

Using the Rate of Genetic Change and the Population Structure of Cattle to Better Target Genetic Progress

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Introduction

Understanding the structure of the beef cattle industry is important for driving genetic improvement. Knowledge of the dynamics of the pedigreed population is the first step toward making genetic improvement recommendations (Koots and Crow, 1989). In beef cattle populations, not all herds contribute the same amount of genetics to the breed. There are two different kinds of herds that make up beef production in the United States: pedigreed or seedstock herds and herds that sell their product commercially for slaughter (Baker and Davey, 1960; Lush, 1946). The pedigreed portion of the beef cattle industry is made up of more than one type of breeder. This sector includes the “nucleus” herds that supply genetics to the rest of the “multiplier” herds. These multiplier herds in turn supply genetic material to commercial producers (Lush, 1946). There is overlap between the two, as many of the nucleus herds also sell animals to the commercial herds.

In an analysis of the American Red Angus Association Pedigree from 1985 to 1989, currently under way at Colorado State University, 3,829 herds (81.75% of the total) did not appear in the pedigree as having bred sires of sires, and 3,087 herds (66.63% of the total) did not contribute to any sires of dams in the pedigree. These herds are most likely multiplier herds that pass their animal’s genetics, obtained from the nucleus herds, further down to commercial producers. On the other hand, in the same analysis of the Red Angus pedigree, 4 herds were found to be responsible for

producing 20.6% of the parental grandsires and 13.4% of the maternal grandsires in the pedigree, this indicates that these four herds are nucleus herds. Genetic change is passed on to commercial producers after the nucleus breeders make the changes (Smith and Banos, 1991). The Red Angus model is similar to what has been reported in other breeds (Gutiérrez et al., 2003; McGuirk, 2000; Robertson, 1953). There is great potential for genetic improvement in beef cattle, by better analyzing and understanding the structure of the pedigrees and targeting genetic improvement programs to the true drivers of genetic change.

Knowing the rate and direction of genetic change in a breed can influence our ultimate decision regarding genetic improvement. The main factors contributing to the rate of genetic change are the selection intensity, generation interval, genetic variation, and accuracy of selection (Bourdon, 2001). We can make the rate of genetic change faster by intensifying selection, shortening generation intervals, improving accuracy or having more genetic variation. These factors contribute to genetic change in different ways. Some, like the intensity of selection or generation interval can be manipulated relatively easily by beef cattle breeders. On the other hand, genetic variation and accuracy of selection are difficult to manipulate. There are interactions between all these factors that have to be taken into account when making selection decisions. The nucleus breeders are the ones that make the greatest impact in the rate of genetic change of a breed,

because their animals have the greatest representation in the pedigrees of the breeds.

Review of Literature

Rate of genetic change. In cattle populations, the rate of genetic change is driven by accuracy of selection, selection intensity, genetic variation and generation interval (Bourdon,

2000):
$$\Delta BV / t = \frac{r_{BV, \hat{BV}} i \sigma_{BV}}{L}$$
 Where

$\Delta BV / t$ is the change in breeding values over time, or rate of genetic change over time. $r_{BV, \hat{BV}}$ is the accuracy of selection, i is the selection intensity, σ_{BV} is the genetic variation, and L is the generation interval (Bourdon, 2000). From this equation we see that the rate of genetic change can be increased by reducing the generation interval, or by increasing selection intensity, accuracy of selection, or genetic variation.

In populations like the beef cattle population of the United States, where matings are not random, genetic change occurs, or should occur, constantly from generation to generation, but it can be positive or negative. The key to achieving genetic improvement is that the value of all the positive changes outweigh the value of all the negative changes (Garrick, 2006). This involves identifying the animals with the best breeding values, and selecting them to become the parents for the next generation (Bichard, 2002). On an individual basis genetic improvement requires that the net benefit per animal be greater than the total cost of achieving the improvement (Garrick, 2006). In any situation, the goal of the breeder should be to produce future generations that are more profitable than the last (Bichard, 2002).

Accuracy. The accuracy of selection is defined as “the correlation between true breeding values and their predictions for a trait under selection” (Bourdon, 2000). Increasing accuracy can enhance the rate of genetic change, by having

more appropriate estimates of true breeding values. Harris and Newman (1994) reason that, if we have accurate estimations of genetic parameters, response to selection can be maximized because we know more about the animals used for breeding.

Statistics is a very important tool for animal breeders, and techniques that have been developed over the years, such as best linear unbiased prediction, among others, have improved the accuracy of reported breeding values for cattle (Harris and Newman, 1994). Accuracy has also been improved through progeny testing, which commonly takes place in the dairy industry. Individual animals, with large numbers of offspring, have more accurate records than animals where only the individuals are tested (Harris and Newman, 1994). Nicholas and Smith (1983) propose that reproductive technologies, such as embryo splitting and cloning, act as a way to increase accuracy because records on genetically identical individuals are available, therefore improving the animal’s accuracy. Accuracy is important for making mating decisions and genetic improvement, but Harris and Newman (1994) suggest that the influence of selection intensity and generation interval on genetic improvement is greater.

Selection intensity. Bourdon (2001), defines selection intensity as the “difference between the mean selection criterion of the individuals selected to be parents (\overline{SC}_s) and the average selection criterion of all potential parents (\overline{SC}), expressed in standard deviations from the mean”

or,
$$i = \frac{\overline{SC}_s - \overline{SC}}{\sigma_{sc}}$$
 Selection is a function of

reproduction, replacement rate, and recognizing genetically superior animals in time for breeding (Bichard, 2002). In the beef industry, the selection that drives genetic improvement is usually performed at the level of the nucleus herds, and this genetic improvement is passed down to other herds through the multiplier herds

(Harris and Newman, 1994). Selection is most effective and can therefore be more intense, when traits are more highly heritable (Wright, 1923). Historically there has tended to be a higher emphasis of selection in males, which can be more intensely selected because they are able to have more offspring in the same period of time as females (Lush, 1946).

Reproductive physiology places limits on the amount of selection intensity that can be achieved (Harris and Newman, 1994). Selection has intensified with progress in reproductive technologies, which results in fewer parents contributing to the next generation of offspring (McParland et al., 2007). As mentioned above, in beef cattle herds, selection intensity is usually higher in males because of their reproductive physiology, and technologies like artificial insemination, that make it possible for reproductive rates of one animal to be artificially high (Smith and Banos, 1991). This makes it more feasible to select a few popular sires out of the population, driving up selection intensity. More intensive selection of females also improves the rate of genetic change, and can be achieved by technologies like embryo transfer and in vitro fertilization, but these technologies are so far limited to animals that have proven their genetic superiority and does not take place in the majority of beef herds (Smith and Banos, 1991). One negative aspect of more intense selection is the loss of genetic diversity, which will be discussed later (Cleveland et al., 2005).

Generation Intervals. Generation interval also affects the rate of genetic change, it is desirable to have a lower generation interval for a greater rate of change (Comstock et al., 1998). The generation interval is the time required to replace one generation with the next, and is measured as the average age of the parents at the birth of their offspring (Bourdon, 2000). The generation interval is calculated by taking the age of each of the parents at the birth of its

offspring and averaging it over all the parents (Baker and Davey, 1960).

Three recent studies report generation intervals in different breeds. Gutiérrez et al. (2003) found, that in some breeds of Spanish beef cattle generation intervals were longer in larger populations, but there was a trend towards shorter generation intervals due to improvements in reproductive management and the use of genetic evaluations for replacement decisions. McParland et al. (2007), in an analysis of Irish Charolais, Limousin, Hereford, Angus and Simmental and Holstein-Friesian cattle populations found that generation intervals were increasing, but at decreasing rates. Bozzi et al. (2006) studied Chianina, Marchigiana and Romagnola cattle pedigrees and found that sire-offspring pathways had shorter generation intervals, they proposed that this was due to early replacement of sires, especially when artificial insemination was used. In these papers we see a trend toward shorter generation intervals, which could result in a faster rate of genetic change in the breeds, by using younger parents to produce new generations.

Genetic Variation and Inbreeding. It is important to maintain genetic variation and diversity in a population. Inbreeding lowers genetic diversity (Bourdon, 2000), it increases homozygosity in a population and has deleterious effects towards traits such as weight and fertility (Wright, 1923). Burrow (1993) in a review of the effects of inbreeding in cattle found that inbreeding caused a decrease in performance in traits such as male and female reproduction, feed intake, conformation, and also in growth and maternal traits. The effects were minor at low levels of inbreeding, and increased at high levels of inbreeding. One of the biggest consequences of inbreeding is the loss of hybrid vigor, which causes declines in the traits mentioned above (Wright, 1922). Heterozygosity can be recovered through outbreeding or crossbreeding, thus recovering

hybrid vigor (Wright, 1923). Cleveland et al. (2005) found inbreeding to be decreasing and then increasing in the population of USA Herefords. In other studies inbreeding has also been found to be increasing slightly, but at a manageable rate (McParland et al. 2007; Bozzi et al. 2006; Gutiérrez et al. 2003). Keeping inbreeding at low levels is important so that performance ability is not lost in the animals. In reported populations inbreeding is being kept sufficiently low to avoid most of its negative consequences.

In the 1920's Wright developed a coefficient of relationship that describes the probability that an individual's genes are identical by descent to the genes of another individual. Comstock et al. (1998) describe it as the relationship of an animal to itself. Wright's coefficient of relationship measures how closely an animal is related to the population being studied (Comstock et al., 1998). Comstock et al. (1998) list Wright's coefficients, along with inbreeding coefficients and the coefficient of direct relationship, for some of the most influential sires of the American Red Angus Association pedigree in an article for the American Red Angus trade publication.

Another reason why genetic variation is important is because cattle need to be adaptable to differing beef production trends. Adaptation can be achieved by maintaining access to genetics that provide the potential for adaptation in individual breeds (Notter, 1999). In this paper, Notter states that in order to maintain a potential for adaptation, allelic diversity, or the range of potentially adaptive alleles present in a species, must be maintained. It is important to maintain adaptive capabilities in beef cattle populations because they are catering to a consumer oriented market and the final product needs to be able to change with changes in consumer preferences in order to be more profitable.

Knowledge of genetic diversity is important in managing beef cattle populations in both small

and large populations where only a few sires are used (Nomura et al., 2001), and in populations where there is not much exchange of breeding animals (Bozzi et al., 2006). Modifying breeding programs to include more sires can lead to an increase in genetic diversity and increased adaptation potential (Bozzi et al., 2006). Nomura et al. (2001) analyzed the effects of inbreeding in Japanese beef cattle breeds and recommended that there be an upper limit on the use of artificial insemination in order to keep diversity and inbreeding at appropriate levels, so the genetic improvement achieved in the Japanese breeds would not be lost. Koots and Crow (1989) found that, in the Canadian Hereford population, there is little variation among herds due to the high level of transfer of breeding animals from one herd to the next. This limits the adaptive potential of this population, and does not take advantage of possible hybrid vigor.

Dissemination of Genetics. We can achieve genetic progress if we know how genetics are disseminated in a breed. When accurate pedigree information is available, the genetic structure of a population can be inferred, we can know which animals and which herds have made the greatest contribution of genetics to the whole breed (Cole et al., 2004). Lush (1946) was one of the first to describe that there are two types of herds in breeds of beef cattle. One type are the registered herds that appear in the breed association's pedigrees, and the second type are the commercial herds, where cattle are sold for slaughter (Baker and Davey, 1960). Registered herds can be further broken down into two categories: nucleus herds that provide the core genetics for the breed, and multiplier herds that act as an intermediate between the nucleus herds and the commercial producers (Baker and Davey, 1960; Lush, 1946). Robertson (1953) described that the genetics of a breed as a whole depend on a relatively small group of nucleus herds that dominate the breed. The multipliers herds' role is to multiply the genes from the nucleus herds and pass them on to other herds.

The remaining commercial herds that do not always appear in the pedigree receive their genetics from the multiplier herds. There is some direct exchange of animals between the nucleus herds and the commercial herds, but the nucleus-multiplier-commercial model applies widely to many breeds. Lush (1946) suggested that the distribution of genetic quality from one herd to another is approximately continuous, so that the drivers of genetic progress are the nucleus herds and the rest of the breed is being changed to reflect the composition of the nucleus herds. Beef cattle breeding is part of a dynamic system where all of the components interact, but the structure described above can be taken as a rough description of what happens (Robertson, 1953). This line of thinking has been corroborated in other studies where a small number of herds behave as selection nucleus which supply sires for the rest of the population. The rate of genetic change in the rest of the herds should mimic the rate achieved in the nucleus herds, since the nucleus genetics are ultimately being passed down (Gutiérrez et al., 2003; McGuirk, 2000).

Robertson and Asker (1951), in an analysis of British Friesian cattle, found that over 80% of the sires used in a herd were bred in outside herds. They found that 80% of the grandsires of females born in 1945 were bred in what they classified as nucleus herds. As a result of this breed structure, the rest of the herds are behind the nucleus group in terms of genetic progress, and the nucleus group needs to continue improving in order to stay on top. Koots and Crow (1989) found that in Canadian Herefords, over two thirds of the sires used and one third of dams used were bred in outside herds. Because genetics are being transferred from the nucleus herds to the rest, the genetic superiority of the nucleus herds is constantly being eroded by the use of its animals in the other groups (Robertson and Asker, 1951). Koots and Crow (1989) suggest that herds adopt positions in the breed hierarchy as a result of the popularity of their breeding animals, the breeding methods they

use and other market forces. They found that, in the Canadian population of Herefords, the more popular herds had higher calving ease scores, lower pre-weaning gain and higher gain from birth to yearling age. Bichard (1971) suggests that in order to have the most productive commercial herds available, the lag in genetic progress between the top herds and the rest of the herds must be minimized. It is clear that there is a structure in beef cattle breeding, and we can take advantage of it to improve genetics faster by targeting the herds that are actually making the genetic changes, and minimizing the lag between them and the rest of the breed.

Reproductive Technologies. An additional factor has to be taken into account when talking about genetic improvement. Advances in reproductive technologies such as artificial insemination, embryo transfer and splitting, cloning, etc., have changed many aspects of animal agriculture including beef cattle breeding and genetics. By making reproductive rates artificially high we can select the best animals more intensively and get more offspring out of them. The same well-proven Mendelian inheritance principles are involved with these technologies so results on genetic improvement can be predicted (Nicholas and Smith, 1983). Nicholas and Smith (1983) suggest that with well designed selection experiments, the rate of genetic improvement can be increased and theoretically even doubled with the use of embryo transfer and splitting. When a superior bull is identified, artificial insemination allows for rapid transfer of genetic material and leads to rapid genetic progress (Bichard, 2001). Vozzi et al., 2006 found in the Nelore breed in Brazil, that artificial insemination lead to a high genetic contribution of just a few sires, presumably genetically superior. By identifying the best animals and using them for breeding at higher rates than the rest of the population, we are making genetic progress much faster than would be permissible without these reproductive technologies.

Conclusion and Implications To Genetic Improvement Of Beef Cattle

A point has been made in the literature that there are, within breeds, nucleus herds that act as drivers of genetic change (Baker and Davey, 1960; Robertson, 1953; Lush, 1946). Subsequent studies in different breeds have suggested that this is in fact still the case (McParland et al., 2007; Gutiérrez et al., 2003; Bozzi et al., 2006; Bichard, 2001). These nucleus herds supply much of the genetic material that is passed down to the rest of the herds, and are responsible for much of the genetic change in beef cattle breeds. Identifying these herds in different beef cattle breeds would be beneficial to hasten genetic improvement in the breed as a whole, thus making producers of all different levels more profitable. As Harris (1998) points out, in an industry where a producer is rewarded for a high relative quality of their product, everyone is better off concentrating genetic improvement efforts with the superior breeders, who will pass this improvement on to other producers. The nucleus breeders can make changes faster than many small breeders working toward different goals.

None of the components that affect the rate of genetic change: the accuracy, intensity of selection, genetic variation and genetic interval, are isolated from one another. More often than not tradeoffs have to be made in practical situations. A higher intensity can be achieved if we use older and fewer animals, which will have a negative impact on generation intervals. Accuracy can also be improved if we use fewer, proven, individuals as parents, but this would result in a loss of genetic diversity, because we are using fewer parents for the next generation, and therefore fewer genes. Every breeder must make choices that will affect the rate of genetic change in his or her herd, and not all breeders will have the same goals, because of differences in the markets they cater to, environmental limitations, etc. Recommendations on practical issues must be made on the basis of achieving

genetic improvement. Making genetic improvement is a never ending process and the result will be cattle that are better adapted to their environment and more profitable for all kinds of producers.

In order to keep up with consumer demands and market pressures, constant genetic improvement in beef cattle is needed. A lot can be learned about the movement of genetics in a breed by analyzing pedigreed populations. If we identify superior nucleus breeders and target them with scientific recommendations on traits to select for, we will be targeting the breed as a whole and everyone will benefit, especially if the lag of genetic transfer between one group and the other is low. One of the main challenges facing the beef industry is to have producers that are more economically efficient. If positive genetic change can be made at a higher rate, this goal can be achieved. Studying pedigrees and understanding the dissemination of genes and the rate of genetic change within breeds is a way to make genetic improvement faster.

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