Single nucleotide polymorphisms for parentage testing, individual identification, and traceability[1]

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Summary

Molecular markers have become the chosen technology for parentage determination, individual identification, and traceability. Types of markers have varied over time, but the advantages of single nucleotide polymorphisms (SNPs) have led to the increasing adoption of these particular molecular markers for identification and diagnostic testing for qualitative and quantitative traits. SNP advantages include highly abundant, more accurate allele calling, high-throughput capability, low mutation rate, very abundant in the genome, amenable to multiplexing, and low per marker cost. Molecular marker panels ranging in size from hundreds to as large as 50,000+ SNPs are currently being used commercially worldwide for genetic identification and diagnostic testing.

***Key words**: SNP, Parentage, Identification, Traceability.*

Introduction

Sites in the genome with at least two different bases at the same location are referred to as single nucleotide polymorphisms (SNPs). Almost all SNPs are biallelic, i.e., two different bases can be found at the location under consideration. SNPs are highly abundant and can be found, on average, at one in 1 000 nucleotide positions throughout the genome. SNPs represent, in fact, the most abundant class of polymorphisms. The enormous interest in SNPs is due primarily to their use as markers to identify genes associated with complex genetic diseases (human and veterinary medicine) and to identify genes and quantitative trait loci underlying complex health, production, and reproduction traits (animal science). Over the last

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few years, the interest in using SNPs for what may be referred to collectively as SNP-based identification has increased substantially. SNP-based genetic identification includes parentage testing (Werner *et al*., 2004; Ayres, 2005; Rohrer *et al*., 2007; Van Eenennaam *et al*., 2007; Fisher *et al*., 2008), individual identification (Kerr *et al*., 2004; Werner *et al*., 2004; Sobrino *et al*., 2005; Li *et al*., 2006; Pakstis *et al*., 2007, Rohrer *et al*., 2007), and traceability (Heaton *et al*., 2005; Hurnik, 2005; Loftus, 2005; Weller *et al*., 2006; Cunningham, 2008).

SNP-based genetic identification

Traditionally, genetic identification is based on highly polymorphic microsatellite markers (short tandem repeat markers or STRs). At present, the interest in using SNPs for genetic identification is increasing rapidly. The reasons for this increase are (see, e.g., Krawczak, 1999; Werner *et al*., 2004; Ayres 2005; Weller *et al*., 2006; Van Eenennaam *et al*., 2007):

- SNPs are abundant.
- SNPs are robust in terms of laboratory handling.
- SNPs are amendable to fast semi-automatic multiplex typing (high throughput, low cost).
- SNPs have a low rate of genotyping errors.
- SNPs have a relatively stable inheritance.
- SNPs have a low mutation rate.
- SNPs are compatible with easy standardization between laboratories.
- SNPs specifically chosen for genetic identification are included as part of the 50 000+ SNP chip being used worldwide to genotype tens of thousands of influential animals in many breeds.

The informative value of a single biallelic SNP is less than that of a multiallelic STR. Therefore, genetic identification requires larger SNP panels than STR panels for similar discriminatory power (Ayres, 2005, Weller *et al*., 2006; Van Eenennaam *et al*., 2007). However, because of the advantages of SNPs over STRs mentioned above, it is expected that the use of SNPs for genetic identification will be broadly accepted as the preferred method for genetic identification. Commercial genetic testing laboratories currently offer genetic identification using SNPs and thus, it is only a matter of time until SNPs replace the use of STRs in many applications. Lower costs associated with genotyping animals with SNPs in contrast to STRs will be one of the primary drivers of this shift from STRs to SNPs.

SNP selection for genetic identification

SNPs included in a SNP panel for universal genetic identification (including parentage inference) should span a large portion of the genome and should have high heterozygosity in each population (or for example, breed within species) in which the SNP panel is to be used. This means that for each SNP included in the panel the fixation index (Wright's Fst) should be globally low, and the average minor allele frequency (MAF) should preferably approach 0.5 (see, e.g., Krawczak, 1999 and Pakstis *et al*., 2007). Heaton *et al*. (2007) developed a panel of 121 SNPs with a MAF of 0.41 based on a group of 216 diverse sires that represent 19 beef and 4 dairy breeds. Most of these markers were included on the 50 000+ SNP chip developed by a consortium of researchers in 2007 and offered commercially by Illumina, Inc. Since then, this 121 SNP panel has been evaluated in additional cattle breeds of the world, bringing the total number involved to 44 beef and dairy cattle breeds using 24 diverse animals from each breed (Mike Heaton, personal communication).

Use of SNPs for genetic identification: State of the art

In humans, using a panel of 31 informative SNPs (4 medium informative, 27 high informative), combined with 28 SNP loci on HLA-DRB1 and ABO genes (major histocompatibility complex and blood group genes, respectively), Li *et al*. (2006) found a matching ability of $9.02x10^{-15}$ and exclusion probabilities in duos (parent-offspring) and trios (both parents/offspring) of 98.94% and 99.92%, respectively. These authors concluded that these 59 SNPs yield the same power in forensic identification as the 13 CODIS (Combined DNA Index System) STRs (selected by the FBI for forensics) used at the time of their study. Pakstis *et al*. (2007) reported the selection of 40 low Fst, high heterozygosity SNPs for universal individual identification of humans. This panel had a match probability that ranged from $2.02x10^{-17}$ to $1.29x10^{-13}$ in 40 populations investigated. (These authors did not consider parentage testing.) Each of the selected SNPs had an Fst of less than 0.06 for all 40 populations. The average heterozygosity in the 40 populations was higher than 0.43 (maximum reachable is 0.50) for each of the 40 selected SNPs.

Weller *et al*. (2006) used analytical and simulation approaches to determine how many genetic markers, SNPs and STRs, might be required for individual animal identification when accounting for genotyping errors. They report STRs have an inherent genotyping error rate of approximately 1%, whereas the rate for SNPs is lower. However, more SNPs are required to attain the same exclusion probabilities. By simulating STRs with five alleles and SNPs with two, Weller *et al*. (2006) concluded exclusion probabilities were approximately the same when using 2 to 2.25 SNPs for each STR.

The successful use of SNPs for genetic identification of cattle and pigs has been reported by Heaton *et al*. (2002, 2007), Werner *et al*. (2004), and Rohrer *et al*. (2007). In cattle, Heaton *et al*. (2002) used a panel of 32 SNPs distributed among 18 autosomes and estimated that the probability that two randomly selected, unrelated individuals will possess identical genotypes for all 32 loci (probability of identity) was $2.0x10^{-13}$ for multi-breed composite populations and $1.9x10^{-10}$ for purebred Angus populations. The 121 SNP panel Heaton *et al*. (2007) developed using 23 breeds of cattle has an exclusion power of 0.99999 when no dam is available. Also in cattle, using a panel of 38 SNPs (including one gender-specific SNP), Werner *et al*. (2004) found theoretical probabilities of identity of $8.59x10^{-15}$, $8.54x10^{-13}$ and $1.30x10^{-13}$ in German Holstein (GH), German Fleckvieh (GF), and German Braunvieh (GB), respectively. The MAF varied largely for these SNPs within each of the three breeds studied (GH: 0.11 to 0.48; GF: 0.05 to 0.50; GB: 0.02 to 0.50; average per breed not given). The theoretical exclusion power of the SNP panel when used for parentage testing was estimated to exceed 99.99% in all three breeds. In pigs, Rohrer *et al*. (2007) used a panel of 60 SNPs, each with a MAF greater than 0.15, and found the overall identity power across the four breeds studied (US purebred Duroc, Hampshire, Landrace, and Yorkshire) was $4.6x10^{-23}$, but within-breed values ranged from $4.3x10^{-14}$ (Hampshire) to $2.6x10^{-23}$ (Yorkshire). Parentage exclusion probabilities with only one sampled parent ranged from 95.94% (Hampshire) to 99.63% (Yorkshire). Sire exclusion probabilities when the dam's genotype was known ranged from 99.87% (Hampshire) to 99.97% (Yorkshire). Rohrer *et al*. (2007) concluded that the power of exclusion with the 60 SNPs is similar to that of 10 STRs. However, the SNP panel was more sensitive for individual identification.

SNPs can also be used for whole herd parentage assignment or parentage verification (see, e.g., Anderson and Garza, 2006 and Van Eenennaam *et al*., 2007). Anderson and Garza (2006) have shown by Monte Carlo simulation studies that 60 to 100 SNPs may allow accurate pedigree reconstruction, even in situations involving thousands of potential mothers, fathers and offspring, both in large managed and/or natural populations. Recently, Fisher *et al*. (2008) used simulation and empirical

data to show that the combination of 40 SNPs (average MAF=0.35) and on-farm data (i.e., mating records, birth dates of progeny, and calving dates of dams) is extremely powerful for parentage assignment. Without the on-farm data, even a 60 SNP panel was not as powerful as the 40 SNP panel with on-farm data. Independent of on-farm data, 40 SNPs were at least comparable to, if not more powerful than, a commercial STR panel consisting of 14 STRs for dairy cattle parentage in New Zealand.

Baruch and Weller (2008) evaluated three different minimum MAFs (0.10, 0.20, and 0.30) for each of three scenarios:

1. single putative parent,
2. two putative parents, and
3. one known parent and one putative parent.

"The numbers of markers required to obtain 99% exclusion probabilities based on a single conflict for the three minimum MAFs were 54, 45, and 39 for scenario 1; 17, 16, and 15 for scenario 2; and 28, 25, and 24 for scenario 3." If one allows at least two conflicts for exclusion, the number of markers required increased by approximately 45% for all three scenarios and all three minimum MAFs.

Successful use of SNPs for verification of sample tracking in beef processing has been described by Heaton *et al*. (2005). They used a selected panel of 20 bovine SNP markers located on 12 different chromosomes. The panel was sufficiently informative to verify the accuracy of sample tracking in slaughter plants. The average MAF of this SNP panel was 0.36 in 96 selected beef cattle and 0.33 in 168 randomly selected market cattle. Not unexpectedly, this study indicates that the reliability of tracking necessitates great accuracy in tissue sampling procedures and sample labeling. Mistakes were largely due to human errors and rarely due to genotyping errors. Weller *et al*., 2006 point out SNPs have a lower genotyping error rate than STRs and used simulation to determine that a single STR was approximately equivalent to 2 to 2.25 SNPs for traceability. At least 8 SNPs were required to reach a 99% probability of exclusion between two individuals; 25 SNPs resulted in a <1% chance of a match between any five million individuals.

Effect of genetic identification on selection and genetic gain

Genetic markers have been used to determine that the misidentification rate contributing to pedigree recording errors in recent studies involving dairy cattle ranges from 7 to 15% (Spelman, 2002; Visscher *et al*., 2002; Weller *et al*. 2004; Sanders *et al*. 2006). Several studies have used actual estimates of pedigree errors or simulated misidentification rates in the reported range to determine that these errors decrease genetic gain anywhere from 2.5 to 15% (Israel and Weller, 2000; Banos *et al*., 2001; Spelman, 2002; Visscher *et al*., 2002;). It should be noted that the magnitude of the decrease in gain is affected by the heritability of the trait, misidentification rate, and number of daughters per progeny test sire. Sanders *et al*. (2006) showed that pedigrees with wrong sire information reduced the efficiency of genetic gain from a breeding program 1.4 times more in comparison to pedigrees with missing sire information. Beef producers also have the opportunity to realize greater genetic gains at a lower cost through more accurate sire selection and/or culling by determining which bulls in multi-sire mating pastures actually sired the resulting calves. Van Eenennaam *et al*. (2007) used STRs and SNPs to assign paternity on 625 calves and found that 5 out of 27 bulls exposed to the cow herd through AI and natural service sired 50% of the calves. In contrast, 10 bulls produced no progeny. There is a clear trend for business-minded producers, companies whose business model requires accurate parentage, and breed associations needing pedigree integrity to choose

DNA marker technology for genetic identification. Those interested in increased precision, faster turnaround time, the ability to include diagnostic markers for quantitative and qualitative traits, multiplexing that can lead to lower costs, and being on the cutting edge are choosing SNPs.

Commercial Examples – STRs and SNPs

Breed associations have processes in place to verify parentage on certain animals that are registered by its members. Currently, multiple breed associations conduct both SNP and STR parentage with IGENITY®[2]. One of the primary downsides of STR marker usage for parentage is the frequent need for re-reading STR gels to see if changing one or more calls by two base pairs will allow a match between parent and progeny. This does not occur with SNPs, which is a fully automated process and thus less prone to errors (Vignal *et al*., 2002; Weller *et al*., 2006). For clarification, a re-check, or re-read, of the genotyping result is conducted if a sire/dam does not qualify as a parent with one to three exclusions. The amount of time required for a data technician to prepare each re-check request averages about 11 min. This re-check time does not include the amount of time required by a lab technician to find and re-read the STR gel. Because all of the re-checking and re-reading processes are manual, there is an increased likelihood of introducing additional human errors with STRs that does not occur with SNPs. Note that when one or more sire or dam STR genotype call is changed, it will impact all other previously assigned matches between progeny and those parents. These changes can also result in a sire or dam no longer qualifying to be the progeny of their parents, resulting in a ripple effect occurring as a result of changing the STR call. Furthermore, it is not possible to re-read STR gels to revise genotype calls when outside labs have conducted the original genotyping work and transferred only the final calls to IGENITY, which obviates the benefit of having ISAG STRs to some extent.

In a large-scale project to evaluate parentage assignment in registered dairy cattle, 6 302 animals were genotyped in 1 639 herds. The IGENITY parentage and identity panel of 99 SNPs used for this project was a subset of those developed by Heaton *et al*. (2007). More than 85% of the animals had 80 or more successful genotype calls for comparison between sire and progeny; 11.8% had between 61 and 80 genotypes. The power of the SNP panel is evident in the distribution in number of exclusions: 76.2% with 0 exclusions, 5.2% with 1 exclusion, 1.1% with 2 exclusions, and 0.5% with 3. (In contrast, the percentage of samples with 1 or more exclusions genotyped with STRs is much higher.) The misidentification rate ranged from an average of 10.3% in herds with <100 cows to a high of 24.2% in herds with more than 2 000 cows; however, there were herds with a misidentification rate approaching 100%.

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[2]IGENITY is a registered trademark of Merial in the United States of America and elsewhere.

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Overview of herd testing

Figure 1 provides a schematic for the flow of dairy within the milk recording industry in the United States. While this view is simplified for demonstration purposes, the diagram clearly demonstrates the interconnectivity of allied and industry partners.

All data generated from the various components of the recording entity are processed at one of four dairy records processing centers prior to submission to the Genetic Evaluation Program (GEP). Like the field service, meter center and laboratory entities, these processing centers have diverse business structures and compete in an open-market environment.

One of the challenges in this open-market climate is to maintain standards among competing organizations. The dairy industry in the United States has long realized the need for a quality certification program to ensure that the minimum standards of services are maintained and to assure the accuracy of data flowing between milk recording industry entities and flowing to the Animal Improvement Programs Laboratory (AIPL) and Interbull.

Figure 2 illustrates the areas reviewed for compliance by Quality Certification Services. The multi-level quality certification programs provides numerous checkpoints to assure data accuracy prior to reaching one of the dairy records processsing centers, and then a final checkpoint of accuracy of processed data leaving each processing center. One important point is that Quality Certification Services does not determine if an entity should exist, only if each entity is operating with compliance to mutally agreed upon guidelines for the recording industry. In addition to providing a review of compliance at all levels, Quality Certification Services Inc. and its auditors serve in an educational and resource role to aid all herd testing program participants.

Field collection of data and milk samples

At the present time, there are 27 certified field service providers working directly with dairy producers participating in herd recording programs in the United States. Each of these field services is unique in their business structure and services offered to dairy producers, but all operate under uniform operating procedures and abide by a code of ethics. Combined these 27 field service organizations have 3 018 well-trained field technicians that work directly with over 4.4 million dairy

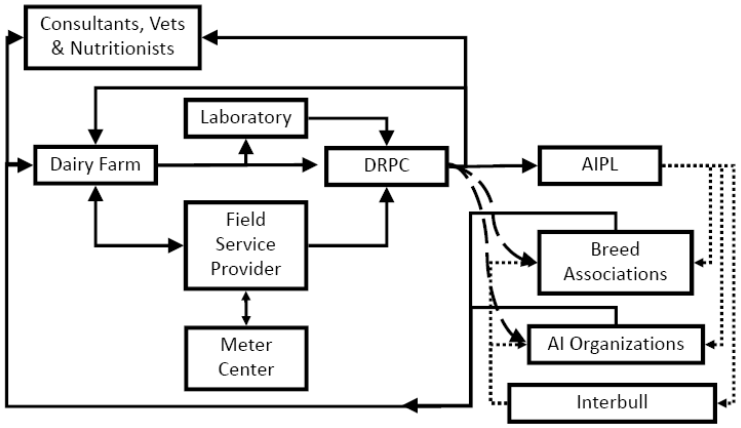

Figure 1. Overview of herd testing in the United States.

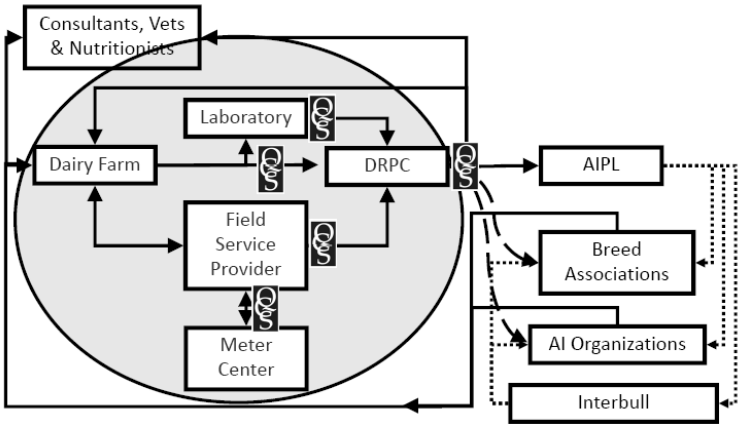

Figure 2. The Role of Quality Certification Programs in the United States.

Figure 3. Certified Providers of Field Services in the United States.

cows on a regular basis. As expected, these field service affiliates are located near areas of concentrated dairy cattle populations (Figure 3), but the entire United States and Puerto Rico are served by at least one field service provider.

Participation in milk recording programs has seen a steady growth over the last five years in the United States (Figure 4). At the end of 2007, there was approximately 47% of the United States dairy cow population participating in DHI (herd recording) programs. Contributing to the growth in dairy cows on recording programs is the fact that each of the individual field service affiliates working with dairies in their respective trade area continue to develop, build value, and market recording services to herds that aid not only provide data to the nationwide genetic evaluation program, but provide timely and useful data to individual dairy producers to aid in the daily management of their respective operations. As detailed in Figure 5, there is a relatively flat distribution of dairy herd size when looking at participation in herd recording programs. While it is probable that the herds of the smallest and largest size (dairy cow numbers) are not on an identical recording program, each of these herds is enrolled in an approved test plan with a certified provider. As a result, dairy cattle

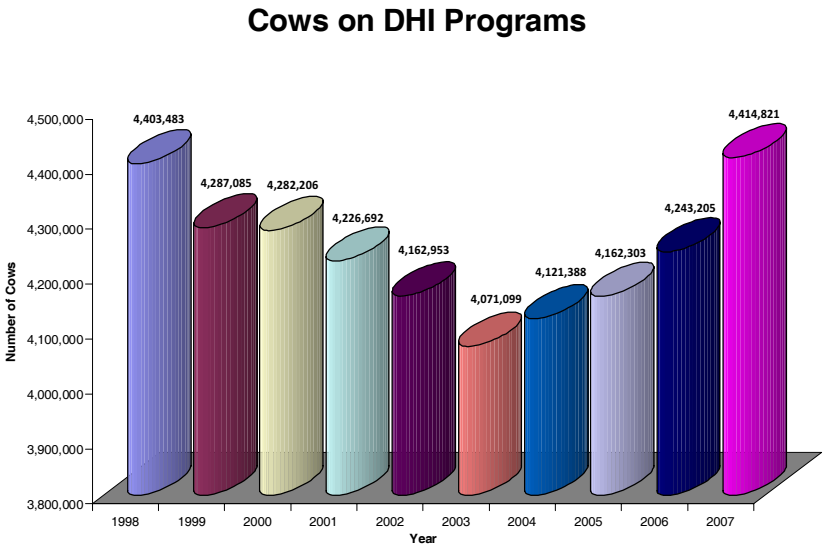

Figure 4. Participation in milk recording programs in the United States (1998-2007).

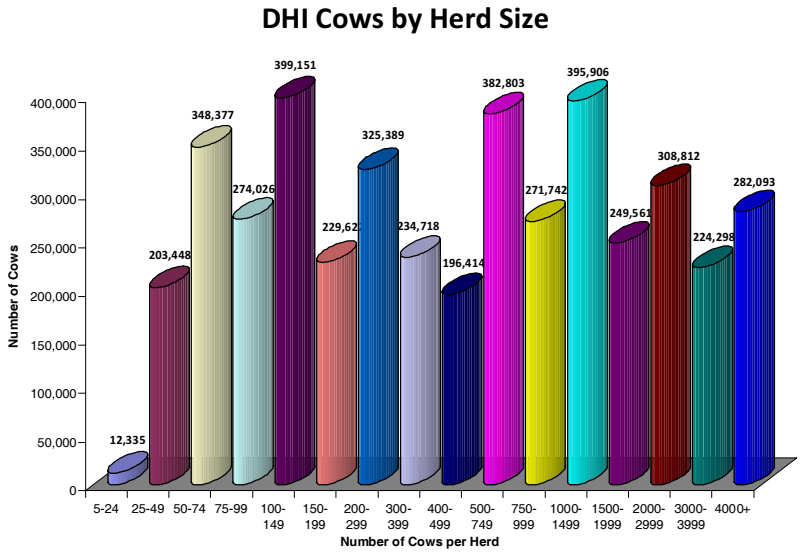

Figure 5. Distribution of herd size for cows enrolled in milk recording programs in the United States, 2007.

from herds of all sizes, geographic locations, and varying management programs are included in the genetic evaluations generated from the United States dairy cattle population.

Use and calibration of recording devices in herd recording

As required by the quality certification program in the Untied States, all recording devices used in herd recording programs must be approved by ICAR and National DHIA. Serving the DHI industry in the United States are 45 certified meter calibration and repair centers, once again located near concentrations of dairy cattle populations. Each meter center is inspected and audited on-site biennally. Further, all meter technicians performing calibration and repair services are also audited biennally as well as attend periodic training schools or seminars.

All portable (monthly) meters are required to be calibrated at least once every 12 months in the United States. During 2007, the 45 certified meter centers calibrated 108 139 portable meters. In addition, over 66 000 electronic (daily) meters were evaluated for performance on their respective dairies. Calibration data from both daily and monthly meters are reported to Quality Certificaiton Services each year for review as part of the certification audit for each of the aforementioned 27 field service providers.

DHI laboratories in the United States

The DHI laboratories providing services to the recording industry have seen similar changes in business structure, trade area and competition. At the end of 2007, the milk recording industry in the United States was served by 49 certified laboratories (Figure 6). Based on reported statistics, the cumulative total of samples analyzed by all laboratories is approximately 4.7 million samples monthly, with a range of 8 000 samples monthly at the smallest laboratory to 410 000 samples at the largest. These samples were analyzed on 204 unique instruments from three different manufacturers. As part of a comprehensive quality certification program, each laboratory is inspected and audited biennally on-site. In addition, each laboratory participates in a monthly unknown samples program to monitor and assess performance and accuracy.

Each of these laboratories competes in an open marketplace, offering a range of services to dairies participating in recording programs. All laboratories provide milk component and somatic cell count analysis of samples. Other services provided to dairy farmer include analysis of milk urea nitrogen (MUN), ELISA analysis of milk samples for Johne's and/or luekosis, and microbioloy analysis. Figure 1 highlights the locations of the certified DHI laboratories operating withing

Figure 6. Certified DHI Laboratories in the United States.

the United States. These labs are located near dairy cow populations (Figure 6) and provide for rapid analysis of milk samples. The average turn-around time from milk sample collection at the dairy farm to lab analysis is 1.45 days across all nationwide DHI laboratories.

Processing data from participating herds

Handling the data on over 4.4 million cows the 23 005 enrolled in herd testing programs in the United States are four distinct dairy records processing centers (DRPC). Each of these DRPC are voluntary participants in the quality certication program as well – audited both monthly and annually for accuracy of data calculations and data transfer. As with DHI field service providers and DHI laboratories, these processing centers compete in an open-marketplace environment for business. In addition to providing data to the Animal Improvement Programs Laboratory (AIPL), they each provide reports and tools direct to dairy producers to aid in the daily management of invidual dairy operations.

Conclusion

The United States milk recording industry is served by a dynamic herd testing system that efficiently and cost effictively meets the needs of dairy producers of any herd size in all geographic locations. Participation in herd recording programs continues to grow, and the United States DHI system is flexible to adapt to the needs of our nation's diverse dairy operations. Each organization, though distinct in business structure and size, participates in a common certification program. The quality certification program in the United States is neutral on many fronts – business structure, size, geography or other external factors – and provides a basis for compliance by all entities within the recording industry without providing a barrier to entry. As a result, users from within the system along with industry partners such dairy studs, breed associations, and other interested parties can be assured of the accuracy of data generated from the United States dairy cow population.