

## SELECTION PLATEAUX IN POULTRY (1)

G. A. CLAYTON

*Institute of animal Genetics,  
West Mains Road,  
Edinburgh 9 - Scotland*

---

### SUMMARY

1. Absolute gains continue to be recorded in weight for age in the cases of chickens, turkeys and ducks but signs of attenuation are appearing.

2. Absolute gains in egg production are imperceptible if they have not ceased altogether. The total gain in hen housed average egg production to 500 days in this century is of the order of 50-60 eggs. The proportions attributable to the various technologies, genetics, nutrition, husbandry and pathology are uncertain and to some extent inextricable.

3. If it can be established that the *Cornell* Control is genetically unaltered then the rapidly expanding divergence between it and breeders stocks is more likely explained in terms of a genotype environment interaction because of the lack of field evidence of absolute trends in improvement. It is postulated that genetic changes in pathogens might explain the paradox.

4. If plateaux for egg production are caused by exhaustion of genetic variability then the crossing of the best performing and least related lines or the extraction of inbred lines from such plateaued populations and the subsequent crossing of the best among them seem to be the most likely techniques to permit further gains.

---

The convening of a conference for the specific purpose of discussing selection plateaux in poultry is evidence that at least some poultry breeders consider that a problem may exist. CLAYTON (1968) poses a general question concerning a limit to economical egg production in the hen, though others have reported cases of zero gain in particular selection experiments. LERNER (1951) in his study of attenuation of response to selection for shank length encountered a plateau after making appreciable gains in the first half of his experiment. He was able to show that this was due, at least in part to natural selection working against him though he was unable to find similar evidence for egg production.

The literature on selection plateaux derive mainly from work on laboratory

(1) Cet article a été présenté à la Réunion du Groupe de travail « Sélection et Testage » de la *Fédération des Branches européennes de la W. P. S. A.*, Tours et St-Brieux (France) 7 septembre 1971.

animals. It may be helpful to consider separately the results on traits of high heritability from those of low heritability. In the first category came the classical selection experiments on body size in mice. ROBERTS (1966) discusses the earlier work of GOODALE, Mac ARTHUR and FALCONER and KING and shows responses to selection in closed populations plateauing ultimately in all cases. ROBERTS (1967) showed that crossing of unrelated plateaued lines permitted further response but only in the direction of increased size. This further gain was marked by a reduction in fitness and extinction of one of the lines, points which should be noted by poultry breeders, as should the fact the crossing of the small lines did not permit advances greater than those previously attained.

GALL (1971), KRESS, ENFIELD and BRACKERAO (1971), PAPA (1971) and CLAYTON and ROBERTSON (1957) report long term selection experiments in flour beetles, a fungus and fruit flies respectively, all of which show marked reductions in fitness and cessation of response in many cases. Maximum responses appear to result from the use of large populations and the lowest rates of inbreeding, another point which should be noted by poultry breeders.

Selection experiments on traits of low heritability are sparse and the results achieved are modest or unconvincing. One of the most successful is that reported by FALCONER (1971) who, in 64 generations of selection, increased litter size in mice by some 20 p. 100 over the starting level: his population appeared to have plateaued some 20 generations previously but his results are of great interest to poultry breeders because crossing of inbred lines derived from this plateaued population gave an unexpectedly large improvement over the selected line itself. Repetition of this procedure in lines of poultry that have been extensively selected for egg production would be extremely interesting and might prove highly rewarding, a suggestion supported by the results of BLYTH and SANG (1960). ROBERTSON and REEVE (1955) and KOJIMA and KELLEHER (1963) report some unusually high egg production figures in crosses between inbred lines of flies, as do BELL, MOORE and WARREN (1955) in the case of flour beetles. OSMAN and ROBERTSON (1968) present experimental evidence from flies showing crossing and selection techniques which permitted them to transgress earlier limits. As they point out the limits they encountered were artefacts of the selection programme caused by the small sizes of the populations involved.

Turning now to poultry, the limited amount of work published on traits of high heritability, for example live weight gain, has indicated unambiguous responses to selection. DEV, JAAP and HARVEY (1969) and CARTE and SIEGEL (1968) may be consulted for the relevant literature concerning chickens. Unlike egg production there is no gain saying a steady improvement in performance in the commercial world and this is reflected by the increasing proportion of chicken in total meat consumption. There is no clear cut evidence as yet of a plateau for body size at an early age in chickens though field experience suggests that the rate of advance is considerably less than it was in the 1940's. There is ground for optimism that further improvements will be made in efficiency of meat production in chickens and other poultry but the indications of attenuation suggest that this will be limited. In the case of ducks no good evidence concerning improved efficiency of meat production has been published though observation of commercial results suggests considerable gains in weight for age. In turkeys substantial increases in weight for age have been

recorded. CLAYTON (1971) gives an example and some of the references. Figure 1 contains a suggestion that a plateau may have been reached though the weight for 1971, not shown in the figure, at 29.60 kg is probably the highest authenticated weight ever recorded. The weights shown in figure 1 are for turkeys in the so called « New York Dressed » condition. The apparently abrupt cessation of response in 1965 arose from the breed change to white turkeys. The latest results indicate that the lost ground has been recovered but that the rate of progress has been greatly slowed. The weights shown in figure 1 are for mature birds and represent the top end of the spectrum but the trend they suggest probably applies to the specialized meat varieties in the breed as a whole. Reports from commercial breeders suggest that lines extreme for weight and conformation are difficult to reproduce and it is likely that their greatly reduced fitness will inhibit much further progress in body size.

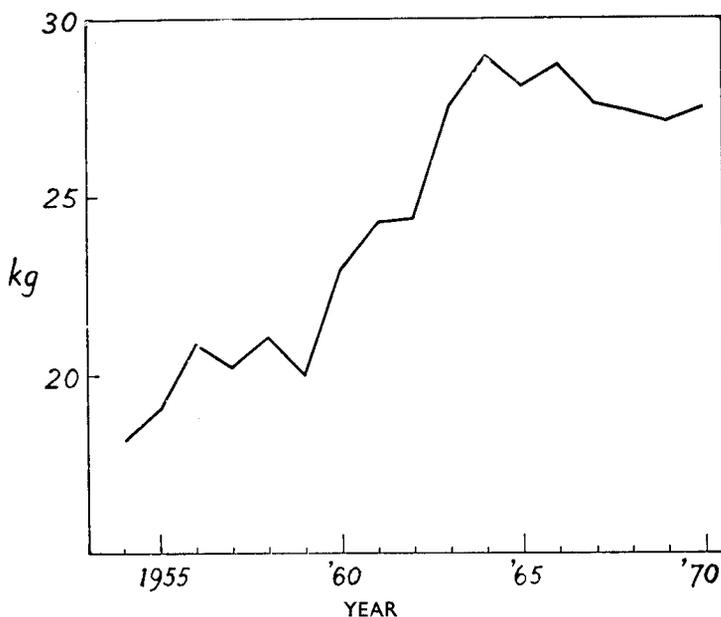


FIG. 1. — *Weight Gain in Turkeys.* (Heaviest Turkey, National Poultry Show U. K.)

*Gain de poids chez les Dindons*

The problem of a plateau for egg production is still a subject of controversy. CLAYTON (1968) presented a rather pessimistic picture, a point of view criticized by DICKERSON (1968). There is no significant new evidence to add to the debate though figures 2 and 3 include more recent results of the U. S. D. A. random sample trials. In absolute terms both breeders and the control population show a continuing decline but expressed as deviations from the control the leading breeders are improving their position by some 2-3 eggs per generation. The argument against the plateau hypothesis has it that the continuous decline over the past ten years is attributable to an increasingly harsh environment encountered in the testing stations. The steady increase in mortality shown in figure 3 does not contradict

this view though whether this increase is due to changes in the nature or type of the pathogens or to physical factors such as increased crowding is not clear.

Included on figure 2 are four points indicating the mean level of performance attained in the random sample trials conducted at Godalming in England. Also shown is the performance of the stocks of two breeders B and S who are also represented in the U. S. D. A. trials. The results are based on substantial numbers, some

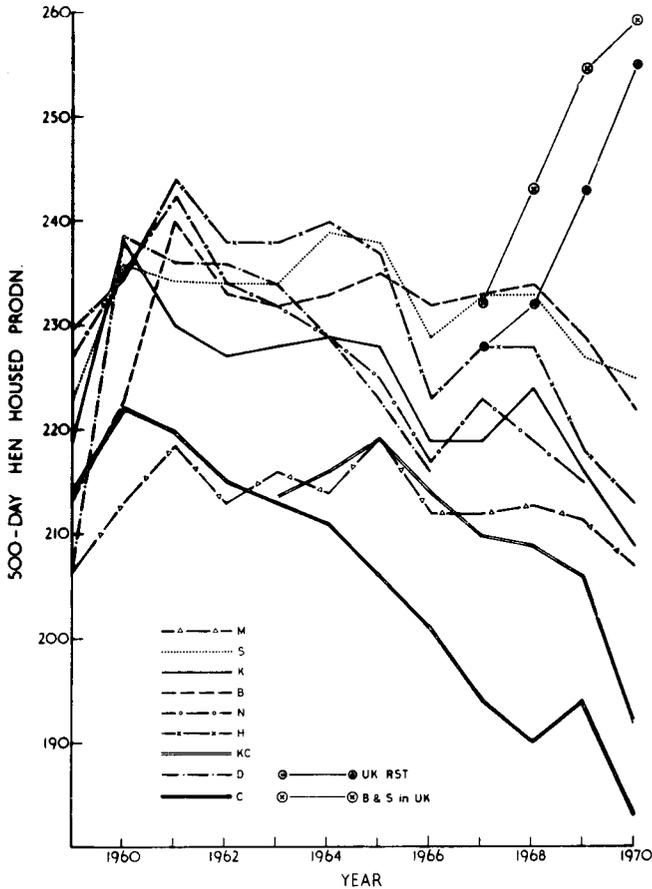


FIG. 2. — Hen housed average production to 500 days of age. Some leading breeders compared with the Cornell Control (C) and the Kentville Control (K. C.) Some recent results from the U. K. Random Sample Test are also shown

*Production moyenne à 500 jours d'âge rapportée aux poules mises en poulailler, pour quelques souches « de pointe » comparées aux témoins Cornell (C) et Keutville (K. C.)*  
Des résultats récents de testage du Royaume-Uni sont également présentés.

288 birds pre entry being housed in the laying quarters. The striking improvement of over thirty eggs in mean performance over the four years for which results are available can only be attributed to environmental changes, the nature of which unfortunately cannot be defined. Little if any of this improvement can be attributed to the withdrawal of inferior stocks as evidence by the virtually parallel response of the B and S lines. Standards of management, which have been kept as

constant as possible, are of a very high order. Preliminary information on the current test suggests that the mean will fall short of the peak attained in 1970. Comparison of the results of the single U. K. test with the U. S. D. A. two year regressed means involving eleven or more separate tests is of very little value. The UK results are only included in figure 2 to demonstrate two points. Firstly the extraordinary magnitude of envi-

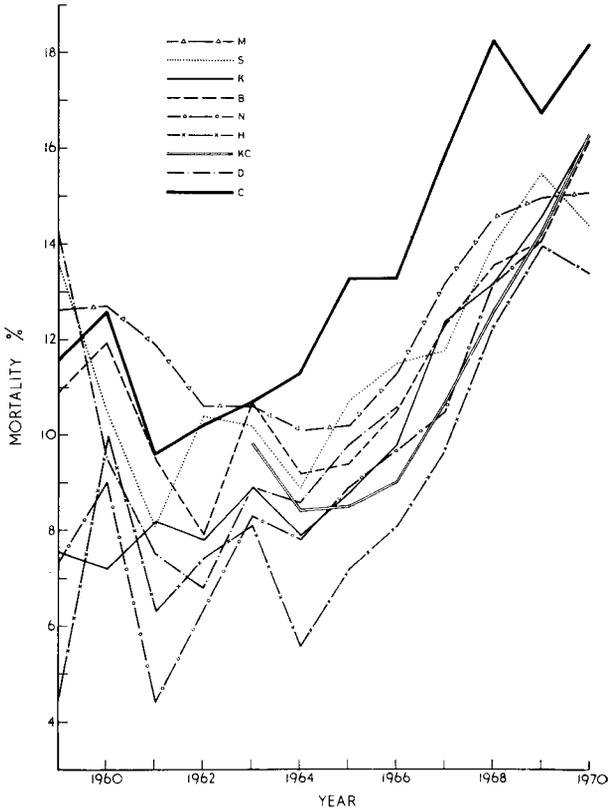


FIG. 3. — Laying house mortality in the U. S. D. A. random sample trials

*Mortalité en poulaillers de ponte dans les tests U. S. D. A. sur échantillons pris au hasard*

ronmental fluctuation which can occur and secondly to draw attention to one of the highest levels of mean performance ever recorded under satisfactorily objective and controlled circumstances. There is ample evidence (CLAYTON, 1972) of the existence of stocks in the first two decades of this century capable of producing a hen housed average to 500 d. of 200-210 eggs. These figures lend support to the assumption that the total improvement in egg productivity in this century is of the order of 40-60 eggs. Allowing for advances in nutritional, husbandry and disease technology the evidence suggests a tenacious resistance to genetic progress that is as yet far from understandable. It is recognized that egg number is not the only criterion of economic efficiency and improvements in the more highly heritable traits, egg and body size, have made a significant contribution though changes in these traits too are becoming less and less perceptible.

In terms of deviations from the control line the breeders in figure 2 are making substantial genetic progress—averaging some three eggs improvement per generation. The crude historical comparison above and current commercial experience, does not accord with this apparent rapid rate of advance. If the control line has changed genetically its use would be invalidated. HILL (1972) in a discussion of control population summarizes the evidence showing significant declines in egg size, early body size and sexual maturity in the *Cornell* Control population at Lafayette and non significant declines in p. 100 production. He also notes significant divergences between this and the *Reginal Red* Control line maintained at the same station. He also quotes other evidence based on smaller numbers but over a longer period showing a significant improvement in p. 100 production but non significant changes in the other traits. His conclusion would appear to be, though not specifically stated as such, that genetic changes in the *Cornell* Control strain, if any, are relatively unimportant. In evaluating the USDA data he considers the most reasonable hypothesis to be that the test environments are deteriorating associated with increased disease levels or changes in management.

If the *Cornell* Control has remained genetically stable then other explanations of the contradiction must be sought. By far the most likely is the probability of genetic changes among the pathogens, particularly the viruses, which afflict poultry. Evidence for genetic variability among viral agents of disease is widespread and the evidence published by FENNER, RATCLIFFE (1965) on myxomatosis is a convincing example. The experiences of the plant breeders in selecting for disease resistance should be a warning of the genetic versatility many pathogens possess in overcoming the various barriers interposed by man. It is a matter of common veterinary knowledge that the manner and severity of disease is greatly influenced by factors such as population size, densities and housing types. The vast monoculture systems increasingly practised today offer unprecedented opportunity to pathogens of enhanced virulence. Under more dispersed conditions and smaller population numbers the more virulent pathogen is at a lower selective advantage because of the shortage of suitable hosts. As exemplified in the case of myxomatosis there are strong selection pressures towards stages of intermediate virulence under natural conditions. The poultry breeder testing and selecting under a range of field conditions is, consciously or not, selecting against the pathogens of the moment. The appearance of more resistant strains of poultry to a given agent immediately present an exploitable opportunity to mutant forms of the disease by analogy with the screening techniques used for isolating mutant forms of bacteria and fungi.

It is postulated that the poultry breeder in a state of constant war with the agents of disease has to work extremely hard for the little progress he may make and that the genes affecting resistance in the host and the pathogenicity of the organism are constantly changing. If this hypothesis be valid then the genotype of a host assumedly held constant since 1955 in the case of the *Cornell* Control might be expected to react increasingly adversely to the changing pathogens of later years, while at the same time explaining the disappointingly small absolute progress which is being made. This hypothesis has the merit of being testable as was done in the case of myxomatosis. By retaining samples of the original virus in deep freeze it was possible to challenge later generations of rabbits and measure the degree of genetic resistance developed by the latter. It would be interesting to make similar

tests in poultry. By maintaining naive populations of poultry in effective isolation the reciprocal tests could be done evaluating the genetic changes occurring in field strains of the virus.

To the extent that disease causing agents are the block to further progress in economic efficiency the solution is more likely to lie in the hands of those who can develop vaccines with a broad spectrum of resistance because it is highly unlikely that the geneticist will be able to compete with the natural advantages of the pathogen viz. numbers and generation interval.

*Reçu pour publication en avril 1972.*

### ACKNOWLEDGEMENTS

I am indebted to *British United Turkeys Ltd.*, Hockenhull, Tarvin, Chester for the data on turkey weights shown in figure 1.

### RÉSUMÉ

#### PLATEAUX DE SÉLECTION CHEZ LA VOLAILLE

1. Des gains absolus continuent à être observés pour le poids à un âge donné dans le cas des poulets et des dindons, mais des signes de ralentissement apparaissent.

2. Les gains absolus pour la production d'œufs sont imperceptibles s'ils n'ont pas totalement cessé. Le gain total réalisé dans le siècle présent, sur la production d'œufs moyenne jusqu'à 500 jours rapportée aux poules mises en poulailler, est de l'ordre de 50-60 œufs. Les proportions de ce gain attribuables aux divers progrès technologiques, en génétique, nutrition, élevage et pathologie, sont incertaines et, dans un certain sens, leur analyse est inextricable.

3. Si l'on peut établir que la population témoin *Cornell* est restée génétiquement inchangée, la divergence qui augmente rapidement entre elle et les souches sélectionnées a son explication la plus vraisemblable en termes d'interaction génotype-milieu, par suite de l'absence de preuves d'une tendance absolue à l'amélioration. Il est suggéré que des changements génétiques dans les agents pathogènes pourraient résoudre le paradoxe apparent.

4. Si des « plateaux » pour la production d'œufs sont causés par l'épuisement de la variabilité génétique, le croisement des lignées les moins apparentées et ayant les meilleures performances ou l'extraction de lignées consanguines à partir de telles populations en « plateau », puis le croisement ultérieur des meilleures d'entre elles, semblent être les techniques ayant le plus de chances de permettre des gains ultérieurs.

### RÉFÉRENCES BIBLIOGRAPHIQUES

- BELL A. E., MOORE C. H., WARREN D. C., 1955. The evaluation of new method for the improvement of quantitative characteristics. *Cold Spring Harbor Symposia on Quantitative Biology*, **20**, 197-212.
- BLYTH J. S. S., SANG J. H., 1960. Survey of line crosses in a *Brown Leghorn* flock. 1. Egg production. *Genet. Res. Camb.*, **1**, 408-421.
- CARTE I. F., SIEGEL P. B., 1968. Correlated heritabilities of unselected traits : a check on procedure. *Poult. Sci.*, **47**, 1831-1827.
- CLAYTON G. A., 1968. Some implications of selection results in poultry. *World's Poult. Sci. J.*, **24**, 37-57.
- CLAYTON G. A., 1971. Egg production in turkeys. *Br. Poult. Sci.*, **12**, 463-474.

- CLAYTON G. A., 1972. Effects of selection on reproduction in asian species. *Symp. Vol. J. Reprod. and Fertil.*, (in press).
- CLAYTON R. A., ROBERTSON, ALAN, 1957. An experimental check on quantitative genetic theory. II. The long term effects of selection. *J. Genet.*, **55**, 152-170.
- DEV D. S., JAAP R. G., HARVEY W. R., 1969. Results of selection for eight-week body weight in three broiler populations of chickens. *Poult. Sci.*, **48**, 1336-1348.
- DICKERSON G. E., 1965. Experimental evaluation of selection theory in poultry. In *Genetics Today. Proc. XIth Int. Cong. Genet.*, The Hague 1963. 3, 747-760.
- DICKERSON G. E., 1968. Lessons to be learned from poultry breeding. In *Animal Breeding in the age of A. I. Univ. Wisconsin. Amer. Breeding Serv. Inc.* 69-93.
- FALCONER D. S., 1971. Improvement of litter size in a strain of mice at a selection limit. *Genet. Res., Camb.*, **17**, 215-235.
- FENNER, RATCLIFFE, 1965. Myxomatosis. *Camb. Univ. Press.* XIII, 379.
- GALL G. A. E., 1971. Replicated selection for 21-day pupa weight of *Tribolium castaneum*. *Theoret. Appl. Genetics*, **41**, 164-173.
- HILL W. G., 1972. Estimation of genetic change. II. Experimental evaluation of control populations. *Am. Breed. Abstr.*, (in press).
- KOJIMA K., KELLEHER T. M., 1963. A comparison of purebred and crossbred selection schemes with two populations of *Drosophila pseudoobscura*. *Genetics*, **48**, 57-72.
- KRESS D. D., ENFIELD F. D., BRACKREED O., 1971. Correlated response in male and female sterility to selection for pupa weight in *Tribolium castaneum*. *Theoret. Appl. Genetics*, **41**, 197-202.
- LERNER I. M., 1958. *The Genetic Basis of Selection*. John Wiley and Sons, New York.
- PAPA K. E., 1971. Continuous selection for increased growth rate in *Neurospora crassa*. *J. Hered.*, **62**, 87.
- OSMAN H., EL SAYED, ROBERTSON, ALAN 1968. The introduction of genetic material from inferior into superior strains. *Genet. Res. Camb.*, **12**, 221.
- ROBERTS R. C., 1966. The limits to artificial selection for body weight in the mouse. I. The limits attained in earlier experiments. *Genet. Res., Camb.*, **8**, 347-360.
- ROBERTS R. C., 1967. The limits to artificial selection for body weight in the mouse. III. Selection from crosses between previously selected lines. *Genet. Res., Camb.*, **9**, 73-85.
- ROBERTSON F. W., REEVE E. C. R., 1955. Studies in quantitative inheritance. VIII. Further analysis of heterosis in crosses between inbred lines of *Drosophila melanogaster*. *Zeit. induk. Abstam. Vererblehre*, **86**, 439-458.