Integration of Classical and Molecular Approaches of Genetic Selection: Egg Production

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ABSTRACT Poultry breeding has demonstrated success from the use of a complex mixture of assessment tools. New proposals are regularly sought out and tested for their ability to translate data into information that enhances genetic gain from selection. Details long hidden from view are already being uncovered by molecular genetics, calling for great skill and discipline to discern and harness their real potential. Some aspects of egg production grudgingly may yield to the influence of new associations suggested from molecular work. In particular, diverse environments call for the kind of genetic variation found only under expensive multiple-location testing, longer flock production life calls for better early predictors, and new egg products call for novel measures of egg component value. In the final analysis, selection on a mix of phenotypic and molecular data is an essential step in evaluating its worth for improving a physiologically complex trait like egg production.

(Key words: poultry breeding, genotype by environment interactions, egg, selection, biotechnology)

INTRODUCTION

Each housed bird of today’s commercial layers can be expected to produce almost 20 kg of egg mass in 52 wk of production with feed conversion rates approaching 2.0 kg of feed for each kilogram of egg. The biological engineering required to reach this level of performance has taken its toll on the poultry business community, leaving only a handful of breeding companies to compete for the diverse world market. Every available tool, time-tested and new, must be scrutinized to assess its potential for improving a company’s ability to sustain market growth under a wide variety of environmental conditions and market profiles. With complex, sex-limited traits such as egg production, the task of evaluating new molecular approaches must be multifaceted. Given the fact that time-tested approaches to layer selection programs historically have been multifaceted, the prospects for a suitable mixture of time-tested and molecular techniques seem good, offering leverage for improving performance already approaching levels close to biological thresholds in some environments. Furthermore, there has been a major shift in world markets toward further-processed eggs, raising questions about the nature of egg constituents and our ability to add value genetically to what has been traditionally a commodity product.

THE GOAL

Simply put, egg producers would like to grow a pullet to sexual maturity as quickly as possible and expect her to lay an egg every day of her adult life. Not just any egg, but one that is marketable; which is to say that it must be of acceptable size (not too big or too small), with a shell strong enough to withstand mechanical handling, provide sanitary protection to the food enclosed, and, in most of the marketplace, be aesthetically pleasing to the consumer. Not at any price either, but one that maximizes product yield for a given amount of nutrients. Additionally, it must be remembered that egg production at the primary breeding and multiplication sectors of the industry is also a reproductive trait with important effects on rate of genetic gain and hatchery utilization.

One measure of flock egg productivity used around the world is “eggs per hen housed” (HHE). It is more easily understood in terms of its biological basis if it is defined in terms of component traits, each with some basis in physiology or immunology, namely average age at sexual maturity (first egg); average daily rate of lay; and average rate of mortality. These are not independent measures, but are correlated genetically and environmentally, sometimes antagonistically, with one another and with other traits of economic importance in the overall plan for genetic gain. Mortality, the third component trait listed, is important enough in its own right to be dealt with elsewhere in this symposium.

Time-tested selection procedures to improve population averages for the other two component traits involve
TABLE 1. Univariate restricted maximum likelihood (REML) estimates of heritabilities and standard errors for egg production traits, egg characteristics, and body weights of hens for two pure lines

<table>
<thead>
<tr>
<th>Trait</th>
<th>Line A</th>
<th>Line B</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eggs in Period 1</td>
<td>0.25 ± 0.010</td>
<td>0.27 ± 0.010</td>
</tr>
<tr>
<td>Eggs in Period 2</td>
<td>0.09 ± 0.004</td>
<td>0.13 ± 0.010</td>
</tr>
<tr>
<td>Eggs in Period 3</td>
<td>0.18 ± 0.010</td>
<td>0.16 ± 0.010</td>
</tr>
<tr>
<td>Egg weight 1</td>
<td>0.47 ± 0.010</td>
<td>0.48 ± 0.010</td>
</tr>
<tr>
<td>Egg weight 2</td>
<td>0.47 ± 0.010</td>
<td>0.44 ± 0.010</td>
</tr>
<tr>
<td>Body weight, 40 wk</td>
<td>0.50 ± 0.010</td>
<td>0.51 ± 0.010</td>
</tr>
<tr>
<td>Specific gravity</td>
<td>0.34 ± 0.005</td>
<td>0.34 ± 0.020</td>
</tr>
</tbody>
</table>

1Adapted from Besbes et al., 1991.
2Periods 1, 2 and 3, were between 19 and 26, 26 and 38, and 26 and 54 wk of age, respectively.
3Weights 1 and 2 were for 30 and 50 wk of age, respectively.

assessing a kaleidoscope of genomic expression filtered and blended through a screen of environmental effects. Selection decisions are based on breeding values estimated from phenotypic measurements on a variety of sources, including pure line individuals and their relatives, whether pure line or cross, in order to give gene interactions that are important in the commercial genotype a chance to contribute to genetic variation and selection discrimination. Furthermore, to ensure that gene expression important in some production environments but not in others has a chance to influence the selection decision, relatives of the breeding individuals are tested in several environments that sample or mimic the commercial setting. The goal is to concentrate data-gathering on that which is informative about future performance of crossline progeny of selected pure line individuals.

Egg production is a trait that has low to moderate heritability (Besbes et al., 1991) (Table 1), and, depending on the period involved, may require a lot of data to be informative. Because it is a sex-limited trait, evaluation of the genetic potential of males for this trait can only be achieved through data collected on their relatives. A major opportunity for improvement in this trait lies in the period after 40 wk of age, but because the frequency of birds approaching 100% production in the early period continues to increase, the ability of early period performance to predict later performance is reduced. Informative sources of information must be sought elsewhere, at the expense of generation interval and enlarged populations.

Poultry breeding organizations are constantly struggling to prepare their products to combat difficulties in nutrient supply and inhospitable environmental conditions and to improve longevity of productivity (to help producers weather uncontrollable downturns in the economy). A major strength of time-tested methods of genetic improvement, particularly for traits like egg number, has been their ability to take into account great amounts of genetic interaction and physiological complexity without having to know exactly how these relationships worked. To the extent that the genetic and physiological mechanisms became better understood, the models on which time-tested methods were based needed to adapt.

Competitive advantage in the marketplace depends on the integration of informative methods of genetic improvement as they became better understood. Existing models continue to be scrutinized. For example, the persistence of moderate levels of heritability despite generations of selection calls for a re-examination of the importance of mutation in our breeding populations and reconsideration of how heavy use of some family information and, indeed marker-assisted selection (MAS), might work against the accumulation of new genes (Hill, 1996). Today, the industry is offered, in the form of molecular genetics technology, an additional means of gathering genetic data, a more direct and very particulate measure of the genomic landscape. Can we find the forest in all those trees? How might the myriad of individual colors help us find the rainbow? How much information is in the data?

THE ALTERNATIVES

Bulfield (1992) has described two ways in which future molecular genetics could impact poultry breeding: 1) MAS using cloned genes closely linked to quantitative trait loci (QTL); 2) genetic manipulation of the “trait-genes” themselves. Given that transgenic techniques themselves are still in development (Petitte, 1996), the appropriate option in the near future will be MAS, employing methods such as those of Goddard (1992) using best linear unbiased prediction (BLUP) and Lande and Thompson (1990) in an extended use of selection index methodology. Muir (1994:9) has suggested that, “with layers, the added efficiency of MAS is less than 10%”. In a typical breeding program, this would mean only three more eggs per hen per production year after 10 generations of selection.

Furthermore, with MAS, even given a set of genes with good ties to QTL, time is of the essence. Without identification of the QTL themselves, the value of markers is reduced with each successive generation, requiring a periodic re-evaluation of the goodness of the tie between the QTL and the markers. If, however, the differences in heritability between rate of lay in different periods are related directly to opportunities to identify important QTL, then greater opportunity may exist in the more important periods of lay at older ages. Kuhnlein et al. (1997), in an attempt to increase the likelihood of finding meaningful QTL, have used a “candidate gene” approach, wherein alleles of certain genes suspected of being directly associated with a trait are investigated for the level of correlation with the trait.

Ultimately, QTL of any reasonable import to the genetic variance of a trait would need to be identified, a formidable task in itself. Furthermore, with any but the simplest of traits, the interaction between genes at different loci must be taken into account in designing...
the test in which the net value of the QTL is measured. Even dividing egg production into its component parts does not yield simple traits. With the increasing demand for performance under diverse conditions, often different from those under which lines have traditionally been selected, there is a reasonable chance for polymorphisms at some loci to be expressed only in tests run under those conditions. In fact, the same rules of testing under commercial conditions that apply to time-tested evaluation techniques apply in the search for important QTL. If QTL with important effects can be identified, there will certainly be interest in moving those genes into populations in which they are lacking, either by introgression or by transgenics. However, it will be vital to know that the net effect of a transferred gene in its new genetic environment would be worth the additional investment in technology, resources and time required to effect the transfer when compared to time-tested methods of achieving the same end. Neither can we ignore the potential difficulties in developing acceptance of food produced from transgenic animals. (Payne, 1994).

WORK IN PROGRESS

At latest count, close to 600 markers have been mapped on the East Lansing reference population and almost 400 on the Compton reference population, netting between 700 and 800 between them. It falls to those with resource populations on which egg production characteristics have been, or could be measured, to obtain estimates of relationships between markers or candidate genes and the various component traits of egg production. A few of these populations exist in publicly funded institutions, where the results of the analyses will become public knowledge. But many more probably exist in private breeding companies, where the derived information will be used to modify the selection procedure in ways that are considered cost-effective for that company and may not be openly publicized. Competitive market success is ultimately the goal of this work within breeding companies.

Recent work by Lamont et al. (1996) on a population derived by crossing two genetically diverse commercial egg lines tested the accuracy of tail-analysis against gradient-analysis in identifying variable-number-of-tandem-repeat (VNTR) markers that appeared to be related to performance traits including age at first egg, percentage production, and total egg number. However, by testing progeny of selected sires carrying appropriate markers, they confirmed that a high percentage (> 95%) of markers identified in this way were, in fact, falsely indicating linkage. Underscoring the need for genetic testing of hypothesized relationships (or lack of them) was the fact that they found “many trait-linked bands that did not appear to be significant in the earlier gradient analysis” (Lamont et al., 1996:5). The marker R14 was related to several traits, suggesting either a pleitropic QTL nearby or a clustering of separate QTL affecting body weight, sexual maturity, and rate of lay.

Kuhnlein et al. (1997) have shown that homozygosity for the GH allele associated with Marek’s disease resistance was correlated with an overall increase of 17% (190 vs 162 eggs) in egg production, primarily because of an associated higher rate in ovulation as age progressed, overcoming even the associated delay in sexual maturity. The resistance-associated growth hormone (GH) allele behaved as dominant for sexual maturity and recessive for persistency. As in the work by Lamont et al. (1996), the test of useful marker information requires a selection stage. This important step, to test the consequences in production-selected, high-performance layers of selecting on GH alleles, is the subject of a study being conducted jointly by Kuhnlein at McGill College in Montreal, QC, Canada, and researchers at the Centre for Food and Animal Research (CFAR) in Ottawa, ON, Canada.

Crooijmans et al. (1996) reported on the need for increasing the number of microsatellite markers from 128 to over 300 in order to do a complete genome search for QTL. Almost in the time between doing the research work and the publishing of the results (June, 1996), that goal of 300 has been virtually achieved (personal communication, Dodgson, 1996) although 77 of them are the subject of patent applications, which could affect their availability.

Over the last four decades, few publications dealing with the genetics of egg production could have avoided mentioning the work of R. S. Gowe and his team at Ottawa. Even today, in the sunset of their short but very productive existence, the populations that have given the poultry industry so much, and in which so much relevant selection was invested, are participants with the USDA’s Avian Disease and Oncology Laboratory (ADOL) at East Lansing, Michigan in the work of associating markers with performance traits including egg production characteristics. It is bittersweet that the work in progress, joining government research across international boundaries, will not be carried forward beyond identifying possible associations to enable testing of those associations in planned matings (personal communication, Gavora, 1996, Agriculture Canada, Centre for Food and Agriculture, Central Experimental Farm, Ottawa, Ontario, Canada K1A 0C6).

THE FUTURE

Although the prospects for the use of molecular genetics in directly improving egg production are difficult to measure at the present time, this should not be construed to mean that there is a lack of interest in it. On the contrary, industry quantitative geneticists are not daunted by formidable odds. There have been other technological obstacles that creative persistence has overcome. The work already done in public research institutions with limited funds has been remarkable, but the pressure to reduce public funding will inevitably
reduce public knowledge of the progress being made. It will hide mistakes that will delay progress, ultimately delaying improvement of food production efficiency to the consumer. Joint research between public institutions and private breeders can and does work, provided the interests of both sides are served. Those who participate in the research stand to benefit earliest from the answers it generates, but it should be recognized that industry funding will be more easily attracted to questions likely to yield useful answers. Thus, industry-supplied resource populations on which trait associations could be measured may need to be designed to fit within existing testing programs and optimum strategies for doing so could be very interesting.

Hopefully, the synteny between chickens and mammals, including humans, will allow for some targeting of chromosomal regions whose functions are inferred by sequence similarity with that of the mammalian genome. A major contributor of such information could be the work on the Human Genome Mapping Project. In seeking QTL for egg production in chickens, mammalian genomic sites with demonstrated relationships to reproductive hormone functions would be suitable targets for investigation.

An interesting new horizon for genetic improvement in egg quality has been created by the upsurge in further processing of eggs and their components (Sim and Nakai, 1994). The major egg constituents, yolk and albumen, represent a potential gold mine of opportunity. Many of the genetic pathways are already well-understood (Burley and Vahedra, 1989; Deeley et al., 1993). Manipulation of some of these components through genes expressed only in the hen producing the final product might be a fruitful avenue of research. Like transgenics work, it will require understanding of the timing and tissue-specificity of gene expression and, of course, would need to be subject to the same rigorous testing of effects on other measures of productivity.

In conclusion, it seems that there are still enough unanswered questions to justify continuing the search for novel ways to improve rates of genetic improvement in component traits of egg production and to be sure that breeding companies are sufficiently familiar with various forms of technology, quantitative and molecular, to respond quickly to opportunities when they become evident.

REFERENCES


