SELECTION AND HOMEOSTASIS

E. A. Dunnington
Virginia Polytechnic Institute and State University
Poultry Science Department, Blacksburg, Virginia, USA 24061

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SUMMARY

Artificial selection for traits of economic importance in poultry has resulted in considerable genetic change. As in all animal systems, however, the force of natural selection balances the changes produced by artificial selection. This balancing is a direct function of allocation of resources available to an individual at any particular time, divided among maintenance, growth, reproduction, disease resistance and other demands. Success or failure of artificial selection generally depends on the criterion of selection and its rate of change. In some cases, human intervention or the ability of the animal to adapt to changes have allowed successful progress. In other instances, limits to selection have been reached, beyond which genetic response cannot be obtained. Recent developments of molecular techniques that may enhance artificial selection and speed genetic change suggest that much greater progress might be possible in altering poultry to suit the needs and desires of humankind. Past progress and problems concerning the balance of natural and artificial selection, however, must be considered seriously in evaluating the methods and rates of change possible with new techniques.

HOMEOSTASIS

Homeostasis is "the tendency of the physiological system of higher animals to maintain an environment of organic stability even when its natural function or condition has been disrupted" (Webster's dictionary, 1973). This phenomenon undoubtedly has contributed to the success of higher life forms on earth. The concept of genetic homeostasis has been described in various works throughout the development of natural history. Darwin (1859) described the concept of balance in nature - balance both among species and among members within a species. His descriptions of populations under the pressures of natural selection resulting in survival of the fittest individuals and, consequently, the fittest populations, have become a cornerstone of biological thinking. Darwin (1896) also recognized the tendency of mankind to select, either consciously or unconsciously, those individual in domestic populations with favorable attributes, thus altering the generation at hand, and the generations to come, by chosing particular individuals to perpetuate a species.

ARTIFICIAL SELECTION

The situation in which most of us find ourselves today, is not in dealing with animals in wild or natural settings, but, as the title of this conference suggests, in dealing with animals developed for livestock production. Thus, we are concerned with a very strong and effective force in the shaping of animal populations, that of artificial selection. From vantagepoints of both convenience and economic gain, altering and shaping future generations of livestock would be considerably more rapid and less complicated if we could limit the forces that effect our species of livestock to only artificial selection. This is not the case, however. No matter what constraints and protections we place upon the animals in our charge, no matter how well we feed them, maintain them and protect them from environmental insults such as disease organisms, climatic fluctuations, and aggressive encounters with others of their species, we cannot eliminate the omnipotent forces of natural selection which demand absolutely that certain biological balances and relationships remain intact. Our quest to bring about changes in form or function of domestic animals can be successful to a certain extent but, depending on the selection criterion and rate of change, an eventual limit may be reached. Those changes that we consider improvements for a quantitative trait may be delayed or stopped completely by the forces of natural selection.

A very clear and instructive discussion of this balance between natural and artificial selection is found in Genetic Homeostasis, by I. Michael Lerner (1954). The methods by which homeostasis is maintained, such as heterozygote advantage, stabilizing selection and negative genetic correlations between certain traits are explained. Lerner differentiates between homeostasis on an individual level and on a population level with the following definitions:

> Developmental homeostasis or ontogenetic self-regulation is based on the greater ability of the heterozygote to stay within the norms of canalized development.
>
> Genetic homeostasis or self-regulation of populations is based on natural selection favoring intermediate rather than extreme phenotypes.

For purposes of this discussion, we will consider both of these types of homeostasis, because they are so closely intertwined. In fact, self-regulation of populations can be considered the result of self-regulation of individuals. Therefore, let us deal with both concepts, one considered a logical extension of the other.

RESOURCE ALLOCATION

A phrase pertinent to this discussion is "resource allocation", which should convey the following meaning. Each individual has a finite package of resources available to it at any particular time, consisting of the food it has ingested, the body stores of fat and protein it has assimilated in the past, and its physiological state. As that individual is challenged by everyday activities and stresses, it must allocate these available resources to various demands, such as maintenance, growth, action, reproduction and responses to pathogens, parasites and stress. With natural selection, the selection criterion is fitness, which encourages two phenomena: (1) an intermediate optimum for many traits such as body weight and growth rate, and (2) maintenance of heterozygosity which imparts buffering capacity to a wide range of environmental conditions. If natural selection is successful, then the individual should be ready at any time to divide its resources among growth, maintenance and reproduction, with a margin left over for unexpected stresses and challenges.

If, however, an individual is the product of artificial selection for a particular trait of importance to its human handlers, a very different situation arises. Depending on the genetic and physiological makeup of the individual, it may be genetically programmed to allocate a large portion of its resources to a particular one of these demands, leaving it lacking in ability to respond to other demands. Often this situation is manifested by a negative correlation which results from the expression of one trait leaving limited resources available for expression of another trait (Rendel, 1963). The outcome of potential problems faced by an individual under such an artificial selection program can be classified as: (1) changes that are successful due to human intervention, (2) changes that are successful due to adaptability of the animal, (3) reaching selection limits. The body of this presentation will be devoted to these three situations. It should be remembered that, in many cases, the level of success achieved will depend on the traits being changed and the rate at which those changes occur.

CHANGES THAT ARE SUCCESSFUL DUE TO HUMAN INTERVENTION

A vivid cases of opposition between artificial and natural selection is the situation encountered with male turkeys. Long-term selection for increased breast muscle has produced males that are not physically capable of natural mating, because of correlated changes in body form. Intervention by handlers through artificial insemination has allowed this situation to be successfully handled, but has certainly changed the husbandry and management procedures necessary for production of these birds.

Artificial selection for high levels of egg production, particularly in White Leghorn stocks, has resulted in hens that do not have the instinct or inclination to incubate eggs. When considered in the context of a natural environment, the production of eggs and their successful incubation are critical to survival of a species. Artificial selection in egg-type chickens has placed intense selection on the production of eggs, and subsequently selection against broodiness. Of course, this is the preferred state in terms of domestic populations, and human intervention for artificial incubation and hatching of eggs has insured survival of the stocks.

Those familiar with the production of broiler chickens are aware of correlated changes that have occurred with selection for a high rate of growth. Over the last 50 years, the number of days necessary to reach market weight has been reduced one day per year (Cahaner and Siegel, 1986). This considerable genetic progress in growth rate has been due to several factors, some of which are: intense selection for increased body weight, maintenance of large populations, routine introduction of new genetic material, mutations, and improvements in husbandry, disease control and nutrition. Along with the progress that has been achieved, however, have been many problems in reproductive capabilities of broiler breeders. The propensities for voracious appetite and rapid growth have produced chickens that have erratic ovulation and defective egg syndrome (e.g., Jaap and Muir, 1968; van Middelkoop and Siegel, 1976). As the severity of reproductive complications increased with increasing growth rate, non-genetic means were employed to alleviate the problem. While genetic selection is applied for increased body weight, broiler breeders are subjected to feed restriction programs that greatly reduce body weight and reproductive problems. The offspring of these broiler breeders inherit growth potential from their parents and are fed ad libitum so that they grow at their maximum genetic potential. This procedure of developing stocks with the genetic ability to grow rapidly while reducing growth rate of their parents by non-genetic means to allow successful reproduction has been a logical and successful approach to bypassing the limiting forces of natural selection which prevents reproduction in extremely heavy parents. New management techniques are continually being implemented for improving reproduction by parents. Separate feeders for males and females in breeder flocks have been used to help maximize fertility even in the heaviest stocks.

Another correlated response to selection for increased growth rate in chickens is reduced immunoresponsiveness (e.g., Siegel and Gross, 1980; van der Zijpp et al., 1987; Martin et al., 1988; Donker, 1989). The negative correlation between body weight and antibody response may be due to limited resources and preferential allocation. White Rocks selected for high (HW) and low (LW) 8-week body weight and White Leghorns selected for high (HA) and low (LA) antibody response to sheep erythrocytes were compared for antibody response (Martin et al., 1988). Selection for high body weight resulted in general response to a foreign antigen of the same low magnitude as genetic selection for reduced antibody response. Chickens from the low-weight selected population have significantly higher antibody responses than those in the high-weight population.

Commercial broilers also have extremely low levels of antibody response to sheep erythrocytes (e.g., Dunnington et al., 1987), as a great proportion of their resources are allocated to rapid growth (Katanbaf et al., 1989a,b). This trade-off of immunity for growth rate can be successful if excellent husbandry conditions prevail, but the potential for a disasterous situation exists when chickens do not have the ability to respond to foreign antibodies. In an experimental situation, chickens from a commercial broiler parent stock were raised on one of three feeding regimes and then inoculated with E. coli (Katanbaf et al., 1988). Mortalities of inoculated chicks at 72 h after inoculation at 47 days of age were: 20% for the ad libitum fed group, 7% for chicks fed a recommended restricted diet and 50% for the group that had been restricted and were then released to ad libitum feed. The broilers given ad libitum access to feed after restriction exhibited accelerated growth to fulfill their genetic potential to grow rapidly, but did not have additional resources to withstand the bacterial infection. This example is another situation where genetic selection has produced chickens with desirable characteristics, but that must be protected by human intervention to withstand environmental challenges.

CHANGES THAT ARE SUCCESSFUL DUE TO ADAPTABILITY OF THE ANIMAL

Methods of selection discussed thus far have caused changes in poultry which are considered by their human handlers to be an improvement. These changes have been achieved successfully because of attention to the correlated responses accompanying selection and the proper circumvention of those correlated responses through non-genetic techniques. Successful alteration of such animals and their ability to survive in spite of radical changes in their body form or production ability may also occur as a result of the animals' ability to adapt to and accomodate change. Evidence of that ability is supplied by experiments where selection is conducted for a period of time and then relaxed. Selection for high and low 8-week body weight was accompanied by relaxation of selection in randomly chosen subgroups in generations 6, 13 and 19 (Dunnington and Siegel, 1985). Each round of relaxed lines was continued for 7 or 8 generations. Body weight of the relaxed populations did not regress towards the original mean for the first or second rounds of relaxation. Only in the third round of relaxation, from generations 19 to 27, did regression towards the mean for 8-week body weight occur. This result indicates that opposition between artificial and natural selection was not severe or, more likely, that natural selection was constantly involved so that opposition between the two types of selection was never very intense.

When comparing the four populations in generation 26, after 7 generations of relaxation for the relaxed groups, there were several traits which were unchanged in all populations with ad libitum feeding, even though body weights had changed significantly (Dunnington et al., 1986). These traits were cloacal temperature and weights of liver, abdominal fat pad and carcass lipid expressed as proportions of body weight. Thus, throughout the process of artificial selection for high or low body weight, genetic homeostasis maintained proportionate sizes of particular organs. Opposition between artificial and natural selection for these traits was a constant force throughout the experiment.

REACHING SELECTION LIMITS

Success or failure of a selection program depends heavily on intensity of selection, effective population size (Robertson, 1960) and subsequent rate of change in the selection criterion and correlated responses. If changes are too radical or are sought too rapidly, the biological balance of the selected organism is lost and a limit is reached, beyond which the organism will no longer respond. Such a limit may arise as a consequence of loss of some alleles and fixation of others, which may be the objective of the artificial selection, but unacceptable in terms of fitness (Robertson, 1960). Several such limits have been documented and will be discussed here.

Selection for decreased body weight in chickens has resulted in a population which is anorexic, to the point that a proportion of the pullets each generation will not achieve sexual maturity with *ad libitum* feeding (Zelenka et al., 1988). In order to reproduce the line, selection must actually be reversed in some generations, because the very smallest pullets are the ones that do not mature and cannot reproduce. The limit in terms of the selection criterion is approximately 168 g body weight at 8 weeks of age. The mean body weight for the whole population of low-weight pullets has been reduced to that level several times, but has never gone below it. In this situation, natural selection has prevented further genetic selection by halting the capacity for reproduction. To the present time, several experimental procedures have been attempted to break the selection limit, but none has been successful.

Selection for increased growth in broilers as discussed above has been successful, in part, because of human intervention with non-genetic means. The problem ameliorated in that situation was reproductive dysfunction in broiler breeders. Two other correlated responses to rapid growth, which may be more difficult to overcome, are sudden death syndrome (SDS) and ascites. Within a flock of broilers under *ad libitum* feeding, it is generally the heaviest, fastest growing chickens that are afflicted with SDS. Because these problems affect the most rapidly growing individuals, and occur just before marketing age, the economic losses due to its occurrence are great. Recent research has indicated that symptoms may include cardiac arythmia, ventricular fibrillation and respiratory distress, and that the disease may actually result from high carbohydrate intake and subsequent rapid growth rate (Julian, 1989). Similarly, ascites or water belly affects fast-growing broiler stocks and is manifested in increased pulmonary arterial pressure, resulting in excessive strain on the heart muscle and eventual leakage of fluid from the liver which accumulates in the abdomen (Julian, 1989). Both of these conditions have been recognized for years, but are increasing in incidence. The influence of natural selection against the extreme phenotype of large body size at an early age demonstrates intense opposition between natural and artificial selection. At the present time, these two conditions may represent a limit to genetic progress, as any increase in growth rate of broilers will probably exacerbate the problems. The challenge to the the poultry industry at present is to find genetic or non-genetic means to alleviate these two problems, so that genetic progress for increased growth rate may continue.

THE FUTURE

This discussion has dealt with a history of artificial selection in the poultry industry and in experimental situations. It has touched upon various traits that are of economic importance and that have been changed, to either a small or large extent, by genetic selection. Success or failure has depended on the selection criterion and the rate at which progress is achieved. Successful changes have been attributable to intervention by human handlers, generally by modifications in husbandry procedures, or to buffering capacity of the animals themselves. Opposition of artificial and natural selection has, in other cases, caused a cessation of response to selection which cannot be circumvented by human intervention or by adaptability of the animals, resulting in limits to selection progress.

In assessing the future of poultry genetics and breeding, there is great anticipation. New molecular techniques are being introduced and refined rapidly; the expectation is that they will be useful in assessing genetic makeup of individuals and in introgressing desirable genes into available populations. These techniques are expected to streamline artificial selection, greatly increasing responses to selection and allowing us to mold animals into the forms that we desire in a more rapid and efficient manner than possible with traditional methods. The examples described in this paper, however, provide a warning for those of us attempting to employ these techniques. We must constantly remind ourselves of the following:

> Historically it has been necessary to make changes slowly, giving the whole animal time to equilibrate to both direct and correlated responses, for fitness to be maintained.
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> Genes introduced in one generation that cause production of a new gene product or alter some characteristic may disrupt resource allocation that has evolved gradually, at the expense of reproduction and other forms of fitness.
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> With a radical change in one generation, as with introgression, human handlers may not have time to recognize correlated responses and devise methods of intervention to ameliorate accompanying problems.

The success of new techniques in improving genetic progress of poultry populations will depend heavily on the ability of molecular and quantitative geneticists to anticipate and compensate for deleterious correlated responses to selection.

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