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# The Importance of Genetic Diversity in Livestock Populations of the Future<sup>1</sup>

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**ABSTRACT:** Farm animal genetic diversity is required to meet current production needs in various environments, to allow sustained genetic improvement, and to facilitate rapid adaptation to changing breeding objectives. Production efficiency in pastoral species is closely tied to the use of diverse genetic types, but greater genetic uniformity has evolved in intensively raised species. In poultry, breeding decisions are directed by a few multinational companies and involve intense selection, the use of distinct production lines, and very large populations. In dairy cattle, the Holstein breed dominates production. Intensive sire selection is leading to relatively rapid inbreeding rates and raises questions about long-term effects of genetic drift. Key questions in management of farm animal genetic diversity involve the distribution of potentially useful quantitative trait locus alleles among global livestock breeds. Experiments

with tomato, maize, and mice suggest that favorable alleles can exist in otherwise lowly productive stocks; this cryptic variation may potentially contribute to future selection response. Genetic improvement under relatively intense unidirectional selection may involve both increases in the frequency of favorable additive alleles as well as the progressive breakdown of homeostatic regulatory mechanisms established under the stabilizing selection that is characteristic of natural populations. Recombination among closely linked regulatory loci and new, potentially favorable mutations are possible sources of long-term genetic variation. A greater understanding of the potential that these alternative mechanisms have for supporting long-term genetic improvement and of genetic relationships among global livestock populations are priorities for managing farm animal genetic diversity.

Key Words: Genetic Resources, Livestock, Genetic Variation, Recombination, Selection

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## Introduction

Discussions of needs and opportunities for improved management of national and global farm animal genetic resources began in the United States by 1984 (CAST, 1984; OTA, 1987; NRC, 1993). Discussions generally focused on strategies for preserving rare breeds. Yet a clear and critical element of the discussion involves debate on the need for, and future opportunities presented by, widespread conservation of diverse livestock breeds. This situation differs from

that in plants, for which the need to maintain a core collection of germplasm for major crop plants is seldom questioned, although debate on magnitude, methodologies, and use of that collection is ongoing (e.g., see NRC, 1991).

Much of the discussion on management of farm animal genetic resources has focused on developing nations. From a global perspective, this focus is appropriate. Most of the world's domestic animals are found in these regions, and livestock breeds in developing nations have been less thoroughly characterized (Mason and Crawford, 1993). However, opportunities and challenges for animal genetic resource management in developed countries have been correspondingly neglected. This article, therefore, specifically considers questions of animal genetic resource management from a domestic U.S. perspective. Key issues include the importance of synchronizing germplasm to production-management environments and appropriate strategies for long-term maintenance and use of genetic variation within livestock species.

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## Use of Farm Animal Genetic Diversity in Current Production Systems

An essential first step in management of farm animal genetic resources is to recognize the full range of production and management systems present in the United States and to identify germplasm that is optimal for each system. The long-term prognosis for livestock breeds is most positive for breeds that occupy secure, widely recognized positions of importance in the commercial livestock industry. Genetic diversity maintained within a species will thus be correspondingly high when production conditions are diversified and can be correspondingly low if production conditions are highly standardized.

Opportunities for active utilization of a wide range of breeds vary among domestic species within the United States. For pastoral species (cattle, sheep, and goats), opportunity for use and maintenance of diverse genetic types remains high. The diversity of production environments, the great importance of adaptation to the grazing environment, and (in sheep and goats) the production of multiple products (meat, milk, and fiber) provide for and, in many cases, demand the use of multiple genetic types. Interbreed genetic diversity in beef cattle, sheep, and goats in the United States has clearly increased during the past 25 yr (Table 1). The overall impact of recent importations, as judged by the contributions of a number of the breeds shown in Table 1 to the U.S. livestock industry, has been generally positive for all species. In small ruminants, the interest in sheep dairying, cashmere production, and meat goats suggests that this trend will continue. Admittedly, some breeds within these species have declined in popularity, and the uniformity of selection criteria has tended to promote increased uniformity among meat breeds (e.g., Notter and Cundiff, 1991). However, the diversity in origin of these breeds (Table 1), coupled with relatively low selection intensities, large numbers of breeders, and limited use of AI and other advanced reproductive technologies suggest little concern for maintenance of genetic diversity over the next few decades.

At the other extreme, interbreed diversity has declined in poultry and dairy cattle owing, in part, to increased standardization of products and production conditions. These two groups of animals provide useful, but quite distinct, models of future changes that could occur in other species.

Production of broiler and layer chickens and turkeys is dominated by at most 10 multinational breeding companies (Merritt, 1996; Warren, 1996). Commercial birds are primarily two- and four-breed crosses among proprietary lines. In chickens, most lines were developed by widespread sampling and testing of commercial breeds in the 1950s, and degrees of relatedness among these lines in terms of breed

ancestry is high. Each primary breeder maintains an array of lines for use in producing commercial hybrids as well as sets of resource populations that they believe may contribute to future line development. However, breed-level genetic diversity within industrial lines is low relative to that available within the species (Crawford, 1990), and essentially no new sources of genetic variation have been introduced into commercial chicken and turkey stocks during the last 20 yr. Periodic exchange of germplasm among breeding companies occurs on a sporadic basis but is not publicly documented.

Within poultry stocks, very large population sizes are coupled with intense selection. Effective population sizes remain substantial (Warren, 1996), but rates of inbreeding are generally not reported. Subdivision and isolation of stocks, interspersed with

Table 1. A partial list of livestock breeds imported to the United States from 1970 to 1996

Species	Breed	Origin
Cattle	Simmental	Switzerland, France, Germany
	Limousin	France
	Gelbvieh	Germany
	Salers	France
	Pinzgauer	Austria
	Maine-Anjou	France
	Normande	France
	Sahiwal	Australia
	Murray Grey	Australia
	Tarentaise	France
	Nellore	Brazil
	Belgian Blue	Belgium
	Tuli	Botswana
	Boran	Kenya
	Chianina	Italy
	Romagnola	Italy
	Marchigiana	Italy
Piedmontese	Italy	
Wagyu	Japan	
Sheep	Finnish Landrace	Finland
	Romanov	Russia
	Merino	Australia
	Cormo	Australia
	Texel	Netherlands
	Coopworth	New Zealand
	East Friesian	Germany
	Dorper	South Africa
	Charolais	France
	Bleu du Maine	France
Goat	Boer	South Africa
	Kiko	New Zealand
Pig	Large White	United Kingdom
	Landrace	Europe
	Piétrain	Belgium
	Meishan	China
	Fengjing	China
	Min	China
	Gloucester Old Spot	United Kingdom
Large Black	United Kingdom	

occasional sampling and recombination, provide a reasonable structure for prevention of genetic drift and maintenance of allelic diversity at loci that are currently selectively neutral. Production conditions are quite standardized, with birds derived from the same parent stocks often used for commercial production worldwide. Opportunity for selection to meet specific production conditions thus occurs only at the multiplier level. However, market diversity has increased somewhat in recent years, and specific lines have been targeted for use in specific product markets (e.g., variable final weights, brown egg production). These variable markets provide some potential for multiple selection objectives and corresponding maintenance of genetic diversity. However, if alleles that promote fitness in nonindustrial or potential future production systems have negative pleiotropic effects on primary production traits (growth rate, egg production), they are likely to rapidly decrease in frequency throughout the industry.

In dairy cattle, the Holstein breed dominates production in the United States and, increasingly, internationally. Globally, the number of Holstein cows is very large. Wiggans et al. (1995) used dairy herd improvement (**DHI**) records and pedigrees from the American Holstein Association to identify 887,809 U.S. Holsteins (registered and grade) born in 1990. Miglior and Burnside (1995) identified an average of 118,206 Canadian Holstein cows born each year from 1986 through 1990. However, international use of AI and embryo transfer is widespread, and sons of limited numbers of sires and grandsires from previous generations dominate U.S., and, increasingly, global lists of active AI sires (Holstein Assoc. USA, 1996). Reliance on a single population rather than on an array of somewhat distinctive lines increases opportunities for genetic drift, and chance losses of neutral or slightly favorable alleles from the population seem likely. Other U.S. and European dairy breeds provide little buffering against loss of alleles as they continue to decline in popularity. Both in the United States and internationally, Jersey cattle are still important, but the breed is experiencing the same changes in breed structure as is the Holstein breed (Miglior et al., 1992; Wiggans et al., 1995). Efforts by Agriculture Canada to develop a competitive, non-Holstein dairy breed for use in crossbreeding with Holstein may have been marginally successful in terms of net economic merit of  $F_1$  crosses (McAllister et al., 1994) but did not result in establishment of a viable commercial breed. Use of other cattle types to support dairy production may be optimal in some places (McDowell et al., 1996) but seems to be currently impractical in the United States.

Goddard (1991) estimated that if all nations had the same breeding objective (most likely the yield of protein), optimization of net genetic improvement allowing for inbreeding depression within the global

Holstein population would lead to an effective population size ( $N_e$ ) of approximately 80. This number is small relative to the global census number, but at  $N_e = 80$ , the rate of inbreeding [ $\Delta F = 1/(2N_e)$ ] is .625%/generation, or, for a generation interval of 6 yr (Nizamani and Berger, 1996), only about .1%/yr. Over 100 yr, accumulated inbreeding would be less than 10%. Inbreeding coefficients are increasing in U.S. dairy breeds but probably still remain at 5% or less. Wiggans et al. (1995) estimated that the rate of increase in inbreeding was about .2%/yr for all U.S. dairy breeds and found that inbreeding coefficients were increasing at an increasing rate for all breeds. For Holsteins, estimated inbreeding rates in 1990 were .2%/yr, which, for a generation interval of 6 yr, corresponds to 1.2%/generation, or an effective population size of 41. Young and Seykora (1996) reported similar results based on changes in coefficients of relationship among U.S. registered Holsteins from 1970 through 1990. Inbreeding has undesirable effects on milk yield (averaging -20 to -25 kg milk/%) and somatic cell count (Miglior et al., 1995a,b; Wiggans et al., 1995). Several authors have proposed including a restriction of inbreeding in the breeding objective (Quinton et al., 1992; Brisbane and Gibson, 1995), but annual losses in 305-d cumulative milk production of 4 to 5 kg/yr at  $\Delta F = .2\%/yr$  remain trivial compared with current realized annual genetic trends of over 100 kg/yr (Nizamani and Berger, 1996; van Raden et al., 1996).

Today's swine industry is similar in structure to the poultry industry of the early 1960s: regional, national, and multinational companies are involved in development of proprietary lines for use in crossbreeding. Individual breeders and breed associations remain important, but their impact is declining. Breed composition of proprietary lines has not yet been fixed, although the Large White/Yorkshire and various Landrace strains contribute heavily to almost all maternal lines. Within the past 25 yr, the Piétrain breed, from Belgium, and the Meishan, Min, and Fengjing breeds from China, have been evaluated for use in intensive production, and the Gloucester Old Spot and Large Black have been reintroduced, from Britain, for use in outdoor production. However, the eventual contributions of these breeds remain unclear.

Reduced breed diversity in U.S. swine seems inevitable, although the extent cannot be predicted. The industry currently seems to be moving toward a single confinement production system and a single lean pork market. Questions of palatability associated with ongoing reductions in intramuscular fat have been raised (Wood and Cameron, 1994), and producers of some breeds, such as the Berkshire, are pursuing niche markets for high-palatability product (Pettigrew, 1995) based on comparative breed evaluations (NPPC, 1995). However, at this time, all commercial breeds likely still possess adequate

amounts of genetic variation to permit restoration of acceptable levels of intramuscular fat.

### **Opportunities for Maintenance and Use of Genetic Diversity in Long-Term Animal Improvement Programs**

The core goal of long-term farm animal genetic resource management programs should be to maintain access to the full adaptive potential of the species. Actions taken today should not reduce our ability to adjust future genetic levels of production and fitness. A great deal of sometimes conflicting information on genetic management of endangered populations exists (e.g., Bodo, 1992; Maijala, 1992). Most studies focus on the population size and structure required to retard inbreeding rates to an "acceptable" level with attendant maintenance of heterozygosity and adaptive potential, which is usually equated with additive genetic variation. Guidelines have generally been adapted from studies on management of endangered species, and focus is usually on maintenance of genetic diversity within the breed itself rather than on genetic management strategies appropriate to the species as a whole.

Management strategies that emphasize maintenance of heterozygosity are probably less useful than those that directly address the broader objective of retention of the allelic diversity present in the species. Allelic diversity is here defined as the full range of potentially adaptive alleles present in the species. An allele is defined as a unique nucleotide sequence that results in production of an identifiable gene product or is capable of exerting a specific regulatory effect on other such sequences. Denniston (1977) demonstrated that the effective population size required to maintain several alleles at a locus in a single random-mating population is much larger than the number required to keep inbreeding rates within their commonly accepted ranges. Notter and Foote (1986) also demonstrated that maintenance of allelic diversity within a species is more efficiently achieved in subdivided rather than panmictic populations so long as the subpopulations are large enough to withstand accumulated effects of inbreeding or are managed to allow occasional strategic crossing of subpopulations to renew heterozygosity.

The estimated number of breeds of mammalian livestock is about 4,000, roughly comparable to the total number of recognized mammalian species, and of these, about 1,000 are estimated to be at risk (Loftus and Scherf, 1993). Long-term maintenance of 4,000 breeds at a viable population size appropriate to an endangered species will not occur and is not necessary to retain the adaptive potential of the species. However, maintenance of a broad, properly constituted, global sample of breeds within each species is

critical and deserves support. The FAO (1996) lists 783 breeds of cattle in its global data base. Of these, only 45 (5.5%) are from North America. These 45 breeds, even if maintained at very large population sizes, seem unlikely to encompass the full allelic diversity of cattle.

Once we have sampled and evaluated breeds that may be of immediate value in current production systems, the larger question concerns the potential long-term value of allelic diversity within the array of breeds that may not have immediate commercial value. An answer to this question requires knowledge of the distribution of potentially valuable alleles at quantitative trait loci (QTL) within each species. Little objective information on this question exists. Studies of isozyme polymorphisms representing presumably neutral variation in structural alleles generally reveal a few (perhaps 2 to 10) alleles per locus (Oxford and Rollinson, 1983). Polymorphisms at the DNA level (e.g., RFLP and microsatellite polymorphisms) are predictably more variable but again represent presumably neutral variants. These highly polymorphic loci may be useful as genetic markers for linked QTL but provide no direct information on the numbers of alleles at associated QTL. A few loci, such as those of the major histocompatibility complex (Warner et al., 1988), are both adaptive and highly polymorphic, but are not necessarily representative of QTL in general.

Maintenance of allelic diversity within a livestock species in a way that will facilitate future access to potentially useful alleles is challenging. Optimal strategies will likely differ, depending on whether the trait of interest is under polygenic or primarily single-gene control. Creation of composite or "gene pool" populations constructed by intercrossing large numbers of breeds has been suggested as a strategy for maintaining high levels of genetic diversity but should be used with caution. If the number of breeds in the composite is large and if they are highly diverse, long-term maintenance of more than two or three alleles per locus will require very large population sizes (Denniston, 1977; Notter and Foote, 1986). Also, even though access to individual genes of large effect may be reasonably efficient in composite lines, ready access to polygenic complexes will be effectively lost. For example, the prolific Finnish Landrace sheep was used in development of the Polypay breed, a semiprolific four-breed composite (Hulet et al., 1984). Yet, without retention of the original Finnish Landrace, creation of other semiprolific breeds would be much more difficult to accomplish. However, the creation of composite populations using breeds possessing similar production characteristics (e.g., tropically adapted breeds) may be useful for developing new commercial stocks. Notter et al. (1994) thus concluded that composite populations were useful for utilization, but not unnecessarily for preservation, of genetic diversity.

Quantitative trait locus alleles of large effect can exist in low-production populations. In  $F_2$  crosses of domestic tomato (*Lycopersicon esculentum*) with wild Peruvian *L. pennellii*, de Vicente and Tanksley (1993) observed that 36% of the alleles at 74 QTL had effects opposite to the mean effect of wild *L. pennellii*. In crosses of *L. esculentum* with wild *L. pimpinellifolium*, Weller et al. (1988) reported that 14 of 18 traits measured had at least one highly significant marker allele effect of opposite sign to the difference in parental means. In maize, crosses between an elite temperate inbred and a tropical Peruvian race revealed a QTL allele from the tropical race with an effect of 662 kg/ha (8.7% of the check mean) on yield (Furbeck, 1995). At the 30 marker loci screened, at least one allele from the tropical race contributed favorable agronomic characters for nearly every character measured.

In mice, Cheverud et al. (1996) crossed unrelated inbred strains of large and small mice differing by about 8 SD in body weight and screened for QTL in resulting  $F_2$  crosses. Even though most QTL for large size and rapid growth came from the large line, three favorable QTL alleles for early (1 to 3 wk) growth and two other favorable QTL alleles for late (6 to 10 wk) growth originated in the small line. Crosses between an inbred line of laboratory mice (*Mus musculus domesticus*) selected for postweaning weight gain and an inbred line derived from a small wild strain (*M. m. castaneus*) were used to identify QTL for body weight in backcrosses to females of the large line (D. Pomp, personal communication). At 12 and 21 d of age, the majority of favorable QTL alleles detected originated in the wild line, whereas alleles for later growth came almost exclusively from the large line. However, one QTL allele from the wild line had a significant effect on body weight through 9 wk of age. In contrast to results in mice, in  $F_2$  pig families derived from crosses of Large White and wild boar, Andersson et al. (1994) did not observe favorable QTL alleles for growth or leanness from wild boar. Similarly, Milan et al. (1998) identified QTL for growth and backfat thickness on porcine chromosome 7 in  $F_2$  Large White  $\times$  Meishan crosses, but favorable alleles came exclusively from the Large White. However, Moser et al. (1998) described a favorable allele for fatness of Meishan origin on chromosome 7 in Piétrain  $\times$  Meishan crosses.

This so-called transgressive (de Vicente and Tanksley, 1993) or cryptic (Weller et al., 1988) variation in crosses among lines that differ widely in mean performance suggests that useful alleles may be found in low-producing, high-fitness lines. Genetic marker studies using  $F_2$  and backcross families from highly divergent parents can identify transgressive variation and clarify its importance in domestic species. At this time, the hypothesis that low-production breeds may carry QTL with positive effects on commercially important traits cannot be rejected.

Mechanisms that permit maintenance of QTL alleles of large favorable effect in otherwise lowly productive breeds have been identified, and some are under genetic control. Most relate to mechanisms regulating gene expression. As knowledge of gene action at the molecular level has expanded, appreciation of the intricate role of various DNA promoter, enhancer, and suppressor sequences on gene expression has increased. These regulatory mechanisms provide opportunity for suppression of QTL alleles of large effect in low-output, high-fitness breeds, and the establishment of appropriate regulatory complexes may allow animals to adapt to highly restrictive environments. These models are consistent with the integrated genomes postulated to evolve under stabilizing selection in natural populations and with losses in fitness ("outbreeding depression" or "recombination loss") observed in  $F_2$  crosses of natural populations (Wallace and Vetukov, 1955; Thornhill, 1993). Regulatory interactions are anticipated to be expressed as epistatic effects in traditional genetic models. Even though epistatic effects investigated under these models have not been pervasive, Cheverud and Routman (1995) and Mayo and Franklin (1998) argue that such results may be artifacts of the infinitesimal model and not necessarily reflective of epistatic effects at the physiological level.

Regulatory sequences may be *trans* acting, involving interactions among gene products at separate loci, which may reside in either the same or different linkage groups. Such independent regulatory sequences could permit expression of recombination loss or of transgressive variation in  $F_2$  crosses. Alternatively, regulatory sequences may be *cis* acting, working through direct interactions at the DNA level with structural alleles. For *cis* acting regulatory complexes, selection for specific allelic combinations would favor closely linked genes in order to minimize recombination load within the population (Charlesworth and Barton, 1996). Closely linked regulatory complexes would then tend to behave as single genes except in rare cases of recombination (Mackay, 1989).

A case can be made that genetic improvement under directional selection in highly controlled environments primarily represents progressive loss of regulatory control mechanisms. Several major genes for quantitative traits—such as fecundity genes (Fahmy, 1996) and the *callipyge* gene for muscular hypertrophy in sheep (Cockett et al., 1994), the *hg* gene for rapid postweaning gain in mice (Bradford and Famula, 1984), and perhaps even the defective *spider* gene in sheep (Thomas et al., 1988)—may represent a loss of regulatory control. In particular, if a high proportion of these control mechanisms involve *cis* acting interactions among closely linked loci, rates of genetic change may be sustained at modest levels over long periods of gradual recombination between structural and regulatory loci. Recombination among

tightly linked loci can be an important source of additive genetic variation (Hospital and Chevalet, 1996) and can produce patterns of selection response similar to those attributed to effects of new mutations. Charlesworth (1993) concluded that a steadily moving optimum, similar to that present under intense selection in increasingly standardized environments, is most favorable to the evolution of increased recombination. However, in comparing mutation and recombination as sources of genetic variation, it is important to recognize that potential for generation of additive genetic variation through recombination of linked loci can still be lost through genetic drift in populations of small  $N_e$ , whereas mutation can generate new genetic variation even in isogenic lines.

Evidence exists for genetic variation in recombination rates. In *Drosophila*, Brooks (1988) reviewed evidence for intraspecific genetic variation in recombination rates, and Charlesworth and Charlesworth (1985) reported significant changes in recombination rates in response to selection. In most cases, evidence points toward reduced recombination rates in natural populations and  $F_1$  crosses of these populations. This result is consistent with the hypothesis that levels of regulatory control are more stringent in natural populations and that strong directional selection produces progressive loss in regulatory control, including higher recombination rates, in domestic species (Burt and Bell, 1987). In tomatoes, presence in *L. esculentum* of an introgressed DNA segment from wild *L. peruvianum* on chromosome 6 resulted in suppression of recombination rates to as little as one-sixth their value in domestic germplasm, providing a mechanism for conservation of allelic combinations present on the introgressed segment (Liharska et al., 1996). Also, estimates of recombination frequencies in the  $F_1$  and total map length of the pig genome in three published linkage maps declined as the frequency of wild boar genome in the reference families increased (Ollivier, 1995).

The role of new mutants in creation of genetic variation in quantitative traits has been widely discussed (Hill, 1982, 1989), although evidence for mutational effects in livestock is not yet available. Results from laboratory species suggest that the contribution of new mutations to additive genetic variance ( $V_M$ ) may be approximately  $10^{-3} V_E$  per generation, where  $V_E$  is the environmental variance in isogenic lines. Asymptotic rates of response from fixation of new mutations are expected to be  $2N_e i V_M / \sigma_P$  for standardized selection differential  $i$  and phenotypic SD of  $\sigma_P$ , and assuming that mutant gene effects are symmetric about zero (Hill, 1982). For 305-d cumulative milk production in dairy cattle,  $V_E$  is approximately  $1.5 \times 10^6 \text{ kg}^2$ . For  $i = 1.75$  and  $N_e = 100$ , resulting genetic trend/generation would be 429 kg/generation, or approximately 70 kg/yr. However, these results are sensitive to assumptions regarding the

distribution of mutant effects (Hill, 1989). If most new mutations are deleterious, estimates of genetic change will be correspondingly reduced. Note also that the effective population size required to achieve this potential level of response is approximately 2.5 times the current estimate of  $N_e$  from Wiggans et al. (1995). Necessary parameters to estimate effects of new mutations on long-term selection responses are not available for livestock. Likewise, the potential role of transposable elements in the generation of mutation in livestock species remains unknown (Mackay, 1989). However, Ruvinsky and Flood (1998) reported that inherited deactivation and reactivation of the *fused* gene in mice are associated with transpositional events.

Other mechanisms that allow conservation of genetic variation in unexpressed form include various forms of genetic imprinting (Latham et al., 1995), which permit differential expression of maternal vs paternal alleles for some genes, in some cases through methylation of DNA during gametogenesis (Ohlsson et al., 1995; Chadwick and Cardew, 1998). The imprinting process itself also seems to be genetically regulated. Lethality associated with maternal inheritance of the  $T^{hp}$  deletion in wild mice (*M. m. musculus*) was not observed when  $T^{hp}$  was introduced through crossing with carrier female domestic mice (*M. m. domesticus*) (Forejt and Gregorova, 1992).

A novel form of allelic inactivation has been reported for the ovine *callipyge* (muscular hypertrophy) gene (Cockett et al., 1996) and can lead to very high levels of masking of this gene's effect. Expression of *callipyge* seems to require that the allele be present in heterozygous form and be inherited from the sire. Animals that inherit *callipyge* from the dam appear normal regardless of the allele contributed from the sire. In a random-mating population in Hardy-Weinberg equilibrium and with the *callipyge* allele at frequency  $p$ , the frequency of the *callipyge* phenotype would be  $p(1 - p)$ , with maximum value of .25 at  $p = .5$ . At larger or smaller values of  $p$ , the frequency of expression would be reduced, reaching a limit of zero at  $p$  equals zero or one. However, mating of rams homozygous for, but therefore not expressing, *callipyge* to ewes that did not carry the allele would result in expression of *callipyge* in all offspring. *Callipyge* therefore expresses apparent overdominance, but with maximum frequency of expression of .25 instead of .5.

## Recommendations

*Develop Appropriate Organizational Structures and Adequate Funding Levels to Support a National Animal Germplasm System.* The existing U.S. animal germplasm system provides for coordination of germplasm-related activities and for some monitoring and inven-

tory of livestock breeds, but it is not supported at a level that permits active involvement in animal genetic resource management or preservation. This is in contrast to the national plant germplasm system, which maintains extensive collections of plant materials (NRC, 1991). In 1989, research appropriations by the U.S. Agricultural Research Service for plant germplasm activities totaled some \$28.5 million (NRC, 1991). Of this amount, half (\$13.9 million) was directed toward acquisition and preservation of plant germplasm; the remainder was used for evaluation and enhancement of collected materials. Additional support for the plant germplasm system comes from the Cooperative State Research, Education, and Extension Service (perhaps \$1 million in 1989; NRC, 1991) and from state experiment stations. Even though contributions of plant products to national agricultural income clearly exceed those of livestock, a more balanced approach to funding of germplasm-related activities is nonetheless needed. Subsequent recommendations are presented here in the context of an appropriately funded national animal germplasm system.

*Maintain an Aggressive Program of Sampling and Evaluation of Exotic Breeds with Potential for Immediate Use.* Various models for acquisition and distribution of exotic germplasm have been used in the United States, involving either the public sector (e.g., Texel sheep), the private sector (e.g., Boer goat), or both (e.g., Meishan pigs). Regardless of the sector involved in acquisition, public evaluation and comparative characterization of imported germplasm should be a priority to facilitate optimal use. Importations of prolific Finnish Landrace sheep (Dickerson, 1977) provide an example of public/private partnership to evaluate and further develop exotic germplasm.

*Closely Monitor Rates of Genetic Change and Inbreeding in Intensively Managed, Highly Selected Populations and Develop Efficient, Strategic Mechanisms for Conservation of Genetic Diversity.* For Holstein dairy cattle, a workable and efficient procedure would be to sample frozen semen of current sires at intervals of one to two generations (6 to 12 yr), storing perhaps 1,000 doses of semen from a total of 50 sires. These samples would be stored for perhaps four cattle generations (25 yr) to form a "working collection" of 2,000 doses of semen from 100 sires. At the end of 25 yr, a subsample of semen from the 10 sires with the lowest relationships to one another could be transferred to a "resource collection" for long-term storage. The remainder of the working collection could be discarded. Similar collections could be established for other dairy breeds; working collections could be smaller, but resource collections should be of similar size. Monitoring of poultry populations will likely be done within the breeding companies in this highly competitive industry. The existence of multiple lines in several companies reduces overall levels of risk, and

careful monitoring of inbreeding and genetic trends should provide early warning of potential problems within industrial flocks. A similar situation will probably evolve for pigs, but with use of frozen semen as a more likely component of the program.

*Support Global Programs to Determine Genetic Distances Among Livestock Breeds and to Establish "Core Collections" of Diversity Within Each Species.* These core collections would be designed to ensure maintenance of the full range of genetic variation within the species. The structure of these collections could vary widely among species and would likely involve a combination of live animals and frozen semen and embryos under both private and public control. For cattle, sheep, and goats, global acceptance of the importance of synchronizing germplasm to the production/management environment and of the critical role of native breeds in livestock production in developing countries would do much to establish a viable core collection, especially if supplemented with strategic stores of frozen semen and embryos from genetically unique, endangered breeds (Notter et al., 1994).

For poultry, establishment of measures of genetic distance among breeds and industrial stocks will be important for identifying unique genetic types not represented in industrial stocks. Many such stocks may exist, likely in the hands of either hobbyists in developed nations or subsistence producers in developing nations. Once these unique genetic types have been identified, their security can be assessed and monitored, with public action taken as needed. Careful monitoring of unique swine breeds will also be required as industrial production systems and germplasm expand. Sampling and evaluation of extreme types should be a priority.

These core collections should be used to search for unique, useful QTL alleles and to develop strategies for their use. They will also provide a strategic reservoir of genetic diversity for use in new and as yet unforeseen production/management systems and markets. Their establishment will be facilitated by accumulating information on genetic distances among breeds. Systematic global efforts to quantify relationships among breeds using modern molecular techniques (Barker, 1994) should be supported.

*Encourage and Provide Limited Technical Support for Private Initiatives to Maintain Farm Animal Genetic Diversity.* The private sector in developed nations has both the resources and motivation to make important contributions to maintenance of farm animal genetic diversity. Public/private cooperation in maintenance of endangered populations should be encouraged whenever possible. Breed associations play a key role in maintaining breeds in pure form and in promoting and managing breed resources. Opportunities to develop breeders' groups in developing countries are increasingly being pursued. In poultry, various fancier

groups have effectively been given de facto control of remaining nonindustrial breeds and will play an important role in long-term maintenance of diversity. Use of public resources to encourage these efforts and provide limited technical support for activities that facilitate application of appropriate genetic management techniques within these populations should be encouraged.

### Implications

Status and trends in genetic diversity in livestock vary importantly among domestic species. In the United States, breed-level genetic diversity is the most limited for poultry and dairy cattle, is declining in swine, and is still substantial in pastoral species. However, it is not yet possible to draw definitive conclusions regarding the impact of these reductions in diversity on selection responses or future productivity. Evidence from plants indicates that useful genes may exist in lowly productive types and suggests a need for systematic programs of genetic resource conservation, evaluation, and use in livestock comparable to those that already exist for crop plants.

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