

samples stored for potential future molecular studies.

Body composition and meat quality

Recent DNA-based research in the areas of meat yield and meat quality (Table 1, #10) has focussed around linkage studies on two selected chromosome regions. These contain the *Carwell* locus (Jopson *et al.*, 2001), which results in increased area and weight of the *M. longissimus dorsi* muscle, and the myostatin (or *GDF8*) gene (Broad *et al.*, 2000; Johnson, 2003; Johnson *et al.*, 2005), leading to an overall increase in carcass muscle and decrease in carcass fat. The two genes are under study at AgResearch in collaboration with Landcorp and Massey University, respectively. Haplotype tests around these two QTL are now being used commercially in sheep breeding programmes (Campbell & McLaren, 2007).

A large study to identify QTL for body composition, meat quality and bone density was initiated in 1995-1996. The QTL data were derived from backcrosses within AgResearch's lean x fat Coopworth lines and a number of QTL have been identified for bone density, a trait associated with osteoporosis in humans (Campbell *et al.*, 2003). Additional QTL for body composition, particularly fat depth, meat tenderness and meat colour have been identified as part of this backcross experiment, and results are currently being prepared for publication.

A new genome scan is now underway at AgResearch to identify further meat quality QTL. The animals used are part of the Rissington Breedline Primera progeny test programme (Table 1, #10). The main trait to be analysed in this trial is meat colour stability, which has been shown in recent phenotypic studies of sire groups to be highly heritable (Campbell, unpublished data). Consumers judge meat freshness by its colour, so meat colour stability is important for chilled meat in the New Zealand export trade. Other traits collected for QTL analysis are tenderness, muscle and fat density (via computerised tomography scanning) and marbling.

Wool traits

A double backcross design was set up in 1992-94 with Merino and Romney grandparents, to study genomic variation in wool production traits, wool quality traits and horns (Table 1, #11). There were in total 792 backcross animals in the study. In spite of very large differences between the means of traits from the two breeds involved, there was only one significant wool QTL, for fibre diameter, with an effect of 1.7 μm (Henry *et al.*, 1998). The position of the horn locus was also mapped in this resource (Montgomery *et al.*, 1996).

Reproduction

Litter size, which is one of the most intractable and lowly heritable traits in the sheep production spectrum, turned out to be the first trait to succumb to molecular techniques on major genes for production in sheep, as a result of the phenotypic measurement of ovulation rate. The first production gene published at the molecular level was the *Inverdale* gene which is a mutation in *BMP15* (Galloway *et al.,* 2000), followed closely by the *Booroola* which is a mutation in *BMPR1B* (Wilson *et al.*, 2001). There is now evidence of other major genes for ovulation rate segregating in New Zealand sheep, the *Woodlands* gene (Davis *et al.*, 2001) and the *Wishart* gene (Davis *et al.*, 2006b), although these have not yet been identified at the molecular level. Molecular studies with DNA from flocks of Woodlands and Wishart sheep maintained by AgResearch are still in progress. There are other ovulation rate genes now explained by mutations in similar genes overseas, *e.g.*, in the Belclare and Cambridge breeds (Hanrahan *et al.*, 2004) and in the Lacaune breed (Bodin *et al.*, 2006). More details are given by Davis *et al.* (2006a).

In order to identify the first four of these litter size genes above, AgResearch's team at Invermay first used ram progeny-testing (Table 1, #12), to demonstrate the segregation of a ram's alleles through his daughters' ovulation rates. Each gene effect was first identified at the chromosomal level; two of the genes (*Booroola* and *Wishart*) are on different autosomes, whilst the *Inverdale* and *Woodlands* genes are both on the X chromosome. Much early work was then carried out by fine mapping, and this was first applied to the *Booroola* gene (Montgomery *et al.*, 1993). After fine mapping, it was necessary to rely on breakpoint mapping to demonstrate that cross-overs in the ancestry of progeny-tested sires were consistent with the phenotypic performance of daughter groups inheriting sire-derived alleles. Generally these approaches can only narrow the causal variant to a few contiguous genes on a chromosome; from there it is necessary to search for physiological differences traceable to just one candidate gene. In the case of the sex-linked *Inverdale* gene, this last process was facilitated by the field discovery of two different mutant phenotypes, *Inverdale* (*FecX^I*) and *Hanna* (*FecX^H*), both of which were traceable to mutations of the *BMP15* gene.

Lamb survival and cold tolerance

Resources for a large AgResearch study on perinatal lamb survival (Table 1, #13) are being built up by Invermay staff, with the considerable assistance of ram breeders in industry. Data and samples from a total of 390 progeny-tested sires are available at this stage. One component of perinatal survival is cold tolerance, and staff at Lincoln University have used a candidate gene approach (Table 1, #14) to screen DNA from 89 Merino sires (with 4486 progeny), and have reported an association with the *β₃-adrenergic receptor* (*ADRB3*) locus (Forrest *et al.*, 2006).

Footrot

Footrot in sheep is a serious management problem, and it has been shown to have a heritable component (Skerman *et al*., 1988). Sire-progeny group data have been accumulated, and an association with a gene in the ovine major histocompatibility complex (class II locus) has been identified in Corriedales (Escayg *et al*., 1997). These results have also been followed up in South Island Merinos.

Other

A test has been developed for a recessive gene in sheep causing microphthalmia (congenital blindness), which is present in the Texel breed and in composites carrying a Texel component (van der Linde-Sipman *et al*., 2003). The trait has been mapped by linkage and then LD. The haplotype defined was validated in separate resources, and breed frequencies were estimated (McEwan, pers. comm.). A gene test is offered commercially as "i-scan" by Catapult Genetics in New Zealand, Australia and Europe.

Deer

Tate *et al.* (1997a; b) described the creation of interspecific hybrids between the Père David's deer (*Elaphurus davidianus*) and red deer (*Cervus elaphus*). The authors generated backcrosses out of red deer dams for QTL and gene mapping studies targeted at growth and morphological traits, which differ considerably between these two species (Table 1, #16).

Knowledge of the deer genome is much more limited than for the cattle and sheep genomes. However, a genetic map has been compiled using the interspecific hybrids (Slate *et al*., 2002), and the linkage groups have now been assigned to chromosomes (Bonnet *et al*., 2001). QTL have been identified for liveweight traits by Goosen *et al*. (1999), and for pubertal and seasonality traits by Goosen *et al.* (2000). Interestingly, three QTL have been identified that account for a major proportion of the morphological differences between these two species, with each QTL having effects on multiple phenotypes that include foot, tail and leg length, and various cranial morphologies (Maqbool *et al*., 2007). These data suggest that only a few genes of major effect can account for the morphological differences observed between species.

A panel of DNA markers is now used routinely for commercial deer pedigree work (Tate *et al*., 1998), which avoids the difficulties of tagging newborn animals (Ward *et al*., 2001). Molecular DNA markers are also being used to determine levels of hybridisation between farmed red deer and the heavier wapiti breed. This has been useful for farmers interested in breed composition in their herds, and also for research into the effects of wapiti x red deer hybridisation on pubertal development and pregnancy in 18-month animals (Asher *et al*., 2005). Current work in deer genomics is focusing on reproductive seasonality and muscling. This work uses a strategy based on candidate genes, and on sequence information derived from genomic studies for equivalent traits in other species.

Table 1: Summary of QTL experiments in New Zealand.

Resource	Design	Main Trait Groups	Additional Trait Groups	Number	Dates: Birth Years	Notes	Reference*
CATTLE							
1. AgR Jersey x Limousin	Double BX	Carcass composition & meat quality	FE, FEC, temperament, puberty, minerals	416	1996 & 1997	Another approx. 400 also generated in Adelaide; 6 sires	Morris *et al.* (2001)
2. AgR Angus puberty lines	Double BX	Puberty traits, both sexes	Carcass comp, tenderness, FEC, temperament	419	2000-03	3 sires	Morris *et al.* (2006a), Phase 3
3. AgR Facial Eczema study (FE)	LD	FE susceptibility (GGT enzyme)		6300	2004-06 seasons	Association study; 164 sires	Cullen *et al.* (2006)
4. LIC Friesian x Jersey trial	F2	Milk yield & composition	Health, reprod., intake, efficiency	800	2000-01	6 F1 sires	Spelman *et al.* (2004)
5. AgR Milk Composition trial	Sire prog.	Milkfat: fatty acid composition	Milk composition traits	4109	2000/01 season	Association study	Morris *et al.* (2007)
6. AgR Bloat trial	BX to Susc. line	Bloat susceptibility (score)		100	1996-2002		Morris *et al.* (1997)
SHEEP**							
7. Romney FEC selection lines	Outcross	Parasite burden, FEC, antibodies		940	1993-95	Natural challenge	Crawford *et al.* (2006)
Romney FEC selection lines	BX	Parasite burden, FEC, antibodies		600	1995-96	Natural challenge	Crawford, pers. comm.
Texel x Coopworth cross	BX	Parasite burden, FEC, antibodies	Muscling	273	1995	Artificial challenge	McEwan, pers. comm.
Industry sires	LD	FEC	SIL production traits	100000	1997-2006	Natural challenge, 1000	McEwan, pers. comm.
8. Romney FE selection lines	Outcross	FE susceptibility		595	1992-93	Artificial challenge	Duncan *et al.* (2007)
Romney FE selection lines	Double BX	FE susceptibility		155	1997-98	Artificial challenge	Phua, pers. comm.
(Finn x Texel) x Coopworth	Outcross	FE susceptibility	Wool traits, minerals in liver	600	2001	Artificial challenge	Phua, pers. comm.
9. Ryegrass staggers seln lines	BX & Outcross	Ryegrass staggers score		624	1999-2002	Mainly BX; 3 F1 sires	Amyes *et al.* (2002)
10. Coopworth Fat/Lean study	Double BX	Carc composition, meat quality	Bone density	631	1995-96	5 sires	Campbell *et al.* (2003)
Massey Texel & Tex x CPW sires	Outcross	Body composition	Meat quality traits	540	2001	6 sires	Johnson *et al.* (2005)
Rissington Breedline Primera	3-gen. families	Meat quality traits	Weights of primal cuts, colour stability, musc & fat density, marbling	2500	2005?		Campbell, pers. comm.
Landcorp Carwell flock	Multi-	Carcass composition	Meat quality	3000	1995-2006	CT scanning	Jopson *et al.* (2001)
11. Merino x Romney	Double BX	Wool traits	Horns	792	1992-94		Henry *et al.* (1998)
12. Ewe litter size***	Sire prog. tests	Ovulation rate and/or Litter size				Laparoscopy & lambing	Davis *et al.* (2006a)
13. Lamb Survival Resource	Sire prog. groups	Perinatal lamb survival, birth wt.	Ewe body condition, maternal behaviour score	46000	2003-2004	Association study, 390 sires	Everett-Hincks, pers. comm.
14. Lincoln Cold tol'nce (Merino)	Sire prog. groups	Perinatal lamb survival	Total pre-weaning mortality	4488		89 sires	Forrest *et al.* (2006)
15. Lincoln Footrot (Corriedale)	Sire prog. groups	Footrot rating		144+254		2 trials	Escayg *et al.* (1997)
DEER (AgResearch)							
16. Père David x Red Deer hybrids	BX to red deer	Growth & morphological traits		346	1990-95		Tate *et al.* (1997a)

BX = backcross; CPW = Coopworth; CT = computerised tomography; FE = facial eczema; FEC = faecal egg count; GGT = gamma glutamyltransferase; LD = linkage disequilibrium; SIL = Sheep Improvement Ltd.

* One reference only per experiment, describing the animal resource.

** All are AgResearch studies, except where stated otherwise.

*** Four genes identified in New Zealand by this same method (Booroola, Inverdale, Woodlands, Wishart), but with differing modes of action.