J. Dairy Sci. 101:1–21
https://doi.org/10.3168/jds.2017-13309

Breeding a better cow—Will she be adaptable?[1]

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ABSTRACT

Adaption is a process that makes an individual or population more suited to their environment. Long-term adaptation is predicated on ample usable genetic variation. Evolutionary forces influencing the extent and dynamics of genetic variation in a population include random drift, mutation, recombination, selection, and migration; the relative importance of each differs by population (i.e., drift is likely to be more influential in smaller populations) and number of generations exposed to selection (i.e., mutation is expected to contribute substantially to genetic variability following many generations of selection). The infinitesimal model, which underpins most genetic and genomic evaluations, assumes that each quantitative trait is controlled by an infinitely large number of unlinked and non-epistatic loci, each with an infinitely small effect. Under the infinitesimal model, selection is not expected to noticeably alter the allele frequencies, despite a potential substantial change in the population mean; the exception is in the first few generations of selection when genetic variance is expected to decline, after which it stabilizes. Despite the common use of the heritability statistic in quantitative genetics as a descriptor of adaption or response to selection, it is arguably the coefficient of genetic variation that is more informative to gauge adaptation potential and should, therefore, always be cited in such studies; for example, the heritability of fertility traits in dairy cows is generally low, yet the coefficient of genetic variation for most traits is comparable to many other performance traits, thus supporting the observed rapid genetic gain in fertility performance in dairy populations. Empirical evidence from long-term selection studies, across a range of animal and plant species, fails to support the premise that selection will deplete genetic variability. Even after 100 yr (synonymous with 100 generations) of selection in corn for high protein or oil content, there appears to be no obvious plateauing in the response to selection. Although populations in several selection experiments did reach a selection limit after multiple generations of directional selection, this does not equate to an exhaustion of genetic variance; such a declaration is supported by the observed rapid responses to reverse selection once implemented in long-term selection studies. New technologies such as genome-wide enabled selection and genome editing, as well as having the potential to accelerate genetic gain, could also increase the genetic variation, or at least reduce the erosion of genetic variance over time. In conclusion, there is no evidence, either theoretical or empirical, to indicate that dairy cow breeding programs will be unable to adapt to evolving challenges and opportunities, at least not because of an absence of ample genetic variability.
Key words: evolution, dairy, genetic, selection, genomic

INTRODUCTION

Adaption is a process that makes an individual or population better suited to their environment. Adaptation itself refers to both the current state of being adapted, as well as the dynamic evolutionary process that leads to the adaptation. The effect of recent artificial selection in various animal breeding programs is well established and proven (Merks, 2000; Chen et al., 2003; Havenstein et al., 2003; Macdonald et al., 2008). In a controlled experimental study comparing grazing Friesian dairy cows representative of germplasm from the 1970s (n = 45) versus the 1990s (n = 60), Macdonald et al. (2008) documented a 23% greater fat plus protein lactation yield in the latter when evaluated at 6 t of DM offered per cow. Figure 1 illustrates the change in phenotypic milk yield per cow in the US Holstein population (https://queries.uscdcb.com/eval/summary/trend.cfm) and apportions it out to genetic and nongenetic influences. The slope of a simple linear regression fitted through the annual phenotypic and genetic means from the years 1970 to 2015 is 305 lb (i.e., 138 kg) and 173 lb (i.e., 78 kg), respectively, implying that genetic gain has accounted for over half

Received June 8, 2017.
Accepted October 12, 2017.
[1]Presented as part of the ADSA MILK Symposium at the ADSA Annual Meeting, Pittsburgh, Pennsylvania, June 2017.
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the gains in phenotypic milk yield; the R^2 of the regression on genetic merit for milk yield was 0.998, implying very little deviation from linearity. It should be noted, nonetheless, that the observed annual gain in nongenetic performance (Figure 1), is in part attributable to genetic improvement, and vice versa. For example, the highly energy-dense diets fed to the modern dairy cows would elicit little milk output advantage if the cow was not bred to exploit such a diet. Therefore, in dairy cow production systems, genetic merit and environment are actually co-evolving. In fact, the environment can have quite a considerable effect on the population dynamics of genetic variance. Certain environmental conditions can favor particular genotypes, thus affecting the genetic variability within the population; this is especially true for relatively rapid and acute changes in the environmental conditions where adaptation of the entire population through genetic change is simply not fast enough. Similarly, a relatively stable environment such as confinement production systems (or indeed vaccination and reproduction synchronization) can, in some instances, reduce selection pressures on a population.

A question that is often raised, however, is if the heretofore observed year-on-year rate of improvement in performance from (dairy cow) breeding programs is sustainable, or if there is a risk of exhausting the genetic variability and thus adaptation capacity. On closer examination of the first derivative of the US Holstein milk yield genetic (and nongenetic) trends in Figure 1, there is a noticeable erosion in the rate at which the annual genetic gain is increasing from the mid-1970s; the first derivative of the annual genetic gain is still positive though, implying that genetic gain in milk production is at least still occurring. Historical genetic trends are a function of the available exploitable genetic variance (and covariances with other traits such as survival) as well as the relative selection pressure on the trait(s). Although one may initially consider a deceleration in genetic gain to be synonymous with an exhaustion of genetic variability, this may not necessarily be true. Exhaustion of genetic variability, in the absence of evolutionary forces that introduce new variability (discussed later), will indeed reduce the rate of genetic gain; in contrast, however, an observed reduction in genetic gain does not necessarily imply an exhaustion of genetic variability (discussed in detail later), and therefore even if the rate of genetic gain diminishes, it does not equate to an inability of a population to adapt, either phenotypically or genetically.

This review will focus on the theory and evolutionary forces underpinning genetic variability and the ability of an animal to adapt, as well as providing empirical evidence of long-term sustainable genetic gain in a range of different animal and plant species. The review concludes with speculation on the possible contributions of developments in key technologies to building a more adaptable cow for the future, as well as strategies that can be exercised to mitigate the risk of breeding a cow that cannot readily adapt to ensuing challenges and opportunities.

IMPORTANCE OF ADAPTATION, AND EVIDENCE OF SUCH IN DAIRY COWS

Agricultural practices in the past century have changed dramatically, and dairy production is no exception (VandeHaar and St-Pierre, 2006). The dairy cow has had to adapt to such changes, the greatest of which in most countries has probably been a change from low-input pasture-based production systems to higher input, highly energy-dense diets fed in confinement. The consequence of aggressive single-trait selection for increased milk production in (predominantly Holstein) dairy cows was a very noticeable deterioration in cow reproductive performance (Berry et al., 2014), the rationale for which has been extensively discussed elsewhere (Berry et al., 2016). The ensuing erosion in farm profit necessitated the adaption or evolution of the Holstein to become more fertile. Figure 2 illustrates the phenotypic change in daughter pregnancy rate in US dairy cows from 1957 to 2015 (https://queries.uscdcb.com/eval/summary/trend.cfm?R_Menu=HO.d#StartBody); genetic merit for reproductive performance declined until approximately the year 2010, after which it improved. Similar trends in reproductive performance in dairy cows have been observed in other international populations, signifying that, despite the low heritability for reproductive performance in dairy cows, (rapid) gains in reproductive performance were achieved (Berry et al., 2014).

Climate change will affect dairy cattle production directly (i.e., heat stress, exotic vector-borne diseases) as well as indirectly (e.g., water and feed quality as well as quality). Furthermore, not only are ruminant production systems affected by climate change, but these production systems themselves are cited as contributing substantially to such climate change (Opio et al., 2013). The consequences and challenges of climate change for dairy cow production have been documented elsewhere (Gauly et al., 2013) and the necessity for ruminant production systems to adapt, in the pursuit of reducing environmental footprint, has also been extensively discussed (Monteny et al., 2006; Weiske et al., 2006). The greater competition for water, energy, and land supply (owing to urbanization and population growth) will require a further adaptive capacity in dairy cows.

Nongenetic interventions or strategies (e.g., nutrition, vaccination) can undoubtedly help circumvent