Termination Report for NC1170 2008-2013

Membership and Institutional Abbreviations: Beckman Research Institute at the City of Hope (BRI: M. Miller); Iowa State University (IA: S. Lamont, J. Dekkers); Michigan State University (MSU: J. Dodgson); Mississippi State University (MS: M. Edelmann); North Carolina State University (NCSU: C. Ashwell, J. Petitte), Oregon State University (OSU: D. Froman); Purdue University (PU: W. Muir); University of Arizona (UAZ: F. McCarthy, S. Burgess); University of Arkansas (UA: W. Kuenzel, B. Kong, D. Rhoads); University of California, Davis (UCD: M. Delany, H. Zhou), University of Delaware (UD: B. Abasht); University of Georgia (GA: S. Aggrey); University of Maryland (UMD: T. Porter, J. Song); University of Minnesota (MN: K. Reed, D. Foster, F. A. Ponce de Leon); Virginia Tech (VT: Eric Wong); University of Wisconsin (UW: G. Guilherme); USDA-ARS-Avian Disease and Oncology Lab (ADOL: H. Cheng, H. Zhang).

This document summarizes by objective the major accomplishments achieved by the NC1170 Multistate Research Project covering 2008 through 2013. Achievements included the application of next generation technologies in sequencing to poultry genomes and numerous contributions to advances in bioinformatics, annotation, and transcriptomics as applied to a variety of fundamental disciplines in poultry biology. Our work is conducted under the auspices of many collaborative arrangements with stakeholders involved in the allied poultry industries for the purpose of improving poultry production. The scholarly publications resulting from this project (see appendix) includes over [update] articles in peer-reviewed journals, books and proceedings. Special note should be made of the large number of publications involving collaboration between members of this Project as well as international scholars located around the world.

Objective 1: Create and share data and technology to enhance the development and application of genomics and systems biology in poultry.

MSU, UCD and MN, with collaborators, generated a detailed turkey BAC contig-based physical map, one of the most complete for any vertebrate genome. This turkey BAC contig map provided the primary platform for assembly of the first draft sequence of the turkey genome using next-generation sequencing (NGS) as part of the Turkey Genome Sequencing Consortium. Comparison to the chicken genome confirmed the high evolutionary stability of avian chromosomes and elucidated 20-27 major rearrangements between turkey and chicken genomes over 40 million years of separate evolution. ADOL contributed the (1) generation of a consensus genetic map that consolidated the East Lansing, Wageningen, and Uppsala maps and contained 9,285 genetic markers, (2) generation of a 60K chicken SNP chip that was distributed worldwide, and (3) development and field evaluation of genomic selection in commercial broilers and layers in collaboration with PU. MN and BRI elucidated genetic variation at the MHC present in wild turkeys. UAZ contributed (1) 81,114 functional annotations for 24,460chicken genes (including data from 224 papaers), subsequently expanded to include turkey annotation, (2) new tools for functional modeling of high-throughput data now freely available on AgBase or via iAnimal, (3) to the Chicken Gene Nomenclature Committee (CGNC) which manually approved 1,300 chicken genes, (4) a tissue expression atlas for chicken (Chickspress) that currently displays data from 37 different experiments with more being added, and (5) the development of a comparative genome browser for birds that contains 50 bird genomes (including chicken, turkey and duck). UA, UAZ, and UD contributed RNAseq data to Roslin Institute for a new chicken transcriptome assembly that is being used for a more complete annotation of the most recent (2011) chicken genome assembly. UCD contributed to the comparative analysis of poultry genomes providing cytogenetic evidence for the chromosome structural changes between

chicken and turkey, in collaboration with MN and MSU. UCD contributed to the molecular analysis of genomic diversity within and among chicken breeds and strains using the 60K SNP array, collaborating with PU and ADOL. The same array was used to establish the chromosomal regions of interest responsible for a series of chicken developmental mutations and determination of priority candidate genes for continued study. UCD, ADOL, PU and MSU also used whole genome sequence analysis to narrow candidate gene intervals for several developmental mutations and associate the talpid2 mutation with the C2CD3 gene. UCD developed a chicken whole genome 44K gene expression array that has been widely used by the poultry community. BRI, in collaboration with other members, contributed detailed binding motifs for two MHC-B class I molecules, extensive sequence data for the MHC-B region, identification of BG1 as a Marek's disease (MD) tumor suppressor gene, revelation of the MHC-YF class I protein as a new type antigen presentation molecule, and characterization of chicken natural killer cells. BRI collaborated with UCD to find the correct order of MHC genes on GGA-16 revealing the presence of a heretofore unknown gene segment within the MHC and shared this data with UAZ to improve annotation and nomenclature in this region. Very recently BRI and UCD mapped olfactory and scavenger receptor genes to a position near the MHC on GGA-16. MN collaborated on construction of genetic linkage maps and sequencing of the turkey genome (the latter with VT, MSU and UCD); investigated immune system genomics to enhance disease resistance in turkeys, including sequencing the core turkey MHC gene cluster, estimation of MHC haplotype diversity within the species through SNP analysis and quantification of MHC gene expression in immune system tissues; identified, mapped and analyzed differential expression of skeletal muscle genes in genetically selected turkeys; applied genomics to increase aflatoxin resistance in turkeys, including sequencing key genes; and investigated the genetics of round heart disease, including expression analysis of cardiac genes. UA investigated neuroendocrine regulation of stress in chickens using the vasotocin receptor family, with a focus on the vasotocin two and vasotocin four receptors. Both receptors are highly expressed in the anterior pituitary specifically in corticotropes that contain adrenocorticotropic hormone. Gene expression of these receptors and two corticotropin releasing hormone receptors were shown to be significantly altered following several different stress models. The data suggest that these four receptors play critical roles in the neuroendocrine regulation of stress in birds. MS used chemical proteomics to identify chicken deubiquitinating enzymes (DUBs), especially ones regulated during Salmonella infection, and to identify ubiquitinated proteins in chicken. They established an enrichment technique for ubiquitinated proteins in chicken macrophages and optimized ubiquitin-specific probe labeling to identify new chicken DUBs or confirm their annotation. Further, new chicken DUBs were identified with consistent differences in abundance during infection with Salmonella. UMD used genome-wide histone methylation analysis and pathway predictions to identify virus-induced DNA methylation changes during Marek's disease virus (MDV) infections, and identified associations between lipoprotein metabolism and MDV infection. Computational epigenetics methods were developed for evaluating the similarity between epigenetics patterns.

Objective 2: Facilitate the creation and sharing of poultry research populations and the collection and analysis of relevant new phenotypes including those produced by gene transfer.

IA maintained unique chicken research lines [including highly inbred; MHC-congenic; closed populations; and advanced intercross lines (AIL)] as resources for identifying genes and QTL of economic importance. Genetic material (chicks, fertile eggs, blood, tissue, DNA or RNA) was shared with cooperating investigators to expand studies on the chicken genome. Financial constraints resulted in the termination of 11 of the 24 lines in 2009-2010. MSU, in collaboration with ADOL, demonstrated that retroviral short hairpin microRNA vectors were capable of generating antiviral

RNA interference against MDV, both in cell culture and in vivo. ADOL maintains a large number of chicken lines that are characterized for a number of traits, especially those associated with viral diseases, including maintenance under specific pathogen free (SPF) conditions. Besides providing unique genetic resources to their location, ~1500 embryos or chicks are supplied yearly to academic institutions or companies throughout the United States. UAZ supported avian phenotype analysis by developing chicken anatomy ontology. The ontology currently contains 1,829 adult chicken anatomical terms from 11 anatomical systems. MN developed the SC-2 immortal chicken embryo fibroblast (CEF) cell line; analyzed gene expression in senescent and immortal chicken CEF cells; performed SAGE analysis of chicken primordial germ cells; used reverse genetics to generating a biomarker avian metapneumovirus vaccine; investigated development of chicken inducible pluripotent stem cells; developed immunogens to protect against turkey cellulitis; and induced chicken embryonic stem-like cells using recombinant SV40 large T antigen. NCSU established lines of chicken primordial germ cells (PGCs) from transgenic chickens expressing green fluorescent protein. Retinoid acid (RA) was found to induce chicken PGCs of both sexes to enter meiosis, act directly on the PGCs, and up-regulate Stra8 expression in PGCs with similar increases in the expression of Dmc1 and Sycp3. In collaboration with Zhejiang University, Epidermal Growth Factor (EGF) was found to stimulate proliferation of chicken PGCs via activation of Ca(2+)/PKC involving the NFKB1 signaling pathway.

Objective 3: Elucidate genetic mechanisms that underlie economic traits and develop new methods to apply that knowledge to poultry breeding practices.

OSU and UA identified genetic regions contributing to low sperm mobility in roosters, a major determinant of male fertility. Proteomic analysis with UA and UAZ indicated reduced energy metabolism in low mobility sperm. A model was developed to explain mobility through stochastic processes arising from reduced energy reserves and transit time in the excurrent ducts. UA studied the basis of ascites in broilers. Experimental lines were generated and used to map some of the genes involved in susceptibility and to study production traits associated with ascites susceptibility. Genomes of the experimental lines were sequenced to 10x to identify genomic differences. UA performed microarray analyses to find differentially expressed host genes in cultured chicken cells infected by wild type and vaccine strain infectious laryngotracheitis virus (ILTV) to identify gene networks and functional roles of candidate genes in host-ILTV interactions. ILTV encoding microRNAs were identified using next generation sequencing (NGS). Microarray analyses were used to identify differentially expressed genes in DF-1 chicken embryo fibroblast (CEF) cells and in senescent CEF cells compared to primary CEF cells. Hundreds of differentially expressed genes were identified and bioinformatics was used to interpret gene network and functional roles of candidate genes in cellular proliferation and lifespan in avian cells. UA examined genetic mechanisms for neuroendocrine regulation of testes development to identify the distribution of specialized neurons in the brain that respond to changes in photoperiod and their neuroanatomical pathway responsible for activating the reproductive system for the production of semen. Identification of key genes and specific neurons comprising the neural pathway could aid in the future sustainability of fertility over a typical reproductive cycle thereby assisting in elucidating markers for the selection of poultry male breeders. IA focused on the host response to bacterial infections, including Salmonella, for which many new candidate genes and quantitative trait loci associated with resistance to bacterial colonization were identified. Research in resistance to pathology resulting from infection with avian pathogenic E. coli (APEC) using microarrays identified many gene networks that are important in host genetic resistance. A new area of focus on resistance to heat stress was recently initiated, and large-scale animal trials generated samples and data for future analysis by transcriptomic and

bioinformatics study. Several statistical methods for the analysis of high-density SNP genotype data were implemented and evaluated, using both simulated and real data. This included whole-genome association analyses and whole-genome prediction of breeding values. Further strategies to implement whole-genome selection methods based on the use of less-costly low-density SNP panels combined with genotype imputation were developed and evaluated. The latter strategies have now become the norm for most applications of whole-genome selection for production animals. ADOL focused on genes and biological pathways that confer genetic resistance to MD. Using a combination of (1) allele-specific expression (ASE) in response to viral challenge, (2) ChIP seq for Meq, the viral oncogene and a bZIP transcription factor, and (3) selective sweeps using next generation sequencing, we identified 5,360 SNPs in 3,773 genes that are involved in the transcriptional response to viral infection and are overrepresented in selective sweeps. Efforts are underway to validate these SNPs and other SNPs using a custom 15K SNP chip and an ~1,000 6x7 F6 MD resource population. ADOL identified a set of 172 SNPs highly associated with MD, on chromosomes 1, 3, 5, and Z; (2) a series of challenge trials provided experimental evidence that host genetics, in addition to the major histocompatibility complex, plays an important role in modulating vaccinal protective efficacy; (3) challenge trials also suggested HVT, a low efficacy MD vaccine, conveys comparable protection against very virulent MD virus challenge as CVI988/Rispens (gold standard); (4) differential DNA methylation patterns and microRNA profiles were found between MD resistant and susceptible lines of chickens in collaboration with UMD.

UCD created new knowledge regarding host virus genome interactions involved in MD by establishing the integration profiles of the virus into chicken telomeres and determined that tumors within birds are largely clonally-derived. UCD mapped the location and variation of mega-telomere arrays in well-utilized cell line systems and UCD 001 (Red Jungle fowl sequenced genome). UCD discovered evidence for the alternate lengthening of telomeres in chicken in vitro cell systems. Genes and signaling pathways associated with host response to Campylobacter and Salmonella infection in the chicken and genes, microRNAs and signaling pathways related to avian influenza virus infection in chickens were identified using high-throughput technology including microarray and next-generation sequencing. PU, in collaboration with ADOL, used NGS to identify genetic adaptations associated with chicken domestication and trait selection, including aggression and MD resistance, and developed software to call SNPs. We explored the use of genomic selection (GWMAS) to address social and ethical concerns while at the same time demonstrating the power and limitations of GWMAS in a multi-generational selection experiment. We found that accuracy was up to 50% greater with ssGBLUP than BLUP. Genetic trends mirrored the increase in accuracy with near 50% increase in response of the index over the 3 traits. GA developed miRNA target programs based on specific features of a particular miRNA class. Selection studies for residual feed intake were undertaken which will lead to reduced feed intake and no changes in weight gain. High feed efficiency birds are characterized by rapid conversion of carbohydrates to ATP, high fat oxidation, increased de novo amino acid synthesis, cell division and proliferation, and efficient nitrogen recycling. Low feed efficiency birds are characterized by low ATP production, increased apoptosis, increased lipogenesis and increased ammonium production and excretion. BRI, in collaboration with other members helped to elucidate genetic mechanisms controlling immune responses that underlie disease resistance traits in poultry including mechanisms underlying the activation of natural killer cells and of T lymphocyte responses. UW focused on four main areas: (1) Statistical modeling approaches and optimal experimental design strategies for gene expression assays, including genomics experiments; (2) Genomic selection models, especially on kernel models, genotype x environment interaction, and non-additive genetic effects; (3) Computational strategies for implementation of genomic selection models, with focus on R software and high throughput

computing using clusters; and (4) Inferring causal phenotypic networks. VT focused on uptake of nutrients (amino acid, peptide, sugar) mediated by transporter proteins and digestive enzymes located in or at the cell membrane. Expression of these genes in the intestine during pre- and post-hatch showed differential expression in the small intestinal segments and throughout development. Expression profiles of some of these genes changed in response to changes in dietary protein quality and composition. In addition, the yolk sac membrane expresses many of the digestive enzyme and transporter genes normally associated with the intestine. UMD used microarrays to identify differentially expressed genes in the anterior pituitary glands and hypothalami of fat line and lean line chickens. SNPs in the promoters of candidate genes were associated with fat yield and breast yield. Microarrays were also used to analyze gene expression in hypothalamus of newly hatched chicks following fasting and re-feeding and in the cecae of neonatal chicks following Salmonella and probiotic treatment to determine gene networks involved in feed intake and Salmonella reduction by probiotics. Promoter and chromatin precipitation analysis of the growth hormone gene identified transcription factors that regulate growth hormone production. UD conducted RNA sequencing to characterize the biological basis of variation in feed efficiency in broiler chickens and also to study a novel muscle disorder in chickens. The results indicated that many biological pathways, molecular, cellular and physiological functions are differentially regulated in broiler chickens with high and low feed efficiencies. The information will be useful in developing strategies for improving broiler's feed efficiency. Results from RNA-seq study of a novel muscle identified over 1000 genes that are deferentially expressed between affected and unaffected chickens. Research is continuing to determine biological pathways and upstream regulatory factors that are involved in this disorder.

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