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THE NECESSARY PARADIGM CHANGE IN QUANTITATIVE GENETICS

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SUMMARY

The availability of environmental resources limits the development of all organisms in all aspects of life, and strongly influences the outcome of natural selection. Regrettably, quantitative genetic theory has failed to incorporate this fact, and this failure has led to unexpected and often undesirable outcomes in a number of domestic animal breeding programs. This paper demonstrates that many apparent problems in animal breeding, and in our understanding of evolution, disappear when one looks at life from the wider perspective, which includes recognition of the limitations imposed on organisms by the environment.

INTRODUCTION - HOW DARWIN UNDERSTOOD EVOLUTION

Darwin knew that every living species produced more offspring than were required to replace the present living members. This being so, a mechanism must exist that effectively removes the surplus. Given that every species, in its specific environment, utilises all available resources, those individuals that use the resources most efficiently will leave the most offspring, and their descendents will become the best adapted, most successful, individuals of the species in its particular environmental niche. Conversely, the descendents of the less efficient individuals are less likely to survive and themselves produce offspring.

CONSEQUENCES

One consequence of Darwin's theory is that, provided its environmental niche does not change, a given species can be expected to remain stable, exhibiting at the most only mild fluctuations. In other words, although natural selection is constantly active, it actually ***prevents*** evolutionary change unless and until the environment changes. This obvious consequence of Darwin's theory of natural selection means that ***evolutionary changes take place when environmental changes occur and they stop once the new environment has stopped changing***. Huge evolutionary extinctions followed by rapid evolution of many new species are the results of major catastrophes on our earth, with the consequent generation of new environmental niches.

Genes provide the mechanism by means of which each form of life reproduces itself (Dawkins 1976). Natural selection in each species selects ***those individual organisms*** whose whole set of genes (genomes) achieve the most surviving young in the next generation. Thus, despite Dawkins' other statements about selfish genes, ***natural selection acts at the level of individual whole organisms, not of genes***. The current interest in understanding the function of individual genes (Neo-Darwinism) arose during the synthesis of Genetics and Evolution in the 1940s. This focus on genes prevents people seeing that the true driver of evolution is the ***environment***, which also limits what genes can achieve in domestic organisms.

Although Falconer and McKay (1996) and Falconer (in his earlier editions) drew attention to the importance of the environment, certain statements in the discussion, such as "that is to say, natural selection was assumed to be absent", seem to have been put aside as unimportant. Apparently geneticists have seen no problem with this confessed simplification. Although computer technologies have enabled great progress to be made in genetics, few people have questioned the basis on which quantitative genetics stands, and Neo-Darwinism has taken over the science of genetic improvement of domestic animals and plants. This leaves quantitative genetics as a complex science which, however, cannot describe the real world. It is imperative that we reintroduce into quantitative genetic theory the understanding that all life is limited by the availability of resources.

The ever-present natural selection selects those individuals whose genes result in the most efficient lifetime production of surviving descendents in the available environment. Applying resources most effectively over a lifetime requires organisms to use resources available ***in that harmony in which each trait is at its optimal level for achieving the maximum number of descendents (maximum fitness)***. This fact, which describes what happens when resources are used to gain maximum fitness, was recognised by Jim Crow (1986), a respected quantitative geneticist, and described by him as a direct result of genes. Unfortunately, restricting our vision to the genetic level prevents us seeing the real cause of limited genetic improvement which is, that ***resources are limited***.

SOME EXAMPLES

What should we expect of beef cattle being selected for more rapid growth and greater size as early as possible in their lifetime? Natural selection will already have selected the lifetime track which results in highest fitness over the whole length of life. When cattle respond to artificial selection on size and rapidity of growth early in life, they must necessarily use more resources early in life than they had been selected for under natural conditions. Unless extra resources are provided, they must use resources normally kept for later in life. As a result, lower performance later in life must result and, typically, fitness and length of life will decline. Experiments with mice by Eklund and Bradford (1977) and Barria and Bradford (1981) clearly showed that selecting for more rapid growth shortened lifetime, and relaxing or reversing this selection led again to increased length of life.

David Barker (1994) is a medical researcher who has evaluated human data from this (Bradford's) point of view from a large population of people in England with data from birth and from death. He has found that what happens in early stages of life has great influence on diseases contracted in later life and the causes of death. Here is a quote from the summary. 'Studies of programming in foetal life and infancy are now established in the agenda for medical research. They have two goals: preventing disease in the next generation and understanding disease in the present one. The search for the causes of coronary heart disease has hitherto been guided by a 'destructive' model. The causes to be identified act in adult life and accelerate destructive processes - the formation of atheroma, rise in blood pressure, loss of glucose tolerance. This book has proposed a new "developmental" model. The causes to be identified act on the baby. In adapting to them, the baby ensures its continued survival and growth at the expense of its longevity. Premature death from coronary heart disease may be viewed as the price of successful adaptations in utero. We need to know more about these adaptations: what are they; what induces them; how they leave a lasting mark on the body; and how this gives rise to the diseases of later life?' Another comment (about sheep): 'In general terms, the enhancement of a component such as early production means suppression of other components which may also include long life' (Gillies 2004).

HOW PROBLEMS ARISE

When domestic animals are selected for increased production, there will be a period during which more resources can be provided, for example by the provision of more food and the consequent reduction in the need to walk and search to obtain food (the downside of this approach, of course, is that it adds to the farmer's costs). However, the provision of extra resources may be difficult and, even if successful, will soon become limiting again. This must have a deleterious effect on the animal, which is no longer in the environment with which it had been in harmony. When resources are insufficient, the trait most affected by conditions is fitness. Pushing milk production above the level at which the cows were naturally in balance with their environment (that is, at which they were at maximum fitness) will inevitably cause problems in other traits. Hence, modern dairy cows, which are pushed to the limits with regard to milk production, often have difficulties conceiving and typically have shorter productive lives than cows had 20 or 30 years ago

YOU GET EXACTLY WHAT YOU SELECT FOR, BUT NOT ALWAYS QUITE WHAT YOU EXPECT

A well-accepted CSIRO program for the selection of fine wool diameter in sheep produced unexpected consequences. It affected the wool clip of my former PhD student, Dr Ian Gillies (2004), whose research involved the analysis of data from his merino sheep flock. After encouragement from the Australian Wool Testing Authority Ltd. he put the wool from his finest wool sheep into a special bale in order to get a high price, selecting the finest wool according to the fibre diameter at the mid-side of the sheep. This mid-side sample has been the accepted way to measure wool fibre diameter for 40 or more years since the CSIRO found that this sample gave the best average measurement. Ian also took two more samples from each of his sheep, one from the front of the fleece and one from the breech. Before wool is sold in Australia a core sample is taken from different parts of the bale. The core sample of this particular bale was coarser than Ian's average mid-side sample, on which he had based his estimate of the value of the bale. When Ian also included the two other samples for each sheep into his bale average, his result was the same as that of the core sample. It has long been assumed that fleece from the back is coarser than that from the mid-side, but traditionally the neck was presumed to be finer and balanced the britch to produce an average result expressed in the mid-side sample (Gillies, 1994). I see another possible reason which might be responsible for this result. After 40 years of selection for fine wool on the mid-side sample, the diameter of mid-side fibres has decreased more than the diameters of fibre from the other parts of the body. ***You get what you select for but not always quite what you expect.***

Another of my PhD students, Dr Brian Luxford (1987), collected data from experiments with caged mice on artificial selection for different components of fitness. He selected single aspects of the total reproduction process, e.g. numbers born, numbers weaned, weight of total number born, and weight of total number weaned, including some over length of life. Most individual components of fitness could be raised by selection at least to some extent. But in no case was the total number or total weight of progeny increased over the lifetime, and in several experiments total lifetime fitness decreased. There are possible genetic explanations for each result. But 'disturbing what natural selection had achieved in its earlier harmonious allocation of available resources over the lifetime' also explains each of the results obtained.

NATURE DOES NOT CHANGE A WELL-WORKING SYSTEM, UNTIL THE ENVIRONMENT DEMANDS AN IMPROVEMENT

Why do the zygotes of humans go through exactly the same procedures after fertilization as most other animals? My answer is that there has been no need to change what happens to the zygote inside eggs or wombs of possibly all organisms that have sexual recombination. The environment of the zygote is protected similarly in fluids whether the grownup lives are in the oceans, deserts forests, etc. As long as the environment of the zygote remains the same no change will occur. Organisms will change when their environment demands a better system.

In my opinion, the reproductive problems exhibited by modern dairy cows are the consequence of the enormous amount of resources required to enable them to maintain the high level of milk production imposed on them as the result of (unknowingly) inappropriate artificial selection.

CONCLUSION

Natural selection always selects the surviving descendents of each individual, using all resources available. If new resources become available, best use of these will occur automatically. In unchanging environments, species are constantly maintained at the most efficient level of use of available resources. Domestic animals are artificially selected above existing resources needed by natural selection. The more resources that genes cause to be diverted to commercial traits the more likely it is that the animal will show strained health and reduced fitness. Consequently, genetically highly productive animals are unsuitable for many commercial farms. It is imperative that we factor into quantitative genetic theory the understanding that all life is limited by the availability of resources in its environmental niche.

My goal in this article is to alert geneticists to a problem that has crept into Quantitative Genetics. By restricting our thinking to the level of genes only, as Falconer had recorded, we have removed ourselves from seeing what in most other biology is obvious common sense: All organisms, through natural selection, adapt themselves to their environment. And if we want to change them successfully, we must ensure that the new environment can supply all the resources necessary for achieving healthy new animals.

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