INHERITANCE AND IMPORTANCE OF BEHAVIORAL TRAITS IN LIVESTOCK

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As a first approximation, livestock or poultry production can be thought of as a manufacturing process. Inputs (such as feed, labor and housing) are converted into outputs (such as meat, milk or eggs) by a "black box," the herds and flocks that constitute our populations. As geneticists we have long been concerned with the biological and economic properties of our black boxes, the quantities of their input needs and their outputs, their efficiency and their health. Less frequently, though, have we studied or even been particularly cognizant of their behavior. Recently behavior has emerged as an organized discipline with potential both to increase our basic understanding of animal biology and to enhance production efficiency and animal welfare.

One objective of this manuscript is to describe several experiments in which inter- or intrapopulation genetic variation for behavioral traits has been documented. The second is to discuss several studies which suggest applications and directions for research in inheritance of behavior in livestock.

GENETIC DIFFERENCES AMONG POPULATIONS

Many experiments have identified differences in behavior among populations of livestock, with "populations" representing genetic diversity ranging from subspecies to breeds to breed crosses. Traits involving aspects of ingestive, reproductive, maternal, social and temperamental behavior have been examined.

Using microhistological analysis of fecal samples to estimate diet composition, Walker et al. (1981) compared forage preferences of Hereford, Angus x Hereford and Charolais x Hereford cows, all nursing Angus crossbred calves on eastern Colorado rangeland. The groups did not differ in forage preferences and, what is more, they did not differ in an index of diet diversity. Murphey et al. (1981), however, using similar methods did identify apparent differences among genetics groups of cattle in diet composition. In their experiment, Creole cattle (descendants of Bos taurus types introduced to the new world by Spanish explorers), "modern" European cattle and Zebu cattle were represented, so genotypes were more diverse than those examined by Walker et al. (1981). The cattle were located on unimproved desert range in Sonora, Mexico; it is likely this environment was more heterogeneous than in the Colorado study. Thirty-four plant species were identifiable in the fecal samples, and differences among genotypes for relative preference were significant for six of them, two at P<.05 and four at P<.01. Plant species for which significant differences existed accounted for some 34% of total estimated forage intake. The Creole animals resembled European types more nearly, in diet composition, than the Zebu types. The Creole and European groups selected more diverse diets than did the Zebu individuals.

Bennett et al. (1985) studied shade seeking behavior of Brahman, Shorthorn and Brahman x Hereford-Shorthorn cattle in tropical Australia. In a yard affording a choice between sun and shade, breeds did not differ in time spent lying, standing or ruminating; but the Shorthorns spent twice as much time in the shade as the Brahman or crossbred steers. On pasture, steers of all three breeds increased the amount of time spent in the shade as exposure
to solar radiation increased, but the slope of the regression was steepest for Shorthorns and flattest for Brahmans. The Shorthorns spent less time grazing than either Brahmans or crossbreds. Earlier Finch et al. (1984), also in tropical Australia, showed that coat color in cattle (white versus red pigmentation as well as differences among individuals in intensity of red pigmentation) influenced grazing and loafing behavior. White and more lightly pigmented cattle were less inclined to seek shade and were more inclined to graze during periods of heat stress and high solar radiation than were their more darkly pigmented contemporaries. The color genotypes therefore exerted a pleiotropic effect on behavioral traits. Both of these experiments provide interesting clues about factors possibly responsible for genetic differences in adaptation to tropical conditions.

Sharafeldin and Shafie (1965) studied the behavior of indigenous Ossimi ewes in comparison to imported Dutch Texels, Russian Caucasian Merinos and German Fleisch Merinos in subtropical, arid conditions in Egypt. The Ossimi sheep walked more rapidly to and from pasture, with little difference among the remaining groups. In addition, unlike the other groups, they showed little sign of exhaustion or stress. The authors relate anatomical confirmation of the Ossimi ewes (high ratio of body height to body weight, for example) to their superior ability to travel under the hot, arid and dusty conditions. On pasture, the Ossimi ewes grazed a longer time, ruminated less and were more indifferent to solar radiation and heat than were the imported breeds. Also they were observed to be more indiscriminate in grazing preference, "sometimes cropping straw and dry weeds while better plants were within their reach." Texels were observed to be the most selective grazers. The Fleisch Merinos seemed most sensitive to solar radiation.

Dudzinski and Arnold (1979), using automatic and continuous recording devices, studied grazing behavior of Romney, Dorset Horn, Cheviot, Suffolk, Southdown and Border Leicester sheep in Western Australia. The breeds differed in the times at which morning and afternoon grazing periods began and ended. Total grazing times also differed among breeds, with Suffolks longest (8.1 hr) and Cheviots and Southdowns least (5.5 and 5.4 hr respectively). Values for Border Leicesters, Dorset Horns and Romneys were 6.6, 6.0 and 5.8 hr, respectively. The authors used principal component analysis in a creative attempt to explain differences in overall grazing behavior of the breeds as varying reactions to environmental stimuli (such as time of dawn and dusk, temperature and rate of change in temperature). They concluded that differences in diurnal grazing patterns likely reflected differences in physiological responses to the environment. Border Leicesters were most sensitive to changes in the environment (i.e., their grazing behavior changed most dramatically as environmental factors changed); Dorset Horns were least sensitive by this same criterion.

Chenoweth (1981) reported that Brahman, Africander, Hereford, Brahman crossbred, Africander crossbred and Shorthorn x Hereford bulls in Queensland, Australia differed for libido and mating ability. In general, Africander and Africander crossbred bulls were highest, British breeds and crosses were intermediate and Brahmans and Brahman crosses were lowest for the mating behaviors measured. Subsequently, Chenoweth et al. (1984) studied libido in Colorado and Wyoming Angus and Hereford bulls of variable ages. The breeds did not differ in any of the variables measuring sex drive, and breed x age interactions also were not important. Schanbacher and Lunstra (1976) studied
seasonal changes in reproductive behavior of Finnish Landrace and Suffolk rams using indexes that incorporated courtship, mounting and copulation behaviors. Rams of both breeds expressed seasonal variation in libido and successful matings, but the Finn rams were consistently higher than the Suffolks for both traits; and their decline in libido after the normal mating season was later in coming and less marked than was that of the Suffolks. Neely and Robison (1983) studied sexual activity in Duroc, Yorkshire and reciprocal crossbred boars. Yorkshires exceeded Durocs and crossbreds exceeded the purebred average for most of the measures of sexual activity. More crossbred than purebred boars completed a mating during the test situation, and their subjective sexual interest scores were higher. They mounted estrous gilts more often and had a higher proportion of properly oriented mounts. In addition, latency times to initiation and termination of sexual activity were less in crossbred than in straightbred boars.

As part of a larger experiment, discussed elsewhere in this paper, Whateley et al. (1974) studied maternal behavior of hill sheep breeds in New Zealand. Of six breed and crossbred groups, mothering ability was poorest among Romney and Merino ewes and best among Border Leicester x Romney crosses. Romneys also scored poorly for failure to lamb, in inclement weather, in sheltered positions. Border Leicester x Romney ewes were least apt, Merinos most apt to desert their lambs. Cheviots were quick to desert their lamb when approached by a shepherd and dog, but they also were quick to reclaim the lamb when the trespassers moved away. When ewes and lambs were separated temporarily at docking, a higher proportion of Cheviot ewes remained near the lamb pen than for ewes of other breeds, possibly suggesting stronger maternal behavioral instincts.

Obst and Ellis (1977) studied maternal behavior, particularly as it was related to weather and lamb survival, of Merino and Corriedale ewes in South Australia. Increasing wind speed in the absence of rain had little effect on the behavior of either group, nor did rain when winds were low. In the presence of both wind and rain, however, the Merino ewes reacted by orienting themselves away from the wind and forming tight groupings sooner, and under less severe conditions, than the Corriedales. Interestingly a mixed flock of both breeds behaved similarly to the Merino only group. Lamb survival percentage in both breeds was closely related to the joint effects of wind and rain.

Alexander et al. (1983) studied maternal behavior in twin-bearing Merino, Dorset Horn and Border Leicester ewes in New South Wales, Australia, and in twin-bearing New Zealand Romney ewes selected for net lamb producing ability. Several very interesting breed differences were observed. For example, when lambs were handled at tagging, Dorset Horn and Romney ewes were much more likely to remain with or near their lambs, while Merinos and Merino crosses were more likely to retreat a distance in excess of 5 m. However, when lambs were handled at tagging, Dorset Horn and Romney ewes were much more likely to remain with or near their lambs, while Merinos and Merino crosses were more likely to retreat a distance in excess of 5 m. Most of the remaining groups in Australia left the birth site much sooner than the New Zealand Romneys, and many twin-bearing Merinos did not ensure that they were accompanied by both of their lambs. Permanent separations of a ewe from one of her lambs were much higher in Merinos than in any of the remaining groups, and the authors thoroughly and creatively speculate upon possible genetic and environmental reasons for the difference.
Tulloh (1961) studied behavior of Angus, Hereford and Shorthorn steer and heifer calves in Australia by assigning carefully defined but subjective scores to their temperament during handling and to handling ease as the calves were worked through lanes and a headgate. He concluded that Herefords were more difficult to handle, that is, to work through the chute and to secure in the headgate, than calves of the other breeds. Temperament, however, favored both Herefords and Angus over Shorthorns. The author concluded that "Herefords were docile, Angus were restless or nervous and Shorthorns were unpredictable." Credibility of the results is enhanced by the fact that steers and heifers were handled separately, but results from both led to similar conclusions. There was a weak but positive relationship between docility and live weight.

Wagnon et al. (1966) studied social dominance in a mixed herd of like-aged Angus, Hereford and Shorthorn cows. Feeding space purposely was limited to create a situation in which dominance would more likely be expressed. In observations about one year apart, rank order of the 30 cows remained fairly stable. That is, although there were numerous changes in rank, most were minor. The top seven cows, based upon the first year's observations, all were Angus. Statistical tests confirmed dominance of Angus over Shorthorns and of Shorthorns over Herefords for both years. Within breeds, dominance rank and weight were positively related; among breeds, this relationship was negative. Subjective judgments of temperament by the authors were in general accord with the study of Tulloh (1961) in that Herefords were considered most docile and the Angus "most nervous in their relations with man." The Shorthorns were "of mild disposition but ... quite vocal regarding their frustrations." An interesting observation was that in loafing groups of cows, Herefords generally were found on the periphery of the group, with Angus and Shorthorns intermingled within the group.

In related work Stricklin (1983) studied dominance and spacing behavior of maternal-lineage families in a mixed herd of Angus and Herefords. Like Wagnon et al. (1966), he found that Angus cows dominated Herefords (despite being lighter in weight) and that in groups, Angus tended to occupy central positions, Herefords the periphery of the group. For several measures of voluntary spacing behavior, distances from Angus cows to other cows were closer than those from Hereford cows to their neighbors. Earlier Stricklin et al. (1980) had assigned temperament ratings to purebred bulls and crossbred steers and heifers restrained in a squeeze chute. British breed cattle were more docile than "exotics", while of British breeds, Herefords were considered more docile.

One aspect of temperament in cattle is ease of handling, possibly reflected by wariness of cattle to their human handlers. Murphey et al. (1980) measured "approachability" or the distance between a human observer and the cow when the cow first showed avoidance behavior. The work was conducted in Brazil and involved 12 Bos taurus and Bos indicus breeds and their crosses. Both beef and dairy types were represented. Large breed differences were found. The most interesting contrast was that dairy breeds were uniformly more approachable than beef breeds, despite the fact that none of the cows of either type was being milked at the time observations were made. The effect still could result largely if not completely from earlier handling. Fortunately, though, three groups (two generally considered dairy breeds, the Red Sindhi and Gyr, and the other, Guzerat, a beef breed) were
represented by separate groups raised and managed as dairy cattle and beef cattle. In an analysis of those data, cows of the beef breed, whether raised as beef or dairy animals, were more wary of humans than cows of the dairy breeds raised by either method. Whether Bos taurus and Bos indicus cattle differed in approachability could not be answered definitively in their research. The same authors subsequently studied investigatory behavior of cows toward an unfamiliar human subject and to a large beach ball (Murphey et al., 1981). The same breed groups and environment were involved as in the previous study. Investigative behavior of beef vs. dairy types was not distinctly different, as had been the case for avoidance behavior. Red Sindhi cows raised as dairy and beef cattle were very similar in their investigative behavior, as were Gyr cows raised in both ways and Guzerat cows raised both ways, suggesting inherent breed differences. There was a low positive interbreed-group correlation between approachability and investigative behavior.

Torres-Hernandez and Hohenboken (1979) studied emotional behavior of ewes of eight crossbred groups. Variables evaluated as possible indices of emotionality were vocalizations, steps taken, urinations, defecations and foot stamping occurrences in an isolated open-field test of 90 s duration. The same behaviors were then scored for a second 90 s after ewes were exposed to a tethered dog. Subjective scores also were assigned for emotional and investigative behavior. High ambulation during the first 90 s and relative immobility after exposure of the dog seemed to be indicative of more nervous behavior. Foot stamping occurred primarily while a ewe was oriented toward the dog. Vocalizations were much more common during the time that ewes were isolated than during their exposure to the dog. Differences between ewes with Columbia vs. Suffolk maternal parentage were small and not consistent, but the Columbia crossbreds were more prone to foot stamping behavior during the second 90 s. Romney crossbred ewes had higher values for ambulation, vocalization and emotional and investigative behavior scores, while ewes from Finnsheep rams were above average for eliminative behavior and vocalizations. (Interestingly, Shillito and Alexander (1975) noted that Finnsheep ewes were more vocal than Soays, Jacobs or Clun Forests in a test situation in which ewes and lambs had been separated, then united.) Dorset and (contrary to expectations) North Country Cheviot crossbred ewes were average or below for most of the traits indicative of emotional behavior.

Willham et al. (1963, 1964) studied learning ability in 3-week-old Hampshire and Duroc pigs. The test situation involved responses, over the course of ten trials, to a signal warning of an impending electrical shock. In four different experiments, Durocs (throughout the ten trials) consistently had higher proportions of correct responses than Hampshires, though by the later trials, differences were not large. In other words, Durocs learned more quickly, but Hampshires eventually tended to catch up. In extinction trials, the breeds did not differ in the rate at which they abandoned avoidance behavior after the warning stimulus was no longer followed by the shock. The authors commented that herdsmen rated Durocs as "more docile and less emotional than Hampshires" and speculated upon the possible effect of such differences upon the differences in learning ability that were identified.
GENETIC DIFFERENCES WITHIN POPULATIONS

Fewer experiments have documented the existence of intrapopulation than of interpopulation genetic variation in livestock behavior. Nevertheless, a number of papers have reported strain differences, correlated responses to single trait selection, differences among sets of identical twins, heritability and single gene effects on various behavioral traits.

Grazing behavior of six sets of monozygous twin dairy cows on eight days (spanning one year) was examined by Hancock (1950). Variation between sets was very large and variation within twin sets practically nonexistent for time per 24 h spent grazing. Twin sets had been selected to represent widely different levels of milk production and probably energy requirement, but evidence was presented that twin sets varied much more in grazing time than could be explained by apparent need for nutrients. Evidence also was presented to dispel mimicry between twins in a set as a major cause of similarity in grazing behavior. Twins sets also were similar in daily loaing time, lying down time, distance walked, number of drinking episodes and number of defecations, though the concordances were not as great as for grazing time. From detailed observations on only two sets of twins, there was little variation between sets in grazing rate (bites per minute). Sets did differ in behavioral characteristics of rumination (number of boluses regurgitated, number of bites per bolus, number of periods for rumination and duration of a rumination period). Hancock's work suggests a strong genetic component to ingestive behavior in cattle, but effects of common rearing and environment of the twin sets cannot totally be discounted.

Williams and Miller (1965) studied voluntary feed intake of Merino rams from lines selected for increased or decreased wool production or at random (the control line). Clean wool weights of the three lines were in a ratio of 118:100:68 for high, control and low, but for body weights the ratio was 103:100:103. The genetic groups were not a significant source of variation for feed intake, but there was a tendency for greater total consumption in less time causing a higher rate of consumption for the increased wool line compared to the control and for the control compared to the decreased wool line.

Bane (1954) studied behavior of six pairs of monozygous twin bulls as they were subjected to semen collection procedures. For a variety of observations, "twin brothers were, on the average, extraordinarily alike in mating behavior" while "differences between twin pairs were great." Both members of a twin pair also often showed similar fluctuations and long-term changes in mating behavior with time. Posture during mating and latency times also were quite characteristic within a pair but quite different among pairs. The effects of prenatal maternal effects and(or) of common environment and handling early in life cannot, of course, be excluded from studies of monozygotic twins. Nevertheless, there is a strong suggestion from Bane's work of an important genetic influence on mating behavior and on temperament as well.

Blockey et al. (1978) computed the heritability of serving capacity from 157 paternal half sib bull groups on 24 farms in Australia. A total of 438 Hereford and 331 Angus bulls, ranging from 16 to 22 months of age, were involved. Whether body weight was included as a covariate or not, the
estimate of heritability was .59 ± .16. Serving capacity was not correlated with scrotal circumference or temperament rating. Hereford herds had higher mean values for serving capacity than Angus herds, 6.28 vs. 3.98. Blockey (1978) also has reported a close correspondence between monozygous twin bulls for serving capacity, with large variation among twin sets.

Tulley and Burfening (1983) studied mating behavior and scrotal circumference of Rambouillet rams throughout the year under ambient environmental conditions. The rams were from a randomly selected control line and lines selected for increased and decreased prolificacy. Line and season effects generally were important, but the line x season interaction was never significant. High prolificacy line rams had more mounts and services and lower latency times to first mount than control line rams, while the low prolificacy line rams were lower than controls for mounts and services, longer than controls for latency time. The high prolificacy line rams had the smallest scrotal circumference, while low prolificacy line rams were highest for this trait.

Sato (1981) studied heritability of temperament in Japanese Black and Japanese Shorthorn cattle. From paternal half sibs, the estimate was .45, and from dam-daughter pairs, it was .67, suggesting the possible existence of maternal effects on temperament of offspring. Shrode and Hammack (1971) also analyzed subjective temperament scores, in their case of bulls and heifers restrained in squeeze chutes. Breeds did not differ in temperament assessed by the scores; and within Herefords, paternal half sib groups did not differ significantly. Differences among sire groups in Angus, though, suggested a heritability of .40 ± .30 for the trait. Stricklin et al. (1980) studied temperament of beef cattle by assigning subjective scores to resistance to handling in a squeeze chute. Heritability estimated from paternal half sib correlations equalled .48 ± .29 from scores of purebred bulls and .44 ± .18 from crossbred calves. The authors did not recommend selection for improved temperament, advocating instead correct handling and provision of appropriate early-life experiences of young calves to improve handling ease. They did, however, suggest culling of unmanageable cattle. In a Wisconsin study (Dickson et al., 1970), theheritabilities of both temperament during milking and social dominance score were computed. Heritability of temperament (.53) was similar to the values from Shrode and Hammack (1971), Stricklin et al. (1980) and Sato (1981), despite different classes of cattle (dairy and beef), different scoring systems and different experimental settings in the trials. Social dominance in the Wisconsin study had an estimated heritability near zero.

There is little evidence in the literature of effects of major genes on behavioral traits of livestock, probably because of the relative paucity of experiments involving major genes. Holmes et al. (1972), however, have reported that cattle homozygous for "double muscling" or muscular hypertrophy are more temperamental than heterozygotes which, in turn, are more temperamental than homozygous normal individuals. Their conclusions are based upon small numbers, but they cite "experience gained by working with a large number of double muscled cattle over a number of years." The homozygous double muscled animals were said to be more fearful than aggressive. They were described as excitable and incapable of adopting reasonable evasive actions. Despite very frequent handling, many never adapted to human handling.
Willham et al. (1963) tested nearly 600 3-week-old Hampshire and Duroc pigs from 143 litters for avoidance learning behavior. Percentage of correct responses to a warning preceding an electrical shock on the third of ten trials was the criterion of learning, because the third trial was the one for which the percentage averaged near 50, leading to maximum variance and maximum opportunity accurately to partition the variance. From the full sib analysis of variance, the dam within sire component was slightly larger than the sire component of variance, suggesting that maternal effects, common litter environment and non-additive genetic variance were not important influences on learning. Heritability, estimated from sire and dam components, was .45 ± .12. Willham et al. (1964) subsequently reported a heritability estimate of .52 for avoidance learning in pigs, based upon further trials with similar experimental subjects, where the main experimental emphasis was identification of breed differences. That work was discussed elsewhere in this report.

EXPERIMENTS SUGGESTING FUTURE APPLICATIONS AND RESEARCH DIRECTIONS

Many crossbreeding experiments are conducted by mating sires of a variety of breeds to dams from a more limited number of breeds. Dam breeds often are chosen for adaptability to local conditions and/or for commercial availability. Germ plasm evaluation work at the U.S. Meat Animal Research Center, for example, involved crossing sires from a variety of British, continental European, dairy, dual-purpose and Bos indicus breeds to Angus and Hereford females (Smith et al., 1976). Langlands (1973), Carter and Kirton (1975) and Wolf et al. (1980) report experiments in sheep in which a number of "exotic" sire breeds were crossed to locally adapted and available ewe breeds. Seldom considered in these experiments is the extent to which differences among F1 crossbred groups might be masked by the maternal behavior of the breed or breeds of females to whom the male breeds to be evaluated were mated. Early life and even adult behavior and performance of the crossbred offspring could be influenced by maternal behavioral effects. The offspring might learn habits from their dams that influence their subsequent productivity. Such effects could be a source of error or bias in breed evaluation experiments. They might also, however, be beneficial to breed introduction or substitution efforts, as speculated by Berggren-Thomas and Hohenboken (1985). They proposed that crossbred offspring possibly could benefit from the exotic genes of their sires while simultaneously benefiting from accumulated "cultural wisdom" (grazing site preferences, means to cope with environmental stress, predator avoidance strategies, for example) learned from their indigenous dams.

Admittedly such effects are speculative. Berggren-Thomas and Hohenboken were led to such musings by their experiment in which differences among F1 crossbred groups (all with common maternal breed parentage) for grazing behavior were less than experiments from the literature involving straightbreds had led them to expect. Asiedu (1978) also found little difference in grazing behavior among West African Dwarf sheep and two crossbred groups of 50% West African Dwarf parentage. It is most likely that his crossbreds were produced (and trained?) by West African Dwarf dams. Perhaps common maternal parentage contributed to the lack of variation in grazing behavior among the genetic groups in that experiment.

Key and Maciver (1980) creatively demonstrated that behavior of the offspring can, in fact, be learned from the dam. They crossfostered lambs
between two genetically diverse sheep breeds, the Welsh Mountain, which evolved under harsh hill land conditions, and the Clun Forest, developed under milder environmental conditions. The two breeds differ markedly in size, wool type and fecundity, and different types of maintenance behavior would certainly have been favored during the past history of each breed. In the experiment, rams were mated only to ewes of their own breed. At lambing, some lambs stayed with ewes of their own breed, others were reciprocally cross-fostered. Lambs of both breeds reared by Clun Forest ewes tended to aggregate together more closely than lambs of both breeds reared by Welsh Mountain ewes. In addition, there was a strong tendency for Clun Forest reared lambs of both breeds to prefer improved areas within a heterogeneous pasture. The Welsh Mountain reared lambs of both breeds preferred unimproved areas within the same pasture. The authors concluded that "sheep are not born with innate behavioral patterns determining their grazing habits, but rather ... the latter are acquired by copying the habits of their natural or foster mother." My conservative inclination would be to modify their conclusion to "sheep are not born with innate behavioral patterns determining all of their grazing habits, but rather ... at least some of the latter are acquired by copying the habits of their natural or foster mother." They have provided a well done and relevant study, establishing the existence of maternal behavioral effects and suggesting topics for future research.

Hunter and Milner (1963) reported that in a long established flock of South Country Cheviot sheep, maternal families (dam and daughters) occupied similar home ranges within the large pasture area available. Since plant communities varied within the pasture, diets of dams and daughters likely were more similar than those of non-related individuals. They concluded that heritability estimates from dam-daughter regressions, for traits influenced by nutrition and(or) the physical micro-environment, could be inflated by the common environmental component.

Often, an unstated assumption of experiments in animal genetics or production is that each animal exists in a biological vacuum. That is, we ignore the possibility that the behavior and(or) performance of some animals in the experiment could be influenced by their herd mates. In breed or crossbred group evaluations, groups very frequently are maintained together. This has the desired effect of ensuring that all groups are subjected to the same physical and management environment, in so far as that is possible to accomplish. It simultaneously creates, however, the opportunity for groups to have different psychological and(or) emotional environments. Consider the results of Wagnon et al. (1966) and Stricklin (1983), for example, that Angus cows dominate Herefords. Herefords intermingled with Angus may not respond the same as Herefords in a breed homogeneous group. Also, as described earlier, Obst and Ellis (1977) reported that in a mixed flock, Corriedales displayed similar behavior to Merinos (in response to inclement weather conditions), whereas in single breed flocks, behavior of the two breeds was distinct. Oldenbroek and Jansen (1979) compared the grazing behavior, milk yield and body weights of cows of three breeds (Holstein Friesian, Dutch Red and White and Dutch Friesian), each maintained as a single breed group, with the same variables from cows of each breed maintained in two-breed mixed groups. The grazing behavior of a group of cows of one breed was, in fact, influenced by the cows of the breed with whom they grazed, but such effects were rather small and not consistent. In their experiment, differences among breeds in average social rank were small. Had there been a clear linear
dominance hierarchy among breeds, behavioral effects of one breed on another might have been larger. The only way to determine whether behavior and/or performance of individuals of one genetic group is influenced importantly by the presence of individuals of other genetic groups is to conduct the appropriate experiments; more of them probably should be done in our research programs.

Labor cost, partly determined by ease of handling, is an important aspect of production efficiency. Little attention has been devoted to it in animal production research, even less to variation in the ease with which various management practices can be accomplished on different genetic groups. Whateley et al. (1974) reported on the behavior of sheep of different hill breeds during various farming routines. Included were behavior at lambing, docking (both discussed elsewhere in this paper), weaning, yarding, shearing and mating. In addition, shepherds with several years' experience with the various breeds were asked subjectively to rate them for ease of handling during management routines. When groups of ewes of each breed were run through a complex yarding exercise, breed differences emerged. Cheviots and Merinos were fastest, Romneys slowest to work, with all Romney crossbred groups also tending to be slow. The objective findings were generally similar to the subjective evaluations of the shepherds. There was little difference among breeds in the time required to catch ewes for shearing. Shearing of Merinos and Corriedales required the longest time, with little difference among the remaining groups. Cheviots were unpopular with shearers because of their propensity to struggle and kick. Additional studies of this sort, in all species of livestock, are warranted. Not only might breeds and breed crosses with particular adaptability for a given environmental and management system be identified. In addition, desirable behavioral characteristics to be enhanced by selection, management or manipulation of early life experiences might be found.

Czako and Santha (1978) also examined behavioral adaptations of different breeds of dairy cattle to farming routines. They introduced the concept of "technological tolerance," commenting that livestock in modern, mechanized, intensive farming systems face changes in their physical and social environment possibly more dramatic than those faced by their distant ancestors at the time of animal domestication. At any rate, changes in livestock environments are occurring at a very rapid rate, especially in terms of the ability of populations genetically to adapt to them. Czako and Santha, in a series of experiments, compared Holstein-Friesian to Hungarian breeds of cattle for behavior during milking, for behavior during work done in the loafing sheds, for reactions to an unfamiliar human, for accommodation to a changed environment, for inter-animal distance maintained by the cows and for ability of a cow easily to locate her own tie stall. Breeds differed for some of the behaviors, but the authors concluded that no one breed was clearly superior for "technological tolerance." Individual cow variation within breeds was much greater than variation among breeds, even when the latter was significant.

A number of experiments (reviewed earlier in this paper) utilized the behavior of monozygous twin cattle to infer the importance of genetic effects on behavior. In such experiments, it is not possible clearly to partition additive from non-additive genetic variation. More importantly, it also is difficult if not impossible to partition genetic variation from that
attributable to prenatal maternal effects, contemporaneity and(or) common postnatal environment. Recently it has become possible, through embryo microsurgery, to create monozygous twins, or even higher multiples in cattle and sheep (Willadsen, 1979; Ozil et al., 1982; Williams et al., 1982). Transferring monozygous embryos into different recipient females creates a powerful tool to interrupt the confounding between nature and nurture in naturally occurring monozygous twins. Total hereditary effects on all manner of behavioral characteristics could be studied very effectively using the animals created by embryo microsurgery.

CONCLUSIONS

It is my belief that future experimentation in the inheritance of farm animal behavior should:

1. Document breed and crossbred group differences in behavior only when attempts are made to relate the behavioral differences found to the ecological and evolutionary history of the breeds and(or) to relate differences found to adaptability of the genetic groups to physical and management production environments of interest.

2. Place greater emphasis on heritability of behavioral traits and their phenotypic and genetic correlations with traits contributing to bioeconomic efficiency.

3. Examine correlated responses in behavioral traits to selection practiced upon other characteristics, utilizing lines from selection experiments already in progress.

Important questions for future research are not so much "Do hereditary differences exist?" but rather "Why do they exist?" and "How can such differences best be manipulated to enhance human and animal welfare?"
LITERATURE CITED


Dr. R. N. Shoffner: Could the mothering ability of Romney ewes be partly due to selection, because they had previously lambed twins and had the opportunity to learn to handle twins?

Answer: In the Alexander et al. experiment, the Romney ewes that exhibited the ability to accept, recognize and rear twin lambs mostly were descendents of ewes that originally were selected, from a very large population, for lamb production ability. Thus selection had been exerted for ability not only to bear but also to rear twins. Some of the ewes in their experiment were first lambers, but some surely had past experience rearing twins. Maternal behavior of the ewes could very well have resulted from a combination of learned and inherited effects.

Dr. W. E. Rempel: Dr. Michael Fox has used a term which he calls "telos." This refers to a pig's pigginess, a sheep's sheepiness, etc. In terms of your technological adaptation, animals would lose some of their telos. What are your views on this?

Answer: Czako and Santha (1978) call "technological tolerance" the ability of an animal or breed to adapt to modern, often industrialized, management systems. By adapt, they mean (and this is my interpretation of their work) to produce satisfactorily and not to exhibit aberrant behaviors. The aberrant behaviors they envision generally would be detrimental to production efficiency and often would be detrimental to animal welfare as well. If conscious or inadvertant selection were to eliminate from populations such aberrant behavior, I think this particular loss of pigginess, sheepiness, etc. would be justified and desirable. I expect that a considerable amount of such selection already has occurred, during the course of animal domestication and breed formation.

Dr. Rodger Johnson: In the Dutch experiment (Oldenbroek and Jansen, 1979), were the differences among breed groups for grazing time significant? They appear to be large. If significant, is there an explanation for the relatively small differences among breeds in milk yield?

Answer: The differences, some of them at least, were significant. Other workers have reported a low correlation between grazing time and feed intake. A faster grazing group would consume the same amount of forage in less time than a slower grazing group. Neither grazing rate nor total intake were measured in their experiment, so this could be the explanation.