IMPORTANCE OF WHOLE ORGANISMS IN UNDERSTANDING GENETIC IMPROVEMENT AND EVOLUTION

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SUMMARY
The environment selects whole organisms, not genes. Organisms need environmental resources to live and reproduce. Genetics and biotechnology effectively ignore the environment and thus cannot fully explain evolution and animal improvement. The Resource Allocation theory adds to quantitative genetics $E(r)$, the local environment with its resources and challenges. This greatly increases understanding of evolution and improvement of animals.

Keywords: Organisms, genomes, phenotypes, genetic improvement, evolution

INTRODUCTION
Modern evolutionists, geneticists and molecular biologists focus on DNA and genomes when they consider evolution of the past and improving animal production now. This was not always so. Darwin introduced the idea “progress in organisms” in 1859. He saw that the local environment selected the fittest individuals and, in time, adapted populations of organisms to it. After Mendel’s results resurfaced in 1900, the understanding that environment selected organisms metamorphosed into the modern conviction that genes and genomes explain both evolution and genetic progress. This metamorphosis of ideas was gradual and diffuse. No one questioned that genetic changes drive evolution and animal improvement. Beilharz et al. (1993), Beilharz (1998) and Beilharz and Nitter (1998) now challenge this view with the Resource Allocation (RA) theory.

We need to define exactly what selection by the environment is, what natural selection achieves and whether the resulting organisms are free to change or constrained in the changes they can make. I briefly outline RA theory and discuss its consequences for “genetic improvement of animals”.

DISCUSSION
Organisms need environmental resources. Genes and genomes initiate and control growth, development, survival and reproduction of animals. Yet, in evolution and animal breeding, whole animals are selected. Genes are selected if they are in successful phenotypes. Surely this is obvious. But have we accepted its consequence? Whole animals need food (environmental resources) to be successful! With rare exceptions (e.g. Sölkner and James, 1994), a need for resources has been ignored in genetics (“natural selection was assumed to be absent”; Falconer and Mackay, 1996)!
Resources limit phenotypes of organisms. Natural selection on fitness never disappears in any population of organisms. In laboratories and on farms one can remove individual stressors and challenges. But, those animals with most surviving young continue to be selected as the fittest. By definition, neither natural nor artificial selection can produce phenotypes fitter than those of animals metabolising all available resources as efficiently as possible. Stable environmental niches continually select animals metabolising efficiently. Genomes producing efficient phenotypes will be selected, and varying genomes may produce equally efficient optimum phenotypes. Beilharz et al. (1993) demonstrated that, in environmentally limited conditions, individual characters important to phenotypes are all selected to intermediate optimum values. This fact is not new and its empirical occurrence was well discussed by Crow (1986). Crow also stated that such “stabilizing” selection would retain much additive genetic variation in each trait and hence allow rapid responses towards new optimum values for each trait when environments change.

Hence, in stable environmental niches, selection on fitness prevents animals changing from optimum phenotypes (sizes, developmental paths, behaviours etc.). Maximum adaptation of a population of animals to its niche exists when animals use all resources most efficiently. Animals cannot surpass complete adaptation. Any phenotypic change from optimum values results in lower fitness. This may be the reason why, as genomes evolved, important genes were conserved, while unimportant genes changed “rapidly” by allelic substitution. Neutral evolution (unimportant genes drift by chance and evolve faster than important genes; Kimura, 1983) and Punctuated Equilibrium (evolution occurs in bursts, after extinctions, interspersed by long periods of stasis; Eldredge and Gould, 1972) describe exactly how Darwin’s natural selection of organisms acts for unimportant and important genes, respectively, in a world where environments are tranquil between infrequent calamities caused by major catastrophes.

Necessary addition to quantitative genetics. Beilharz and Nitter (1998) defined E(r) as the effect of local environment to which organisms adapt. This allows the basic equation of quantitative genetics to define contributions to the phenotype of individual (i) precisely, as follows:

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P(i) = \mu + G(i) + E(r) + E(rt) + E(rte)
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where the phenotype of the individual P(i) equals the population mean plus the contributions of the individual Genotype G(i), the local environment E(r), and, within the local environment, any treatment or other fixed effects E(rt) and error E(rte).

E(r) specifies the resources and challenges of the local environment. Animals adapt to and are limited by levels of E(r). Genotype-Environment interactions occur between genotypes adapted to differing local environments. Natural selection acts within each level of E(r) and both individuals that are genetically poor and genetically “too good” (demanding too many resources) are culled. When the environment is limiting, there is no “slack” in fitness available to accommodate a response to artificial selection without a cost in fitness.
Domestic environments have been improved in many small steps, e.g. whenever a particular stressor was removed, climate was controlled or amount or quality of feed rose. In domestic environments, genomes demanding more resources than are available produce unwanted side effects in their phenotypes. These often constitute animal welfare problems. Unwanted side effects and reduced fitness in modern breeding programs indicate that even intensive environments already have insufficient resources for the genomes present. Focussing only on genetic explanations (e.g. changing genetic breeding goals, selfish genes hypothesis, Fisher’s fundamental theorem of natural selection, 1958) prevents seeing the real problem, that environments limit phenotypes.

**Practical consequences.** Animals already adapted are constrained within their optimised phenotypes. Artificial selection achieves only those changes demanded by the actual selection criteria applied (e.g. Merinos selected for fine fibre using mid-side samples get finer wool on mid-sides). Indirect selection fails when environment is limiting. It is useful to define “economic fitness”, maximising profit, so that profit is achieved despite reduced biological finess.

Lifetime development is movement along a path in time. Predictable needs select anticipatory resource storage. The lifetime path becomes efficient for the local environment. Artificially selected deviations in size and developmental path reduce fitness (poor reproduction, shorter life).

Genes are not expressed equally in both sexes as environmental challenges for the two sexes differ. Selection based on phenotypic traits in males does not guarantee a response in daughters. Yet, using different breeding goals for the two sexes should increase overall efficiency. Group selection can improve cooperative behaviour, e.g. in group-caged poultry. Egg production above that from individual selection can be achieved by selecting cage groups on egg numbers. (Muir, 1995).

Breeding with individuals of highest breeding value, in large, loosely defined production systems (e.g. Australian dairy herd), produces many offspring that demand too many resources in poorer parts of the environment. This creates welfare problems. The remedy is to restrict breeding populations to defined local environments, i.e. specifying E(r) for the total, localised system.

Natural selection has perfected the sexual recombination mechanism in all complex forms of animal life including humans. It has long ago stopped doing this for cloning in complex animals.

**CONCLUSIONS**

Using current quantitative genetics and biotechnology in animal production is inefficient, as theory in these sciences ignores environment. Limiting breeding programs to a local environment or breeding system achieves efficient animals for existing situations. This removes the need to create costly environments to maintain highly productive individuals of low fitness. All individual genes must work in harmony with all other genes and the environment. In biotechnology, changes in individual pieces of DNA are unlikely to achieve overall harmony. Sexual reproduction replaced
cloning early in the evolution of multicellular life. It seems dangerously unwise to use technology
to try to reverse such a major, successful step in the evolution of complex life?

REFERENCES
Freeman, New York.
Eldredge, N. and Gould, S.J. (1972) In “Models in Paleobiology”, p.82, ed. T.J.M. Schopf,
Freeman Cooper, San Francisco.
Harlow.
151.