

ANNUAL REPORT OF MULTI-STATE RESEARCH ACTIVITY

PROJECT: NRSP-8

PROJECT TITLE: NRSP-8 Sheep/Goats Species Committee

PERIOD COVERED: January 1 to December 31, 2017

DATE OF THIS REPORT: February 1, 2018

ANNUAL MEETING DATES: January 13-14, 2018

PARTICIPANTS:

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¹In attendance at the 2018 NRSP-8 meeting.

BRIEF SUMMARY OF MINUTES OF ANNUAL MEETING:

The 2018 annual meeting of the NRSP-8 Cattle, Sheep, and Goat committee was held on Jan 13-14 in conjunction with the Plant and Animal Genome XXVI meeting. The morning session of the scientific meeting on Jan 13th was held as a joint session in with the Swine Committee with a total of 6 presentations. Theses presentations included an over view of the genomic tools and improvements, genomic resources, manual annotation, the identification of regulatory region, disease challenge models and complex trait, and implications for genomic prediction from sequence data. The Saturday afternoon and Sunday morning sessions of the combined Cattle/Sheep/Goat workshops included 17 presentations covering a wide variety of topics, from the numerous different cattle genome assemblies, imputation, copy number variation, annotation of immune gene clusters, analyses of the microbiome, methylation, feed efficiency, genetic signatures, and high resolution atlas of gene expression in sheep. Attendance at the sessions was good with more than 220 people attending the Cattle/ Swine scientific session, including delegates from Academia, Industry and Governments and at least 24 countries. Attendance at the Cattle/Sheep/Goat 1 workshop included 100 people from 16 countries, and in attendance at the Cattle/Sheep/Goat 2 workshop there were

128 people from 22 different countries. Additionally, there were 42 cattle and 25 sheep and goat posters presented. Brenda Murdoch was thanked for serving as President of the NRSP-8 Cattle, Sheep and Goat Committee in 2017-18. Rebecca Cockrum will serve as President in 2018-19. Ben Rosen was elected as the 2018-2019 Secretary, and he will serve as President in 2019-2020.

ACCOMPLISHMENTS AND IMPACTS:

Objective 1: Advance the status of reference genomes for all species, including basic annotation of worldwide genetic variation, by broad sequencing among different lines and breeds of animals.

The NRSP-8 sheep co-coordinators are participants in the International Sheep Genome Consortium (ISGC) (<http://www.sheepmap.org/>). This multi-institutional organization has assumed a key role in the coordination and prioritization of ovine genomic resources. An ongoing project of the ISGC is development of a whole genome reference assembly. In 2010, sequence data were generated at two sequencing facilities (Beijing Genomics Institute and the Roslin Institute) from DNA of a Texel ewe and a Texel ram, respectively. The ovine whole genome assembly built on these two sequences was released in October, 2012 as Oar v3.1 through NCBI. Kim Worley (BCM-HGSC) has used PacBio sequence data with PBJelly to fill in gaps and improve the male Texel sheep assembly. The assembly is more contiguous, with the contig N50 increasing from 41.7 kb to 165.2 kb. Also, almost 25% of the contigs are larger than 100kb (8,527; increased from 2,355). This version of the ovine genome reference sequence (Oar v4.0) was released in August, 2015 through NCBI. Using funds from a 2013 NIFA/AFRI grant (K. Worley, PD), a very high quality “de novo” whole genome sequence has been constructed using genomic DNA from a Rambouillet ewe (Benz 2616) and 66-fold PacBio long-read sequence data with Hi-C proximity ligation sequence data for scaffolding. This version (Oar_rambouillet_v1.0), which has a total sequence length of 2.87 Gbp, a contig N50 of 2.5Mb and 0 gaps between scaffolds, has been released in GenBank (https://www.ncbi.nlm.nih.gov/assembly/GCA_002742125.1).

The Ovine FAANG Project, which has been awarded a 2016 NIFA/AFRI grant (B. Murdoch PD), includes investigators from several US institutions (USDA/ARS MARC, Washington State University, Utah State University, University of Idaho, BCM-HGSC and Virginia Tech), CSIRO (Australia), Roslin Institute (UK) and AgResearch (New Zealand). This project will contribute to the core activities of FAANG by providing transcriptome data and detailed annotation of genes and regulatory features in the sheep. All transcriptome and regulatory data generated in the Ovine FAANG Project will directly connect to the *de novo* reference genome sequence generated from Benz 2616. Over 100 tissues were collected from Benz 2616 in April 2016; these tissues are archived in EMBL-EBI BioSamples under identifier GSB-7268 and sample accession number SAMEA104495037. The protocols used in collection can be found on the FAANG ftp site:

ftp://ftp.faaang.ebi.ac.uk/ftp/protocols/samples/USU_SOP_Ovine_Benz2616_Cell_Isolation_20160426.pdf
ftp://ftp.faaang.ebi.ac.uk/ftp/protocols/samples/USU_SOP_Ovine_Benz2616_Tissue_Collection_20160426.pdf

Ovine FAANG sequence was generated by K. Worley (BCM-HGSC) during the first half of 2017 from 20 samples for miRNA sequence, 9 samples for mRNA sequence and 5 samples for long-read mRNA sequence. Ongoing efforts by BCM-HGSC will phase the genome and incorporate the long-read transcript data into the annotations of the Oar_rambouillet_v1.0 assembly. B. Murdoch (U. of Idaho) is using cap analysis of gene expression (CAGE) to identify active promoters and confirm transcription start sites, and

ATAC-seq will be used by S. White and M. Mousel (USDA-ARS/Washington State U.) to assess chromatin accessibility.

WC1 co-receptors belong to the scavenger receptor cysteine-rich (SRCR) superfamily and are encoded by a multi-gene family. Each type I transmembrane bovine WC1 protein contains an extracellular SRCR domain arrangement that can be characterized as [a1-(b2-c3-d4-e5-d6)-(b7-c8-d9-e10-d'11)] or [a1-(b2-c3-d4-e5-d'11)]. The repetitive nature of the exon duplication and gene duplication makes annotation of the WC1 locus challenging; thus techniques worked out in this project will have an impact on annotation of other gene and exon duplicated loci.

Expression of particular WC1 genes defines functional subpopulations of lymphocytes known as WC1 gamma delta T cells. WC1 genes can be grouped as WC1.1-type or WC1.2-type based on the sequence of their N-terminal a1 SRCR domain, which is 4 amino acids longer for WC1.2 type a1 SRCR domains. Reciprocal expression of either WC1.1-type or WC1.2-type proteins is correlated with gamma delta T cell responsiveness to pathogens, which explains how so many large homologous open reading frames have been maintained for millions of years. We have previously identified complete genomic sequences for 13 different bovine WC1 genes through annotation of the bovine genome Btau_3.1 build. In 2017, we made significant progress in verifying caprine gene models obtained through annotation of the PacBio sequenced San Clemente goat genome, by comparison to the Yunan goat genome and cloning of corresponding full-length WC1 cDNA from the UMass Boer goat herd. We also cloned homologous WC1 cDNA from the UMass Dorset sheep flock. Because each goat breed contains non-overlapping WC1 genes or cDNA, we estimate that there are 28 caprine and ovine WC1 genes, some of which may be pseudogenes or encode soluble SRCR domains instead of a transmembrane receptor. In order to resolve this question, we are pursuing a next generation sequencing overview of WC1 gene transcripts. We have almost completed the cloning and sequencing of 7 porcine WC1 cDNA from Yorkshire x Duroc cross piglets from a local farm, with sequence from the 5' UTR to the 3' UTR. Only 2 of the 7 are currently annotated in the swine genome; thus we plan to complete swine WC1 gene annotation and database deposition in 2018.

Objective 2: Develop strategies to identify and exploit genes and allelic variation that contribute to economically relevant phenotypes and traits, in part through improving functional annotation of the genomes of our species.

While sheep scrapie has well-defined genetic resistance, the genetics of goat scrapie have not been as well understood. There are multiple amino acid substitutions in the PRNP gene which are known to be underrepresented in scrapie positive goats, but for which the incubation times from inoculation to development of disease have not been characterized. An oral challenge experiment has demonstrated highly significant extended scrapie incubation in animals singly heterozygous for either PRNP S146 or K222 that now extend beyond an average age of 6 years, which is also longer than the commercial lifetimes of many goats.

Entropion is thought to be a recessive genetic disorder and is defined as a laxity of the horizontal lid margin allowing inversion of the eyelid causing lashes or external hairs to rub against the ocular surface. A GWAS was conducted with the severity of entropion categorized as 0, 1, or 2 eyes afflicted in 513 white-faced sheep. Six genomic regions were significantly associated severity of entropion. Further evaluation of these data is ongoing to narrow the region which contains the underlying causal mutation(s). Once the causal

mutation(s) are identified producers could use marker assisted selection to more quickly progress to an entropion free flock.

Coxiella burnetii is a zoonotic gram-negative organism broadly endemic in most of the world, and domestic ruminants (especially small ruminants) are blamed for disease outbreaks in human populations. We are generating phenotypic data in small ruminants to enable additional research on *C. burnetii* related traits.

An association of sheep KCC3b with blood sodium concentration suggested a role for the R31I variant in dimer function. To our knowledge, this is the first report of any KCC3 genotype association with sodium phenotypes in any mammal. KCC3 is an important hypertension gene with known roles in potassium transport, but the mechanism underlying this association with blood sodium is not well understood at present.

Understanding parasite resistance in sheep. This project was funded in the beginning of 2016 with the aim understanding parasite resistance and resilience and generating estimated breeding value regarding this trait for the industry. To date this project has collected fecal samples, performed FEC and collected blood samples for year one animal and is now entering year two of collections.

Meiotic recombination is an essential process in gametogenesis that ensures proper chromosome segregation and contributes to genetic variation. Interestingly, genetic recombination can differ in different breeds of sheep (Suffolk exhibit 61, Icelandic 64 and Targhee 66 meiotic recombination event per spermatocyte) and is approximately 20% higher than what has been observed in cattle breeds. The characterization and quantification of meiotic recombination should provide valuable information towards improved reproduction and genetic predictions in sheep.

To encourage and enable increased phenotypic collection of carcass trait in sheep data the University of Idaho and WSU were awarded funds to host a carcass scanning school. This school is intended to train personnel in the collection of accurate carcass data.

Estimation of the effective population size in sheep based on recombination rate by the LD method. Effective population size (N_e) is a key parameter in population genetics and is widely applied in determining the rate of genetic drift and loss of genetic variability. It is crucial to consider in animal breeding, selection and conservation. The linkage disequilibrium (LD) method performs better in the N_e estimation when genome-wide SNPs applied. Genome-wide SNP data of three commercial sheep breeds, including Texel, Merino and Suffolk, were downloaded from the ISGC database. Chromosome-specific recombination rates were estimated for all autosomes from estimated LD between SNP pairs and the known map length of chromosome. We found that the decay in LD over distance between SNPs within sheep populations is consistent with the recent population decrease. However, our estimated N_e for these sheep populations were about 40% higher than the previously report, possibly because we used the estimated recombination rate, not the theoretical value of 1 Mb=1 centi-Morgan.

Identifying genetic variants responsible for photosensitivity and hyperbilirubinemia in Southdown sheep: A photosensitivity and hyperbilirubinemia disease was first described in New Zealand Southdown sheep in 1942. It was determined to be a sub-lethal recessively inherited trait. It was subsequently seen in

California in the 1960s. In collaboration with Drs. Bud Tennant (deceased) and Nate Sutter, whole genome sequencing was performed on a known heterozygote individual. Sequencing identified a deleterious mutation within *Slco1b3*, a gene expressed in the liver known to be involved in bilirubin uptake. This manuscript has been accepted and is in press in *American Journal of Veterinary Research*.

Increasing Annual Lamb Productivity through the Identification of Genes and Diagnostic for Selection of Out of Season Breeding: Several approaches were taken to identify regions of the genome contributing to out of season breeding. GWAS was performed using HD SNP chip data on 257 ewes of various breeds. Analysis across breed and within the Dorset and Polypay breeds identified several QTLs that are biologically plausible in genetic control of out of season lambing. In particular, identified pathways involved eye development and known hormones involved in reproductive capability. This manuscript will be submitted to *BMC Genomics* this month.

Identification of genes associated with mature body size and growth: 615 ewes, across 22 breed, were characterized for mature body size using 28 measures of various body parts to get an accurate representation of skeletal size. Principal component analysis was performed on the measurements to represent overall body size (PC1) and body thickness (PC2). 184 of these ewes are genotyped on the HD SNP chip. We plan to perform GWAS for mature body size and body thickness both across and within breed. We have birth weight and weaning weight data on 104 individuals we plan to analyze for growth trait associations along with mature body size. Analysis is ongoing.

Characterizing genetic variants responsible for coat color changes in United States sheep breeds: The genetic basis for brown coat color has been identified in several US sheep breeds. Experiment.com/moorit-sheep was used to raise funds to perform Sanger sequencing of *TYRPI* in several U.S. sheep breeds known to have color variation. Two mutations were associated with brown versus black. This project will be presented at the 11th World Congress on Genetics Applied to Livestock Production.

Genome-wide association studies identify candidate genes for coat color and mohair traits in the Iranian Markhoz goat: The Iranian Markhoz goat is an Angora type goat that was investigated for genetic variants related to coat color and fleece traits. Significant associations to coat color were found within or near the *ASIP*, *ITCH*, *AHCY*, and *RALY* genes on chromosome 13 for black and brown coat color and the *KIT* gene on chromosome 6 for white coat color. Individual mohair traits were analyzed for genetic association along with principal components that allowed for a broader perspective of combined traits reflecting overall mohair quality and volume. A multitude of markers demonstrated significant association to mohair traits highlighting potential candidate genes of *POU1F1* on chromosome 1 for mohair quality, *MREG* on chromosome 2 for mohair volume, *DUOX1* on chromosome 10 for yearling fleece weight, and *ADGRVI* on chromosome 7 for grease percentage. Variation in allele frequencies and haplotypes were identified for coat color and differentiated common markers associated with both brown and black coat color. This manuscript is under revision in *Frontiers in Genetics*.

Objective 3: Facilitate analysis, curation, storage, distribution and application of the enormous datasets now being generated by next-generation sequencing and related "omics" technologies with regard to animal species of agricultural interest.

A sheep genomes database, created by the ISGC using funds from a second 2013 NIFA/AFRI grant (N. Cockett, PD), currently contains whole genome sequences from 935 sheep from 21 countries and 69 breeds. H. Daetwyler (La Trobe University, Australia) presented the analyses of these sequences (Run 2) and alignment to Oar v3.1 during the January, 2018 ISGC meeting. Over 50 million SNPs and indels were identified with high confidence using two variant-calling platforms. Data in the database is publicly available (<http://www.ebi.ac.uk/eva/?eva-study=PRJEB14685>) via European Variation Archive (EVA), which provides public access of genome information, data storage and variant accessioning. Variants are available as raw (unfiltered) or filtered data following application of a comprehensive QC protocol and information about the variants can be found through dbSNP. Run 3 will align all Run2 sequences and any new sheep genomes to the Oar_rambouillet_v1.0 assembly and will be available at the end of 2018 to coincide with annotation of the assembly.

The whole genome sequence for the photosensitivity and hyperbilirubinemia heterozygote was submitted to NCBI's SRA (SRR5749462).

IMPACT / USEFULNESS OF FINDINGS:

USEFULNESS OF FINDINGS:

The Ovine FAANG project will provide the enhanced functional annotation of the ovine genome in order to enable research in this sheep. Furthermore, this project will facilitate the understanding of gene regulation in sheep and other livestock species by generating and distributing curated transcriptome data.

The European Food Safety Authority (EFSA) convened a large expert panel that recognized the goat *PRNP* S146 and K222 alleles as scrapie resistance alleles in the latter half of 2017 (Ricci et al 2017), based in part on NRSP8 member data. They concluded that the evidence for scrapie resistance from both the S146 and K222 alleles is stronger today than the public evidence was in 2001 at the time of an important decision recommending use of scrapie resistant sheep bearing R171 (ARR haplotype). They also recommended European member states adopt genetic selection for these alleles as part of scrapie eradication efforts. While no implementation rules have been issued at present, the EFSA decision confirms the strength of the scientific evidence and sets the stage for formal adoption in government-run scrapie eradication efforts.

The KCC3b R31I substitution data open new avenues of research into the relationship of a known potassium transporter with sodium handling in mammals. Furthermore, they suggest sheep as a biomedical model for studying function in the hypertension gene KCC3.

The characterization of WC1 genes in ruminants and swine has utility in several areas: improved vaccine design against multiple important pathogens targeted to recruit gamma delta T cells, potential selective breeding based on SNPs in WC1 genes linked to resistance to pathogens, and the possible involvement of WC1 as a receptor in PRRSV infection of swine. Because WC1 genes are present in most mammalian and avian species, elucidation of WC1 genes in agriculturally important ruminants and swine has global application potential in improving food security and in containing zoonotic diseases in non-human animal reservoirs. This project also helps support undergraduate and graduate agricultural research training.

Total Leveraged Funding Summary for 2015-2017

Federal Funding:	\$ 3,138,500
State/Local/Institutional:	\$ 360,500
<u>Industry:</u>	<u>\$ 46,200</u>
Total	\$ 3,545,200

PUBLICATIONS:

Refereed manuscripts and book chapters: 19

- Baldwin, C.L. et. al. (11 authors on committee) National Academies of Sciences, Engineering, and Medicine. 2017. Revisiting Brucellosis in the Greater Yellowstone Area. The National Academies Press: Washington, DC. 209 pgs; ISBN 978-0-309-45831-3 | DOI 10.17226/24750
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- Dechow, C.D., Liu, W.-S. (2017) Genome-wide DNA methylation patterns and differential methylation in leukocytes from Holstein cattle with variable milk yield. *BMC Genomics* (manuscript under revision).
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- Notter, D. R., Mousel, M. R., Lewis, G. S., Leymaster, K. A., and Taylor, J. B. Evaluation of Rambouillet, Polypay, and Romanove-White Dorper x Rambouillet ewes mated to terminal sires in an extensive rangeland production system: lamb production. *J. Anim. Sci.* 95:3851-3862. 2017.

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Posbergh, C.J. & Huson, H.J., (2018) Making Moorit: Mutations in TYRP1 are responsible for brown coat color in different United States sheep breeds, *Proceedings 11th World Congress of Genetics Applied to Livestock Production*, (accepted, under revision Nov 2017).

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Ph.D. thesis:

Payal Damani Yokota “Regulation of expression of the gamma delta T cell co-receptor and pattern recognition receptor multi-gene family WC1.” 2017.

Kimberly Davenport “Understanding the ramification of meiotic recombination variation in male sheep” 2017.

Published abstracts and proceedings: 25

Cinar, M.U., Mousel, M.R., Herndon, M.K., Taylor, J.B., White, S.N. Tenascin-XB (TNXB) amino acid substitution E2004G is associated with mature weight and milk score in American Rambouillet, Targhee, Polypay, and Suffolk sheep. 2018. *Plant & Animal Genomes XXVI*, San Diego, CA, USA. *Plant & Animal Genomes XXVI*, San Diego, CA, USA.

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- Mousel, M.R., White, S.N. Genomic regions associated with entropion in Columbia, Polypay, and Rambouillet breeds of sheep. 2017. International Society for Animal Genetics, Dublin, Ireland.
- Mousel, M.R., White, S.N., Herndon, M.K. Genomic regions associated with entropion affecting one or both eyes of domestic sheep. 2018. Plant & Animal Genomes XXVI, San Diego, CA, USA.
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- Oliveira, R.D., Mousel, M.R., Gonzalez, M.V., Taylor, J.B., Knowles, D.P., White, S.N. Genome-wide association with monocyte count in domestic sheep. 2018. Plant & Animal Genomes XXVI, San Diego, CA, USA.
- Stewart, W.C., Murphy, T.W., Notter, D.R., Mousel, M.R., Lewis, G.S., Leymaster, K.A., Taylor, J.B. Wool characteristics of Rambouillet, Polypay and Romanov-White Dorper x Rambouillet ewes in an extensive rangeland production system. 2017. American Society of Animal Science, Western Section Meeting. Fargo, ND, USA.
- Telfer, J.C. and Baldwin, C.L. (invited talk) "WC1 hybrid pathogen recognition receptors and signaling co-receptors direct immune responses by bovine $\gamma\delta$ T cells to pathogens" CRWAD meeting, December 2017.
- White, S.N., Oliveira, R.D., Mousel, M.R., Gonzalez, M.V., Highland, M.A., Taylor, J.B., Knowles, D.P.

Underdominant KCC3b R31I association with blood sodium concentration in domestic sheep suggests role in dimerization. 2017. International Society for Animal Genetics, Dublin, Ireland.

Zhang, Y.Y., Liu, W.-S., Deng, X.M. (2017) Estimation of the effective population size in sheep based on recombination rate by the LD method. Conference Abstract, International Plant and Animal Genome Research (PAG) XXVI, January 13-18, 2017. San Diego, CA. P1148.

Invited Seminars:

1. Developing the functional annotation of the sheep genome. Murdoch BM, White SN, Mousel MR, Massa AT, Worley KC, Archibald AL, Clark EL, Dalrymple B, Kijas J, Clarke S, Brauning R, Smith TPL, Hadfield T, Cockett N. International Sheep Genomics Consortium. Jan 15, 2018.
2. The Ovine FAANG Project. Murdoch BM, White SN, Mousel MR, Massa AT, Worley KC, Archibald AL, Clark EL, Dalrymple B, Kijas J, Clarke S, Brauning R, Smith TPL, Hadfield T, Cockett N. International Sheep Genomics Consortium. Jan 15, 2018.
3. Rambouillet Sheep Genomic Resources. Liu Y, Harris RA., Qin X, Richards S, Rogers J, Han Y, Vee V, Wang M, Meng Q, Heaton MP, Smith T.P.L., Dalrymple B, White SN, Murdoch BM, Kijas JW, Cockett N, Muzny DM, Gibbs R, Worley K. Plant & Animal Genomes XXV Conference, January 14, 2017.
4. Update on the Rambouillet Assembly, the 5.0 Reference, and plans for FAANG RNA Sequencing. Liu Y, Harris RA, Qin X, Richards S, Rogers J, Han Y, Vee V, Wang M, Meng Q, Heaton MP, Smith TPL, Dalrymple B, White SN, Murdoch BM, Kijas JW, Cockett N, Muzny DM, Gibbs R, Worley K. Plant & Animal Genomes XXV Conference, January 16, 2017.
5. Genome-Wide Landscape of Active Enhancers in Sheep Alveolar Macrophages. Massa A, Mousel M, Murdoch BM, White S. Plant & Animal Genomes XXV Conference, January 16, 2017.
6. Understanding the Ramification of Recombination Variation in Sheep. Davenport K and Murdoch BM. Plant & Animal Genomes XXV Conference, January 16, 2017.
7. Gene regulation in Sheep Alveolar Macrophages: Genome-Wide Identification of Active Enhancers. Massa A, Mousel M, Murdoch BM, White S. 36th International Society of Animal Genetic Conference, Dublin July 20, 2017.
8. Investigating Genetic Associations with Meiotic Recombination in Rams. Davenport K, Rodriguez AM, Sawyer RJ, Badigian TM, Jaeger H, Follet MA, Murdoch BM. 36th International Society of Animal Genetic Conference, Dublin July 20, 2017.
9. Strategies to employ molecular markers towards improved prediction of carcass quality. Murdoch B. Increased Efficiency of Sheep Production NCERA214 Lansing, Michigan June 11-14, 2017.
10. The Future of Sheep Production: Capturing Genetic Variation. Cockett N and Murdoch B. American Sheep Industry. Superior Farms board meeting. Denver, CO January 25-28, 2017.
11. Idaho cow-calf herds; a genetic resource for understanding and improving cow reproduction and calf growth efficiency. Murdoch B. NRSP8 Hatch report. San Diego Jan 14, 2017.
12. Ovine FAANG Project. Murdoch B. International Sheep Genome Consortium. San Diego Jan 16, 2017.

13. Ovine FAANG progress Murdoch B. FAANG consortium meeting International Plant and Animal Genome San Diego Jan 17, 2017.

WORK PLANNED FOR NEXT YEAR:

1. Generation of Ovine FAANG Project data.
2. Annotation of sheep macrophage regulatory sites.
3. Development of *Coxiella burnetii* phenotypes.
4. Evaluation of genomic regions identified in GWAS of entropion.
5. Continued characterization of meiotic recombination differences.
6. Annotation of swine WC1 genes based on sequencing of full-length cDNA clones
7. Continued characterization of ovine and caprine WC1 genes and cDNA discovered via next generation sequencing overview
8. Completion of annotation of new Pac-Bio sequenced genomes and deposition of sequence into GenBank database
9. We will continue to work on the transcriptome of the bovine and ovine Y chromosome
10. WC1-pathogen binding studies