

GENETIC IMPROVEMENT OF BEEF CATTLE ADAPTATION IN AMERICA

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Introduction

Management systems and *environments*^f differ widely for beef cattle populations across the United States. A typical animal occupies several environments during its lifetime, each presenting a unique set of challenges. No animal or breed maximizes the conversion of input to salable product across all environments, nor is the genetic makeup of any animal or breed optimally suited to the challenges encountered in any one environment. To a certain degree, therefore, all beef cattle in America are less than optimally adapted. The opportunity exists to improve profitability of beef cattle production and to maintain integrity of cattle production environments through programs designed to achieve balanced genetic potential for adaptation, production and product quality within specific environments.

With financial support from the USDA Agricultural Research Service and the Beef Improvement Federation and under the auspices of the National Beef Cattle Evaluation Consortium, concerned geneticists and cattle producers met in March, 2004^g to define *adaptation* in beef cattle, characterize important *stressors* in major production environments, and identify opportunities to improve adaptation through genetic means. Results were presented to the beef cattle industry in a symposium in October, 2004. Participants and registrants agreed that the problem was critically important to profitable and sustainable beef cattle production and that new programs should be designed to foster the genetic improvement of adaptation of beef cattle in America. The goal of this document is to present those conclusions to a wider audience of stakeholders.

Why are American beef cattle less than optimally adapted?

Response mechanisms to environmental challenges have been evolving in cattle populations for millions of years. Adaptation has been successful, and populations capable of sustained production now exist throughout most inhabited regions of the world. Why, then, are American beef cattle less than optimally adapted? There are several reasons.

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Prior to domestication, cattle had a demanding but uncomplicated job description; they had first to survive and then to reproduce. To accomplish these goals, they evolved anatomical, physiological, immunological and behavioral mechanisms appropriate to conditions in Eurasia, their center of origin. Thousands of bovine generations hence, domestic descendents in contemporary America face vastly different parasites, diseases, stresses and nutritional challenges. It is not surprising that **a *gene pool* conferring adaptation to past and distant environments confers less than optimum adaptation to current and, indeed, to future conditions.**

Cattle were domesticated in western Asia some 10,000 years ago. Cattle and cattle production technologies subsequently migrated outward from centers of domestication, eventually to colonize much of Europe, Africa and Asia. With an estimated initial migration rate of six miles per decade^{a1}, natural *selection* could easily accommodate adaptation of cattle to their newly encountered environments. During recent times, however, the speed of migration has accelerated (air freight can transport animals, gametes and embryos throughout the world in a matter of hours). Beef cattle management systems are changing more rapidly as well, typically in the direction of greater intensification. Compared to only a few decades ago, for example, cows now produce their first calf at two rather than three years of age, animals are maintained at a higher density per unit of land area, and cattle are fed to market on higher energy diets. In many instances, **management systems and environments are changing more rapidly than animal populations can adapt to such changes through natural selection².**

Domestication created opportunities for the formation of and differentiation among many locally adapted cattle populations. Our ancestors lived in a society of small tribes at that time, with limited material and cultural exchange among groups³. The role of cattle was determined by the needs of each tribe- milk and meat production, power generation, the accumulation of wealth and religious or cultural iconography, for example. Tribal definition of value thus imposed a new 'environmental' challenge on cattle populations, that of fulfilling an economic role. *Phenotypic selection* was applied⁴, as animals more successful in meeting the community standard of value were allowed to reproduce while less successful individuals were not. *Planned matings* and natural selection exerted by local environmental challenges also promoted the creation of populations well adapted to local requirements. As social organization gradually evolved from tribes to communities, communities to villages, villages to cities, cities to states and states to nations, interactions among human populations increased⁵, and the isolation of local cattle populations diminished. When *allele* frequencies and *gene* combinations favorable to production in a local environment were disrupted through exchange of breeding animals, adaptation to specific environments declined. National and international trade in breeding animals, gametes and embryos now allows an animal to produce offspring in environments very different from the one to which that individual is adapted. While providing many benefits to efficient livestock production, **movement of genes into new environments also can reduce adaptation of a resident herd to its unique conditions and challenges.**

^a Numerical footnotes correspond to literature citations listed at the end of the document.

An idea whose time has come back

Beef cattle geneticists in the American South and West concluded in the 1970s that “genetic adaptation to local environments is important in commercial beef cattle production”⁶. Furthermore, “indiscriminate distribution of breeding stock (or their semen) to different environments” should be avoided until something is known of the adaptive merit of that stock. They advised that animals be performance tested^a under environmental conditions similar to those that their progeny were likely to encounter. Evidence supporting these recommendations was provided by their classical experiment to investigate genotype by environment interaction. They started with two genotypes, a line of Hereford cattle selected in and adapted to Montana and another Hereford line selected in and adapted to Florida. These states also constituted the production environments; half of each herd was transferred to the other location, where production of the cows and their descendants was monitored over an 11-year span. Genotype by environment interaction would occur if the production difference between cows of Montana versus Florida origin differed depending upon the location in which they were compared. Such was the case. At Miles City, Montana, the Montana cows and their descendants exceeded Florida cows and their descendants by an average of 14 pounds in calf production per year. In Brooksville, Florida, average annual calf production of Florida cows and their descendants was 84 pounds greater than that of Montana cows and their descendants! As might have been expected, cows from each origin were most productive in the environment to which they were adapted.

Gradual response to mild selection to increase *production traits*, as occurred during most of the history of the co-dependence between cattle and man, generally does not detract from an animal’s ability to survive and reproduce. In fact, selection to increase sustained annual production selects automatically for traits important to adaptation. In recent decades, however, the application of refined knowledge of inheritance, improved information technology and advanced reproductive techniques has allowed dramatic increases in *selection intensity* and *selection response*. Rapid response to intense selection for increased product (as opposed to increased sustained production) can sequester resources formerly utilized to support reproduction and survival. **Rapidly increased genetic potential for production may be achieved, therefore, at the expense of decreased genetic merit for adaptation.**

Hidden costs of selection

Among domestic food animals, broiler chickens are the poster species for rapid rate of response to selection. They are highly prolific and turn generations rapidly, allowing for a high intensity of selection. Furthermore, commercial poultry breeding companies have clear, consistent objectives, most prominently to increase growth rate, feed conversion efficiency and breast meat yield. Selection responses in these traits have not been without cost. Undesirable correlated selection responses include reduced fertility of broiler breeders and increased severity and incidence of ascites, sudden death syndrome, distortion of long bones and tibial dyschondroplasia throughout the life cycle⁷. In a

^a Words in regular print within italicized text are defined in the Glossary.

similar manner, progeny testing and artificial insemination have fostered rapid response to selection for increased milk yield in dairy cattle, for which undesirable correlated responses are poor rebreeding performance and increased incidence of metabolic imbalances in lactating cows⁸. In swine, intense selection to increase growth rate and feed conversion efficiency has been accompanied by increased skeletal abnormalities and impaired reproduction⁹. Such undesirable side effects should come as no surprise. Within an environment, an animal can accumulate no more than some fixed level of nutritional resources. When a higher proportion of that total is required to support performance for intensively selected traits, then a smaller proportion is available to meet all other physiological demands.

Who benefits from improved beef cattle adaptation?

Potential benefits from improved beef cattle adaptation include enhanced animal well-being, increased profitability for beef cattle producers, more desirable products for beef consumers, enhanced resource conservation and more effective forage resource utilization.

Improved adaptation enhances animal well-being. Stress is a fact of life. Fortunately, response mechanisms have evolved to stressors commonly encountered in a population's evolutionary past. These physiological, immunological, metabolic and behavioral responses generally are sufficient to maintain biological integrity and physical well-being. However, when responses are inappropriate or inadequate, stress can lead to distress, defined here as ill health or compromised well-being¹⁰. A maladapted population is one in which inherent response mechanisms to prevailing environmental challenges do not maintain satisfactory well-being in many individuals. An adapted population is one in which most individuals do cope successfully with stresses commonly encountered in their environment.

When cows are vertically challenged

Although native to and domesticated in western Asia, cattle are now raised in most semi-arid through humid, tropical through temperate and coastal through alpine regions of the world. Individuals are most likely to be poorly adapted when raised at one or the other extreme of an environmental continuum. One such case is high-altitude disease of cattle, of economic and welfare concern in mountainous regions of the American West. A synonym is 'brisket disease', named for the edema which results when low oxygen pressure at high altitude induces labored respiration, increased heart rate, elevated blood pressure, and fluid accumulation in the thoracic cavity of affected individuals. A tool to select breeding stock resistant to high-altitude disease was developed through research at Colorado State University and elsewhere¹¹. Pulmonary arterial blood pressure (PAP) measured at high altitudes is heritable and is indicative of genetic susceptibility to brisket disease. Individuals with PAP below a specific benchmark produce offspring likely to be resistant to brisket disease; those whose PAP score exceeds that threshold typically produce a higher proportion of susceptible calves.

Improved adaptation enhances financial well-being of beef cattle producers. Beef cattle production cannot be profitable unless cattle are productive, efficient and produce a desirable end product. Selection to improve traits contributing to these ends is desirable if not required. In addition, cattle that are genetically adapted to their environment incur lower costs than unadapted but otherwise comparable cattle. Profitability of beef cattle production would be enhanced by including locally-rational measures of adaptability in industry selection schemes and *breeding objectives*.

When enough is just enough

Selenium (Se) is an essential trace mineral for animal nutrition. Its concentration in the soil varies widely across cattle producing regions of America and in plants grown upon those soils as well. Although many cattle receive an appropriate amount of Se in their diet, some are marginally to severely deficient¹² while others experience selenosis¹³ (toxicity from excess Se). Cattle at the Quinn Cow Company near Pine Ridge, South Dakota, fall into the latter category. Each year, some cows exhibit lameness, ill thrift and reduced calf production (the symptoms of selenosis), leading to premature culling. The Quinns believe that average resistance to Se toxicity is increasing in their herd, although slowly, as natural selection eliminates genes causing increased susceptibility. These detrimental genes could be re-introduced, however, through purchased bulls whose genetic resistance to selenosis is unknown. If a readily measurable trait indicative of ability to absorb Se from the diet could be identified, breeding animals could be selected whose genetic merit for Se absorption was appropriate for forages that their progeny were likely to consume. High absorber bulls could be selected for regions low in Se and low absorbers for regions in which selenosis had been a problem.

Improved adaptation reduces cost and enhances quality of beef. Typically, a portion of the economic benefit of improved agricultural efficiency is passed on to the consumer as lower prices and/or better quality of product.

Improved adaptation enhances food security. Well-adapted populations are resilient to temporal variation in their environment, differences among years in weather, feed quantity and feed quality, for example. Accordingly, annual product yield from well-adapted herds will vary less than that of poorly-adapted herds. When cow herds and market animals are well adapted to their production environment, it is easier to maintain a safe, reliable and uniform supply of beef.

When less is more

Just as high incidence of infectious disease may signal a poor fit between a population of cattle and its environment, low incidence suggests that a population is well adapted. Because adapted cattle will, in general, be healthier, they should require fewer therapeutic injections of antibiotics. Public health officials are concerned that antibiotic residues in food products may promote antibiotic resistance in organisms that are pathogenic to humans. Reducing the use of antibiotics within the production chain for beef could, therefore, benefit public health and food security as well. Economic benefits

would accompany these social benefits. Each time that an animal is injected, there is a possibility that the injection site may become infected. According to the National Cattlemen's Beef Association 1995 National Beef Quality Audit, resultant blemishes reduce carcass value an average of \$7.05 per steer or heifer slaughtered in America¹⁴. Producers of better adapted and healthier cattle would escape some proportion of this financial burden.

Improved adaptation lessens the need to modify production environments. Beef cows have been called a scavenger species. Their traditional agro-ecological role has been to convert foodstuffs not directly usable by man to wholesome, nutritious meat and other valuable products. They do this best when they are well adapted to the environment in which they find themselves. When they are not well adapted to a prevalent challenge, a management option is to modify the environment to more closely satisfy their needs. Such modifications are never without monetary cost, and they may incur social costs as well. For example, recreational users of public forest and range lands prefer 'natural' to altered environments, and adapted cows are more likely than unadapted cows to prosper on unmodified lands.

One cow's fodder is another cow's poison

*Hank Maxey raises cattle in the Piedmont region of Virginia. Forage grows well on his farm in spring and autumn but not during the hot and often droughty summer. In fact, tall fescue (*Festuca arundinacea*) is the only grass species that tolerates the climatic, nematode and insect stresses characteristic of much of the southeastern United States at that time. It does so because of its symbiotic association with the endophytic fungus, *Neotyphodium coenophialum*¹⁵. Together, fungus and grass produce toxins that are harmful not only to invertebrate consumers of the grass but to livestock as well¹⁶. Affected cattle experience severe discomfort from heat stress, leading to reduced forage intake, lower milk yield, slower growth and impaired reproduction. Lost production exceeds \$800 million per year¹⁷. Farmers in the "fescue belt" report that some cattle within each herd are particularly susceptible to fescue toxicosis while others are largely unaffected. Research suggests that inheritance is partly responsible for observed differences and that tolerance to endophyte-infected fescue could be improved by among-breed¹⁸ and within-breed¹⁹ genetic selection, as several southern cattle breeders are attempting to achieve.*

Improved adaptation enhances resource conservation and utilization. Cattle production has sometimes been criticized for contributing to environmental deterioration. It also, however, can serve to maintain or improve pastoral environments. For example, cattle are grazed in the Grayson Highlands State Park in southwestern Virginia to prevent reforestation of meadows that contribute to habitat diversity. Several European countries subsidize traditional cattle production enterprises to maintain rural economies and environments. To contribute effectively to environmental conservation, cattle must be satisfactorily adapted to the particular environment that they are assisting to conserve.

Designing cows for resource conservation

When the right number of cattle consume the right amounts of the right forages at the right times, according to the physical and ecological characteristics of a specific site, range beef cattle production is a remarkably sustainable enterprise. This requires skillful and judicious management. Cattle, and the wild ungulates with which they share the range, prefer grazing near streams. Therefore, one of the most intractable problems on mountainous, semi-arid ranges has been to prevent over-utilization of riparian zones before there has been adequate utilization of upland terrain. Can beef cattle be selected genetically for more uniform utilization of a forage resource? Researchers from Montana State University reported that Tarentaise cattle (native to the alpine region of France) spent a higher proportion of time grazing on slopes distant from water sources than Hereford cattle (native to a farming region of the British Isles)²⁰. They reported heritable variation within the Hereford breed in propensity to graze steeper, drier areas of the range as well. New Mexico State University researchers reported among-breed²¹ and within-breed²² genetic variation in diet selection, an important component of forage utilization of native range. Perhaps cattle can be selected for improved utilization of a heterogeneous forage resource, reduced degradation of riparian habitats and reducing grazing pressure on especially palatable plant species.

Proposed actions

The Agricultural Research Service of the U. S. Department of Agriculture should initiate and support research and development programs to enhance genetic adaptation of beef cattle to United States environments and challenges. In order to achieve genetic improvement for adaptation of beef cattle in America, the following actions are recommended:

I. Identify important stressors and environmental challenges

- A. Convene a Beef Cattle Adaptation Coordinating Committee to include beef cattle producers, advisors to the beef cattle industry and scientists from pertinent disciplines (genetics, physiology, nutrition, reproduction, behavior, veterinary science and economics).
- B. Identify major beef cattle production environments in America, and characterize their nutritional, physical, climatic, management and economic characteristics.
- C. Identify the major physical, biotic, social and management stressors within each defined environment.

II. Quantify genetic variation and covariation of adaptive and production traits

- A. Through review of national and international literature, analysis of field data and designed experimentation, quantify within-breed transmissible genetic variation (*heritability*), among-breed genetic variation (breed differences), *inbreeding depression* and *heterosis* for *adaptive traits*.

- B. Through review of national and international literature, analysis of field data and designed experimentation, quantify *genetic correlations* among different adaptive traits and between adaptive traits and production traits.

III. Identify *indicator traits, DNA markers and genes important to adaptation*

- A. Identify measurable and heritable indicator traits that accurately reflect variation among cattle in adaptation to specific stresses and challenges.
- B. Identify DNA markers that accurately reflect variation among cattle in adaptation to specific stresses and challenges.
- C. Identify genes and alleles that influence adaptation to specific stresses and challenges.

IV. Develop *breeding value estimation procedures for adaptive traits and for adaptation.*

- A. Modify traditional genetic evaluation procedures to allow estimation of breeding values for specific adaptive traits within specific environments and for specific breeding objectives.

Achieving site-specific adaptation

The number of specific traits contributing to adaptation in any one environment typically is too large to allow all of them to be optimized by selection, even if methods were available to do so. Rex Ranches of Ashby, Nebraska, take a different approach. They define specific accomplishments that a cow must achieve by her fourth birthday in order to be successfully ADAPTED to their ranch and its challenges. Such elite cows are given the opportunity to leave as many descendents as possible in future generations. Cows that fail to meet one or more of the benchmark criteria are prevented from leaving many replacement offspring. This program should increase adaptation but, because of the inherent limitations of bovine reproduction, only slowly. In 2004, scientists from the National Beef Cattle Evaluation Consortium used records from the Rex Ranch to test a program to accelerate genetic improvement for site-specific adaptation. Data from the entire herd were analyzed simultaneously to estimate genetic merit for adaptation not only of four-year-old cows but of their male and female relatives as well. (Similar procedures are commonplace for genetic evaluation of production and product quality traits in livestock). Although requiring further development, the method shows promise as a tool for within-herd genetic evaluation of adaptation, as defined for specific needs and conditions.

- B. Develop *marker-assisted selection* procedures (MAS) to incorporate genotypic information for DNA markers and genes into quantitative genetic evaluation for adaptive traits and adaptation.

V. Design selection and mating programs to improve adaptive traits and adaptation

- A. Develop breeding objectives that rationally combine selection for product quality, production and adaptation.
- B. Develop *decision-support programs* to evaluate mating systems and breed choices for specific economic goals within specific environments and for specific challenges.

VI. Identify management practices and environmental modifications that enhance adaptation

- A. As a secondary goal of research programs to enhance genetic merit for adaptation, identify management interventions and environmental modifications that reduce stress and enhance ability of cattle to cope with environmental challenges.

VII. Determine economic and social benefits of genetically enhanced adaptation of beef cattle

- A. Concurrent with accomplishment of the above objectives, estimate the impact of improved genetic adaptation on the cost, revenue and efficiency of beef cattle production.
- B. Concurrent with accomplishment of the above objectives, analyze the impact of genetic improvement of beef cattle adaptation on animal well-being, sustainability of beef cattle production systems, maintenance of the integrity of production environments and the health and economic well-being of beef consumers.

Glossary

Adaptation. Adaptation to a particular environment exists when an animal or breed has the ability to survive, produce and reproduce within that environment at an acceptable level to the cattle producer.

Adaptive trait. An adaptive trait is one that contributes to an animal or a breed's ability to survive and reproduce sustainably in a particular environment. Resistance to internal parasites and heat tolerance are important adaptive traits in some environments but not in others.

Allele. Alleles at a gene locus have different nucleotide sequences within the DNA. Because different alleles may have different biological effects, they account for the genetic variation necessary for response to selection. See also *gene*.

Breeding objective. The precise goal of a beef cattle breeding program is known as its breeding objective. An example would be “to produce high-quality, lean beef at the lowest possible cost.” The breeding objective typically includes a listing of *production* and *indicator traits* that will be used as selection criteria. Breeding objectives vary among enterprises because of differences in resources, environments, markets and economic goals.

Breeding value. An animal’s breeding value reflects its transmissible genetic merit for a trait. It is twice the amount by which progeny of the individual would differ from progeny of an average individual from the same population when mates of both were chosen at random from the population at large. Breeding value cannot be known with certainty, but it can be estimated using performance information from the animal itself and from its relatives. Directional selection is often practiced using expected progeny difference or EPD (one-half of estimated breeding value) as the selection criterion.

Correlated selection response. Correlated response to selection is the change that occurs in one or more traits as some other trait is subjected to *directional selection*. It occurs when some of the same genes affect the direct and correlated traits simultaneously, a phenomenon known as pleiotropy. Correlated responses may be beneficial, neutral or harmful, depending on the biology and economic impact of the traits in question. See also *genetic correlation*.

Decision-support programs. A decision-support program is a set of rules, usually coded into a computer program, which allows a user to evaluate biological and economic impacts of breeding and management strategies on a production system.

DNA marker. A DNA marker is a specific sequence on nucleotides within a particular gene that can be detected through laboratory analysis and can be used to determine which alleles are present at that locus in an individual. See also *marker-assisted selection*.

Environment. In the context of beef cattle breeding, the environment includes the net effect of all nongenetic factors that influence an animal’s phenotype for a particular trait, up until the time that the trait is observed or expressed. Factors that contribute to the ‘environment’ include but are not limited to physical geography, climate, quantity and quality of the diet, management practices and health maintenance programs.

Gene. A gene is a discrete segment of the DNA molecule, located at a specific site on a specific chromosome pair. The unique nucleotide sequence of each gene determines its specific biological function. Many genes specify the amino acid sequence of a protein product. Others produce molecules that are involved in controlling developmental and metabolic events. See also *allele*.

Gene pool. A population’s gene pool is composed of all alleles at all gene loci on all chromosomes of individuals within that population. Its content is dependent upon the population’s ancestry, historical isolation, history of natural and artificial selection and cumulative mutation.

Genetic correlation. The genetic correlation between two traits is a numerical measure of the extent to which variation in both of them is caused by genes at the same loci. It ranges from +1 (indicating that the two traits are genetically equivalent) through zero (indicating that the two traits are totally independent) to -1 (indicating that alleles causing the first trait to increase cause the other trait to decrease concomitantly).

Genotype by environment interaction. Genotype by environment interaction exists when the difference in phenotypic merit between genetic groups is dependent upon the environment in which those groups are compared.

Heritability. Heritability is a numerical measure of the extent to which variation in a trait is genetically determined. Varying from zero to one, it describes the proportion of an individual's phenotypic superiority or inferiority for the trait expected to be transmitted to its offspring.

Heterosis. Heterosis is the difference in average performance for a trait between crossbred individuals and the average performance of parent breeds contributing to the cross. It frequently is economically beneficial, particularly for traits that contribute to reproduction, longevity and health.

Inbreeding coefficient. The inbreeding coefficient is a number between zero and one that quantifies the expected reduction in proportion of heterozygous loci in the inbred individual, compared to the proportion of heterozygous loci in a typical individual from the noninbred population from which the individual descended.

Inbreeding depression. Inbreeding depression is the average change in phenotypic value for a trait that accompanies each unit of change in *inbreeding coefficient* within a population. Generally it is economically detrimental, particularly for traits that contribute to reproduction, longevity and health.

Indicator trait. An indicator trait is one that does not directly influence net profit of commercial livestock production but which is genetically correlated with one or more traits that do. For example, larger scrotal circumference of yearling bulls does not increase revenue or reduce cost of production, but it is predictive of a bull's genetic merit for age at puberty, an economically important trait in many instances.

Marker-assisted selection. In marker-assisted selection, DNA markers are used to predict genotypes of candidates for selection at loci associated with merit for an economically important trait. Such information may then be used in breeding value estimation for the trait.

Performance test. In a performance test, phenotypic values for economically important traits are recorded on animals that have been managed as uniformly as possible, such that performance records will reflect transmissible genetic merit as accurately as possible.

Phenotypic selection. Phenotypic selection occurs when individuals are selected to become the next generation of parents based upon their phenotypic merit for a particular trait or traits. Because “like tends to beget like”, selection of phenotypically superior parents should increase progeny merit for the selected trait.

Planned matings. Planned matings occur when the cattle breeder chooses to mate a particular male with a particular female in an attempt to achieve a desired result. Crossbreeding is a planned mating, for example, when practiced in an attempt to benefit from heterosis. See also *random mating*.

Production trait. Production traits are those that directly influence cost or revenue from beef cattle production; growth rate, feed intake and carcass merit, for example.

Random mating. In random mating, the alternative to *planned mating*, males and females are mated without regard to their genetic relationship or to their phenotypic similarity.

Selection. Selection occurs when individuals of different genetic or phenotypic merit reproduce at different rates. Relevant types of selection include:

Artificial selection. The livestock breeder decides which individuals will reproduce and for how long. Ideally, animals with highest predicted genetic merit for economically important traits are chosen as parents, and those with the poorest estimated genetic merit are rejected or culled.

Natural selection. Whether an animal reproduces, and for how long, is determined by that animal’s ability to cope with environmental challenges, rather than or in addition to breeder decisions.

Directional selection. Animals chosen to be parents are above (or below) the average of their contemporaries for the trait in question. The goal of directional selection is to improve phenotypic merit of the selected traits in progeny of the selected individuals.

Stabilizing selection. Those animals closest to average of their contemporaries are selected as parents, while animals that are either well above or well below average are discriminated against. The goal is to maintain the trait in question at its current level of expression. Stabilizing selection is appropriate for traits for which the optimum phenotype is an intermediate value.

Selection intensity. Selection intensity is a numerical measure of a breeder’s attempt to change a trait by choosing as parents those individuals with better than average estimated transmissible genetic merit for that trait. If all other things are equal, then higher selection intensity leads to higher selection response.

Selection response. Selection response is the amount by which the population mean for a trait is changed by the effects of selection, generally expressed per unit of time. See also *correlated selection response*.

Stressor. A stressor is any external challenge that causes an animal to initiate a physiological, behavioral and(or) immunological response to maintain or achieve its

physical integrity and well-being. Examples include environmental temperatures outside the animal's inherent comfort zone, pathogenic organisms and dietary toxins.

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