BEEF CATTLE BREEDING À LA JEFFERSON¹,²

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Summary

Even more than most disciplines in the Animal Sciences, quantitative genetics is dependent upon models. Models, by definition, are abstractions of reality. Invariably they require simplifying assumptions, which should be but sometimes are not clearly specified. One thesis of this article, illustrated by examples, is that many of the assumptions upon which animal breeding theory and practice are based are not valid. Some proportion of research resources should be devoted to challenging or verifying those assumptions and following up those areas of enquiry suggested by the outcome of such research. A further thesis is that the selection of topics and priorities for animal breeding research should be a matter of choice by individual scientists and should not be determined by steering committees or directed by administrative fiat. Hopefully, the resultant mutation, cross-fertilization, assortment, recombination and selection of ideas that would result would bestow upon our discipline higher fitness from multiple-peak epistasis, and minimal danger of extinction (or petrification) from over-specialization. A final thesis is that true creativity by research scientists should be nurtured and rewarded and that work in traditional areas of breeding and quantitative genetics should be continued—but done better. (Key Words: Animal Breeding, Quantitative Genetics, Beef Cattle.)

Introduction

This essay wanders rather far afield from the theme of quantitative genetics of livestock. Therefore, in order that it at least begin with reference to domestic animals, I remind the reader of the Three Little Pigs. Two suffered dire consequences because their straw and stick houses could not withstand challenges imposed by a changing environment. Only the pig that was wise enough to build his house of durable materials, and on a strong foundation, escaped property destruction by the wolf. This old story paraphrases the scriptural injunction to build upon rock rather than upon shifting sands. Unfortunately time-honored advice such as this sometimes goes unheeded, even in the Animal Sciences.

A thesis of this article is that the foundations upon which beef cattle breeding theory and practice have been built may not be as strong, as accurate or as complete as we frequently allow ourselves to believe. Traditional areas of beef cattle breeding research should be continued, but some of our effort should be devoted to challenging, verifying or modifying the assumptions upon which current methods are based. New work should be initiated in areas suggested by challenges to current assumptions and also in areas suggested by research accomplishments in other species, other countries and other disciplines. This will require of individual scientists and of science administrators, the curiosity, the enthusiasm, the imagination, the open-mindedness and the creativity of a Thomas Jefferson, thus the title—Beef Cattle Breeding à la Jefferson—of this essay.

Current Assumptions

Quantitative genetics, probably more than any other discipline contributing to the animal...
sciences, is dependent upon models. By definition, models are not reality. They are an attempt to approximate reality, often though not invariably using mathematics. They are invariably a simplification of the system or phenomenon which they are designed to represent. Model construction should be accompanied by a clear statement of the simplifying assumptions upon which the model is based. Further, the possible consequences to accuracy and validity of the model if assumptions are not met should be documented.

Quantitative genetics, and the application of quantitative genetic principles to animal breeding and improvement, has been around for a long time. Many models are so familiar to students and practitioners alike that we tend to forget that they are models—that they are an abstraction of reality and that they originally were constructed employing carefully defined simplifying assumptions. As refinements and embellishments were added, more sophisticated models emerged and eventually found their way into animal breeding practice. There is some danger, I believe, that our field may now be akin to an inverted pyramid. A great deal of theory, dogma and practice may be resting upon an unstable base.

Some of the assumptions upon which quantitative genetics theory is based are believed to be true. Others are known or suspected to be false. These latter assumptions fall into two subcategories—those that are believed to be minor in their consequences (so they can safely be ignored) and those we do not have the technical capability to incorporate into models, even if they are thought to be important.

A list of assumptions which I subconsciously accept or blithely ignore includes the following:

1. Qualitative and quantitative genetic variation is caused by structural genes, i.e., genes whose nucleotide sequence codes for the amino acid sequence of an enzyme.

2. Economically important quantitative traits are influenced by joint effects of the environment and of a large number of unlinked, noninteracting loci with additive and equal effects on the phenotype.

3. Inheritance is Mendelian. Cytoplasmic inheritance and nuclear-cytoplasmic gene interactions can safely be ignored.

4. Only directional selection is relevant to beef cattle breeding and improvement.

5. Undesirable correlated response to artificial selection can generally be ignored.

6. Selection goals are stable. They are neither time dependent, population dependent nor environment dependent.

7. Microgenotype x microenvironmental interactions are not important and can be ignored.

8. The individual animal and the herd exist in a biological vacuum. That is, no consideration need be given to cooperating or competing species.

9. Within an animal industry, the individual rather than the nuclear family (dam plus offspring), the herd or the entire population is most important. Also, production per individual is more important than production per unit of land area, per dollar invested or per unit of other inputs.

This list will not be found in any animal breeding text, and I certainly do not teach it to undergraduates in Principles of Animal Breeding. If other animal breeders were to compose their own lists, none would correspond precisely to this one. Each specialist, however, upon reflection probably could compose such a list of personal, subconscious "givens". The important point is that few of the items on my list, or on other lists that could be composed, would bear up under careful scientific scrutiny. And even more importantly, the existence of unchallenged assumptions such as these constitutes a sort of "psychosclerosis" (Morowitz, 1979, pp 225 to 228) that stifles creativity and encourages repetitious research. Exceptions to these assumptions could well provide raw material for future advances in our field.

Challenged Assumptions

The first three assumptions deal with genetics of the individual and of the cell, levels of organization commonly ignored by animal breeders. After all, since most economically important traits are quantitative and appear to be polygenic, it does not seem to make much difference what genes are, how genes function, or how genes are organized within the genome. If we think of them at all, we think of them occasionally mutating but otherwise obeying the central dogma and passively replicating, transcribing and translating, subject to Jacob and Monad (1961)
or Britten and Davidson (1969) control. If
items 1 through 3 are untrue or oversimplifi-
cations, what difference does it make to beef
cattle breeding? Possibly quite a lot. To illus-
trate with some possibilities:

1. Wilson et al. (1977) reviewed evidence
that ruminants differ from other mammals
not in the type of metabolic enzymes (struc-
tural genes) they possess but in the relative
quantities of those metabolic enzymes (pres-
umably under the control of regulatory
genes). Ruminants for example, have vastly
greater quantities than nonruminants of en-
zymes involved in the conversion of propionate
to more complex carbohydrates and of acetate
to fatty acids. In nonruminants, by comparison,
enzymes predominate that catalyze the syn-
thesis of fatty acids from citrate. “Ruminants”
vs “nonruminants” is a macrogenetic dif-
ference. But if genetic variation in enzyme
quantity exists at that level of comparison,
it might also exist within ruminant species,
among and/or within breeds, for example.
Alleles at the regulatory loci causing variation
in enzyme quantity might cause variation in
digestive efficiency as well. Selection for feed
efficiency might be enhanced by selection
for enzyme levels or ratios. It is an issue that
warrants joint investigation by the digestive
physiologist, the protein biochemist and
the quantitative geneticist.

2. Beef cattle have 30 chromosome pairs.
Other agriculturally important species also
have a fairly large number of chromosomes,
ranging down to 19 pairs for swine. This has
caused quantitative geneticists to discount
linkage as an important source of variation
in economically important traits. And even
if traits generally are affected by many more
segregating loci than there are linkage groups,
if the proportional effect per locus on the
phenotype is small, then linkage still can be
ignored.

Or can it? Charlesworth and Charlesworth
(1976) and Turner (1977) document a case
of Batesian mimicry in butterflies in which
at least six tightly linked loci segregating
as a “supergene” cause the mimetic form.
Lewontin (1977) speculates that linkage
of genes with related biochemical or physio-
logical function, or genes influencing related
traits, may be common. Such linkage could
arise through gene duplication from unequal
crossing over, followed by evolution of one
of the copies to a new but related function
(MacIntyre, 1976) or by rearrangement of the
genome by translocation with preservation
of favorable linkages by selection. Specula-
tions on the importance of linkage frequently
are based upon data from species with fewer
chromosome pairs than exist in livestock
species. Also the arguments frequently are
concerned primarily with an evolutionary
time frame rather than with the number of
generations ordinarily of concern to breeders
of domestic animals. Nevertheless, to ignore
linkage may be a luxury we cannot afford.

It is well known that predicted short-term
response to selection is maximized as selection
intensity is maximized, other factors remain-
ning equal. In the long term, however, neither
the duration nor the limit to selection response
is maximized with maximum selection in-
tensity. Robertson (1960) showed that for
the case of free recombination among genes,
the selection limit was maximized when p,
the proportion of potential replacements
retained in truncation selection, was .5. When
genes affecting the trait were linked, a larger p
(lower selection intensity) was necessary to
achieve maximum long-term response to
selection. The change in p was not large,
however, when the number of loci affecting
the trait and size of the selected population
were large and when loci were distributed
evenly along the chromosomes (Hill and
If tight linkage among functionally related
genes is as frequent and as important in
domestic animals as is envisioned by Lewontin,
then he may be correct (Lewontin, 1977)
in stating that linkage “cannot be regarded
as a second-order nuisance to be ignored
except in special cases.” More needs to be
known of the organization of the genome of
domestic animals before optimum selection
strategies can be determined. It may be neces-
sary, for example, to reassess whether maxi-
mum selection intensity is optimum selection
intensity for beef cattle breeding in the long
term.

3. Variation in quantitative traits from
epistasis is difficult to assess, especially in
species such as beef cattle. Probably largely
because of this difficulty, epistasis generally
is ignored. Evidence from experiments in
other species indicates that it likely does
exist, and in subtle forms quite different
from classical dihybrid examples. Harris (1975,
chapter 2) has documented that many func-
tional proteins are polymers, i.e., that they are composed of more than one polypeptide chain. In some cases, the chains are coded by genes at a single locus (peptidase A, for example); but in other cases, the polypeptide subunits are coded by genes at distinct loci. Thus two or more genes commonly "co-operate" in the synthesis of a single functional protein. Adult hemoglobin, with two α chains coded by one locus and two β chains coded by an unlinked locus, is an example. It is not hard to imagine that the phenotypic effect of an amino acid substitution on one chain could be dependent upon the structure and amino acid sequence of the other chain, ergo epistasis. A perplexing result of the extensive research relating hemoglobin variants to economic traits in sheep (reviewed by Agar et al., 1972) is the frequent finding that for a given trait, one variant is favored in some populations, the other variant in others. This observation could be a manifestation of epistasis—either of the traditional sort, or intraprotein, as just described.

Epistasis might even involve nuclear x cytoplasmic gene interactions. Woodward et al. (1970) reviewed evidence that in Neurospora, cytochrome oxidase (an electron transport enzyme) was composed of two subunits specified by nuclear and by mitochondrial gene loci. Further, the effect of certain mitochondrial mutants on respiratory properties was dependent upon the nuclear genotype. Admittedly, Neurospora is a long way from Bos taurus on the phylogenetic tree. The existence of such epistatic interactions in yeast, however, suggests the possibility of their existence throughout eukaryotes, since cells and their mitochondria have coexisted for a long, long time (Thomas, 1974, pp 69 to 74). Consideration of possible interactions of this kind might explain some instances of reciprocal cross differences in livestock and possibly should be included in experimental designs assessing maternal effects.

The contribution of epistasis to variation in quantitative traits could influence breeding programs in at least two ways. First, it could sabotage the effective selection of purebreds for use in crossbreeding schemes. McNew and Bell (1971) showed that certain types of epistasis could cause a negative correlation between a sire's breeding value estimated from purebred vs outcross progeny. Negative purebred x crossbred covariances have been reported for some traits in mice (Bowman, 1960), Drosophila (Bowman, 1960), swine (Wilson et al., 1962) and chickens (Krause et al., 1965). In most of these cases, the correlations were small in relation to their standard errors. For populations and traits for which such epistatic interactions did exist, response from current selection schemes would surely be curtailed. Selection would become much more complicated, since sires to be used in crossing would need to be selected using recurrent or reciprocal recurrent selection. Sire rankings for estimated breeding value could be dependent on the tester population and genetic merit of a sire would be dependent upon the breed of females to which he was mated. Let us hope that this type of epistasis is not common for economically important traits in cattle.

Second, the effectiveness of new breed formation from a crossbred foundation could be diminished. As presented in the form of expectations by Dickerson (1969, 1973), in the absence of selection and maternal effects, an F1 crossbred should be intermediate between parent breeds plus or minus a deviation attributable to heterosis. In populations large enough to avoid inbreeding, an F2 should be intermediate between the parent breeds plus or minus half the original heterotic deviation, since in the F2 half the F1 increase in heterozygosity is lost. In F3 and later generations, there should be no additional change in the population mean. If, however, part of the superiority of the original purebred populations were due to epistatic gene combinations fixed by previous selection, then advanced generations (F2, F3, etc.) would be expected to deteriorate as the favorable gene combinations were lost through recombination. Experimental evidence on the magnitude of such "recombination loss" in mammals is limited. In a study conducted in New Zealand, Hight, Jury and various colleagues compared contemporary unselected F1, F2 and F3 Romney x Border Leicester ewes for several reproductive, wool and lamb production traits (Hight and Jury 1970a,b, 1971, 1973, 1976; Hight et al., 1973, 1976a,b). In their populations, F2 individuals had lower values than F1 individuals for most traits. In addition, either there was little difference between F2 and F3 groups or F3's surpassed the F3's for production, suggesting that recombination loss could be important for some traits. Mc-
Gloughlin (1980), however, detected no significant deviation from a linear relationship between level of performance for reproductive traits and theoretical percentages of heterozygosity in straightline, line-cross and backcross female mice, suggesting that recombination loss was not important. It is encouraging to note that greater attention currently is being directed to epistatic and recombination effects in quantitative traits (Rastogi and Chevalet, 1973; Teehan et al., 1979; Kinghorn, 1980; and research in progress [Project no. 30-1-0] at the Roman L. Hruska U.S. Meat Animal Research Center, Clay Center, NE).

4. With the exception of cytoplasmic effects, inheritance is Mendelian, but even Mendel's laws have their well-documented exceptions. Segregation distortion or meiotic drive, an exception in Drosophila and mice to the law of independent assortment, is of potential use in domestic animal breeding. In segregation distortion systems (as reviewed by Braden, 1972 and Hartl and Harazumi, 1976), matings among males heterozygous for the distorting allele and females homozygous for the normal allele at the locus do not produce progeny in the expected one-to-one ratio. Furthermore, the deficiency in progeny of one type cannot be explained by differential embryonic mortality. In these systems, when heterozygous females are mated to homozygous males, offspring of the two types are produced in equal proportions. In mice, the phenotypic manifestation of distorting alleles is a shortened tail. The gene is autosomal and does not influence sex ratio. Several systems are known in Drosophila, some of which do have a pronounced effect on sex ratio (Policansky, 1974). Manipulating such genes has, in fact, been advocated as a possible means of biological control of insect populations (Hickey and Craig, 1966; Hartl, 1977). Unfortunately, segregation in natural populations of modifiers that lessen the effects of distorting alleles limits the usefulness of this approach.

The ubiquity in natural populations of Drosophila and mice of segregation distortion suggests its existence in other classes of animals as well. If a sex-linked segregation distortion system could be located in beef cattle, it could be used to manipulate sex ratio of the offspring, as discussed by Beatty (1971) and Hartl (1977). Such a system might, in fact account for the aberrant offspring sex ratios of individual sires occasionally reported in livestock species but usually attributed to chance, fraud or inaccurate record-keeping. As discussed by Foote and Miller (1971), sex ratio control would have dramatic effects on the efficiency of beef cattle production.

My next three assumptions deal with selection. If point 4 were true, then by inference “maximum” is “optimum”, (or at least an increase from current levels is desirable) for all economically important traits. This is clearly not true. An example is the well-documented effect of birth weight on survival in sheep (Purser and Young, 1964; Hight and Jury, 1970b). Mortality is greatest for individuals well above average (from dystocia) or well below average (from starvation or exposure), with highest survival for individuals near the mean. The same relationship likely exists in cattle, though most reports document only the higher mortality of calves well above the average birth weight (Anderson and Bellows, 1967; Laster and Gregory, 1973; Smith et al., 1976). There are probably many other instances in livestock production where natural selection favors an intermediate optimum, though we tend to ignore them in designing selection and breeding systems.

Enfield (1977) has documented a case in which very long-term stabilizing selection for pupa weight in tribolium brought about correlated response in several fitness traits. Compared to control lines in which selection was entirely at random, the stabilized selection lines had from 14 to 30% more progeny per fertile mating. In addition, the percentage of fertile matings was from 11 to 26% higher in the lines subjected to stabilizing selection. The stabilizing selection did not cause a significant decrease in genetic variance, phenotypic variance or heritability of pupa weight. It would require some 480 yr to carry out the number of generations of selection in beef cattle that were done in Enfield's experiment. Nevertheless, his results suggest a possible means of improving lowly heritable traits. Stabilizing selection may be more appropriate than directional selection for some traits in agriculturally important species including beef cattle.

We all would agree that assumption 5 is false, but relatively little research has been devoted to estimating genetic correlations among traits, warning breeders of undesirable correlated responses and designing selection strategies to circumvent undesirable corre-
lated responses. It is likely, for example, that past selection for pre- and postweaning growth in beef cattle has caused increased birth weights, which in turn has increased the incidence of dystocia and perinatal calf losses and caused poorer rebreeding performance of cows in commercial herds in this country. To apply an agricultural metaphor, partly because of overly simplistic recommendations in the past, our chickens have come home to roost. In response to this problem, Dickerson et al. (1974) examined selection strategies to increase efficiency of beef production. In so doing, they published indexes that recognized the positive genetic correlation of birth weight and other measures of growth and the undesirable genetic correlations between birth weight and calf mortality and calf mortality and cows' subsequent reproduction.

Another example of undesirable correlated response to directional selection was documented by Hansen et al. (1979). In their experiment, Holstein cows from a line selected for increased milk yield were compared to nonselected contemporaries. Milk production did respond positively to selection, but labor and veterinary expenses also were increased. The value of the added milk production more than offset the added costs, but their experiment pointed out a potential danger to continued directional selection. Many experiments in laboratory mammals confirm that after long-term selection, the genetic correlations between the selected trait and components of fitness become negative, regardless of magnitudes and signs of correlations in the base population (see LaSalle et al., 1974; Frahm and Brown, 1975; Barria and Bradford, 1981, for example). Greater research emphasis on selection methods to constrain responses in correlated traits is warranted (Cunningham et al., 1979; McCarthy and Doolittle, 1977; Evans, 1980), for situations in which genetic correlations are unfavorable—or may be expected to become unfavorable over time.

It is self-evident that assumption 6 is not true. Selection goals have varied over time. This is illustrated by the gradual discrimination (or reduced emphasis) against fat in animal products—first in pork, then in milk and finally in meat animals and poultry. In sheep, meat production continues its eclipse of wool production in economic importance in the United States.

Selection goals probably also should vary from population to population. Extensive breed characterization research in cattle (reviewed by Long, 1980) has documented important differences among breeds for economic traits and has begun to sort breeds into maternal, terminal and general purpose categories. Too much current research could be interpreted to advocate that breeds now ignore differentiation resulting from past selection and that selection within all breeds now be directed toward the same traits, specifically to increased weaning weight and(or) yearling weight. Few researchers would consciously recommend this procedure, but when only preweaning and(or) postweaning growth are evaluated in a research program, the implication is clear that they are the only traits deemed important, regardless of breed.

Selection goals also should be dependent upon the environment in which production is to occur. Milk production in beef cattle, for example, should receive different emphasis in range vs irrigated pasture vs confinement operations. The optimum level of prolificacy in sheep also is dependent upon the environment, with harsh environments not able to benefit from triplet and possibly even from twin births. The "environment" might be economic as well as physical or managerial, as discussed by Cunningham (1978) for European cattle populations. In his study, the beef to milk price ratio was defined as a spatially and temporally variable "environment", the state of which influenced the selection emphasis to be placed on milk, beef or dual purpose production.

Assumption 7 stated that microgenetic x microenvironmental interactions (McBride, 1958) were not important and could be ignored. By definition, microgenetic differences are the continuously distributed genetic differences which exist within a population such as a breed or crossbred group. Micro-environmental differences are those which exist within a group of animals provided access to the same diet, maintained in the same physical location and afforded the same management. They form a continuum and it generally is not possible to assign categorical or quantitative values to such environmental effects on phenotypes of individuals. For that reason, genotype x environment interactions of the micro- x micro-category cannot be analyzed with traditional biometrical models and methods. That they cannot be quantified
does not imply that they are not important nor that they should be ignored.

Although microenvironmental differences could be of many types, social environment in dairy cattle will be used as an illustration. In large commercial dairies, groups of cows at a similar stage of lactation or cows with similar production levels are often maintained together in close confinement. Even though cows share the same physical environment and are provided access to the same diet, the existence of dominance hierarchies within the group (Schein and Fohrman, 1955) means that cows experience different social environments. Dominant cows are classical tyrants in that they occupy more favorable habitats within their environment (e.g., free stalls, Friend and Polan, 1974), maintain a larger personal space (Kilgour, 1969) and eat first and more when feed is provided (McPhee et al., 1964; Friend and Polan, 1974). Despite these advantages, no consistent relationship among dominance order and milk production has been established (Schein and Fohrman, 1955; Friend and Polan, 1974 and others reviewed by Lamb, 1976). Dominance order was, however, related to fat content in milk (Friend and Polan, 1974) and could be related to other economically important traits such as health care expense, labor requirement or longevity. The inheritance of dominance has received little attention in dairy cattle. If dominance is heritable, however, then to a certain extent a cow's microenvironment is dependent upon her genotype, the common assumption of independence between genotype and environment in influencing phenotype is not valid and a microgenotype × microenvironmental interaction will exist.

Again, we cannot quantify such interactions, but we could investigate them and then alter management in such a manner as to reduce their importance. If a genotype × dominance order interaction were important in dairy cattle, increasing space allowance for housing (Donaldson et al., 1972) or redesigning feeders (Albright, 1974) might decrease conflict among cows and reduce the interaction magnitude and effect. Alternatively, the genetic ability of an individual to choose, alter or interact favorably with its microenvironment might be an aspect of that individual's merit that the breeder would not wish to obscure.

Incidentally, if the environment can be altered to lessen “noise” from genotype × environment interactions, it might also be possible to modify the environment to expose genetic variation that would otherwise be masked. Evenson et al. (1980), for example, subjected unheated and heated sperm nuclei from the same bulls to flow cytometry. Normal vs low fertility bulls did not differ in the flow pattern of the unheated nuclei, but they differed markedly in flow patterns of heated nuclei. The low fertility bulls presumably had damaged chromatin structure that altered the denaturation pattern of DNA in the heated cells. This imaginative use of molecular biological techniques illustrates unmasking of variation (possibly genetic) among individuals by altering the environment at the cellular level. The principle might well find application at the level of intact organisms as well.

A final strategy in coping with microgenetic × microenvironmental interactions would be to attempt to estimate breeding values of individuals (through progeny or sib testing, for example) across the entire range of microenvironments in which the individuals' progeny were expected to perform. In any case, recognition that such interactions might be important and reaching conscious decisions of how best to deal with them should lead to more effective selection programs.

Assumption 8 states that in designing mating systems and selection schemes, consideration need be given only to the species we are attempting to alter genetically. Parasites, competitors, symbionts, bystanders and onlookers can be ignored. An example of a case in which the biosphere of beef cattle has been acknowledged is Australian research to identify genetic variation in resistance to external parasites (Utech et al., 1978a,b). Also various researchers have investigated genetic differences in internal parasite infection of sheep (Whitlock, 1957; Scrivner, 1964; Radhabrishnan et al., 1972). Plant breeders include resistance to pests and diseases as selection criteria and sorghum breeders have developed bird-resistant cultivars.

Examples of cases in which additional attention might profitably be devoted to other species in livestock breeding schemes could include the following. In many pastoral farming areas of the world, New Zealand in particular, cattle and sheep are traditionally reared on the same farms. The cattle are often considered primarily a management tool to
improve forage quality for the sheep. This system creates the potential for coordinated selection of the two species to enhance cooperation and reduce competition between them. This might be accomplished through modification of grazing habits or preferences or through modification of the annual production cycle, in order that periods of peak nutritional need match most effectively the production curve of the pasture. To accomplish these modifications by within breed selection would be an extremely slow procedure; selection among breeds or crossbred types would likely be more feasible.

Torres-Hernandez and Hohenboken (1979) reported differences among crossbred types of ewes in their behavior toward a tethered dog and Gluesing et al. (1980) documented behavioral differences between lambs killed by coyotes compared to contemporaries that escaped predation. It is possible that selection could produce sheep more amenable to herding by dogs and(or) less subject to predation by coyotes, though this would likely require a long-term effort. Little is known of the inheritance of behavioral traits or of which traits it would most beneficial to modify.

Finally, attention might be directed toward genetic aspects of the symbiotic relationship between cattle or sheep and their rumen microflora. It is possible that strains of bacteria and protozoa more efficient in carbohydrate digestion, more sparing of dietary protein or better able to synthesize vitamins could be developed—a potential task for genetic engineers (and their patent attorneys) using recombinant DNA techniques (Anonymous, 1979). It is possible that ruminants could be selected to provide a more hospitable environment for their microflora. It may even be possible to achieve coevolution of ruminant and microflora for optimum utilization of particular diets, though natural selection has already achieved an excellent working relationship between the two classes.

Assumption 9, that production per individual is more important than production per family unit (cow-calf pair, for example), per herd, per hectare or per dollar of financial investment, is clearly wrong. Few would subscribe to that notion, but much research still is conducted as if it were true. Experiments and reports with other bases for assessing production efficiency are becoming quite common. For example, Dickerson (1970) presented a formula to quantify production efficiency of producing female plus progeny units and Texas A&M researchers have published a series of papers in which simulated herd production is evaluated according to net income, income per fixed block of land and percentage return on investment (Long et al., 1975; Fitzhugh et al., 1975; Cartwright et al., 1975). Other groups are active in systems analysis work (see Wilton et al., 1974 and Notter et al., 1979, for example), and it is likely that such experimentation will be expanded.

In summary to this point, my list of subconscious assumptions is not valid—but yours probably are not either. Such assumptions should not be taken for granted. They may be the armor of traditional animal breeding theory and practice, but we must be on the lookout for chinks in the armor, to be repaired as appropriate.

Recommendations

The foregoing account should not be construed as an indictment of all past or current beef cattle breeding research. Much excellent research has been done and extension and industry have made effective use of methods and information that have been generated. It is my belief that part of our future research effort should be devoted to further refinements and further advances in traditional areas of breeding research. These areas, with sample citations to recent studies in each, include genetic parameter estimation (reviewed by Woldehawariat et al., 1977), breeding value estimation (Henderson, 1975; Kress et al., 1977; Harvey, 1979), identification of selection criteria (Dickerson et al., 1974; Elofson et al., 1980), identification of heritable indicator traits genetically correlated with production efficiency (Rowlands and Manston, 1976; Coulter and Foote, 1979), evaluation of selection schemes (Koch et al., 1974a,b; Morris et al., 1980), verification of quantitative genetic theory and models (Seifert, 1975; Barlow, 1978), examination of maternal effects (Cundiff et al., 1974), examination of microgenetic or macrogenetic × macro-environmental interactions (Nunn et al., 1978; Geay and Robelin, 1979), evaluation of mating systems (reviewed by Gregory and Cundiff, 1980), breed evaluations (reviewed by Long,
The relative emphasis devoted to each area should not be determined by administrative fiat. Rather it should be decided by a process akin to natural selection. Individual state and federal experiment stations and individual investigators should set their own priorities for the type of research to pursue, subject to the advice of regional technical and coordinating committees, federal and state administrators, breed associations, producer groups, individual producers and colleagues both in research and extension. Some decisions will be inopportune; and some research work—hopefully a minimum—will be redundant. Still the cross-fertilization, the independent assortment, the recombination and the selection of ideas afforded by this process would likely be more effective than allocating research goals by decree—anyone's decree. The variety in the types of research likely chosen by different investigators would be good insurance against beef cattle breeding entering the evolutionary dead end of over-specialization—and the subsequent danger of extinction. The result hopefully would be more like multiple-peak epistasis (Wright, 1978), with researchers in each area contributing to increased average population fitness by generating more and better information in that area. The analogy to natural selection is imperfect, but the point, I hope, is clear. There should not be pressure for individual investigators all to conform to some national plan of research priorities and goals. Individual initiative must be encouraged, not simply tolerated.

With freedom comes responsibility. It is our ethical duty as individual investigators to choose research objectives as wisely as possible, to avoid duplication of effort, to conduct experiments according to sound experimental designs and research protocols, to harvest the maximum information from our data, to interpret it fully and wisely and to ensure that results are made available to consumers of that information.

It is our duty to be creative—"to look where others have looked but to see what others have not seen." Skjervold and Finland (1975) did this when they showed that a sire, through the fetus, could influence milk production of his mate. (Incidentally, their research is a good teaching tool in introductory animal breeding classes. Students readily accept that a sire can influence milk production of his daughters but many do not believe he can affect production of his mates as well—not until the physiology of the situation is explained to them. It is a reminder that common sense cannot always be trusted and it is a lesson many of them remember.) Their research has been verified and expanded upon by others, as reviewed by Thatcher et al. (1979). Another example of creative research was Grimes and Harvey's (1980) use of a traditional statistical definition of variance in a novel fashion. They showed that the squared difference between phenotypic measurements of a trait for all possible pairs of individuals in a population could be equated to expressions for causes of the differences, with results manipulated to estimate genetic parameters simultaneously from all the relationships (not just paternal half sibs, for example) in the population. Their methods likely will be added to those in routine use throughout the animal breeding field.

Our graduate education and postgraduate experience can teach statistics, genetics and physiology. We can learn how to program a computer, analyze a system, stain a chromosome, measure a selection differential and assay a hormone. It is more problematic, though, to know when these things are to be done and in what combinations, to maximize true creativity of research endeavor. Two recommendations that might be helpful to increase creativity or imagination are as follows.

The first is to become more cosmopolitan and less provincial, more open and less circumscribed, more farsighted and less myopic in our approach to biological science. By this I am not advocating a mass exodus from specialization to generalization. Rather I am advocating a more open-minded approach to whatever area of specialization an individual does elect. There are not many renaissance persons in our field, or in any other field for that matter, though there are a few I personally would honor with this designation. Some degree of scientific specialization is necessary. (A colleague whom I consider very successful in his field of biology, for example, has spent his entire career on three problems, but each year he approaches them with fresh insight, fresh methods and greater...
experimental precision. Much of his success is dependent on having chosen important and challenging problems to begin with.) If an individual scientist elects to specialize in modeling of beef production systems, that scientist should consider inputs from associates in genetics, physiology, nutrition, reproduction, health and economics in formulating the models. If an individual scientist decides to study the inheritance of physiological traits and their relationship to production efficiency, then let that scientist pursue results from other taxa to aid in formulating hypotheses and experiments. No matter what area of specialization an individual scientist elects, prohibit that scientist from confining his literature review to North American studies. Neither ignorance, arrogance nor laziness are valid excuses for failing to be aware of research advances from our colleagues abroad, but examination of the literature citations of many Journal of Animal Science or Canadian Journal of Animal Science articles indicates that this is too frequently the case.

Disciplines with which we could cooperate to the potential benefit of both include at least the following: molecular biology, embryology, physiology, endocrinology, nutrition, pathology, toxicology, parasitology, ecology and economics. None of us can be all things to all people, and none of us can keep current in all these areas. We can, however, and should keep an open mind to discoveries from other fields and spend at least some time reading outside our speciality and outside the journals in which we ordinarily publish.

The second recommendation is derived from an essay by Morowitz (1979, pp 28 to 32) entitled “On Computers, Free Will and Creativity”. He describes a hypothetical chess-playing computer that, prior to making a move, calculates the probability of eventual victory from each of the possible moves which could be made. He then defines as “epsilon” a pre-programmed range of probabilities within which the actual move is chosen at random. For example, if epsilon were very narrow, the computer would be free to choose its move from a very limited potential number. A conservatively programmed computer such as this could have an excellent win-loss record, but it would not be likely to discover creative new ways to win the game. Alternatively, epsilon could be wide, and the adventurous computer would then have dozens of moves from which to choose. This computer usually would be check-mated long before it could stumble across an ingenious and innovative win. The ideal epsilon to program into the machine might be conservative enough to prohibit foolish and completely inappropriate moves but large enough to allow an occasional “creative” burst.

As analogues to chess-playing computers, scientists need to question the epsilon that we or our administrators impose upon our research. It should not be so narrow that the outcomes of experiments are known before the experiments even are conducted. It should not be so wide as to allow a shotgun approach to research, i.e., to run experiments, measure traits and correlate variables to see what happens or to determine what is “significant”. It should, however, be wide enough so that we are not slaves to common sense, traditional wisdom and current interpretations and results. There must be room to speculate, to challenge and occasionally to blunder if creativity is to be expressed.

In summary, my recommendations for beef cattle breeding in the years ahead are to nurture, encourage and reward creativity in new areas of enquiry, to continue work in traditional areas of breeding research but to do it better and to devote a portion of our energies to challenging or verifying the assumptions upon which current methods and models are based. It is an exciting time to be in the research business, and I wish all of us good fortune, good ideas, good working conditions, adequate resources, good epsilons and good administrators.

Literature Cited


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