

# Is Continued Genetic Improvement of Livestock Sustainable?

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**ABSTRACT** Large genetic improvements in the quantitative traits of growth, production, and efficiency of farmed livestock have been made over recent decades, and by introduction of genomic technology these are being enhanced. Such continued improvement requires that there be available variation to utilize. The evidence is that little variation has been lost and such rates are indeed sustainable in the future.

SINCE *GENETICS* was founded we have seen an enormous increase in productivity of livestock for food production. Much of that is due to rapid genetic improvement in the past 60 years of quantitative traits such as growth rate, reproductive rate, and feed conversion efficiency. The improvement has been due to selection, recently mainly within populations, and has continued at similar rates for many livestock generations. I consider whether these rates, which depend on a continuing supply of useful genetic variation, can be maintained or indeed enhanced. Chickens provide my main source of examples as they have been under very strong selection pressure for many decades in the developed world and there is well-documented evidence of their genetic improvement, but the principles are not species-dependent. Further background on animal breeding history, quantitative genetics theory, results, and references are given elsewhere by me (Hill 2010, 2014; Hill *et al.* 2016) and of course by many others.

## Genetic Improvement Achieved

To estimate genetic change, Havenstein *et al.* (2003 and associated papers) utilized a control strain of broilers (*i.e.*, poultry for meat) founded from crosses of then commercial strains in 1957 and subsequently maintained without selection. In trials in 1991 and 2001, birds from current commercial broiler crosses were compared to the controls using diets formulated to 1957 or to then current specifications. On the current diet, the 1991 strains at 56 days old were 3.47 times heavier than

the 1957 control, and the 2001 strain 4.36 times heavier, *i.e.*, annual increases of 3.7 and 3.4%, respectively. Differences in diet had only ~10% the effect of that in the genotype. There were corresponding improvements in feed conversion efficiency and in carcass traits: for example, breast meat yield as a proportion of body weight almost doubled by 2001, and fatness was reduced after 1991. In another trial using control stocks, broiler growth rates increased at a compound rate of 3.3%/year, and feed conversion ratio improved by 2.55%/year over the period 1957–2005, such that over this nearly 50-year period the feed required to produce chicken meat has been halved and that required for breast meat has been reduced by 67% (Zuidhof *et al.* 2014). Age at slaughter of commercial broilers has fallen to ~35 days so as to improve feed efficiency and meet market requirements, and industry data from the past decade indicate that genetic trends are continuing at similar rates, with annual trends from 2006 to 2013 of ~2% in body weight and 4% in breast weight (Hill *et al.* 2016).

These increased growth rates require increased appetites, and broiler mothers have to be feed-restricted to reproduce well. Undesirable correlated effects have included increased leg and feet weakness in broilers as they bear a heavier load, but strong selection pressure applied to these traits has been effective in reversing these correlated changes (Kapell *et al.* 2012).

The main broiler traits are moderately highly heritable, but those for poultry egg production are not, and concern about selection plateaus in layer strains was already expressed 60 years ago. Comparative trials using control lines started in 1950, 1960, and 1980 with modern lines in 1989 showed, however, annual rates of improvement in feed conversion efficiency (grams of egg/grams of feed) of 0.7% (Jones *et al.* 2001), and

industry comparisons indicate similar rates continuing to 2009 (Hill *et al.* 2016). Modern birds still rarely lay more than one egg a day, but start younger, weigh less, continue production for longer, and lay relatively larger eggs and so are much more efficient users of feed.

Commercial poultry are typically two-way or higher order crosses to utilize heterosis and complementarity of parent breeds, *e.g.*, meat content in sire lines and reproductive rate in dam lines (respectively, fathers and mothers/grandmothers of the final cross). Selection within lines has been primarily on pure line performance of the individual and its relatives, but may incorporate crossbred relatives' performance for reproductive traits and, as breeders market world-wide, data on relatives kept under different representative commercial environments (*e.g.*, low quality feed, high disease load, and group housing). Data from different relatives and data sources can be combined optimally using best linear unbiased prediction (BLUP).

Population structure in dairy cattle has been very different, with the use of artificial selection across many herds and selection of the best sires based mainly on progeny performance using BLUP. Although increasing emphasis in recent years has been placed on traits that are unfavorably correlated with yield, such as milk protein percentage and cow fertility, and so have reversed the decline, in recent years genetic improvement in milk yield in U.S. Holsteins has still exceeded ~0.5% of the mean per year, or nearly 3% per generation (<https://www.cdcb.us/eval/summary/trend.cfm>). Following the rapid uptake of genomic technology, the breeding structure is changing, and rates of overall improvement are consequently accelerating.

In contrast, racehorses do not run much faster. Over both the periods 1850–2012 and 1997–2012 winning times in British races improved on average by 0.065%/year for middle distance races (~2 km), rather more for shorter and less for longer races (Sharman and Wilson 2015). The current record time for the Kentucky Derby was set in 1973. (Breeders of thoroughbred racehorses do not gamble on employing quantitative geneticists, but there may be other explanations.)

Again in comparison, plant breeders have, dependent on the species, material with a high reproductive rate and access to more flexible breeding systems such as selfing, doubled haploids, and cloning, but the growing conditions of field crops are region- and weather-dependent. Rates of improvement, assessed from contemporary comparisons of varieties bred in different years, are, for example, a little >1%/year for hybrid maize for actual yield and 2% for potential yield under good growing conditions in Iowa, *e.g.*, sufficient rainfall, and less for wheat, 0.6 and 0.7%/year, respectively, in the United Kingdom (Fischer and Edmeades 2010).

Improved stock is distributed differently to crop than to livestock farmers. Cereals such as wheat are marketed as inbred lines and maize as inbred line crosses, and improvement is effected as new varieties replace old after some years. Livestock, whether reared mainly as purebreds (*e.g.*, many dairy cattle) or as crosses (*e.g.*, poultry), are marketed as

segregating outbred individuals or their semen. Although the breed or brand name usually stays the same, the livestock producer expects yearly genetic improvement in the stock.

## Genetic Architecture and Models

The major traits of livestock and crops are quantitative and, as had been surmised from the time of the Mendelian rediscovery, many loci are involved; indeed, progeny distributions and selection responses typically fit well to Fisher's infinitesimal model. Direct information from genome wide association studies has confirmed the highly polygenic nature of quantitative traits, notably in humans (*e.g.*, Yang *et al.* 2010). Similarly, for dairy cattle, by fitting a model ("Bayes R") for 43,000 SNPs in which SNP-associated effects were assumed to be in one of four groups, contributing either no variance or variances of 0.01, 0.1, or 1% of the genic variance. In the non-zero classes, it was estimated that in Holsteins 3968, 53, and 7, respectively, contributed for milk yield and 5685, 241, and 10 for stature (Kemper *et al.* 2015).

Similarly, analyses using dense genomic markers of both selected commercial (Fragomeni *et al.* 2014) and experimental (Pettersson *et al.* 2013) lines of poultry have shown that responses cannot be attributed to just a few sites. For example, the top 10–20 SNP windows for each trait that explained the largest fraction of the genetic variance across generations explained only 0.5–1% of the total variance and was inconsistent across generations (Fragomeni *et al.* 2014). Consequently, apart from a few specific cases such as Marek's disease resistance in poultry (identified in the 1950s from a blood group marker), most genetic progress has come from selection of the traits directly and not from identifying specific genes or linked markers.

The utilization of genomic predictions as first proposed by Meuwissen *et al.* (2001) has led a revolution in livestock breeding research and practice. While it is possible to use genomic data to locate QTL of large effect, the SNP markers and sequence data are primarily routes to increasing the accuracy of selection by utilizing both realized relationship through shared genomic regions and marker-associated effects through linkage disequilibrium using information on distantly related individuals. The determination of optimal ways to weight SNPs and regions to allow for heterogeneity of QTL effects and their distribution in the genome is a major research activity, but there is some robustness to assumptions. For livestock, genomic data are particularly valuable as a way to obtain predictions of breeding value for young males for sex-limited traits in poultry and dairy cattle, enhancing sib records with otherwise low accuracy and progeny records requiring long generation intervals.

The uptake has been fastest in dairy cattle where young bulls with "genomic predictions" are being marketed in competition with old sires with progeny tests, leading to a substantial reduction in generation interval and potentially near doubling in rates of improvement. Selection using genomic prediction remains firmly in the polygenic paradigm, however,

as the primary aim is to utilize improvement from the whole genome rather than by identifying specific sites.

## Sources of Continued Improvement

### Heritability of quantitative traits

If trait improvement is to continue into the future, genetic variation for important traits and trait combinations must remain in the populations. In accordance with the fairly consistent rates of continuing response, estimates of heritability within broiler populations seem to have changed little over many years. Estimates of the heritability of 35-day body weight for three current nucleus broiler populations averaged 36% (Kapell *et al.* 2012), similar to average estimates (38% from half-sibs, 31% from offspring-parent) for 56-day weight (the then market weight) in a 1969 summary of published data. During 50 generations of selection for 8-week body weight in a population derived from inbred line crosses, response upward was almost linear, although that in the low lines has slowed, associated with fitness problems (Dunnington *et al.* 2013). Heritability of lactation milk yield in dairy cattle has risen from ~25% in the 1950s to ~35% currently, likely partly due to improved management. Consistent with steady rates of improvement relative to the mean, the coefficients of variation (CV) and therefore evolvabilities (CV/mean) of growth traits in meat species and of milk yield in dairy cattle also seem to have remained fairly constant. Notwithstanding over 50 generations of intense selection, commercial populations have maintained additive genetic variation in important traits.

### Molecular variability

Polymorphism at the nucleotide level in poultry is  $\sim 4\text{--}5 \times 10^{-3}$  and does not stand out as particularly high or low among species of birds, although it is much higher than in humans (Ellegren 2007). Modern commercial poultry stocks have lost about half the molecular variation of their native Jungle Fowl source, but most of this loss occurred before the current populations, including fanciers' strains, were bred (Muir *et al.* 2008). Estimates of heterozygosity within two broiler and two layer commercial strains averaged 60 and 40% of that in a Red Jungle Fowl population ( $4.1 \times 10^{-3}$ ) (Rubin *et al.* 2010). There are large between- and within-commercial line differences: Kranis *et al.* (2012) found  $78 \times 10^6$  SNPs segregating within one or more of 24 lines representing commercial broiler and layer breeds and several experimental and inbred lines with 10% on average detected in each commercial line. There seems no shortage of molecular genetic variability.

### Maintenance of variation at the quantitative level: mutation

Let us consider how the continuing and consistent rates of improvement that span 50 years or more are being maintained. As a reference point, assume an effective population

size for nucleus populations of 100, likely of the right order as a range of 50–150 is listed for a major international poultry breeder (UK Government 2010).

Variation is lost at a rate of  $1/(2N_e)$  per generation at neutral individual genomic sites and for quantitative traits determined solely by additive gene action. For the variation in the population to remain constant, mutational variation ( $V_M$ ) on the traits must be generated at a similar rate: 0.5%/generation of the current variance if  $N_e = 100$ . Assuming an additive model,  $V_A$  is maintained if  $V_M/V_A = 1/(2N_e)$  or  $V_M/V_E = [h^2/(1 - h^2)]/(2N_e)$ , where  $V_E$  is the environmental variance. To maintain a typical  $h^2 = 1/3$  at  $N_e = 100$ ,  $V_M$  has to be  $\sim 0.25\%$  of  $V_E$ .

Published estimates of mutational variance for a range of species and traits center on  $V_M/V_E = 0.1\%$ /generation (Houle *et al.* 1996), but vary widely around this value. The few estimates for vertebrates are higher: 0.23–0.57% (Keightley 1998) from inbred mice and, with high sampling error, by partitioning variation in outbreds into standing and *de novo* components,  $\sim 1\%$  for mice and 0.6–0.9% for litter size in sheep (Casellas *et al.* 2010, 2014).

In a population under directional selection, only those mutants with effect ( $a$ ) on the trait in the desired direction are useful, while others are removed by selection; therefore, the distribution of the mutant effects is important. Using Robertson's (1960) theory for additive genes, and assuming that the mutants are neutral for fitness (*i.e.*, get no index weighting), the directional selection response from one generation of mutants (the asymptotic rate) is approximately proportional to  $4N_e V_M E^+(a^2)/E(a^2)$ , where  $E^+$  denotes expectation only over positive mutant effects (Hill 1982). Therefore, if the distribution of mutant effects is symmetric, the variance maintained under directional selection remains at  $2N_e V_M$  for any selection intensity or accuracy (correlation of criterion and breeding value). With selection on multiple traits and predicted breeding values weighted by their economic importance, the same arguments would seem to apply at least approximately to the overall index. Thus, in a multi-trait context, if genes beneficial for the index of traits are relatively disadvantageous with respect to other aspects of fitness, constant variance and response for  $N_e = 100$  requires  $V_M/V_E > 0.25\%$ .

This analysis uses the simplistic assumption that selection is based on individual performance, whereas in practice relatives' information is incorporated through pedigree and an increasingly genomic relationship or marker-associated effects. The early fate of the mutant is then no longer simply a feature of its phenotypic effect on the selected trait(s). Under an infinitesimal model, however, for a selection index based on own and relatives' performance with accuracy  $\rho$ , the fixation probability of an additive mutant of effect  $a$  is proportional to  $a\rho N_e$  (from Robertson 1960), which remains a fairly good approximation even if effects are larger (Caballero *et al.* 1996).

Long-term aspects of selection using genomic information have been analyzed by Goddard (2009). The specific role of

effective population size has been discussed more fully in genomic prediction, and Casellas *et al.* (2013) have discussed accounting for mutations. With genomic prediction, the change in gene frequency depends not only on its direct effect on the trait but also on its linkage disequilibrium (LD) with other loci, so the dynamics are more complex. It seems reasonable, however, to assume that the same simplistic arguments apply under the infinitesimal model with genomic selection based on relatives' and LD associations as with direct selection because the fate of the mutant depends on many selection cycles. Hence it is still a function of  $a\rho N_e$ , with the accuracy including the genomic input. Otherwise, we can then argue that the higher responses possible using genomic methods will be translated into higher long-term responses subject to maintaining similar effective population sizes. If gene effects are not small, the LD associations may change rapidly and the simplistic argument rendered invalid.

### Utilizing Intrinsic or Extrinsic Variation?

The above calculations are based on closed populations and on response from intrinsic (within population) variation, but improvement can also come from introducing superior genetic material from other populations, if indeed it is superior. Poultry breeders, for example, maintain several separate strains to provide components for different markets or as reserves (UK Government 2010), although these strains are likely partially related. We can be sure, however, that for many important production traits such nucleus populations of poultry are far ahead of all other populations except those of their few competitor breeders worldwide.

Consequently, although useful genes for traits of poultry likely lurk in the jungle or the fancier's backyard, identifying them is difficult, and only if their effect is sufficiently large, for example, for specific disease resistance, to compensate for deleterious effects on other traits are they potentially useful, although modern molecular methods may enable introgression without reduced linkage drag (Kantanen *et al.* 2015). Indeed, methods for more rapid introgression using genome editing have been suggested recently as a way of incorporating many identified genes via transformed sires without backcrossing (Jenko *et al.* 2015). In view of the polygenic nature of the traits, searches for individual QTL in pre-genomic prediction days have revealed many, but generally have not been very productive in terms of breed improvement. Methods and utilization are likely to be increasingly effective using across population genomics prediction (Kemper *et al.* 2015). It is moot whether the resources expended by international organizations and governments on the maintenance of local genetic resources will be justified, but so far the uptake and consequent economic impact on developed animal production through use of such stocks or genes from them has been limited. In practice, developing countries have introduced housing and management changes and increasingly used nucleus stock or component lines from developed countries.

### Recommended population sizes

A controversial issue in conservation biology is the minimum effective size for a population to be "safe" from genetic disaster, *e.g.*, the "inbreeding vortex." For example, Frankham *et al.* (2014) recommend  $N_e > 100$  to limit total fitness loss to  $< 10\%$  over 5 years and  $N_e > 1000$  to minimize it in perpetuity. The nucleus populations providing the world's chickens are no larger. As commercial birds are crossbred, inbreeding depression is unlikely to extend beyond the parental or grandparental lines maintained by the breeder under good environmental conditions, so maintenance of variation is the main consideration. Nucleus populations are continuously under selection for fitness *per se*, family sizes are regulated to reduce variation and maintain  $N_e$ , and reserve populations are likely held elsewhere to minimize risk from a major pathogen or environmental catastrophe. Maybe the current pragmatic figures for minimum  $N_e$  of  $\sim 100$  for such nucleus populations is a suitable compromise.

### Continuing sources of variation?

An underlying issue that has greatly concerned many quantitative geneticists but not been answered adequately is, what determines the observed level of phenotypic and genetic variances, heritability, and evolvability of the traits? Johnson and Barton (2005) put nicely what remains the regrettable current state: "We are in the somewhat embarrassing position of observing some remarkably robust patterns, that are consistent across traits and species, and yet seeing no compelling explanation for them." While such discussions have mostly been in the context of natural populations, the same unanswered questions arise for livestock under directional selection.

Although experimental populations have reached apparent limits to directional selection, nicely illustrated by experiments in *Drosophila* of Weber (2004) in quite large population sizes and by those of Mackay *et al.* (1994) based on utilizing mutation, in these populations no selection was practiced on fitness traits *per se*. The Illinois maize experiment (Dudley and Lambert 2004) has now continued for  $> 100$  generations (years) with  $N_e$  under 30, yet there is a continuing near linear increase in percentage of oil in the kernel that can be explained only by mutational input (Walsh 2004). Although the low line has reached a real limit, it has almost no oil in its kernel. The long running *Escherichia coli* lines of Lenski are selected for fitness, and all variation is derived from mutation, yet they have continued to respond for 50,000 generations (Wiser *et al.* 2013).

Incorporation of new technology to further increase rates of improvement beyond that which can be achieved using genomic selection methods may come on the scene and render much of the previous discussion obsolete. For example, precise gene editing using CRISPR/Cas9 (Hsu *et al.* 2014) or successor systems surely provides major opportunities. Nevertheless, progress in the past century in livestock improvement has come largely from genetic changes of typically small effect at many loci. While that paradigm has been challenged before in livestock breeding, *e.g.*, in the early days of QTL mapping and of transgenic technology, the technological developments are

now much greater. Overall, I believe that we can justify optimism for continuing responses and increased efficiency of production of desired and nutritious products while minimizing demand on resources and without sacrificing animal health and welfare. Selection has to be multivariate and fitness as well as production trait oriented. Breeders are simply giving evolution a push using the technology available.

## Acknowledgments

I am grateful to colleagues for comments and for contributions to the sounder parts of the arguments.

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Communicating editor: M. Johnston