# ASSOCIATED EFFECTS OF SIXTY YEARS OF COMMERCIAL SELECTION FOR JUVENILE GROWTH RATE IN BROILER CHICKENS : ENDO/EXOPHYSIOLOGICAL, OR GENETIC ?

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## INTRODUCTION

The modern broiler was developed in the past 60 years, from a dual-purpose chicken, reared primarily for egg production. It is now the most efficient converter of grain to meat among all agricultural animals. This is due the early realization that in this species, the key for efficient feed conversion was to shorten time to market through selection for rapid juvenile growth rate (JGR), and later for increased breast weight as a proportion of body weight (%BW).

The initial rapid response to selection for JGR is readily explained by the technical suitability of JGR for mass selection ; the intense selection enabled by the great reproductive capacity of the chicken; and for the same reason, the absence of a significant negative economic correlation between JGR and mature body weight. In 60 years, age at market weight has been reduced from 120 to 40 days; %BW has increased from 14% to 18% (Havenstein *et al.*, 1994a,b). Remarkably, progress continues without a plateau.

The enormous and continued response in JGR and % BW, has been accompanied by deleterious effects on reproductive performance of the parent flocks, and health of the broiler chick (Table 1). A remarkable aspect of the deleterious effects is their apparent coordinated appearance; sequentially in time, and simultaneously in the stocks of all main line breeders.

This history raises questions as to the sources of the genetic variation required for the extended response to selection and the coordinated appearance of the deleterious associated effects. We here present a pair of alternative hypotheses, each providing at least partial answers to both questions.

## A STANDARD GENETIC EXPLANATION : COMBINED GENETIC ENDO/EXOPHYSIOLOGICAL HYPOTHESIS

Initially, there were dozens of independent breeders, so that the total population under selection was very great, and although subdivided, there was continual informal exchange of birds among the breeding nuclei. In this island structure, any genetic innovation (rare allele; recombination in a balanced block ; mutation) arising in one breeding nucleus would soon spread to all. In addition, selection for extreme phenotypic variants is also selection for breakdown of developmental homeostasis. This can release cryptic genetic variation.

**Table 1. Associated effects of selection for juvenile growth rate and breast weight, their postulated endo- or exophysiological mechanisms, and their management solutions**

| Line | Associated effect | Type | Mechanism | Management solution |
|---|---|---|---|---|
| Female | Obesity (1960) | Endo | Lack of appetite control caused by selection for JGR | |
| | Reduced lay (1965) | Endo | Hormonal imbalance caused by Obesity | Quantitative feed restriction |
| | Increase in minimum weight for sexual maturity (1972) | Genetic | Allometric change in weight for onset of sexual maturity as a result of change in growth curve | Adjustment of recommended growth curves |
| | Reduced lay (1980) | Exo | Physiological hunger state caused by feed restriction | Stimulatory lighting |
| | Prolapse/internal lay (2000) | Exo | Stimulatory lighting | Slower release from feed restriction at onset of lay |
| Male | Reduced fertility (1985) | Endo | Hormonal imbalance induced by obesity | Quantitative feed restriction |
| | Reduced fertility (1995) | Exo | Stimulatory lighting: simultaneous induction of sexual maturity in males and females | Males transferred from dark out to laying house before the females. |
| Broiler | Skeletal defects (1980) | Endo | Developmental imbalance, Skeleton: body mass | Mild feed restriction to slow growth |
| | Reduced immune response (1980) | Endo | Muscle growth competes with immune response | Vaccination programs, pathogen free parent flocks |
| | Ascites (1990) | Endo | Developmental imbalance, Heart: body mass, exacerbated by cold | Maintain optimal growing temperature; reduce feed intake. |
| Embryo | Reduced hatchability (2001) | Endo | Increased muscle mass, more embryo heat production | Lower incubator temperature |

**An endo/exophysiological explanation for the coordinated appearance of deleterious associated effects.** Selection for JGR was in large part selection for lack of appetite control (Soller and Eitan, 1984). When the mature animal overeats, it becomes obese, interfering with reproductive performance in male and female. The term “endophysiological effect” was coined by Reuven Bar Anan, to describe associated effects of this nature. These “obesity” effects were successfully controlled by restricting feed intake. However, the restricted feed intake itself may have engendered a secondary endophysiological effect, which we term “exophysiological”. In particular, the reduced photosensitivity causing delayed onset of lay, and failure to reach peak egg production that arose in the 1980’s, may have been a consequence of the lack of satiety caused by the increasing relative degree of feed restriction required by continued selection for JGR (Eitan and Soller, 1996, 2000). This lack of satiety may conflict with the normal signal for onset of lay, namely, increasing photoperiod (day length). To offset this, entry into lay is now managed by “stimulatory lighting”, i.e., keeping the birds under short photoperiod, and then sharply increasing feed and photoperiod. This, in turn, may be generating a new set of exophysiological effects. Males normally enter sexual maturity before the females, so that they settle dominance status before the females become sexually mature. Stimulatory lighting forces males and females into sexual maturity at the same time, disrupting normal relations. As a result the males may mate less actively, putting on fat which reduces their mating activity still further, engendering a self-reinforcing cycle, that eventually results in male reproductive collapse (J. Brake, pers. comm.) The same forced rapid entry into lay may be responsible for an increased incidence of prolapse and internal lay (Robinson *et al*. 1998). In this way a cascade of endo- and exophysiological affects may cause the appearance of the same deleterious associated effects in all breeding nuclei, at about the same time.

**Problem :** Some of these same associated effects are found in turkeys, where feed restriction is not used.

## A UNITARY GENETIC HYPOTHESIS : NEW GENETIC VARIATION RELEASED BY CHANGES IN GENETIC BACKGROUND THROUGH SELECTION

A more novel alternative, proposed by one of us (Y.E.) is that selection itself acts as a bootstrap, changing the genetic background in such a way that genetic variation that was previously present, but cryptic, now comes to expression. On this hypothesis, long term selection itself would iteratively generate at least part of the genetic variation required for its own continuation; as selection proceeds changing the genetic background, new sets of genes would continually come into play as sources of variation, in a “programmed” manner. Pleiotropic effects of allele substitution at these genes would then be responsible for the coordinated appearance of new deleterious effects with continued selection.

**Problem :** Crosses of broiler and layer lines are intermediate in JGR. This is not expected if part of the gene effects depend on background.

## CONCLUSION

Selection of broiler chickens for JGR is an ongoing, and unprecedented instance of long-term, intense and effective directional selection. There has not been any comparable experimental or commercial selection program. Thus, the modern broiler represents a unique genetic resource for studies in mechanisms of long term selection response and associated effects. It also represents an object lesson on the dependence of normal development and function on subtle environmental signals, that may be lost or modified by management (read : civilization). We await with interest the next stage in this fascinating history.

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