

Annales Agriculaurae Fenniae

Maatalouden
tutkimuskeskuksen
aikakauskirja

Journal of the
Agricultural
Research
Centre

Vol. 23,4

SELECTION EXPERIMENTS IN POULTRY
Proceedings of the International Conference,
held at Helsinki, Aug. 7, 1984
Edited by Kalle Maijala

Annales Agriculae Fenniae

JULKAISIJA — PUBLISHER

Maatalouden tutkimuskeskus
Agricultural Research Centre

Ilmestyy 4 numeroa vuodessa
Issued as 4 numbers a year
ISSN 0570-1538

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IMPORTANCE OF GENETIC PROGRESS AND OF SELECTION EXPERIMENTS IN POULTRY¹⁾

K. MAIJALA

MAIJALA, K. 1984. Importance of genetic progress and of selection experiments in poultry. *Ann. Agric. Fenn.* 23: 185—187. (Agric. Res. Centre, Inst. Anim. Breed., SF-31600 Jokioinen, Finland.)

The role of chickens as experimental animals in genetics and animal breeding was pointed out. Attention was paid to the considerable genetic progress made in practical poultry breeding even in the recent decades, although some signs of selection plateaus had been observed by some researchers. Comparisons to randombred controls showed that annual egg yields per hen had, on an average, increased genetically by 2 eggs, hen-day egg yields by 1 %-unit and annual egg mass yields by 0,2 kg per hen. Egg size had increased, while viability had either impaired or remained unchanged. It was realized that many selection experiments have been carried out in poultry in the recent decades.

Index words: chicken, experimental animals, genetic progress, randombred controls, egg yields, selection experiments.

Chickens were important experimental animals in pure genetics in its Mendelian era in the beginning of this century, because of their small size, high reproduction rate and short generation interval. Later on, chickens and quails have been used as laboratory animals for testing various theories of quantitative genetics, methods of selection and mating systems for economic breeding of farm animals. Experiments aiming at genetic progress in chickens have, of course, also been numerous. Some of the lessons learned were discussed by DICKERSON (1968).

Considerable progress in improving egg yields was made in the first half of the century, and signs of diminishing returns or even plateaus were observed and discussed in the 1950's and 1960's (DICKERSON 1955, CLAYTON 1968). In the last 15 years, however, positive estimates of genetic progress in practical breeding, based on utilization of genetically constant, randombred control populations, have still been obtained (Table 1).

Although random drift, inbreeding, natural or artificial selection, environmental trends and diseases may cause problems in the use of

¹⁾ The scientific part of the Opening address

Table 1. Linear regression coefficients on years, of average deviations of commercial hybrids from randombred controls, for various traits in different countries (In Denmark, Finland and Norway common control and only domestic hybrids, including experimental ones).

Trait	North Amer. 1958-70 1)	Ireland 68-73 2)	Australia 66-78 3)	FRG 65-71 4)	70-77 5)	Norway 75-82 6)	Denmark 73-82 7)	Finland 74-82 8)
ASM, d.	-1,3	0,2	-0,5	-0,8	-2,1	-1,4	-1,5	-1,0
HDE, No.	1,7	1,7	1,5		5,9	1,2	2,0	
HHE, No.	1,2		1,7			1,2		
HDE, %	0,7			1,2	1,8			0,3
HHM, kg		,16			,37	,16	,16	,21
EW, g	,30	,21		,40	,37	,36	,21	,60
FEED, g/d	,16	-,06	-,01					
FCR, kg/kg	-,023		-,020			-,120	-,019	-,030
Viability, %	-,33	-,12				-,75	-,03	,01
BW I, g					13	- 3		0
BW II, g					- 3	0		- 10

ASM = age at sexual maturity
HDE = hen-day egg yield
HHE = hen-housed egg yield
HHM = hen-housed egg mass
EW = egg weight

FEED = feed consumption
FCR = feed conv, rate, kg feed/kg
BW = body weight
I = at start of lay
II = at end of lay

- 1) DICKERSON and MATHER (1976)
- 2) FOSTER and WEATHERUP (1977)
- 3) POLKINGHORNE (1981)
- 4) KROSIGK et al. (1973) (Nick-Chick)

- 5) KOLSTAD (1979)
- 6) ANON. (1984)
- 7) PETERSEN (1984)
- 8) MAIJALA (1982)

control populations and in the interpretation of results, it appears that continuous progress has been made in improving egg-layers in many countries. On an average, egg yield per hen has increased genetically by 2 eggs, hen-day egg yields by 1 %-unit and egg mass yields per year by 0,2 kg per hen per year. Age at sexual maturity has decreased by one day per year and feed consumption per kg eggs by 0,04 kg per year. The trend in egg size has still been upwards in spite of that further increase has no more been considered desirable in some countries. Viability has tended to develop to undesirable direction or to remain unchanged. Undesired directions of development have often been observed also in egg quality traits.

The experiences give grounds for attempts to improve egg yields further, especially when one takes into account the changing environments for which the animals should be adapted, concerning feeds, lighting, temperature, density, cage size, disease environment etc. It is

also important to make the selection and progress more manysided, in order to improve the total economic value of layers. The quality of eggs deserves special attention.

In meat-producing birds, the same applies. The progress made in growth rate both in broilers and turkeys has been enormous, and some undesired correlated changes have been observed, e.g. in fertility and product quality.

For these reasons, many selection experiments in chickens, quails and other avian species are being performed in different countries, including the Scandinavian ones, which since 1969 have closely co-operated in poultry breeding research (LILJEDAHL et al. 1979). The objectives, environmental and managerial conditions, animal materials and numbers etc. vary, but it is very obvious that the researchers working with these experiments have a great need of exchanging experiences and ideas, in order to get more out of their own experiments. Since it appeared that it is not possible

to discuss these scientific problems in great details in connection with the XVII World's Poultry Congress at Helsinki on Aug. 8—12, 1984, it was decided to arrange a special satellite conference on this topic. The intention was to complement the genetic sessions of the congress and the symposium on Selection Experiments in Laboratory and Domestic Animals in Harrogate, England, in 1979, where 1/5 of the papers concerned poultry. Taking into account the travel programs of participants, only one day was reserved for the purpose.

In correspondence with researchers who were known to have worked with selection experiments, the programme of this conference became clear. The papers were divided into four groups according to the traits studied. In addition, a review of recent or ongoing selection experiments in Scandinavia was considered appropriate. It is hoped that the discussions will help participants in their work and in their mutual understanding and later collaboration, especially in planning better and better future experiments.

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Manuscript received August 1984

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SELECTION EXPERIMENTS IN POULTRY IN SCANDINAVIA — A REVIEW

NILS KOLSTAD

KOLSTAD, N. 1984. Selection experiments in poultry in Scandinavia. *Ann. Agric. Fenn.* 23: 188—195. (*Inst. Poult. and Fur Anim. Sci., Agric. Univ. of Norway, 1430 Aas-NLH, Norway.*)

Because of limited resources for poultry breeding research in Scandinavia a collaboration between the Scandinavian countries was initiated in 1968. A research program was accepted by the Nordic Contact Agency for Agricultural Research, and recommendations were given to the research councils in Denmark, Finland, Norway and Sweden, which started to support poultry breeding projects from 1970.

The present paper is a review of the most important selection experiments performed during recent years. The experiments briefly discussed are: Scandinavian selection and crossbreeding experiments with laying hens. Tissue antigens (MHC) and productivity in laying hens. Selection for improved feed efficiency in egg production. Selection for better feed efficiency in slaughter chickens. Selection for leg disorders in broilers.

Index words: poultry, selection, experiments, feed efficiency, leg disorders, MHC.

INTRODUCTION

The Scandinavian countries are all relatively small with limited resources for research in poultry breeding. The idea of intensified Scandinavian collaboration in this field of research, forwarded by the Animal Breeding Sub-section of the Scandinavian Association of Agricultural Scientists, was therefore well accepted by the poultry geneticists when proposed in 1966. A working group was immediately set up and a preliminary plan for research was proposed, and accepted by the Nordic Contact Agency for

Agricultural Research in April, 1968. Recommendations were given to the research councils in Denmark, Finland, Norway and Sweden, which in turn started to support poultry breeding projects from 1970.

The first joint project was named "Population Genetic Conditions for Poultry Breeding in Scandinavia". The principal aim of this project was to investigate how modern selection and breeding methods could be applied under conditions typical for the Scandinavian coun-

tries as to previous breeding systems, farm size, degree of specialization, veterinary regulations etc.

This initial project consisted of several smaller projects which were performed either in one, two, three or all of the participating countries (MAIJALA 1974):

- testing of existing egg-laying strains
- estimation of genetic parameters
- development of selection indexes
- testing of strain combinations
- genotype — environment interaction

The most pronounced example on joint operations was the establishment of a common gene pool in Sweden in 1969, — a gene pool which has been used as base population for most of the breeding experiments performed in Scandinavia since then.

The present paper aims at giving a brief review of the selection and breeding experiments performed by the poultry geneticists in Scandinavia during the last years.

EXPERIMENTS

1. Scandinavian selection and crossbreeding experiment with laying hens

During the time when the first poultry breeding project was performed the idea of starting a large-scale selection and breeding experiment arose. The experiment was supposed to follow the same principles in all the four Scandinavian countries starting from the same heterogeneous base population. The principal aim of the experiment was to compare the efficiency of specialized selection in two lines with index selection in one line for the same traits. The traits selected for were laying intensity and egg size, which are clearly antagonistic to each other. The outline of the experiment is shown in Fig. 1 (LILJEDAHL et al. 1979).

Many interesting results both from a theoretical point of view and for the more applied poultry breeding are obtained from this experiment which has now lasted for more than ten years. The experimental results, however, will not be dealt with in the present review as a presentation of the whole experiment followed by a thorough discussion of the most important conclusions will be given in a separate paper by Prof. Liljedahl.

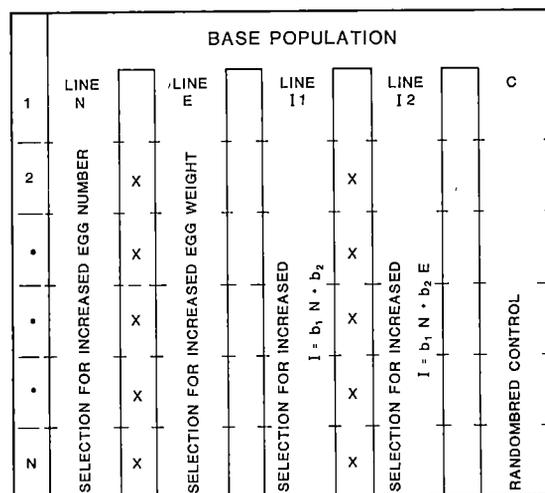


Fig. 1. Scandinavian selection and crossbreeding experiment with laying hens.

2. Tissue antigens (MHC) and productivity in laying hens

During 1980, a total number of 2342 birds from generation 7 in the internordic selection experiment were MHC-typed by Dr. M. Simonsen (Institute of Experimental Immunology, University of Copenhagen). The birds were

Table 1. B-haplotype frequencies in the control lines.*

	Da	No	Sw	Fi
B2	0,0552	0,0189	0,0126	0,0279
B5	0,0316	—	0,0217	0,0099
B6	0,0052	0,0125	0,0162	0,0139
B12	0,0122	0,1056	0,0180	0,0039
B13	0,0515	0,0986	0,0684	0,2014
B15	0,2590	0,2584	0,2854	0,3540
B19	0,3637	0,3339	0,3160	0,1700
B21	0,1435	0,0679	0,0780	0,0972
B21, x	0,0245	0,0415	0,0603	0,0079
Bx, 6	0,0192	0,0063	0,0551	0,0219

* Calculated from BERNSTEIN' formula: $P = 1 - \sqrt{1 - f}$

picked at random from the control line and from all selection lines in Sweden, Denmark and Norway. In 1982 the same typing procedure was carried out with birds from Finland.

Two main conclusions were drawn from this material (SIMONSEN et al. 1982): The control lines did not deviate as regard to frequency of MHC-haplotypes in spite of many years' separation. Four of the B-haplotypes (B13, B15, B19, B21) were far more frequent than the other haplotypes (Table 1). Since the control population originally was formed by crossing several highly productive commercial strains, the observed dominance of certain B-haplotypes may suggest an association between the B-system and productivity. The frequencies of those B-haplotypes also seemed to be affected by the selection in some of the selection lines, and the response in the B-system seemed to differ, depending on the traits included in the selection.

On these background it was decided that these observations should be investigated further in a separate experiment. The experiment was designed as a Scandinavian project, involving Denmark, Sweden, Finland and Norway. It was started during 1982 and was planned to cover a period of three years. According to the plans, the experiment should focus on the association between the four frequent B-haplotypes and productivity. Both the control lines and the selection lines from the Scandinavian selection experiment were included in the experiment. But because of limited re-

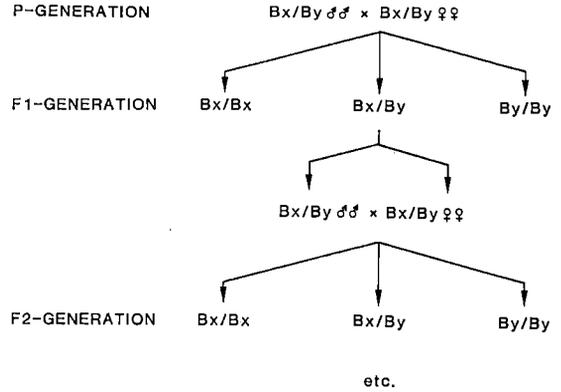


Fig. 2. Mating system.

sources the different participating countries had to concentrate on various parts of the experiment:

- Denmark: B15, B19 and B21 in C and E lines
- Sweden : B13, B15 and B21 in C and I1 lines
- Finland : B13, B15 and B19 in C and N lines
- Norway : B13, B19 and B21 in C and E/W lines

A mating system was designed to produce the homozygous and heterozygous combinations of the B-haplotypes within each line and country (BENTSEN 1984). The mating system is shown in Fig. 2. According to this, six different mating groups were required in each country (three different heterozygotes in each of the two lines). The design would provide two parallels of complete performance records of all B-haplotype combinations in the control population, when the results from all four countries are assembled. The records from the selection lines would be less complete. The entire testing procedure should be repeated three times, each test covering one year, to obtain an adequate number of birds in each group. The following traits should be recorded: Body weight at different ages, age at sexual maturity, rate of laying, egg weight, egg quality, reproductive traits and mortality. The experiment will also provide records for segregation analysis of the B-haplotypes.

The progress of the experiment has not caused any major changes from the original design. The Swedish part has been somewhat delayed, and one of the B-haplotypes that should be investigated in Sweden (B13) had to be replaced with another (B19) because of problems with finding a sufficient number of parents with B13. Some of the mating types in the selection lines in Denmark and Finland have been dropped because of similar problems.

The approximate number of offspring tested from each mating type in each year has been: 100—200 (Denmark), 100—150 (Sweden), 60—100 (Finland), and 50—90 (Norway). In addition to the described experiment, the less frequent B-haplotypes have also been subjected to investigations, particularly in Sweden, where 800 birds have been typed and performance recorded each year in 1982 and 1983. Because of higher frequency of unknown B-haplotypes in the Finnish hens, a separate study on these haplotypes has been carried out in Finland. In Denmark, an extension of the experiment has been planned, to investigate the performance of hens with other B-haplotypes than B13, B15, B19 or B21. For the whole experiment a total of approximately 10 000 birds have been typed up to now. The results until now have been summarized and discussed by the participating countries, but the final computations and the presentation of the results will not be completed until 1985.

3. Selection for improved feed efficiency in egg production

In most countries the feed cost accounts for about 60—70 % of the total expenses in egg production. In spite of this fact, direct selection for feed efficiency is seldom practised among commercial breeders. The main reasons for this are partly that the collection of records on feed consumption on an individual basis is very expensive, and partly that the selection

through reducing body weight and increasing egg mass production has been effective even in improving the feed efficiency. This may, however, change as the level of production increases. Moreover, as pointed out by BENTSEN (1980), even under standardized environment, differences in egg production, body weight and body weight gain explain only 80—90 % of the total variation in feed efficiency between strains, and 70—90 % of the variation between individuals within strains. These suggest that the variation in feed efficiency independent of the variation in body weight and egg production should be large enough to consider the possibility of direct selection for this trait.

During the last few years considerable efforts have been made in many countries to investigate the importance and the possibility of direct selection for feed efficiency in poultry.

As far as egg production is concerned, our contribution in this field may be summarized into three groups of experiments: 1) heritability estimates of energy utilization by White Leghorn chicks, 2) estimates of genetic variation in feed efficiency, and 3) selection experiments for feed efficiency in egg production.

The results from an experiment performed in 1978 showed very clearly that the gross energy utilization calculated as deposited energy in percent of energy consumed differed between sire progeny groups of young chicks (0—4 weeks) from a randombred population. The heritability was estimated to $h^2=0,22$ (ABDOU and KOLSTAD 1979).

The results led to the conclusion that it might be advantageous to utilize such results in a stepwise selection program in laying hens.

The use of multiple regression equations to predict feed consumption from observations on certain traits like egg production, body weight and body weight gain, is well known from the literature (NORDSKOG et al. 1970, 1972, BORDAS and MERAT 1981, BENTSEN 1983 a, PIRCHNER 1983). In our experiments the following models were usually used to estimate

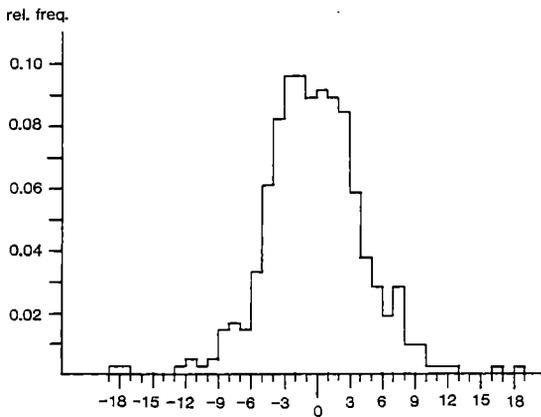


Fig. 3. Distribution of RFC in the WL breed (BENTSEN 1983).

the expected feed consumption, $E(FC)$, in the different parts of the laying period:

$$16-20 \text{ w of age: } E(FC) = a + b_1 MW + b_2 \Delta W$$

$$20-28 \text{ w of age: } E(FC) = a + b_1 MW + b_2 \Delta W + b_3 PR + b_4 SL$$

$$28-66 \text{ w of age: } E(FC) = a + b_1 MW + b_2 \Delta W + b_3 PR$$

where: MW = metabolic weight
 ΔW = body weight change
 PR = egg mass production
 SL = number of days in the recording period affected by the start of lay

The relationship between the recorded feed consumption (FC) of an individual during one of the periods, and the expected feed consumption ($E(FC)$) as predicted from the multiple regression equation for the same period, can be written as: $FC = E(FC) + RFC$, where RFC represents a positive or negative residual, which will reflect the variation in feed consumption not explained by the equations used. Because of a possible connection between $E(FC)$ and the numerical value of RFC, the RFC also was expressed in percent of $E(FC)$.

From Fig. 3 it can be seen that the accumulated percent RFC seems to be a quite normally

Table 2. Heritability estimates for residual feed consumption (BENTSEN 1983).

Age	Heritability
16—22 weeks	0,46 ± 0,13
22—34 „	0,48 ± 0,17
34—66 „	0,23 ± 0,13
16—66 „	0,26 ± 0,14

Table 3. Correlations between feed consumption and some other traits (BENTSEN, 1983).

Trait	r_p	r_G
Shank surface	0,12*	0,11
Comb length	0,15*	-0,08
Feather covering	-0,18*	-0,42
Yolk percentage	0,10*	0,28
Depot fat, chest	-0,01	0,40
Age at first egg	-0,18*	0,36

distributed trait. The distribution of the same trait when measured in actual units (gram) was clearly skewed towards the positive end of the scale.

Estimates of within breed heritabilities and the standard error of estimate in different periods are seen from Table 2. The estimates are in good agreement with the results obtained by WING and NORDSKOG (1982) and HAGGER (1978). As a general impression the heritability seems to show a decreasing trend with increasing age.

Genetic and phenotypic correlations between RFC and other traits which could be thought of having some effect upon feed efficiency, are listed in Table 3. None of the traits seem to represent dominating sources of variation in RFC. However, some significant correlations are found. Poor feather covering at the end of the experiment or large naked body appendices (shank and comb) are associated with increased feed consumption. Delayed sexual maturity seems to be associated with a decrease in feed consumption. An association between high yolk percentage in the eggs and high feed consumption in the laying period is also indicated.

A significant positive correlation between RFC in different recording periods is expected. This leads in turn to a positive correlation be-

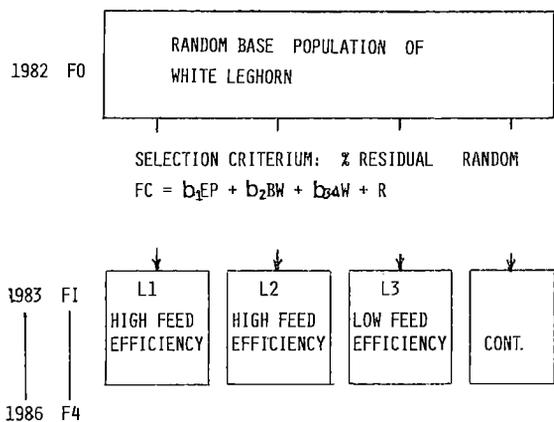


Fig. 4. Selection experiment for feed efficiency.

tween RFC in a single period and the accumulated RFC for the complete laying period. The highest correlations are obtained at an age of 35 weeks or more. The correlation between RFC in a single 4 weeks recording period at this age and RFC for the complete year was in our experiment as high as 0,7, which means that records of feed consumption in a short period at about peak production would provide sufficient information for practical purposes.

The results obtained in our experiments lead to the conclusion that one could expect a genetic response of economic importance, if selection for residual feed consumption was applied in a population of laying hens. To verify this conclusion, selection experiments are started in Norway, Denmark and Finland. The layout of the experiment in Norway is indicated in Fig. 4. Similar outlines are used both in Denmark and Finland. In Denmark the experiment is performed on a normal as well as on a home-grown-plant-product diet to take also the genotype x feeding interaction into consideration (SØRENSEN 1984).

The aim of the projects may be summarized in the following points:

- to see if it is possible by selection to obtain genetic gain in feed efficiency independent of changes in body weight and egg production

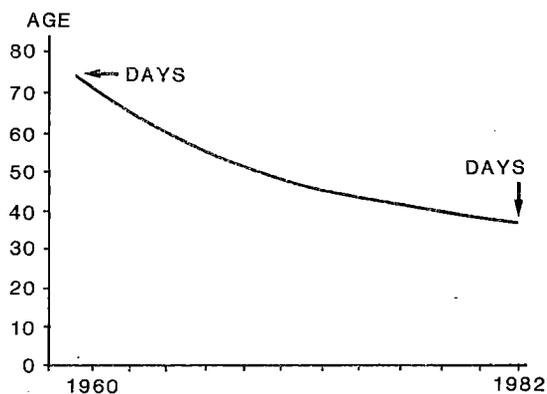


Fig. 5. Number of days to obtain a body weight of 1400 grams (SØRENSEN 1984).

- analyse correlated responses from direct selection for residual feed consumption
- analyse the sources of variation in residual feed consumption

The results so far seem promising, but it is too early to draw important conclusions (KATLE 1984).

In 1982, Institute of Animal Genetics and Breeding, Agricultural University of Norway, initiated some work on estimating body composition in live animals by use of computerized tomography. A Siemens SOMATOM 2 was installed in May 1982, and we are now trying to utilize this new instrument in our research program.

4. Selection for better feed efficiency in slaughter chickens

During the last 25 years or so the breeds and lines used for production of slaughter chickens have increased their growth capacity in such a way that the live weight of 1400 grams is obtained in 36—38 days compared to 75—80 days in 1960 (Fig. 5). This considerable increase in growth capacity is to a large extent due to genetic improvement, which still seems to be appreciable.

However, the law of diminishing returns

Table 4. Selection for food conversion ratio (FCR) in broilers (SØRENSEN 1984).

Line	Weight at 40 days	FCR	
		at 40 d	at 1650 g
FCR	1678	1,70	1,69
FCR	1739	1,74	1,71
Weight	1928	1,88	1,79

leads to the fact that the overall net income from a generation of selection for increased growth rate will decrease, and selection criteria which were not profitable some years ago may become even more important than growth rate itself (SØRENSEN 1984). Such a selection criterion is feed efficiency.

Denmark is the Scandinavian country where most genetic research in this field has been performed. I have extracted three of their recent experiments for this review.

In 1974 a selection experiment was started in which the objective was to compare selection for high growth rate in various feeding regimes. The aim of the experiment was to see if a reasonable selection effect could be obtained in suboptimal environments (low protein level in diet, restricted daily feed intake), and next to see if a genetically based adaptability to that particular environment took place.

SØRENSEN (1984) summarized the results in the following conclusions:

"The chickens selected on a low protein diet showed a considerable adaptability to low protein diets as regards to daily gain. The chickens selected under restricted feeding deviated from the normal line in the way that they ate much faster when the diet was given *ad libitum*. They also showed a tendency to be a little leaner".

In a separate paper during the day's program Dr. Sørensen will present results from a selection experiment on food conversion ratio in broilers (FCR). From a fast growing male line of white Cornish origin two lines were selected for better FCR and a third line for high growth rate. In addition the base population was con-

Table 5. Selection for leg disorder in broilers. Response after two generations of selection (SØRENSEN 1984).

Line	Bending of tibia	Percentage with abnormal		
		toes	tarsus	hocks
"GOOD"	30,4°	5,3	1,3	1,3
"BAD"	37,3°	30,5	6,3	4,6
DIFFERENCE	-7,1°	-25,8	-5,0	-3,3

tinued in the original selection program for male lines.

Until now four generations have been raised, and a considerable divergence can be seen (Table 4). To a fixed age (40 d) the growth line had a much higher body weight than the FCR-lines. On the other hand, to a fixed weight (1650 g) the FCR-lines had a better FCR than the growth line.

5. Selection for leg disorders in broilers

Obviously some broilers suffer from different kinds of leg disorders. According to SØRENSEN (1984) rarely more than 2—5 % of the chickens in a batch suffer so much that they are not able to move, but from time to time one meets batches of chickens in which all birds are very unwilling to move, indicating they have pain when standing.

With the purpose to see what can be done from the genetic point of view, a small scale selection experiment was set up in which two lines were selected divergently for leg disorder in the tibia. The disorder was considered as bending or rotation of tibia, and selection was based on a fullsib index. In the spring of 1984 two generations of selection were carried out and a definite deviation was shown between the "good" and the "bad" lines, as seen from Table 5.

Acknowledgement - Thanks to Dr. P. Sørensen and Mr. H. B. Bentsen for valuable help in preparing the paper.

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Manuscript received August 1984

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EFFECT OF SELECTION FOR PART-RECORD NUMBER OF EGGS FROM HOUSING VS SELECTION FOR HEN-DAY RATE OF PRODUCTION FROM AGE AT FIRST EGG

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GOWE, R. S. and FAIRFULL, R. W. 1984. Effect of selection for part-record number of eggs from housing vs selection for hen-day rate of production from age at first egg. *Ann. Agric. Fenn.* 23: 196—203. (Anim. Res. Centr., Agric. Canada, Ottawa, Ontario, K1A 0C6, Canada.)

Selection for part-record hen-housed egg production was contrasted with selection for part-record hen-day egg production rate from age at first egg in two populations from a highly selected base population. Both strains were also selected for the same complex of other important traits required in egg stocks. Both strains improved in part-record egg production, but the rate selected strain improved much more in full-year egg production measured as hen-housed number or rate of egg production. Both strains were concurrently improved in the array of traits required in egg production stocks.

There was little evidence that either the heritabilities or the genetic correlations changed over the 10 generations, although there were real differences between the two selected strains. Although the heritabilities were generally lower in the selected strains than the control, this could be attributed for the most part to the fact that the sires were heavily selected in the selected populations and randomly selected in the control, and not due to changes in genetic variance associated with the selection program.

It is recommended that breeders of poultry egg stocks select on the basis of a combination of hen-day rate of egg production, sexual maturity and viability rather than using the hen-housed index which puts too heavy an emphasis on early sexual maturity.

Index words: laying hens, part-record selection, multiple trait selection, hen-housed egg production, rate of egg production, control strains, heritabilities, genetic correlations, selection differentials, genetic gains.

INTRODUCTION

BOHREN et al. (1970) and BOHREN (1970) suggested that when the age at sexual maturity had been reduced to as early an age as is practically consistent with the development of adequate body size, poultry selection programs

designed to improve egg production would be more effective if selection was directed at improving the rate of egg production from first egg, rather than to continue selection on part-record egg numbers to a fixed age. The latter

procedure, that is using the hen-housed index (HHP) for a part-record, puts very heavy selection emphasis on reducing age at first egg (AFE) and much less emphasis on improving rate of egg production from AFE (HDR). This report will deal with a 10 generation (1971—1980) test of this hypothesis with two populations derived from a base that previously

had been under selection for egg numbers to a fixed age for about twenty generations and that was characterised by early sexual maturity. Two unselected control populations were used. These data are a part of a larger selection study involving a total of six selected and three control populations.

MATERIAL AND METHODS

Strain 5, an unselected control population, and strain 3, a selected population, originated by a within family division of a common base population of White Leghorn females in 1950. Common males were used to breed both populations of females that year.

Strain 3 was selected for HHP to 273 days of age, fertility, hatchability, viability and egg size. More recently, egg quality traits such as egg specific gravity, Haugh units, blood spot incidence and, to a lesser extent, shell shape and texture, and body weight have been added as selection criteria.

In 1971, strain 1 was derived from strain 3 by a within full-sib family division of females and males. Since then, about 1125 pullets were housed for each selected strain, and 28 sires and 244 dams were used to breed each generation. Strains 1 and 3 have been selected for the same traits except that strain 3 has continued to be selected for HHP to 273 d, and strain 1 was

selected for HDR to 273 d.

In 1958, control strain 7 was developed from four widely used North American commercial stocks and continuously maintained as a random-bred unselected control along with strain 5.

The females were brooded and reared in a 3-deck cage system in a windowless house. After 24 h of light to start, the photoperiod was reduced to 6 h per day during the rearing period. The pullets were randomly housed at maturity in individual 20 x 41 cm cages and fed an all-mash diet and water both supplied *ad libitum*. Day-length was gradually increased after housing to a maximum 16 h photoperiod. Records were maintained to 497 d.

More details on strains, selection procedures, management and test procedures can be found in GOWE et al. (1973), GOWE (1977), GOWE and FAIRFULL (1980, 1982 b, 1984), FAIRFULL and GOWE (1979) and FAIRFULL et al. (1983).

RESULTS

Means and changes

Figure 1 shows HHP to 273 d of the two selected strains and one control strain from their inception. Strain 7 is shown from the time that this control strain was first introduced to Ottawa (GOWE et al. 1973). This report is mainly concerned with the last 10 generations, but

note that part-record egg production to 273 d of strain 3 has been increased by about 30 eggs to 1971. Also, a Marek's disease outbreak in 1969 and 1970 affected all strains. Marek's vaccination started in 1971. From 1974 to 1978, a change in the Marek's vaccine affected all strains negatively, but strain 7 was affected more than the other three strains which are all

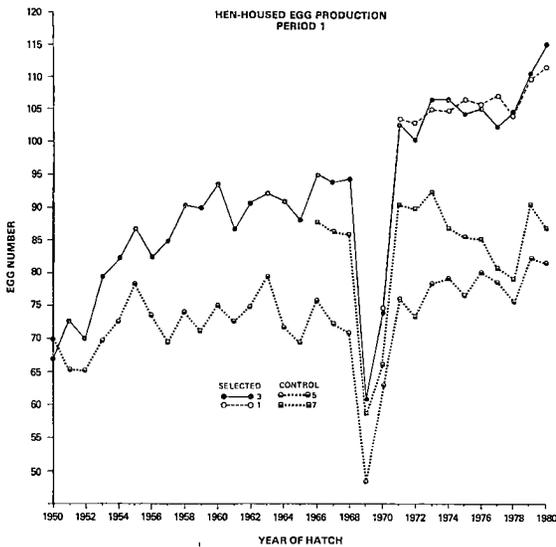


Fig. 1. Hen-housed egg production to 273 d of selected strains 1 and 3, and controls 5 and 7 from 1950 to 1980.

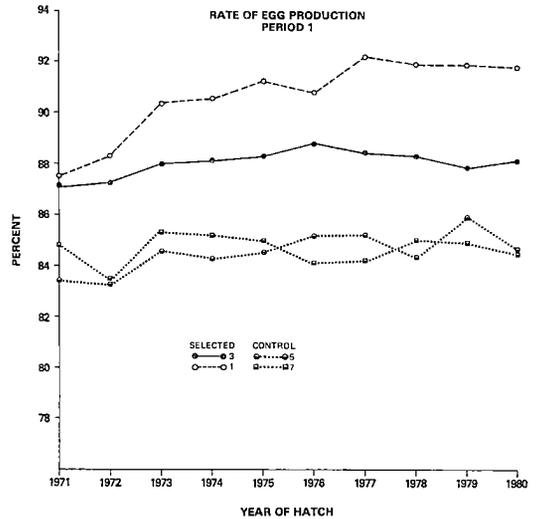


Fig. 2. Hen day rate of egg production from first egg to 273 d of selected strains 1 and 3, and controls 5 and 7 from 1971 to 1980.

related. Nevertheless, it is obvious that progress has been made in improving HHP to 273 d in both selected strains.

Figure 2 illustrates the changes that have taken place in the last 10 generations for the trait HDR to 273 d for the four strains. The much larger increase in response to selection for strain 1 selected for HDR to 273 d is obvious, as is the relative stability of the two controls when the effects of sexual maturity and mortality are removed from egg production.

After 10 generations, selected strains 1 and 3 had similar HHP to 273 d, the primary trait of selection in strain 3 and a correlated trait in strain 1 (Table 1). Both strains had similar selection differentials (Table 2) and genetic gains per generation (Table 3) for this trait although strain 3 had higher values than strain 1. For the correlated trait HHP to 497 d, the results were different. Strain 1 laid 17 eggs more to 497 d than strain 3 in 1980 (Table 1).

Strain 1 (selected for HDR to 273 d) had 4 % higher rate than strain 3 in which this was a correlated trait and this advantage increased in the residual parts of the year, 5 % from 274 to

385 d and 9 % from 386 to 497 d (Table 1). Although both strains had similar selection differentials for HDR to 273 d (Table 2), the genetic gains for HDR from 1971 to 1980 for strain 1 in the early part of the record, the residual parts of the year and the full year were much greater than those of strain 3 (Table 3).

After 10 generations with no direct selection for sexual maturity, strain 1 birds matured 12 days later than strain 3 (Table 1). Given the higher selection differentials (-2.6 days average, Table 2) and consequently greater genetic gain (-0.99 days average, Table 3) for strain 3 relative to strain 1, this difference was expected.

The 1980 population of both selected strains had acceptable performance for the selected egg quality traits: egg weight, egg specific gravity, Haugh units and blood spots; and body weight (Table 1). These strains have been improved genetically for these traits (GOWE and FAIRFULL 1980, 1984, FAIRFULL and GOWE 1979) and this is reflected, in part, by their superiority over the control strains. Both selected strains also had high viability (Table 1), but its

Table 1. Means of selected strains 1 and 3, and control strains 5 and 7 for the population hatched in 1980.

Trait ^a		Strain			
		1	3	5	7
HHP to 273 d	No.	111 ^a	115 ^f	82 ^s	87 ^t
HHP to 497 d	No.	279 ^a	262 ^f	209 ^s	212 ^s
B & RM	%	2,4 ^q	2,8 ^q	6,0 ^r	2,3 ^q
LHM to 497 d	%	4,7 ^q	5,9 ^q	10,0 ^r	5,0 ^q
AFE	d	152 ^q	140 ^r	173 ^s	167 ^t
HDR to 273 d	%	92 ^a	88 ^r	85 ^s	84 ^s
HDR 274 to 385 d	%	85 ^a	80 ^r	74 ^s	74 ^s
HDR 386 to 497 d	%	76 ^a	67 ^r	59 ^s	59 ^s
HDR to 497 d	%	85 ^a	79 ^r	72 ^s	72 ^s
365 d BW	dg	181 ^q	183 ^r	204 ^s	187 ^t
240 d EW	g	57,8 ^q	57,9 ^q	51,8 ^r	54,2 ^s
240 d SG		86,9 ^q	86,0 ^r	84,1 ^s	83,8 ^s
240 d HU		88,1 ^q	85,4 ^r	83,3 ^s	82,4 ^t
240 d BS	%	2,7 ^q	3,5 ^q	3,9 ^q	5,8 ^r
FE		2,06 ^q	2,14 ^f	2,40 ^s	2,41 ^s

^a HHP = hen-housed egg production, HDR = hen day rate of lay from age at first egg (or period specified if start is after first egg), B & RM = brooding and rearing mortality, LHM = laying house mortality, AFE = age at first egg, BW = body weight, EW = egg weight, SG = specific gravity (1,082 reported as 82), HU = Haugh units, BS = blood spots, FE = g feed per g egg mass (measured after peak egg production)

^{q, r, s, t} Means with the same superscript are not significantly different, and those with different superscripts are significantly different ($P < .05$)

genetic improvement in selected strains 1 and 3 over the last 10 generations has been small (GOWE and FAIRFULL 1980, 1984, FAIRFULL and GOWE 1979). For the correlated trait feed efficiency, strain 1 had better performance than strain 3 and both selected strains were better than the controls.

Table 2. Mean selection differentials from 1970 to 1979 of selected strains 1 and 3 for hen-housed egg production (HHP) to 273 days, hen day rate of egg production from first egg (HDR) to 273 days and age at first egg (AFE).

Period	HHP to 273 d		HDR to 273 d		AFE	
	Strain 1	Strain 3	Strain 1	Strain 3	Strain 1	Strain 3
1970	13,2 ^a	13,2	5,2 ^a	5,2	-2,6 ^a	-2,6
1971	8,2	10,8	7,5	6,0	-0,1	-5,1
1972	9,4	9,6	6,3	4,4	-1,7	-4,7
1973	7,9	10,4	5,1	5,4	-2,3	-5,5
1974	6,9	8,8	4,8	5,2	-2,3	-3,8
1975	7,7	11,0	4,2	4,8	-2,0	-5,0
1976	7,0	10,5	4,3	4,4	-0,9	-5,3
1977	8,0	9,6	4,2	4,3	-3,6	-3,4
1978	8,7	10,5	4,4	4,3	-2,0	-4,2
1979	5,0	9,7	4,6	4,8	-0,2	-4,4
1970-79	8,2	10,4	5,1	4,9	-1,8	-4,4

^a A strain 3 population selected for HHP to 273 d was divided into two groups to produce the 1971 populations of both strains 1 and 3

Table 3. Genetic gains per generation of selected strains 1 and 3 from 1971 to 1980 calculated as deviations from control strains 5 and 7.

Trait ^a	Strain 1	Strain 3
HHP to 273 d	0,78 ^{**}	1,02 ^{**}
HHP to 497 d	1,99 ^{**}	0,84
LHM to 497 d	0,18	0,34
AFE	-0,39	-1,38 ^{**}
HDR to 273 d	0,36 ^{**}	-0,01
HDR 274 to 385 d	0,39 ^{**}	0,08
HDR 386 to 497 d	0,59 ^{**}	0,06
HDR to 497 d	0,46 ^{**}	0,07

^a See footnote in Table 1

* $P < 0,05$

** $P < 0,01$

Heritabilities and correlations

Heritabilities based on sire variance components (h_s^2)

For HHP to 273 d, HHP to 497 d and LHM to 497 d, the h_s^2 of selected strains 1 and 3 was approximately a half to third of the estimate of unselected, control strain 5. In strain 1, h_s^2 of

Table 4. Estimates of heritabilities from sire (h_S^2) and dam (h_D^2) components with linear estimates of their change per generation (b) from 1971 to 1980 for selected strains 1 and 3, and control strain 5.

Trait ^c		Strain 1				Strain 3				Strain 5			
		h_S^2		h_D^2		h_S^2		h_D^2		h_S^2		h_D^2	
		x ^a	b	x ^a	b	x ^a	b	x ^a	b	x ^a	b	c	c
HHP to 273 d	No.	,09	-,007	,25	,021	,11	-,005	,29	,004	,31	,40	,28	,33
HHP to 497 d	No.	,07	-,008	,25	,027*	,09	-,008	,39	,006	,24	,49	,18	,39
LHM to 497 d	%	,04	-,001	,10	,025*	,04	,000	,22	,013	,12	,24	—	—
AFE	d	,42	-,023	,41	,006	,29	-,031	,31	-,033*	,68	,58	,38	,56
HDR to 273 d	%	,14	-,024	,24	,022	,22	,002	,29	-,010	,24	,08	,27	,31
HDR 274 to 385 d	%	,21	-,013	,37	,008	,24	-,021	,38	,003	,29	,06	,31	,31
HDR 386 to 497 d	%	,16	,007	,37	-,001	,19	-,022*	,41	,005	,12	,51	,16	,29
HDR to 497 d	%	,20	-,011	,41	,003	,25	-,023	,44	,005	,30	,37	,35	,33

* $P < 0,05$

^a Mean of 1971 to 1980

^c From GOWE et al. (1973)

^e See footnote in Table 1

HDR to 273 d was smaller than that of strain 3 and control strain 5. Also, h_S^2 of HDR to 273 d was higher than that of HHP to 273 d. However, for the residual parts of the year (274 to 385 d, 386 to 497 d) and the whole year in strain 1 and for all parts of the year in strain 3, h_S^2 of HDR was similar to that of the control. For AFE, h_S^2 was slightly reduced in selected strain 3, but not in strain 1 compared to the control. For control strain 5, the h_S^2 estimates from GOWE et al. (1973) are considered the more reliable ones as those populations were larger and structured to estimate h^2 with minimal error while the other populations were structured to reduce inbreeding and drift, and were poorly structured to estimate h^2 (Table 4).

In strain 3 from 1971 to 1980, h_S^2 of HDR 386 to 497 d decreased slightly (Table 4). There were no other significant trends in h_S^2 from 1971 to 1980 (Table 4).

Heritabilities based on dam components (h_D^2)

For the most part, h_D^2 estimates of selected strains 1 and 3, and control 5 were similar. However, the h_D^2 of AFE in both selected strains and of LHM to 497 d in strain 1 were lower than those of control 5. For HDR to 497 d, h_D^2 of the selected strains were higher than

that of control 5 and in the residual part years for HDR, there was a similar, but less certain tendency. From 1971 to 1980, h_D^2 of HHP and LHM to 497 d increased slightly in strain 1, and h_D^2 of AFE decreased slightly in strain 3. There were no other significant trends in h_D^2 values (Table 4).

Genetic correlations from sire variance components (r_g)

The r_g between HHP to 273 d and HHP to 497 d of strain 1 was lower than that of strain 3. However, the corresponding r_g between HDR to 273 d and HDR to 497 d was similar in both selected strains although slightly lower for strain 1.

The r_g between HDR to 497 d and LHM to 497 d was positive in strain 1 and negative in strain 3, but not large in either case. Selection for HHP to 273 d seems to have reduced the r_g of this trait with AFE in strain 3. The r_g 's of LHM to 497 d and HDR for the three egg production periods also differed in the two selected strains. For other correlations, the differences between the selected strains were small and of little significance.

Although all correlations calculated are not presented here, it should be noted that strains 1 and 3 also differed in the size of their r_g 's

Table 5. Estimates of genetic correlations based on sire components with linear estimates of the change per generation (b) from 1971 to 1980 for selected strains 1 (above diagonal) and 3 (below diagonal).

Trait ^a		HHP to 273 d	HHP to 497 d	LHM to 497 d	AFE	HDR to 273 d	HDR 274 to 385 d	HDR 386 to 497 d	HDR to 497 d
HHP to 273 d	x	—	,54	—,39 ^c	—,91	,57 ^c	,25	,13	,28
	b	—	—,018	—,072	—,027*	—,010	—,055	—,055	—,065*
HHP to 497 d	x	,84	—	—,60 ^c	—,40	,66	,86	,82	,91
	b	,033	—	,055	—,017	—,042	—,013	—,002	—,005
LHM to 497 d	x	—,35	—,47	—	,04 ^c	—,08 ^c	,11 ^c	,19 ^c	,36 ^c
	b	—,057	—,111	—	,298*	,149	,350	,338	,455
AFE	x	—,79	—,24	,05	—	—,18 ^c	,01	,07	—,02
	b	,014	—,034	,075	—	—,032	—,005	—,006	—,002
HDR to 273 d	x	,72	,73	—,13	—,24	—	,61 ^c	,42 ^c	,65 ^c
	b	,055	,022	—,081	—,056	—	—,061	—,064	—,048
HDR 274 to 385 d	x	,42	,94	—,32	,03	,74	—	,83	,96
	b	,051	—,012	—,119	—,011	—,003	—	—,021	—,009*
HDR 386 to 497 d	x	,18	,81	,01	,06	,36	,78	—	,94
	b	,032	—,033	—,006	—,012	—,013	—,051	—	—,001
HDR to 497 d	x	,44	,97	—,26	—,05	,72	,98	,83	—
	b	,058	—,002	—,103	—,033	,017	—,009	—,036	—

* P < 0,05

^a See footnote in Table 1

^c Values are based on 1971 to 1979

between egg production traits and egg weight (HDR to 273 d and 240 d EW, —,17 and —,59; HHP to 273 d and 240 d EW, —,15 and —,45, for strains 1 and 3, respectively), and between HDR to 497 d and 365 d body weight (,24 and —,16, respectively).

Similar to heritabilities, there were few sig-

nificant trends from 1971 to 1980 in the r_g values and those that were significant involve only strain 1. The r_g 's of HHP to 273 d with AFE and with HDR to 497 d, decreased as did that of HDR to 497 d with HDR 274 to 385 d, but the r_g of LHM to 497 d with AFE increased (Table 5).

DISCUSSION

When the effect of Marek's disease mortality was removed over the last 10 years of the study, the controls were very constant for part-record egg production measured as either rate or egg numbers and also relatively so for the full-record. The trend in one control suggested a slight improvement in the environment (Fig. 1).

Strains 1 and 3 were selected for ten traits with two others receiving minor consideration. Over 10 generations from 1971 to 1980, the traits under selection as well as important correlated traits improved in almost all cases of both strains. Not all of these changes were statistically significant; however, they were all in the desired direction with the exception of

laying house viability which had a slight, non-significant decrease. This was probably an anomaly due to a change in Marek's disease vaccines (GOWE and FAIRFULL 1982 a, 1984) and the fact that the estimate was a linear one: the true situation was no change in viability except for environmental changes.

The rate (HDR to 273 d) selection was more effective in improving full-record egg numbers (HHP to 497 d) and rate (HDR to 497 d) as well as residual rate (HDR: 274 to 385 d and 386 to 497 d) than egg numbers (HHP to 273 d) selection. In addition, there was more improvement for egg shell quality (egg specific gravity), Haugh units and blood spots in the

rate than in the egg numbers selected strain. However, there was little difference between the selected strains in viability, body weight or egg weight.

Selection for egg numbers reduced sexual maturity (AFE) much more than rate selection by putting more selection pressure on this component of the hen-housed egg production index as BOHREN (1970) predicted. This seems to result because it is biologically easier to increase potential days of lay than to increase rate of lay. Although both are highly correlated with part-record egg numbers, the absolute sizes of variances, selection differentials, etc. are larger for sexual maturity than for rate of lay and at the start of selection, sexual maturity was likely farther from the biological limit. While sexual maturity decreased in the rate selected line as selection proceeded, this appears to be unique to this gene pool. In two other strains, both from different unrelated genetic bases, that have been selected for part-record rate from AFE and the other traits strain 1 has been selected for, progress in rate of egg production was accompanied by later sexual maturity (FAIRFULL and GOWE 1979, GOWE and FAIRFULL 1980).

Neither part-record rate nor part-record egg numbers seem to be optimal for selection to improve full-record egg numbers although selection on rate appears marginally better than selection on egg numbers. Hen-housed egg production is really an index of the three traits — viability, sexual maturity and rate of egg production. In our opinion, including sexual maturity as a selected trait along with selection for rate would be preferable to part-record selec-

tion for either rate or egg numbers without any consideration of sexual maturity. Viability should also be considered as a separate trait.

The h_s^2 of part-record rate was higher in both strains than that of part-record egg numbers. This reinforces the above argument. Not unexpectedly, the h_s^2 of part-record rate was lower in the rate selected strain than in the one selected for egg numbers.

The h_s^2 estimates of traits under direct selection were generally lower in the selected strains than the control. However, there were no indications of substantial changes in h_s^2 estimates over the 10 generations from 1971 to 1980. In an earlier report, GOWE and FAIRFULL (1984) showed that there were no substantive changes in h_s^2 values for two strains (strain 3 discussed here and another unrelated strain 4) over 30 generations after the initial change from a random breeding to a selected population. This change in the breeding status of a population seems to cause an initial reduction in the additive genetic variances and h_s^2 , due to the fact that the sires used were all highly selected, but thereafter, only insignificant or very small gradual changes occur.

There were a few large differences in r_g 's between the two selected strains, however, for the most part, r_g values were similar in both selected strains and there was little evidence of changes over the 10 generations for most of r_g values. It would appear that some r_g 's change early in a selection program as a result of selection emphasis and the underlying biological relationships among traits, and that for the most part these relationships persist.

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ARC Contribution No: 1305
Manuscript received October 1984

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SPECIALISED COMPARED WITH INDEX SELECTION FOR TWO GENETICALLY ANTAGONISTIC TRAITS IN LAYING HENS

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WEYDE, C. & LILJEDAHN, L-E. 1984. Specialised compared with index selection for two genetically antagonistic traits in laying hens. *Ann. Agric. Fenn.* 23: 204—210. (Dept. of Anim. Breed. and Genet., Swed. Univ. of Agric. Sci., S-75007 Uppsala, Sweden.)

The present paper deals with the results of 9 generations of selection from the Swedish part of the Scandinavian breeding experiment with laying hens.

The main object of this experiment was to compare single trait selection for egg number in line N and egg weight in line E followed by crossing with two-trait index selection for egg number and egg weight in line I.

The layers' diet used as a nutritional selection environment was sub-optimal with regard to the contents of energy, protein and essential amino acids.

In general the selection was effective in improving the traits identical with or closely related to the selection objectives in the various lines.

As expected, the direct selection response in each of the two lines specialised for improvement of number of eggs (N) and egg weight (E) was significantly greater than the corresponding responses in the line selected for an index of egg number and egg weight.

The existence of the negative genetic correlation was clearly demonstrated by the marked decline in egg weight as a result of selection for number of eggs in line N and in number of eggs as a result of selection for egg weight in line E.

These results are consistent with the results from analysing the genetic parameters which among other things showed that the genetic correlation between egg number and egg weight changed from values not significantly different from zero in the base population (Gen. 0) to negative values significantly different from zero during the process of selection in lines N, E and I.

The heritability, estimated by means of the resemblance between paternal half sibs, seems to have been reduced during the process of selection (1) in line N for number of eggs (20—42w), (2) in lines N and I for age at first egg, and (3) in lines N, E and I for egg mass (20—42w).

The sub-optimal layers' feed mash was found to be a favourable selection environment, thus allowing the genetic variation to be clearly expressed.

Index words: selection response, antagonistic traits, laying hens, egg number, egg weight, index selection, specialised selection, heritability, genetic correlation.

INTRODUCTION

The present report is based on some of the results of 9 generations of selection from the Swedish part of the Scandinavian breeding experiment with laying hens (cf. LILJEDAHL et al. 1979, LILJEDAHL and WEYDE 1980, KOLSTAD 1980, SØRENSEN 1980).

The background for the design of this experiment was the evidence that the selection response is significantly weakened when two or more genetically antagonistic traits are selected for simultaneously in the same population, i.e. when the genetic correlations between them are negative. Thus, if such traits are combined in a selection index the heritability of the index

would be less than might be expected from the heritabilities of the component traits (DICKERSON 1955, NORDSKOG et al. 1974).

Thus, the present experiment was designed with the main object of investigating if specialised selection for each of two genetically opposed traits, egg number and egg weight, followed by crossing could be a possible method of avoiding the counteractive effect of this antagonism.

Only the results from selection are considered in the present paper. Further, only the most essential traits with regard to the principal problem to be dealt with are included.

MATERIAL AND METHODS

Synthesis of the base population

The base population was formed by mating males and females from seven commercial stocks (1—7) according to a diallel system with the exception that males from one of the stocks were not available. Consequently, birds from 42 combinations were obtained in F_1 . After the formation of the F_1 generation the population was randomly mated for three generations before the breeding experiment was started in 1973 with day-old chicks from the F_4 generation.

System for selection and crossing

In the F_4 generation the base population was divided into four selection lines and a control as follows

- N = line selected for number of eggs (NE)
- E = line selected for egg weight (EW)
- I = line selected for NE and EW combined

into a selection index and divided into two replicates in Gen. 1—4 with $I=0,28$ NE + 1,15 NE; from Gen. 4 on the two replicates were put together with $I = \text{Egg mass (EM)}$

C = control line reproduced by random mating

The selection was based on the production results obtained in the period 20—42 weeks of age such that the generation interval would be about one year.

Environment

The environmental conditions were the same as usually recommended in practice except for the fact (1) that the hens were housed in single-hen cages and (2) that the energy and protein contents of the layers' feed mash were lower than normal (approx. 2,5 Mcal/kg and 13 % crude protein with the level of the essential amino acid leucine being about 20 % below the NRC recommendation).

Traits

The traits considered in the present paper are confined to the following:

Number of eggs	20—42 w = NE (20—42)
	42—63 w = NE (42—63)
Egg weight	20—42 w = EW (20—42)
	42—63 w = EW (42—63)
Egg mass	20—42 w = EM (20—42)
	42—63 w = EM (42—63)
Age at first egg	= AFE
Rate of lay	AFE-63 w = RL (AFE-63)

Principles for construction of the selection indexes

The selection indexes used in the present experiment are of the conventional type (cf.

HAZEL 1943, OSBORNE 1957 a, b, HENDERSON 1963). The prediction of a female's breeding value is obtained from her own performance and the means of her full-sisters and half-sisters while the prediction of a male's breeding value is reduced to the means of his full-sisters and half-sisters for the traits manifested in females only.

At the present time the 9th generation of birds have finished the period 20—42 weeks of age but not the residual period 42—63 weeks. Thus, the results of 9 generations of selection are presented for the former period and the results of 8 generations of selection for the latter period.

For a detailed description of the material and methods the reader is referred to the papers by LILJEDAHL et al. (1979) and LILJEDAHL and WEYDE (1980).

RESULTS

In Table 1 the mean numbers of breeders and the mean selection intensity (%) over the different generations are given together with the expected and realised coefficient of inbreeding in the last generation.

Table 1. Mean numbers of breeders, selection intensity, and the expected and realised coefficient of inbreeding.

Line	Mean numbers of breeders selected from Gen. 0—8		Mean selection intensity (%) in Gen. 0—8		Coefficient of inbreeding (%) in Gen. 9	
	♂♂	♀♀	♂♂	♀♀	Expected	Realised
N	18,7	119,4	13,6	24,7	6,9	12,0
E	18,9	127,7	14,8	30,0	6,8	10,4
I	19,4	114,4	13,7	25,7	6,8	9,1

Selection response

Number of eggs

As shown in Fig. 1 selection for NE (20-42) in line N has resulted in a marked direct response amounting to 3 eggs/gen. A great proportion of

this response is caused by a considerable reduction of age at first egg (—24 days) in this line. This is also the case for the response of about 2 eggs/gen. to selection for an index of NE (20—42) and EW (20—42) in line I (—18 days). In line E selected for EW (20—42) the correlated cumulative response in NE (20—42) first increased moderately up to about 4 eggs in Gen. 3 but decreased suddenly after that with an average of about 2 eggs/gen., thus indicating that the genetic correlation between NE (20—42) and EW (20—42) had turned negative.

The correlated response in NE (42—63) was greatest in line N being about half that of the direct response in NE (20—42). In line I no significant response in NE (42—63) has been obtained up to Gen. 8. Selection for EW (20—42) in line E resulted in a negative response in NE (42—63), being at least as large as for NE (20—42), again demonstrating the genetic antagonism between egg number and egg weight.

CUMULATIVE DEVIATIONS FROM THE CONTROL

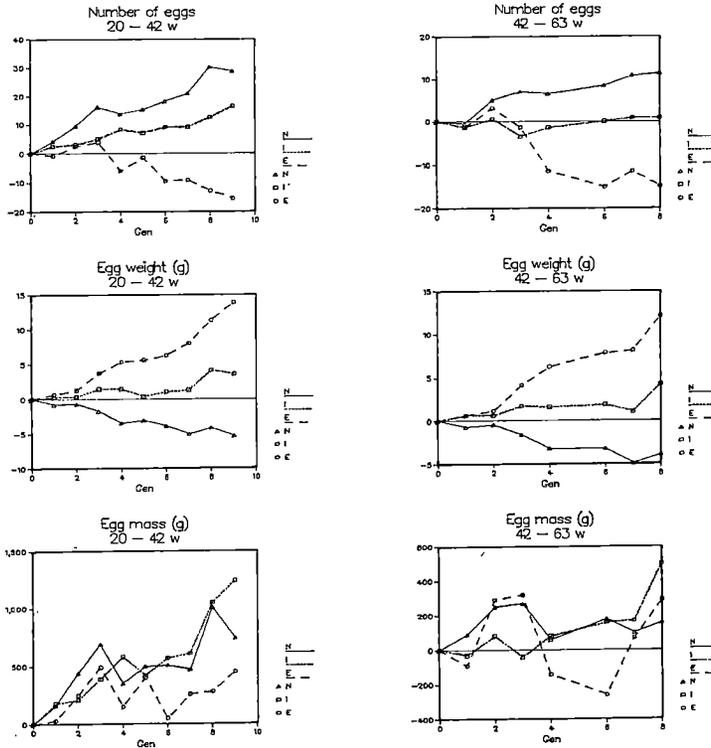


Fig. 1. Selection response by line and generation for number of eggs, egg weight and egg mass in the periods 20—42 and 42—63 weeks of age.

Egg weight

The results for egg weight in Fig. 1 show that the direct selection response for EW (20—42) in line E was very pronounced, thus amounting to about 1,5 g/gen., while the improvement due to index selection in line I was about four times smaller. EW (20—42) decreased already from the start of selection in line N as a further proof of the genetic antagonism between egg number and egg weight, the decline being about 0,7 g/gen.

All the selection responses in EW (42—63) were very similar to the corresponding responses in EW (20—42), thus indicating a genetic correlation between EW (20—42) and EW (42—63) close to unity.

Egg mass

From Fig. 1 it appears that the improvement of EM (20—42) seems to have been greatest in line I, most closely associated with the selection for this trait, by surpassing line N in Gen. 9. Obviously, the selection response for this trait was smallest in line E.

The results for EM (42—63) indicate that the selection response in line I as for EM (20—42) has attained the greatest cumulative value among the three selection lines. However, the improvement was about two and a half times smaller than for EM (20—42).

CUMULATIVE DEVIATIONS FROM THE CONTROL

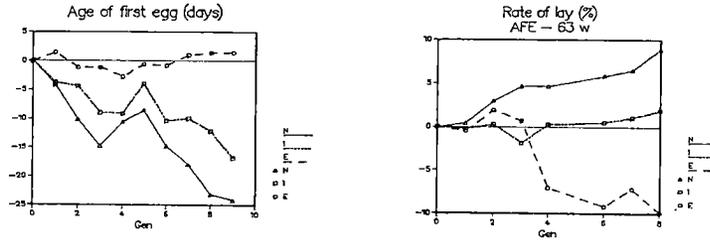


Fig. 2. Selection response by line and generation for age at first egg (AFE) and rate of lay from AFE to 63 weeks of age.

Age at first egg

As shown in Fig. 2 selection for NE (20—42), and for an index of NE (20—42) and EW (20—42) has resulted in marked correlated responses in AFE amounting to —24 days in line N and —18 days in line I while no clearcut response has been obtained as a result of selection for EW (20—42) in line E.

Rate of lay (%)

The results for RL (AFE-63) in Fig. 2 show that the correlated selection response for this trait was at least as large, though negative (—10%), in line E as in line N (9%), which indicates a high negative genetic correlation between rate of lay and egg weight. The correlated selection response in line E was fairly small (2%).

Genetic parameters

The genetic parameters as shown in Tables 2—3 were estimated partly for the base population (Gen. 0) and partly for the various selection

lines as means of the different generations. They are given as paternal half sib estimates.

Since the distribution of heritability (h^2) is unknown it is difficult to judge if the estimates of h^2 in the various selection lines over the generations passed are significantly different from those in the base population (Gen. 0). However, in view of the standard errors it seems reasonable to suppose that h^2 has decreased as a result of the process of selection (1) in line N for number of eggs (20—42 w), (2) in lines N and I for age at first egg, and (3) in lines N, E and I for egg mass (20—42 w). For some unexplicable reason selection seems to have increased h^2 for NE (42—63) and for RL (AFE-63) in line E.

Obviously, the selection has changed the genetic correlation (r_G)

* for both NE (20—42) x EW (20—42) and NE (42—63) x EW (42—63) from values not significantly different from zero in the base population into negative values significantly different from zero in lines N, E and I

* for NE (20—42) x NE (42—63) from about 0,7 to about 0,4 and for EW (20—42) x EW (42—63) from about 0,9 to about 0,8.

Table 2. Estimates of heritabilities and their standard errors for the various traits in the base population (Gen. 0) and in the selection lines.

Line	NE (20—42 w)		NE (42—63 w)		EW (20—42 w)		EW (42—63 w)	
	Gen. 0	Gen. 1—9	Gen. 0	Gen. 1—8	Gen. 0	Gen. 1—9	Gen. 0	Gen. 1—8
N	0,344±0,097	0,206±0,051	0,151±0,054	0,165±0,043	0,605±0,147	0,514±0,053	0,673±0,158	0,536±0,081
E	0,344±0,097	0,353±0,065	0,151±0,054	0,327±0,067	0,605±0,147	0,626±0,087	0,673±0,158	0,675±0,095
I	0,344±0,097	0,344±0,063	0,151±0,054	0,149±0,045	0,605±0,147	0,706±0,088	0,673±0,158	0,578±0,085

Line	EM (20—42 w)		EM (42—63 w)		AFE		RL (AFE-63 w)	
	Gen. 0	Gen. 1—9	Gen. 0	Gen. 1—8	Gen. 0	Gen. 1—9	Gen. 0	Gen. 1—8
N	0,526±0,133	0,216±0,045	0,208±0,067	0,154±0,040	0,601±0,146	0,359±0,061	0,225±0,071	0,230±0,020
E	0,526±0,133	0,251±0,067	0,208±0,067	0,242±0,066	0,601±0,146	0,441±0,073	0,225±0,071	0,373±0,042
I	0,526±0,133	0,236±0,049	0,208±0,067	0,130±0,043	0,601±0,146	0,336±0,058	0,225±0,071	0,295±0,026

Table 3. Estimates of genetic correlations and their standard errors for some trait combinations including number of eggs (NE) and egg weight (EW) in the base population (Gen. 0) and in the selection lines.

Line	Trait combination							
	NE (20—42 w) x EW (20—42 w)		NE (42—63 w) x EW (42—63 w)		NE (20—42 w) x NE (42—63 w)		EW (20—42 w) x EW (42—63 w)	
	Gen. 0	Gen. 1—9	Gen. 0	Gen. 1—8	Gen. 0	Gen. 1—8	Gen. 0	Gen. 1—8
N	0,254±0,157	-0,353±0,108	-0,156±0,178	-0,531±0,169	0,687±0,109	0,413±0,176	0,936±0,021	0,808±0,057
E	0,254±0,157	-0,563±0,106	-0,156±0,178	-0,528±0,118	0,687±0,109	0,652±0,092	0,936±0,021	0,957±0,019
I	0,254±0,157	-0,541±0,083	-0,156±0,178	-0,575±0,151	0,687±0,109	0,662±0,133	0,936±0,021	0,938±0,022

DISCUSSION AND CONCLUSIONS

In general, the selection was effective in improving the traits identical with or closely correlated to the selection objectives in the various lines.

As expected, the direct selection response in each of the two lines specialised for improvement of number of eggs (N) and egg weight (E) was significantly greater than the corresponding responses in the line selected for an index of egg number and egg weight. However, line I was most inferior to line N and line E with regard to the improvement of NE (42—63) and EW (42—63) respectively.

The existence of the negative genetic correlation between egg number and egg weight has been clearly demonstrated by the marked decline in EW (20—42) and EW (42—63) as a result of selection for NE (20—42) in line N, and in NE (20—42) and NE (42—63) as a result of selection for EW (20—42) in line E.

The relatively large selection responses obtained in the present experiment might be explained as resulting from the following preconditions.

- (1) A wide genetic variation was introduced into the base population during the initial phase of its formation.
- (2) A considerable part of the potential genetic variation was released by recombination and crossing-over during the three generations of random mating between F_1 and the first generation of selection (F_4).
- (3) The sub-optimal layers' feed mash with regard to the contents of energy, protein and amino acids has been a favourable environment for selection thus allowing the genetic variation to be clearly expressed.

The results on the genetic parameters indica-

ted among other things that the genetic correlation between egg number and egg weight changed from values not significantly different from zero in the base population (Gen. 0) into negative values significantly different from zero

during the process of selection in lines N, E and I. These results are consistent with the marked decline in egg weight due to selection for egg number in line N and in egg number due to selection for egg weight in line E.

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Manuscript received October 1984

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SELECTION FOR HIGH NUMBERS OF MULTIPLE YOLKED EGGS IN WHITE LEGHORNS

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ABPLANALP, H. 1984. Selection for high numbers of multiple yolked eggs in White Leghorns. *Ann. Agric. Fenn.* 23: 211—215. (Dept. of Avian. Sci., Univ. of California, Davis, California 95616, U.S.A.)

Selection over 18 generations for increased numbers of multiple-yolked eggs in a flock of White Leghorn chickens (DY) resulted in an increase of extra yolks found in multiple-yolked eggs from an average of less than one to approximately forty. The highest numbers of yolks ovulated by individual hens exceeded 200 to 40 weeks of age. Average body weight of hens increased in the course of selection for multiple ovulations, thus confirming the genetic correlation between body weight and ovulation rate found in hens of fast-growing broiler lines. Introduction of the sex-linked gene for dwarfing into the DY-line resulted in a reduction of multiple ovulations from 38,7 to 13, a reduction in the number of rapidly developing ovarian follicles from 11,4 to 7,5, and an increase in the number of single-yolked eggs laid by hens. Dwarf pullets have a lower percentage of abdominal fat than normal-sized hens.

Index words: selection, multiple-yolked eggs, dwarf gene, follicle number, fat.

INTRODUCTION

Continued selection for increased numbers of multiple-yolked eggs in a closed population of Leghorns (Line DY) has been carried out at the University of California since 1963. ABPLANALP et al. (1977) reported an increase in double-yolked eggs from an average of less than 1,0 in the base population (P) selected for high egg number to about 30 in the DY-line after eleven generations. Since then an additional 7 generations of selection have been carried out. Concurrently, the recessive gene for sex-linked dwarfing (dw) was introduced into the DY-line by three repeated backcrosses in order to examine possible similarities of superovulation in

the DY line to that observed in growth selected broiler hens. In the latter the dwarf gene has been shown to reduce superovulation with the attendant undesirable features of multiple-yolked and soft-shelled eggs, as first reported by JAAP (1968).

Selection

Selection for increased incidence of multiple-yolked eggs was on the basis of an individual hen's egg record to 40 weeks of age. All eggs were broken out and examined for yolks; soft-

Table 1. Generation means of combined sub-lines selected for high numbers of double-yolked eggs between 1964 and 1983.

Year and Season of Hatch	Generations Selected	Hens Tested	Eggs to 40 weeks of Age			40 Week Body Wt. (kg)	Egg Weight (gm)		Age at First Egg (days)
			Single	Double	Triple		30 Wk.	40 Wk.	
1964 S	1	283	87,9	2,42	—	1,72	49,8	—	140
1965 S	2	244	75,68	6,39	—	1,71	49,4	—	148
1966 S	3	371	72,69	6,44	—	1,69	51,0	—	153
1967 S	4	496	42,18	8,80	—	1,68	51,4	—	149
1968 S	5	242	69,96	8,68	—	1,80	56,2	—	162
1969 A	6	303	69,03	11,22	—	1,82	52,8	—	158
1970 A	7	311	63,17	19,34	—	1,89	55,2	—	158
1971 A	8	122	64,70	27,03	—	1,90	53,6	—	143
1972 A	9	55	61,35	27,17	—	1,92	55,6	—	142
1974 S	10	55	58,99	27,72	—	1,93	55,0	—	139
1975 S	11	51	59,66	30,63	0,6	1,94	49,6	—	132
1976 S	12	57	51,69	35,91	2,1	1,98	47,1	—	135
1977 S	13	54	46,37	38,74	2,5	1,93	46,0	49,9	137
1978 A	14	64	48,37	36,62	2,2	1,98	—	52,1	146
1979 A	15	51	48,44	39,64	3,7	1,90	—	48,3	140
1980 A	16	53	58,60	26,0	1,3	1,77	—	47,4	150
1981 A	17	89	45,8	37,8	3,5	1,85	—	47,1	148
1982 A	18	38	50,7	30,8	1,4	1,83	—	43,6	150

shelled or misshapen eggs were recorded. Males were selected from families with the highest average number of multiple-yolk eggs. Details about the numbers of birds tested and used in matings were given in an earlier report (ABPLANALP et al. 1977) and are listed for the last 7 generations in Table 1. It should be noted that for the first 10 generations of the experiment two replicate DY lines were selected along with a single control flock (P) from which they had been derived. The latter was maintained concurrently under continued selection for high egg number, with egg size held at a constant level. In 1975, generation 10 birds of the two replicate DY lines were crossed and thereafter reproduced as a single flock. Generations 11 to 18 were based on 12 males mated to two hens each. The results of selection response for combined sublines and their subsequently pooled flock are shown in Table 1. Beginning at an initial level of less than 1 percent double-yolked eggs in the 1963 flock of origin (Production line, P), the number of multiple-yolked eggs rose to 2,42 percent in 1964, gradually increased to 8,7 percent in generation 5, and then to over 30,6 percent by generation 11 when sublines were crossed.

Beginning with generation 11 it became clear that an adequate accounting of multiple ovulations had to include triple-yolked eggs and eggs with even four or five yolks. While these higher multiple-yolked eggs accounted for less than one percent in generation 11, they increased under selection for excess yolks to over 3 percent in generations 15 and 17. Concurrently with this increase in higher multiples, the selection criterion was changed from the number of double-yolked eggs to the number of excess yolks contained in multiple-yolked eggs laid to 40 weeks. On this basis the maximum level of multiple ovulations was observed in generation 15, hatched in the autumn of 1979 when an average of 47,25 excess yolks were laid by the DY hens. It is also clear from the results of the last 4 generations that non-genetic causes influenced the level of superovulation of the selected line. Although generations 15 through 18 were all hatched in the months of October and November, their level of excess yolk production varied between the high of generation 15, just mentioned, to a low of 29,00 the following year, only to rise and fall once again in generations 17 and 18 as shown in Table 2. Since all these experiments were carried out in unheated

Table 2. Effects of the sex-linked gene for dwarfism on the number of normal eggs, total yolks, and excess yolks produced in the genetic background of line DY selected for multiple-yolked eggs.

Year	Genotype	Number of Hens	Eggs to 40 Weeks of Age		
			Single yolks	Total yolks	Extra yolks
1979	Normal	51	48,0	138,6	47,4
	Dwarf	22	74,4	109,5	17,9
1980	Normal	53	58,6	114,9	29,0
	Dwarf	25	82,8	112,3	15,1
1981	Normal	89	45,8	131,8	44,7
	Dwarf	38	87,0	108,7	11,0
1982	Normal	38	50,7	116,7	33,8
	Dwarf	59	85,7	101,7	38,2
Average	Normal	231	50,7	125,5	38,7
	Dwarf	144	82,5	108,0	13,0

houses without light controls other than supplemental lighting to 14 hours daily light, natural changes in temperature and light conditions may have played a role. It would appear that the highly selected DY hens have become sensitive to their environment. Correlated with the increase in multiple ovulations was a gradual decline in the number of normal eggs laid from an initial 88 to a low of 45,8 in generation 17. In that generation the total number of yolks produced had reached 131,8, a 50% increase over generation 1.

Another correlated response to selection is seen for adult body weight of hens which increased from an initial 1,72 kilograms to a high of 1,98 generations 12 and 14, followed by a slight decline thereafter. It thus appears that growth rate and ovulation rate in chickens are under the control of some common factors, possibly hormones, that need to be further identified. The present selection study independently confirms this positive correlation between growth rate and increased ovulation rate observed in broiler lines where the primary selection is for growth rate.

Changes from selection were also observed for egg weight of single-yolked eggs. Initial egg size at 30 weeks of age was approximately 50 grams and increased to 55,6 grams in generation 9. Thereafter, egg weight declined steadily to 46 grams in generation 13. In that year egg weight measurements were changed from 30 to

40 weeks of age and continued to decline to a low of 43 grams in generation 18. On the basis of thirty week measurements, egg size thus increased some 10 percent to a maximum in generation 9, only to fall an estimated 30% in the following 9 generations. The biological basis of these changes remains as yet unclear, although one might speculate that excessive numbers of ovulations result in relatively small yolks and, hence, may cause eggs to decline in size as well. An increase in the flock average for numbers of extra yolks from less than one to approximately 40 demonstrates the high heritability of yolk production. Figure 1 gives the distribution of total yolks laid to 40 weeks in generations 12 through 15, showing that some hens laid in excess of 200 yolks. Apparently there is no discernible physiological limit imposed by daylight upon the number of ovulations and the rate of follicle maturation. Furthermore, it was found that even at these very high rates of yolk production, the formation of eggs, while incorporating multiple yolks, did not result in excessive numbers of the DY line soft-shelled and prematurely laid eggs. Thus in generations 10 through 13, the percentage of eggs without shells or with soft shells accounted for 6,6, 6,4, 9,4, and 6,8 percent of ovipositions respectively or 7,3 percent of all eggs laid by these hens.

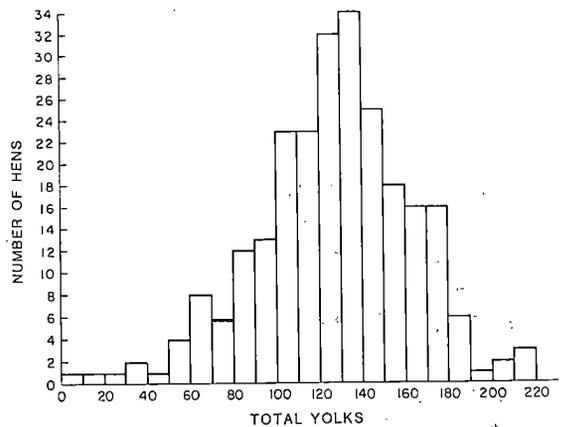


Fig. 1. Distribution of numbers of yolks produced to 40 weeks of age by hens from line DY selected for high numbers of multiple yolked eggs.

These levels of abnormal egg formation are not much higher than those reported by JAAP and MUIR (1968) or REDDY and SIEGEL (1977) for chickens with high growth rates.

Dwarfs

During the last 4 generations beginning with 1979, the sex-linked gene for dwarfing was maintained segregating within families of the DY line following its introduction into the line by 3 successive backcrosses to DY birds. Under this procedure the segregating DY-line was expected to carry about 95 percent of the genes present in the selected DY flock plus 5 percent of genes belonging to a commercial dwarf-line used to supply the sex-linked dwarf genes (*dw*). Segregation of sex-linked dwarfing was accomplished by mating each generation of normal-sized males known to be heterozygous for dwarfing (*Dwdw*) with dwarf hens (*dw-*). Such matings yield dwarf (*dwdw*) and normal-sized but heterozygous (*Dwdw*) males within each family as well as normal (*Dw-*) and dwarf (*dw-*) females. The use of dwarf females in reproducing the line had the advantage of improved production of hatching eggs which had reached critically low levels for normal-sized DY hens. In order to assure that selected hens were dwarfs, only individuals in the lower third of the size distribution weighing less than 1,2 kg were used as breeders. Similarly, only males in the upper third of body weight distribution were used to reproduce the line. Such opposing selection for size in the two sexes was intended to avoid errors in genotype and also assured that genes for growth other than the *dw* gene remained at unchanged frequencies for the line as a whole. Aside from selection on size to retain segregation for dwarfing, selection was also continued for increased incidence of multiple-yolked eggs. Thus dwarf hens were selected on the basis of high numbers of multiple yolks of their own as well as those laid by their normal

sisters. Normal *Dwdw* males were selected on the basis of high numbers of multiple yolks of their normal sisters.

The effects of sex-linked dwarfing on yolk production in the DY-line are shown in Table 2 for generations 14 through 17. Apparently nongenetic effects caused considerable variation from generation to generation, as mentioned earlier. However, the dwarf gene effects were consistent throughout and are well represented by the 4-generation average. Thus, the number of single-yolked normal eggs laid by dwarf hens (82,5) far exceeded those of normal-sized hens (50,7), while just the opposite was true for total yolks produced: normal-sized hens produced an average of 125,5 yolks, while dwarfs laid only 108. The most dramatic effect of the dwarf gene is shown in its reduction of extra yolks, with normals exceeding dwarfs by some 25 extra yolks (38,7 vs 13,0). These effects of the dwarf gene in the genetic background of superovulating hens thus demonstrate its capacity to increase the number of normal eggs by reducing the level of superovulation and thus multiple-yolked eggs. These effects closely parallel the findings of JAAP and MOHAMMADIAN (1969) and REDDY and SIEGEL (1977) who have shown the dwarf gene to have similarly beneficial effects in broiler stocks, which show relatively high levels of superovulation in large size, normal hens. The genetic lines developed for high numbers of multiple-yolked eggs in the selection experiment reported here thus may serve as a model for further studies concerning the effects of dwarfing on inherited superovulation of chickens.

Studies of follicle development and abdominal fat of dwarf and normal-sized DY hens were made in generations 16 and 17, as shown in Table 3. Also included in Table 3 are data from the production selected base population (*P*). As mentioned earlier, body weight of normal DY hens exceeds that of controls by about 15 percent. Dwarfs of the DY line weighed only 1,23 kg: that is, 35 percent less than their normal

Table 3. Effects of sex-linked dwarfism on abdominal fat, follicle number, and liver weight and ovary weight in a White Leghorn line selected for multiple ovulations (DY) and its egg number selected control line (P) for samples of 24 week-old pullets of the 1980 and 81 generations.

Genotype	No. of Hens	Body Weight kg	Abdominal Fat Weight gm	Fat % of Body Wt.	Liver Wt. gm	Follicle No.
DY Normal	28	1,89+0,08	84,4+5,5	4,45+0,2	63,2+2,9	11,4+0,5
DY Dwarf	24	1,23+0,08	44,3+5,9	3,60+0,2	41,2+3,2	7,5+0,6
P Normal	18	1,62+0,05	103,1+8,5	6,40+0,3	51,0+1,9	5,6+0,2
DY Dwarf/ DY Normal		0,65	0,53	0,81	0,65	0,66

sisters. They also had substantially less abdominal fat than normal DY hens. Even when expressed as percentage of body weight, abdominal fat of dwarfs was only 81 percent of normal DY hens. These results are just the opposite of those reported by TOUCHBURN et al. (1980) who found dwarfs from broiler lines to be fatter than their normal sisters. Production selected controls of line P had more fat than normal DY lines.

The number of ovarian follicles exceeding 5 mm in size averaged 11,4 for normal DY hens as compared to 5,6 for P controls, thus demonstrating excessive follicle development to be the principal cause of multiple-yolked eggs. The

dwarf gene, while reducing follicle numbers in DY hens in the same proportion as body weight (65 %), could not completely counteract the effects of DY selection, having 7,5 follicles as compared to 5,6 in the control hens. Thus, ovarian follicle numbers are closely correlated with observed numbers of multiple-yolked eggs in normal and dwarf DY hens as compared to the control (P). The production of multiple-yolked eggs by dwarf hens also demonstrates that superovulation cannot be explained by differences in body size alone, since dwarf hens were much smaller than P-controls, yet laid many more excess yolks and had larger numbers of follicles as shown in Table 2.

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Manuscript received August 1984

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INCREASING EGG YIELD UNDER NORMAL LIGHT CYCLES BY SELECTING FOR SHORT INTERVAL BETWEEN EGGS UNDER CONTINUOUS LIGHT

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SHELDON, B. L., YOO, B. H. & PODGER, R. N. 1984. Increasing egg yield under normal light cycles by selecting for short interval between eggs under continuous light. *Ann. Agric. Fenn.* 23: 216—225. (CSIRO Div. of Anim. Production, Prospect, NSW, Australia.)

Results of selection for short interval between eggs under continuous light are reviewed. The primary selection response in interval and the correlated responses in rate of lay, egg weight, egg specific gravity, age at first egg, and body weight varied widely between the three main selection lines, White Leghorn, Australorp and Synthetic.

In the Australorp and Synthetic lines the mean intra-clutch interval has been reduced to 22,2h and 22,7h respectively in continuous light and to 24,1h and 24,2h respectively in normal 24h light:dark cycles. The results indicate that these selection lines are beginning to break through the barrier of one ovulation per 24h cycle in the normal light regime. Preliminary results of genetic parameters are given for a strain-cross White Leghorn line (LN), which is closer to this barrier than the base populations of the other three lines.

Results are reviewed which indicate that the response in interval is due to the egg spending less time in the oviduct and not to earlier ovulation relative to oviposition. Some effects of breed and selection on plasma levels of luteinizing hormone (LH) and on the time relationship of the pre-ovulatory LH peak to oviposition are summarized.

Results of an analysis of oviposition times and intervals in 27 genotypes are also summarized. Estimates of "free-running period", i.e. the period of the endogenous circadian rhythm controlling the "open period" for LH release, indicate that this period has been reduced by selection for low interval in continuous light.

Index words: selection, interval between eggs, egg production, continuous light, domestic fowl.

INTRODUCTION

Selection for egg production based on the methods of quantitative genetics began in the Australian poultry industry 25 to 30 years ago. Considerable discussion occurred at that time about how long it would take to reach selection plateaux for egg production in poultry and how to deal with them when they did occur, especially the ultimate selection plateau for rate of lay imposed by the 24 h light:dark cycle, i.e. a limit of one ovulation and hence one egg per 24 h cycle (FRAPS 1955). Since hens genetically capable of ovulating at a rate higher than once per 24 h cycle would probably not be identifiable under such an environment, several re-

search groups started selecting under different lighting regimes considered suitable for identifying such genotypes (ABPLANALP 1966, 1968, MARKS, LUCAS and GODFREY 1968; MORRIS 1961).

The CSIRO group chose continuous light as the modified environment and within-clutch interval between eggs as the selection criterion (SHELDON, PODGER and MORRIS 1969). The above authors, FOSTER (1983) and YOO, SHELDON and PODGER (1984) have justified the various approaches. The purpose of the present paper is to summarize the results and significance of the work of the CSIRO group.

MATERIAL AND METHODS

Details of selection and control lines are given in Table 1. Details of flock management, testing and recording facilities and procedures, and selection methods were described in the references under Results. Continuous light (CL) and background noise (radio or recorded music) was the modified environment used. Selection under CL was based on a four week test period between 29 and 37 weeks of age. Time of lay was recorded automatically (PODGER 1983). The primary selection criterion was reduced interval between eggs within clutches. The secondary selection criteria shown in Table

1 were introduced after evaluation of the previous selection and correlated responses. The selection schedule was normally 1 generation per year. Pullets were selected on individual performance, cockerels on performance of their full-sisters. In each selection line correlated responses in mean interval between eggs and other egg production traits were measured every few generations in a normal light environment (NL) of 24 h light:dark cycles. Since 1977 the program has included extensive evaluation of the crossbreeding performance of the selection lines.

Table 1. Details of Selection and Control Lines in Selection Experiments.

Selection or Control Line	Years	Approx. number pullets tested per generation	Number of Parents used per generation	Selection Criteria
			Sires	
			Dams	
<u>White Leghorn Selection (LS)</u>	1959-71 1972-77	300-520 480	10-17 17	100-170 126
	1978-81 1982-84 1967-71	480 — —	17 60 18	126 60-120 108
<u>White Leghorn Control (LC)</u> [Sample of LS base popln. from commercial breeder in 1967]	1972-78	—	30	120
<u>Australorp Selection (AS)</u>	1979-84 1962-65 1967-73 1974-84	— 480 480 480	56-60 16 16 16	56-120 112 112 112
<u>Australorp Control (AC)</u> [Derived from the AS line itself]	1967-77	—	28	112
<u>AS Sub-line Selection (ASS)</u>	1978-84 1980-83 1984	— 480 480	64 20 20	64 120 120
<u>Synthetic Selection (SS)</u>	1968-82 1983-84	480 240	16 16	96 64
<u>Synthetic Control (SC)</u>	1968-77 1978-84	— —	40 96	160 96
<u>SS Subline Selection (SSS)</u> <u>White Leghorn Strain Cross (LN)</u>	1983-84 1977-84	240 450 (1981-82) 1800 (1983-84)	16 — 141	64 — 450
<u>Selection 1 (LN1)</u>	1984	1800	16	128
<u>Selection 2 (LN2)</u>	1985- 1984	240 1800	16 16	64 128
<u>Selection 3 (LN3)</u>	1985- 1984	240 1800	16 16	64 128
<u>Control (LNC)</u>	1985- 1984-	240 240	16 32	64 128

* CL = Continuous light; NL = normal environment

** L-S pattern (see Results; White Leghorn Selection)

Reduced interval between eggs within clutches, in CL*.
 Reduced interval, high egg number in test period, egg weight and egg specific gravity, in NL*.
 Reduced deviation from 24h of oviposition interval, in NL.
 No selection (NL). Random matings.
 No selection, random matings (NL).
 Reduced interval, in CL.
 Reduced interval, high egg number in test period, in CL.
 Reduced interval, high egg number, absence of long-short (L-S)** pattern of lay, in CL.
 No selection, random matings.
 Reduced interval in CL. High egg weight in NL.
 Reduced interval in CL. Hold mean egg weight constant.
 Reduced frequency blood spots.
 Reduced interval, high egg number in test period, absence of L-S pattern, in CL.
 No selection, random matings.
 Reduced interval, high egg no. in CL; high egg weight in NL.
 No selection, form base popln., genetic parameters study.
 Rate of lay to 300 days, high egg weight and egg specific gravity, in NL.
 Reduced interval in CL, high egg weight and egg specific gravity, in NL.
 Reduced interval in NL, high egg weight and egg specific gravity, in NL.
 No selection, random mating.

RESULTS

(i) Selection response and correlated responses

A summary of the main effects of selection is given in Table 2. The **White Leghorn selection line (LS)** showed after 12 generations an

interval between eggs about 4 h below its control line (LC) in both CL and NL. About half this response was ineffective due to a large increase in frequency of long-short (L-S) pattern of lay, i.e. an unusually long interval of over

Table 2. Selection response in mean interval and correlated responses in the three main selection lines.

Lines		Interval (h)		Egg No. (Survivors to 65 weeks)	Age 1st Egg (days)	Egg Weight (g)		Egg S.G. (34 weeks)	Body Weight (g)	
		CL	NL							
<u>White Leghorn</u>										
1967(8)*	LS	25,2	25,0	184,7e	136	43,4a	50,9b	1,0767	1538a	1675b
	LC	27,2	26,6	182,0	138	49,2a	56,8b	1,0781	1652a	1809b
1971(12)	LS	23,6	23,2	178,4	139	44,1a	50,6b	1,0724	1555a	1728b
	LC	27,6	27,0	186,2	140	49,3a	56,0b	1,0826	1702a	1919b
1977(17)	LS	23,8	25,1	178,7	157	46,2c		1,0772		1693d
	LC	26,7	26,6	182,9	156	50,6c		1,0792		1759d
1981(21)	LS	25,4	26,0	198,3	160	47,2c		1,0779		1501a
	LC	27,1	26,9	182,8	151	51,0c		1,0789		1598a
<u>Australorp</u>										
1972(10)	AS	24,2	24,4	194,4	154	51,8a	59,2b	1,0775	2374a	2448b
	AC	26,5	25,6	184,7	144	52,4a	60,0b	1,0793	2279a	2447b
1977(15)	AS	23,5	24,3	207,1	162	49,6c		1,0800		2109d
	AC	26,0	26,6	177,7	153	50,3c		1,0811		1966d
	LS × AS	24,2	24,6	244,7	154	50,9c		1,0809		1991d
	LC × AC	26,1	25,6	223,6	148	51,9c		1,0840		1974d
1979(16.5)	AS	22,9	23,9	207,2	166	50,5c		1,0808		2146d
	LC × AC	25,9	25,5	229,8	146	51,9c		1,0838		1857d
1980(18)	AS	23,0	—	—	—	—		—		—
	ASS	23,4	24,1	211,9	177	51,2c		1,0763		2252b
	LC × AC	26,1	26,1	224,8	149	52,9c		1,0796		2190b
1981(19)	AS	22,8	—	—	—	—		—		—
	ASS	23,4	—	—	—	53,9a		—		—
1982(20)	AS	22,6	—	—	—	—		—		—
	ASS	23,5	24,2	—	—	52,7a		—		—
	LC × AC	25,5	25,1	—	—	—		—		—
1983(21)	AS	22,2	—	—	—	—		—		—
	ASS	23,0	—	—	—	—		—		—
<u>Synthetic</u>										
1974(6)	SS	24,7	24,5	165,6e	146	50,0a	57,7b	1,0797	1990a	2153b
	SC	26,9	25,8	185,8f	144	51,8a	59,5b	1,0819	2010a	2202b
1980(12)	SS	23,2	—	—	—	—		—		—
1981(13)	SS	23,5	24,2	225,6	163	47,8c		1,0808		1672a
	SC	26,8	25,9	192,7	158	50,9c		1,0848		1682a
	LC × AC	26,2	25,9	227,0	150	53,6c		1,0835		1778a
1982(14)	SS	23,1	—	—	—	45,6a		—		—
1983(15)	SS	22,7	—	—	—	—		—		—
	SSS	22,8	—	—	—	48,7a		—		—

* Generation Number in brackets;

a: at 34 weeks; b: at 62 weeks; c: average of all eggs to 65 weeks; d: at 43 weeks; e: n = 113; f: n = 140.

30h or even a clutch break of 35h or more, followed by an unusually short interval of less than 20h (SHELDON and PODGER, 1972, 1974). SHELDON and BOBR (1983) confirmed by radio-telemetry study of body temperature that the long interval of the L-S pattern is due to delayed oviposition of that egg. Other unfavorable features of the response at generation 12 were no increase in egg production, a reduction of 5g in egg weight, and a serious decline in shell quality (egg specific gravity). After the following eight generations of corrective selection the total response in mean interval was less, largely due to a reduction in incidence of L-S pattern, and the unfavorable correlated response in egg weight remained (YOO, SHELDON and PODGER 1983, 1984). There was also an increase in egg production in NL of 8%, after allowance for the effect of inbreeding, and an indication of an increase in age at first egg.

In the **Australorp selection line (AS)** the reduction in mean interval was 2,3h in CL (1,2h in NL) six generations after the control line (AC) was established (SHELDON and PODGER 1974), but only 2,5h in CL (2,3h in NL) after a further five generations (SHELDON, PODGER and YOO 1979). Since then the response has become more rapid again, the mean interval in the selection line in 1983 being just over 22h in CL, i.e. a reduction from the control of over 4h. In NL its mean interval is very close to 24h at 32 weeks of age. There has been no increase in frequency of L-S pattern. A reduction of about 1g in egg weight occurred in this line, much less extreme than in LS (YOO, SHELDON and PODGER 1984). Other correlated responses were increases of 6% in age at first egg, 5% in body weight and 18% in egg production but little change in egg specific gravity. Crossbred progeny of AS dams mated to LS or LC sires had low mean interval, very high egg production and high feed conversion efficiency but egg size below acceptable market levels, largely because the AS base population had a low egg size.

Therefore, the ASS sub-line was derived in 1980, selecting for increased egg size and reduced interval at the same time. Pullet egg size has increased by about 3g over 3 generations while interval has remained around 23h.

In the **Synthetic selection line (SS)** the response in interval was more linear than in AS and showed a reduction from its control (SC) of about 3h in CL (1,7h in NL) after 13 generations of selection (YOO, SHELDON and PODGER 1983). It had a large reduction in egg weight (3g) similar to LS, but an increase in egg production (17%) similar to AS. SS also had a significant reduction in egg specific gravity, smaller than in LS, and a tendency to an increase in age at first egg but no change in body weight. Since then mean interval in CL has dropped below 23h. The crossbred progeny of SS (YOO, SHELDON and PODGER 1981, 1983) also have a low interval, a very high feed conversion efficiency but a low egg size even less acceptable for the market than the AS crossbreds. The SSS sub-line was derived to explore further the genetic correlation between interval, egg size and egg specific gravity. In the first selected generation mean interval in SSS was as low as in SS while its egg weight was higher.

(ii) Genetic Parameters

YOO, SHELDON and PODGER (1976) presented results of a pooled analysis of small samples of the three selection lines and their control lines over five generations. The data had problems of heterogeneity so that the estimates obtained were of limited value. The heritability (h^2) of interval between eggs was medium to high (0,3 to 0,6) and tended to be higher in CL than in NL. The genetic correlation (r_G) of interval in CL with interval in NL ranged from 0,44 to 0,74.

YOO, SHELDON and PODGER (1979) presented further data on genetic parameters esti-

mated in line LS over the first 12 generations of selection. h^2 of interval in CL was lower (0,17) than the above and r_G of interval with egg weight and egg S.G. were positive but low.

In the crossbreeding experiments of 1977 and 1979 (YOO, SHELDON and PODGER 1981, 1984) a commercial strain-cross White Leghorn flock (LN) was included which is much closer to a selection plateau in interval between eggs (24,8h in NL, 25,8h in CL) and in survivors' egg production than the LC, AC and SC lines. In addition it had commercially acceptable egg size (average 55—56g to 65 weeks of age), age at first egg (150 days), egg specific gravity and body weight, and its survivor egg production did not decline in an F2 flock produced by random matings among the strain-cross flock. This population was chosen for an experiment to estimate genetic parameters of interval between eggs in CL and NL and the usual egg production characters. All traits were recorded on a flock of about 455 pullets in 1981—82, and on 1802 pullet progeny in 1983—84 derived from 359 dams and 141 sires. The full results will be published elsewhere. Unusual features were very high h^2 for body weight, egg weight, age at first egg and mean interval in either CL (0,52) or NL (0,59). The latter two are higher than in the previous two studies. Favorable r_G were high negative values for CMIN or NMIN with PHP, AHP, PRL, ARL,* and low values for CMIN or NMIN with BWE and AFE. Unfavorable r_G were medium positive values for CMIN or NMIN with EWE and SGE and for BWE with EWE, high negative values between PRL and EWE, and low to medium negative value for EWE with SGE, AHP and ARL. The genetic correlation of CMIN with NMIN was higher (0,83) than reported in the

previous study. On the basis of our accumulated experience and these results we have defined a selection objective for this LN population as follows: (i) to maximise pullet-year hen-housed egg production (AHP), (ii) to maintain EWE, BWE, SGE and AFE at their present levels.

Theoretical comparison of alternative selection criteria using a restricted selection index (YAMADA, YOKOUCHI and NISHIDA 1975) indicated that indices combining CMIN-EWE-SGE or NMIN-EWE-SGE will be 30% more efficient than those combining PRL-EWE-SGE or PHP-EWE-SGE-AFE. Three LN selection lines and an LN control line (Table 1) have been established to test this hypothesis.

(iii) **Is the selection response in interval due to earlier ovulation or to the egg spending less time in the oviduct**

Since BOBR and SHELDON (1977) did not find a direct body temperature indicator of time of ovulation this question was studied by direct autopsy observations of ovulation and position of the egg in the oviduct at intervals of time after oviposition. Line AS was compared with line AC in both CL and NL in 1980. No difference in timing of ovulation relative to time of oviposition was detected between lines or between CL and NL (SHELDON and BOBR, unpublished). Thus reduced interval between eggs in AS is due to a faster rate of passage of the egg through the oviduct.

Questions on possible changes in the components of the egg arise from this conclusion. In the above study direct measurements were made of egg weight, yolk weight, shell weight and, by difference, albumen weight, in relation to interval between eggs and egg specific gravity (SHELDON and YOO, unpublished). The three components of egg weight were reduced in line AS in CL where the reduction in egg weight was greater than in NL. In NL albumen

* PHP: part-annual hen-housed egg production (to 300 days of age); BWE, EWE, SGE: early body weight, egg weight, egg specific gravity, i.e. at 34 weeks of age; AFE: age at first egg; PRL: part-annual rate of lay (from first egg to 300 days); AHP, ARL: annual hen-housed egg production, rate of lay (to 65 weeks of age); NMIN, CMIN: mean intra-clutch interval between eggs in NL, CL respectively.

weight was not reduced but yolk and shell weight were. Since the reduction in egg weight (2%) is less than the reduction in interval (6–8%), it appears that the efficiency of production of yolk, shell and especially albumen has increased in line AS.

A further characteristic of significance in lines AS and AC is the high frequency (approx. 30%) of ovulation before oviposition (SHELDON and BOBR, unpublished). The mean time of ovulation in these lines is about 10 minutes after oviposition compared with about 30 minutes after in those reported in the literature (e.g. MELEK, MORRIS and JENNINGS 1973), where ovulation before oviposition was extremely rare. The possibility that this variability in our Australorps represents an alternative pathway to surmounting the plateau of one egg per 24h light:dark cycle is now being explored in an experiment started from line AC. In 3 generations of selection for early ovulation, the frequency of pullets which had already ovulated when autopsied 10 m after oviposition appears to have increased to 0,78 compared with 0,56 in the base population (SHELDON, YOO and BOBR, unpublished).

(iv) Hormone differences among the selection and control lines

Plasma levels of luteinizing hormone (LH) during the ovulatory cycle have been studied in lines LS, LC, AS and AC in both NL and CL (GOW et al. a, b; in preparation). The main findings relating to eggs in mid-clutch ovulation cycles were:

(a) a breed difference in plasma LH, line AC being significantly higher than LC in both NL and CL.

(b) plasma LH was significantly higher in AS than AC in CL, but not in NL. In contrast, plasma LH was higher in LS than LC in NL ($P=0,13$) but not in CL. Within lines AC, LS, LC the levels were similar in NL and CL.

(c) The interval from LH peak to oviposition of the egg already in the shell gland was shorter in AS (by 0,6h) than in the other 3 lines in NL. In CL it was shorter (by about 0,6h) in the two Leghorn lines (LS=LC) than in the Australorp lines (AS=AC). In line AC it was the same in NL and CL.

(d) In NL the time of lay in AS was 3,5h earlier than in AC and the time of the LH peak in AS was 2,3h earlier than in AC, i.e. more LH peaks occurred towards the beginning of the "open period" for LH release in AS.

(v) Analyses of oviposition times and intervals in relation to endogenous circadian rhythm controlling the "open period"

YOO, SHELDON and PODGER (in preparation for publication) have recently completed a statistical analysis of data from four crossbreeding experiments, involving the CSIRO selection and control lines, their crosses and commercial strains. Thirtynine populations were analysed covering 27 genotypes, varying in mean interval between eggs from 24,1h to 26,8h in NL, and from 23,1h to 27,6h in CL.

In both NL and CL, the standard deviation of all intervals in the population fell and the coefficients of skewness and kurtosis increased as the mean interval approached 24h. In CL the standard deviation rose, while skewness and kurtosis decreased, as the mean interval (5 populations) decreased below 24h.

The mean time of oviposition in NL decreased, and the degree of entrainment of the endogenous circadian rhythm in NL (proportion of eggs laid in the modal 8h) increased, with reduction in mean interval in CL.

In CL the proportion of eggs laid in the modal 8 hours varied from 0,37 to 0,51 in different populations, compared with the expectation of 0,33. This statistic was used as an indicator of sensitivity to uncontrolled timing cues in CL, and was positively corre-

lated with mean interval in CL.

"Free-running period", i.e. the period of the endogenous circadian rhythm controlling the "open period" for LH release, was estimated by MORRIS' (1977) procedure. The mean free-running period declined linearly with mean interval between eggs in CL, for mean intervals

below 25,75h, suggesting that the period of the endogenous rhythm has been reduced by selection for low interval. The five populations with mean free-running periods below 24h (23,0 to 23,4h) were three samples of the AS line, one of the SS line and one of the cross SS \times AS.

DISCUSSION

The relatively large differences in selection and correlated responses between our lines are relevant to evaluation of the success of selection under abnormal lighting regimes in identifying and increasing the frequency of genotypes capable of surmounting the barrier of one egg per 24h. FOSTER (1983) reviewed the experiments of MARKS (1967), CAHANER and ABPLANALP (1979), and himself using ahemeral light cycles, and some of our results in continuous light (CL). He saw little evidence to support the use of abnormal lighting regimes because no one had yet produced genotypes capable of laying at a rate greater than one egg every 24h in a normal 24h light:dark cycle (NL). He speculated that the responses achieved under abnormal lighting would only be realized in flocks kept under that regime, and that the performance of such genotypes in NL might be achieved equally by selection in NL.

We agree that experiments in ahemeral cycles have not provided support for the use of abnormal lighting to break the selection plateau. However, our experiments in CL show that in lines AS and SS many birds have a capacity to lay in NL slightly more frequently than once per 24h. In AS in NL, up to 50 % of the flock has an individual mean interval less than 24h, range 22,7h to 25,9h. Birds with means of 22,7h to 23,6h range from 18h to 27h.

Birds with means closer to 24h are less variable, a typical range for a 23,9h bird being

23,3h to 24,6h. The proportion of pullets laying 28 eggs in 28 days in NL is 15 %. None of the flock has yet laid more than 28 eggs in 28 days in NL. By contrast in CL 33 % of the flock lays more than 28 eggs in 28 days, the distribution in 1982 being 29 eggs — 16,8 %, 30—10,2 %, 31—4,3 %, 32—1,1 %, 33—0,2 %, 34—0,4 %. Nevertheless, the flock mean in CL was still only 25,3 eggs.

It is important to note that it is not the flock mean, as used by FOSTER (1983), which is the relevant indicator of whether the barrier at 24h and 28 eggs is being broken, but the individual birds which show evidence of surmounting it. In line AS the high proportion of the flock laying a high proportion of their eggs in NL at intervals less than 24h provides a clear indication that selection in CL has, after 15—20 generations, started to break through the 24h barrier in NL. The SS line is following the same course.

If these trends continue with further selection, several factors may have contributed to the absence of useful response in Foster's experiment compared to ours, namely, his different base population, different lighting regimes (23, 22 and 21h ahemeral cycles) and different selection criteria ("presumed number of ovulations" in the first 9 generations and "oviposition frequency" in the next 4 generations of selection). The latter seems the most likely explanation. In addition, Foster's experiment and all others reported so far including

ours, started from populations not at the ultimate physiological plateau, mainly because such were not available. The early generations of selection in abnormal lighting in these populations would have been utilized in bringing them closer to the plateau, as with conventional selection. The 4, 7 and 13 generations of selection by Marks; Cahaner and Abplanalp; and Foster respectively were probably not sufficient to go beyond this point. It has taken about 15 generations in lines AS and SS to achieve a response indicative of starting to break through the barrier in NL, and this work was done in probably a more favorable environment (CL), using a more direct selection criterion with higher h^2 (intra-clutch interval between eggs). It should also be realized that even if the barrier in NL is partly of fully broken by selection in CL, a 24h light:dark cycle might still not be the optimum environment for performance of these lines or

their crosses. If the optimum proves to be, for example, an ahemeral cycle of 21h, consideration will have to be given to using such an environment for commercial egg production.

While our results with CL are more promising than those from ahemeral light cycles reviewed by FOSTER (1983), no experiment has yet been reported showing that selection for reduced interval in NL cannot achieve the same result. The experiment of MCCLUNG, WANG and JONES (1976), while successful in reducing interval, did not last long enough to test this question. The theory of ovulation control on which the ahemeral and CL experiments are based specifies that selection in NL can never break through the barrier imposed by the 24h light:dark cycle. Our experiment just begun with the strain-cross White-Leghorn line (LN) already close to this physiological limit will provide information on this question.

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Manuscript received September 1984

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SELECTION FOR AGE AT FIRST EGG

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KOMIYAMA, T., NIRASAWA, K., NAITO, M., YAMADA, Y. & ONISHI, N. 1984. **Selection for age at first egg.** *Ann. Agric. Fenn.* 23: 226. (Nat. Inst. of Anim. Ind., Tsukuba Norindanchi, P.O. Box 5, Ibaraki 305, Japan.)

Selection was conducted for age at first egg (SM) to find selection responses and selection limit. A crossbred of 2 WL strains, a WR strain and a RIR strain was used as the base population. SM of the base population was 196 days. Marked direct selection responses were obtained from G_4 (179 d) to G_{15} (126 d). It seems to reach the selection limit in this selected line (T-line), because no clear responses were observed from G_{15} to G_{18} . The realized heritability over 12 generation (G_4 — G_{15}) was 0.477. Marked correlated responses were observed in egg weight (EW) and body weight (BW) at first egg, but no response in egg number for 90 days after first egg (EP).

Lighting treatments to delay sexual maturity were conducted with T-line. SM of control and treated group were 122 and 157 days. EW, BW and egg production rate of treated group increased 30 %, 12 % and 28 %, respectively. Standard deviation of SM of treated (5 d) was smaller than that of control (13 d).

Diallel cross of 4 selected lines for early maturity was conducted to study crossing effects on SM, and other traits. SM of crosses were mostly earlier than those of selected lines. Significant GCA, SCA were observed in SM, EW, BW, EW220 d, and EP151—350 d.

Index words: selection, age at first egg, early sexual maturity, lighting, heterosis, chickens.

The full paper published in Proceedings of XVII World's Poultry Congress and Exhibition, Helsinki, Finland August 8.—12.1984.

Manuscript received August 1984

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SELECTION FOR FEED EFFICIENCY OF EGG PRODUCTION IN LAYER-TYPE CHICKENS

A. W. NORDSKOG, Y. H. HOU and HARPAL SINGH

NORDSKOG, A. W., HOU Y. H & SINGH, H. 1984 Selection for feed efficiency of egg production in layer-type chickens, *Ann. Agric. Fenn.* 23: 227—232. (Dept. of Anim. Sci., Iowa State Univ., Ames, Iowa 50011, U.S.A.)

Genetic changes were monitored over 4 generations of selection for feed efficiency in 8 lines of Leghorns, plus 4 control lines. The traits were body weight (BW), egg weight (EW), egg mass output (EM), feed consumption (FC) and feed efficiency (FE) defined as EM/FC. Four lines were selected on an index, I_1 , which contained information on BW, EM, and FC and 4 were selected on index I_2 containing information only on BW and EM. The line-mean contrast of I_1 vs. I_2 was assumed to measure the genetic effect of individual hen feed records on performance. This is called the "feed record effect". A total of 7155 hens was tested in single cages over a 5 year span. Feed consumption was measured in two 4-week periods: 32—36 weeks (Period 1) and 52—56 weeks (Period 2). The results show that selection on I_1 (with FC in the index) increased efficiency more effectively than selection on I_2 in both periods 1 and 2. Age at first egg, however, was delayed by about 6 days.

Index words: selection, feed efficiency, egg production, layer-type chickens, body weight, genetic changes, index, egg weight, egg mass.

Journal Paper No. J- 11557 of the Iowa Agriculture and Home Economics Experiment Station, Ames. Project 2576.

INTRODUCTION

Because feed is a major cost of egg production, the value of genetically efficient egg-laying strains of fowl is self-evident. Body size and egg mass output determine most of the genetic variation in individual-hen feed consumption. Usually, hens that lay at the highest rate with the smallest body size are the most efficient feed converters. If hens differ in their ability to

digest and metabolize feed, an additional genetic component can be estimated from the difference between total feed consumed and that used for egg mass output plus feed for body maintenance. We call this the "residual component" of feed consumption, RC. If the heritability of RC is high, breeders would benefit by keeping individual feed consumption records.

At Iowa State University, selection indexes have been constructed with and without feed consumption records. In our initial study (ARBOLEDA et al. 1976) based on rather limited data, we estimated that feed efficiency could be improved by about 9 % if a selection index were to include feed records.

Using a considerably larger sample of layer-type hens, WING and NORDSKOG (1982) reexamined the question of the heritability of the residual component of feed consumption (h^2_{RC}). Based on 4909 pedigreed White Leghorns in two separate populations, Q and R, the estimates of h^2_{RC} from the sire component of variance were .29 and 15, respectively.

Furthermore, from our results we estimated that the "feed record effect" used in a selection index, should increase income over feed costs by 17 % with truncation selection of the top 38 % of the population.

In the study reported here as a progress report on an experiment still under way, observed genetic gains from the use of two selection indexes were contrasted. Index I_1 contained information on feed consumption (FC); a second index (I_2), contained the same information as I_1 except that FC information was lacking. The results of 4 generations of selection are presented.

MATERIAL AND METHODS

Experimental Stocks

From two unrelated White Leghorn populations, Q and R, 12 lines were formed by using 8 males and 48 female breeders in each generation. Each line averaged about 100 pullets per year. The plan of the selection experiment is shown in Tables 1 and 2.

The I_1 lines were selected on an index containing information on BW, EM and FC. The I_2 lines were selected on an index containing only BW and EM. The contrast of I_1 vs. I_2 is used as a measure of the value of FC

information in the index. We call this the "feed record effect".

As shown in Table 2, two replicates of the independent populations, Q and R, were produced. Six lines were derived from each population for a total of 12. Four were selected on I_1 and 4 on I_2 . Four control lines, originating from the same populations as the selected lines, were produced in each generation with zero selection intensity. The rate of inbreeding expected in each line is taken to be the same because the effective population number (N_e) is the same for all 12 lines. In each generation, the expected gain from selection on I_1 is

Table 1. Traits in the Selection indexes

	Coefficients in Index		FC (g)
	BW (g)	EM (g)	
I_1	+03	+2,80	-.96
I_2	+08	+2,12	0

$(Q.1 - Qc1)$ and $(R.1 - Rc1)$ in populations Q & R, respectively.

For I_2 the corresponding gains expected are,

$(Q.2 - Qc2)$ and $(R.2 - Rc2)$.

Table 2. Selection lines and controls

Populations	I_1	Control	I_2	Control
Q_1	Q_{11}	Q_{c1}	Q_{12}	Q_{c2}
Q_2	Q_{21}		Q_{22}	
R_1	R_{11}	R_{c1}	R_{12}	R_{c2}
R_2	R_{21}		R_{22}	
Mean	$X.1$	X_{c1}	$X.2$	X_{c2}
Av. Sel. Int.	.80	0	.80	0

Differences between Q_{11} vs. Q_{21} , R_{11} vs. R_{21} , etc. represent sampling errors. Differences between $X.1$ vs. $X.2$ measures the feed record effect, i.e., the effect of including FC in the index.

Birds and Management

The data cover 4 generations (5 years) from 1978 through 1983. A total of 7155 pullets was tested for a mean of 119 pullets housed in single cages per lines per year.

March- and April-hatched chicks were floor

brooded and placed in individual laying cages at 20 weeks. Records were kept on age at first egg, body weight, egg size and rate of lay at 32 and 54 weeks. Individual-hen feed consumed over two 4-week periods, at 30–34 weeks and at 52–56 weeks, were measured.

RESULTS

The results are presented graphically over the 4 generations of selection with focus on the trends in performance at 32–36 weeks and at 52–56 weeks of age. Only the pooled averages of lines selected either on I_1 or on I_2 are given.

In each instance, the values presented are taken as the difference from their respective controls (see Table 2). For example:

$$I_1 = X_{.1} - X_{c1} \text{ and}$$

$$I_2 = X_{.2} - X_{c2}.$$

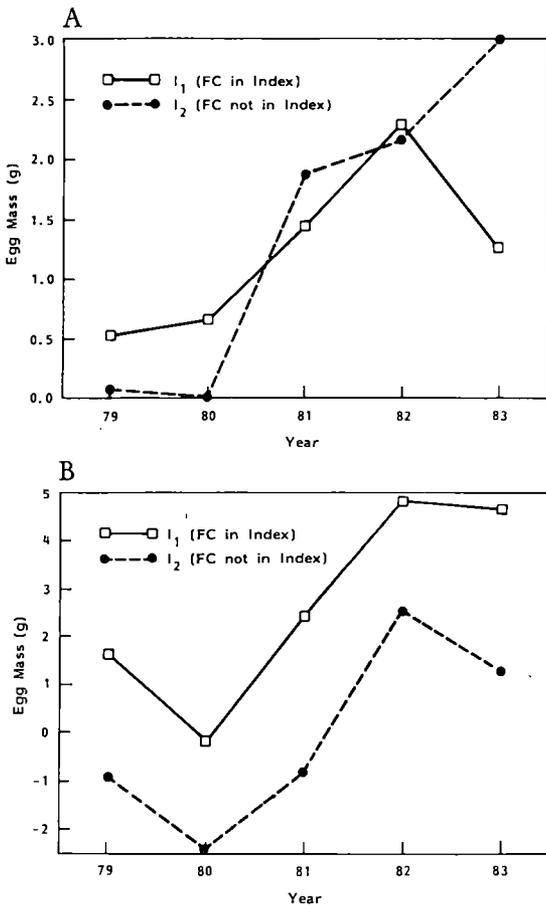


Fig. 1. Difference in egg mass output per day from controls at 32–36 wk. (A) and at 52–56 wk. (B).

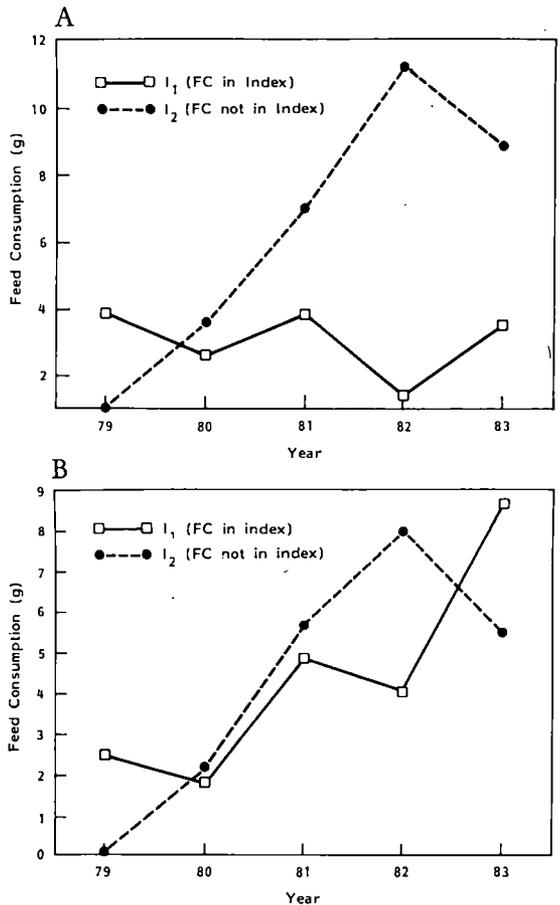


Fig. 2. Difference in feed consumption per day from controls at 32–36 wk. (A) and at 52–56 wk. (B).

In Figure 1, the EM output increased over years in both test periods. Differences, however, in Period 1 were relatively small in 1980, 1981 and 1982 but with considerable divergence noted in 1983. In Period 2, EM was consistently higher for I₁ (i.e. with FC in the selection index) than in I₂, with a difference amounting to about 2,5 g per generation. On the other hand, EM output increased for both types of indexes.

Figure 2 showing feed consumption for I₁ and I₂ gave strikingly different trend curves in Period I but not so in Period 2. In the former case, feed consumption did not increase for I₁, but for I₂ a strong increase of about 7 g is shown over the 4-generation span. In Period 2,

FC increased in both the I₁ and I₂ selected lines. The average increase in FC was about 6 g over the 4-year span.

Figure 3 presents the data on feed efficiency (EM/FC) by periods. In Period 1, the I₁ lines increased consistently except for the year 1983, but, no clearcut trend for I₂ is discernible. In the 1983 year, however, both selection groups were essentially equal in feed efficiency. In Period 2, I₁ was consistently more efficient than I₂ even though there was a dip in the trend in 1983.

Figure 4 presents the body weights at 32 and 52 weeks. For I₁ the trend line is near zero throughout year 1982 in both periods but at the '83 year body weight increased by about 50

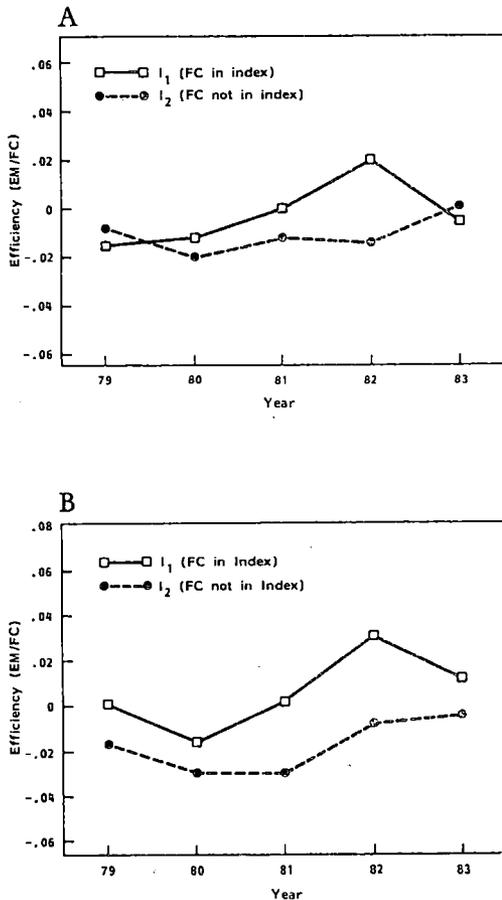


Fig. 3. Difference in feed efficiency (EM/FC) from controls at 32-36 wk. (A) and at 52-56 wk. (B).

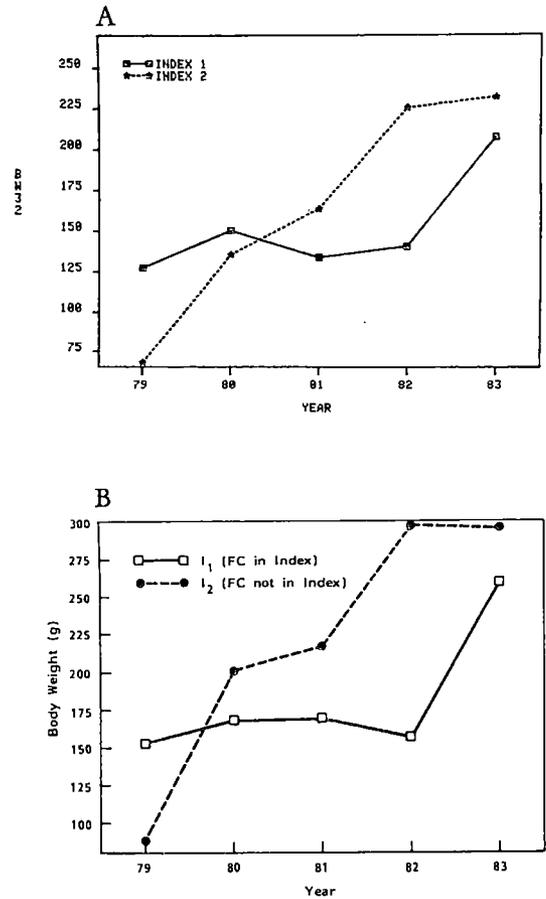


Fig. 4. Difference in body weight from controls at 32-36 wk. (A) and at 52-56 wk. (B).

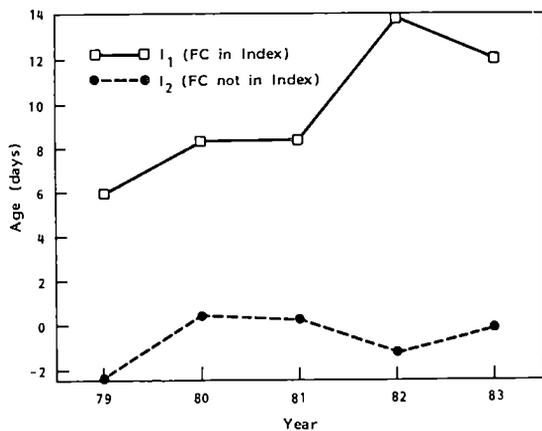


Fig. 5. Difference in age at first egg from controls.

and 100 g in the respective periods. For the I₂ lines the trend is markedly up with a total increase in body weight of more than 200 g in the second period.

Age at first egg is presented in Fig. 5. For I₁ AFE increased by about 6 days but for I₂ no real trend is evident. The difference in age at first egg between I₁ vs. I₂ consistently widened over the 4-year span from about 8 days to 12 days in year 1983.

In Table 3, tests of statistical significance are presented of the linear regressions of traits on years shown in the figures. For the I₁ selected lines, AFE was significant at the 5 % level; FC and EM were significant in the 52 to 56 wk. period between $.05 < P < .10$. For the I₂ lines, various levels of statistical significance for BW, FC and EM were found. Feed efficiency measured as EM/FC, however, did not reach statistical significance.

In summary, selection on I₁ (with FC in the

Table 3. Statistical significance of regression of traits on generation number

Trait	Age wks.	Selection on	
		I ₁	I ₂
BW	32	,15	,01 **
	52	,16	,01 **
FC	32	,63	,03 *
	52	,06(*)	,08(*)
EM	32	,26	,01 *
	52	,09(*)	,14
Effic.	32	,29	,41
	52	,25	,24
AFE	—	,05 *	,53

* $P < .05$, (*) $.05 < P < .10$ ** $P < .01$

index) increased egg mass, feed consumption, and feed efficiency rather consistently at 52—56 weeks of age but less consistently at 32—36 weeks. Body weight showed no upward trend for the first 4 years but markedly increased in the last year. Age at first egg increased about 6 days.

For I₂, egg mass and feed consumption at 52—56 weeks also increased but feed efficiency increased only slightly. No clear-cut increase in body weight could be detected until the 1983 year. Age at first egg remained essentially unchanged.

Finally sampling effects, perhaps associated with environmental exigencies, contributed a considerable amount to the unexplained part of the trend lines. Because the data cover only 4 generations of selection, the opportunity to demonstrate statistical significance in genetic gains in efficiency is quite restricted. Yet, the overall results support our earlier findings that individual feed records can be used in a selection program to increase efficiency of feed utilization for egg production.

DISCUSSION

The heritability estimates of the residual component of feed consumption h^2_{FC} in two populations between ,15 and ,25, as already reported (WING and NORDSKOG 1982), seem sufficiently high to support the hypothesis that

individual feed consumption records should enhance selection for feed efficiency. Furthermore, from our results combined over the two selected populations involving all lines, we calculated that the feed record effect used in a

selection index is expected to improve feed efficiency by 17 % with truncation selection of the top 38 % of the breeder candidates. Taking these results at face value, we might conclude that keeping individual hen records on feed consumption will substantially increase feed efficiency for egg production and, therefore, should be of benefit to breeders. Even if the heritability of the residual component is zero, it can be shown that FC records would still enhance selection for production efficiency. That is, if FC is genetically correlated with EM and BW and if feed efficiency is solely a function of egg mass output and body size, then FC would still be useful as an indicator trait (PURSER 1960) and therefore, should make selection for EM and BW more accurate; this

way, it would increase the rate of genetic improvement for efficiency.

Finally, our studies indicate that, in lieu of direct information on individual FC records, valid estimates of genetic and phenotypic parameters involving FC, BW and EM can be substituted in a selection index. If sufficiently accurate parameter estimates are available, about the same increase in feed efficiency can be expected as might be obtained with actual feed record information. Thus, it would seem that the primary justification for commercial breeders to keep individual feed records is to collect a volume of data sufficiently large so that reliable population parameter estimates on a given population can be obtained for use in a selection index.

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Manuscript received August 1984

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CORRELATED RESPONSES IN A SELECTION EXPERIMENT ON RESIDUAL FEED INTAKE OF ADULT RHODE-ISLAND RED COCKS AND HENS

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BORDAS, A. & MERAT, P. 1984. Correlated responses in a selection experiment on residual feed intake of adult Rhode-Island red cocks and hens. *Ann. Agric. Fenn.* 23: 233—237. (Centr. Nat. de Rech. Zoot., I.N.R.A., 78350-Jouy-en-Josas, France.)

From a R.I.R. strain two lines R⁺ and R⁻ are selected since 1976 respectively for high vs. low "residual" food intake (individual deviation from regression on body weight and weight gain in males, plus egg mass in females). The divergence represents more than 15 p. cent of mean food intake in cocks and 6 to 8 p. cent in hens. No unselected control is kept. Compared to R⁺, the R⁻ line in both sexes has smaller comb and wattles, lower rectal temperature, better hatching rate; females show slightly inferior egg weight, a smaller and possibly fatter body, superior shell strength.

Index words: selection, residual feed intake, laying hens, Rhode-Island cocks and hens, correlated responses, food consumption.

INTRODUCTION

The feed efficiency of laying hens has been considerably improved by increasing their egg production and lowering their body weight. A point which remains to be considered is the component of the variance of feed intake which is independent of the two factors, egg production and body size. Several authors (NORDSKOG et al. 1972, LEE and NORDSKOG 1975, ARBOLEDA et al. 1976) found no significant amount of this "residual" type variation, but it was observed later in other populations (BOR-

DAS and MERAT 1974, 1981, WATANABE et al. 1975, HAGGER 1977, 1978, HAGGER and ABPLANALP 1978, WING and NORDSKOG 1982, BENTSEN 1983).

The correlations between residual food consumption and other traits have been investigated by BORDAS and MERAT (1974, 1981). Following this, divergent selection was undertaken; the preliminary results are presented in this paper.

MATERIAL AND METHODS

From a Rhode-Island Red strain kept in our laboratory (BORDAS and MERAT 1974), two lines have diverged through individual selection of both sexes for the trait, "residual food intake" (high: R⁺ line; low: R⁻ line). In addition, hens with the lowest egg production (less than 10 % of controlled birds) were discarded. The parents of the first generation of both lines, hatched in 1976, came from the same six sire families; within each of these families half of the females were kept for reproduction of the R⁺ lines and half for the R⁻ line. There was no unselected control population. The number of sires per line was formerly 8 but since 1979 it has been 9. The number of dams per line was initially 32, 36 from 1979 to 1981 and 41 thereafter. The average number of controlled progeny per generation in the R⁻ and R⁺ lines, respectively, was close to 104 and 91 for females and 34 and 32 for males. Selection intensity in males varied between 23 and 40% in the R⁻ line and between 25 and 32 % in the R⁺ line; in females it fluctuated between 32 and 63 % in the R⁻ and between 32 and 57 % in the R⁺ line.

Pedigree reproduction (one generation per year hatched in March-April) took place in cages, 4 to 5 females being inseminated by one male. The chicks were raised in floor pens till 18 weeks of age. Pullets and cockerels kept for performance testing were then transferred to individual cages. Both sexes received *ad libitum* a mash containing 16 % total protein and 10, 6 MJ.EM/kg. The feed formula was identical for all the years. Feed wastage was considered as small. The birds were lighted 14 h per day. The mean ambient temperature was 20 ± 2 °C.

For each bird during a period of 28 days from the age of 8 months, we recorded in both sexes food intake (O), mean body weight (W) and body weight variation (ΔW) from the beginning to the end of the period. We also

recorded in hens the total egg mass laid (E) for this period. Predicted food intake (T) was estimated from a multiple regression equation (BYERLY 1941, LEESON et al. 1973, GOUS et al. 1978, MCDONALD 1978) for each sex within each year. For example, for females in 1983 (variables in g), the equation was:

$$T = 78,9 W^{0,5} + 2,8 \Delta W + 1,2 E - 1825$$

The value 0,5 was taken initially as the power of W and it was kept thereafter, although variations of this value between 0,5 and 1 were found to give very similar results. A unique equation could be established for each generation since no significant heterogeneity was found between the lines for the coefficients of W, ΔW and E. The difference between the observed (O) and predicted (T) feed intake of each individual was taken as its residual feed intake (R). The proportion of the total variance explained by the regression equation in both lines was of the order of 80 % in females and only 40 % in males. The coefficients of the variables W and ΔW were not substantially different in males and females in any year.

The other traits were defined as follows: egg number (en) from the onset of laying to the age of 39 weeks; mean egg weight (ew) and percentage of cracked or broken eggs (% c) between 8 and 9 months of age; at 9 months of age, egg shell thickness (st) and albumen height (ah) on 2 eggs per hen. Wattle length (wl) and rectal temperature (rt) between 9 a.m. and 11 a.m. were also measured. For each line as a whole, we recorded the percentage of mortality (% mo) from 18 weeks and the hatching rate (% h) expressed as hatched chicks/egg set.

In each generation and sex, the mean value of the two lines was compared by a t-test.

RESULTS AND DISCUSSION

R variable: direct response to selection

Table 1 shows that for the trait under selection (R), the difference between lines was significant since 1978 for males and since 1979 for females. In percentage of the mean observed feed intake (O) of the two lines, it varied in females between 5,6 (in 1979) and 8,6 (in 1983) and in males between 13,0 (1978) and 19,3 (1983). The lines diverged sooner and to a larger extent in males than in females. A response to selection seemed to exist in both directions, although in the absence of a controlled, unselected population this was not certain.

Table 2 gives the mean selection differential and mean gains per generation on the R variable for males and females in each line.

The larger selection differentials in males was due to two facts: selection intensity on the whole was higher in males (smaller percentage of birds of the male sex chosen as parents) and the phenotypic variance of the residual component of feed intake in males was higher than in females (the within-years pooled estimate of the

variance of R was: 81581 for males and 41955 for females in R⁻; 143104 for males and 56970 for females in R⁺).

If the genetic correlation between the R variable in males and females is equal to unity, the realized heritability, estimated from the previous figures, is equal to 0,20 and 0,08 in males and females, respectively. Conversely, assuming that there was no correlation between the sexes as to the trait measured, the corresponding estimates of realized heritability in males and females would be 0,29 and 0,24, respectively. The optimal estimates are likely to be intermediate between these extreme figures, as the mean values over generations for the correlations between relatives are the following; between dam and son: -0,03 and +0,10 in the R⁻ and R⁺ lines, respectively; between brother and sister, +0,04 and -0,17; and for comparison, between dam and daughter, +0,09 and +0,13, respectively.

The appreciable gains obtained on the R variable seem encouraging because our population has been closed since 1953, and the two lines originated from a limited number of breeding birds. It is too early to detect a tendency to plateau.

Table 1. Response to selection on the R variable.

Sex and line	Mean value per year (g)							
	1976	1977	1978	1979	1980	1981	1982	1983
Males								
R ⁻	+33	-42	-222	-205	-77	-163	-268	-259
R ⁺	-41	+41	+222	+242	+195	+215	+291	+314
			***	***	***	***	***	***
Females								
R ⁻	+3	+8	-3	-70	-100	-105	-64	-122
R ⁺	-1	-9	+3	+106	+102	+121	+100	+121
				***	***	***	***	***

*** : significant difference at the 0,1 p. cent level.

Table 2. Mean selection differentials and responses to selection per generation (1976 to 1983 included) on residual feed intake.

Line	Mean selection differential (g)		Mean responses to selection (g)	
	Males	Females	Males	Females
R ⁻	-150	-64	-43	-18
R ⁺	+177	+93	+51	+18

Other traits: correlated responses

Tables 3 and 4 show the evolution of the other traits in females and males since 1977. Food intake (O) was considerably modified in response to selection on its residual component; in 1983 the lines differed for the former trait by 15,1 % in females and by 17,6 % in males. In the same year, food efficiency for egg production (O/E ratio) was 2,69 and 2,97 in R⁻ and R⁺, respectively. The body weight of males did not differ in the two lines, except for the year 1983 which must be confirmed. Since 1980, the R⁻ line females are lighter and have a

Table 3. Correlated responses on other traits : females.

Trait and Line	Mean values per year							
	1977	1978	1979	1980	1981	1982	1983	
w(g)	R ⁻	2118	1950	1923	1988	1952	1910	1997
	R ⁺	2169	2095	2006	2205	2186	2041	2140
			***		**		**	***
E(g)	R ⁻	1149	1035	1013	1073	1057	1029	974
	R ⁺	1060	1073	1067	1045	979	1019	1025
O(g)	R ⁻	3277	3051	3003	3005	2858	2810	2619
	R ⁺	3220	3205	3306	3418	3044	3075	3048
			***	***	***	***	***	***
en	R ⁻	73,7	67,5	58,6	72,7	72,5	73,5	50,4
	R ⁺	70,0	66,5	57,5	65,0	62,1	71,9	46,1
					**	***		
ew(g)	R ⁻	56,5	53,5	55,5	56,7	53,6	54,2	54,6
	R ⁺	55,0	55,6	56,6	57,3	55,1	55,0	56,4
			**	*		*	*	***
st (0,01 mm)	R ⁻	37,1	37,0	37,2	—	—	36,1	35,4
	R ⁺	36,7	37,3	37,2	—	—	34,3	33,6
							*	***
ah (0,1 mm)	R ⁻	75	69	72	—	—	76	77
	R ⁺	71	63	65	—	—	72	70
				***			***	***
% C	R ⁻	—	—	—	8,5	4,9	5,0	5,4
	R ⁺	—	—	—	11,3	7,7	8,5	8,0
					**			*
wl (mm)	R ⁻	28,8	27,2	26,2	26,6	25,5	24,3	24,6
	R ⁺	31,3	32,0	31,3	34,2	32,4	31,3	30,7
			***	***	***	***	***	***
rt (°C)	R ⁻	—	—	—	—	—	40,31	40,41
	R ⁺	—	—	—	—	—	40,37	40,58
							***	***
% h	R ⁻	72,1	52,1	62,2	73,1	56,7	64,9	66,6
	R ⁺	64,1	54,0	48,4	56,5	39,7	41,3	63,9
				***	***	***	***	***
% morta- lity (after 18 wks)	R ⁻	13,7	12,6	7,0	2,3	28,2	5,7	11,3
	R ⁺	15,5	3,0	10,1	3,8	14,5	3,0	11,9

* ** *** : respectively P < 0,05 P < 0,01 P < 0,001

Table 4. Correlated responses on other traits : males.

Trait and Line	Mean value per year							
	1977	1978	1979	1980	1981	1982	1983	
w (g)	R ⁻	3268	3007	3049	3099	2850	3200	3252
	R ⁺	3311	3035	3072	3126	2956	2149	3070
								*
O (g)	R ⁻	2760	3235	2511	2437	2565	2345	2648
	R ⁺	2794	3604	2927	2709	2911	2865	3155
			*	***	**	***	***	***
wl (mm)	R ⁻	66,6	64,8	61,4	62,1	60,6	64,2	62,9
	R ⁺	71,6	69,8	70,1	69,1	69,6	73,3	70,3
		**	***	***	**	***	***	***
rt (°C)	R ⁻						40,80	40,93
	R ⁺						41,10	41,23
							***	***

* ** *** : respectively P < 0,05 P < 0,01 P < 0,001

slightly reduced egg weight. On the contrary, egg number differences are not significant within any year, but on the whole the R⁻ line tended to be slightly superior so that the lines did not differ for egg mass. Shell thickness was higher and fewer broken or cracked eggs were recorded in the R⁻ line.

A physiological interpretation of the correlated responses would be premature. However, the early divergence between R⁻ and R⁺ for wattle and comb size suggests that selection for better food efficiency consisted partly in reducing the unfeathered appendages contributing to heat loss. The difference in rectal temperature in 1982 and 1983 suggests the appearance of a divergence between the lines for thermogenesis. In any case, the divergence in thermogenesis and in thermolysis reflected by the correlated responses cited above can explain only a part of the difference between the two lines for food intake.

The better hatching rate of the R⁻ line clearly concerns embryonic mortality: out of a total of 7 generations recorded on table 3, this line had about 10 % more hatched chicks in proportion to eggs set. On the other hand, it showed about 8,5 % fewer dead embryos. A like difference between lines was evident for embryonic mortality in 6 out of 7 years, with a difference of only 1,9 % in the opposite direction in 1978. The better shell strength in the R⁻ line probably explains at least part of this superiority of embryo survival. The post-hatching mortality of young chicks was generally low. It did not differ significantly between lines for females after 18 weeks of age in any separate generation, but for all pooled years it was 10,4 % in the R⁻ lines compared to 7,4 % in the R⁺ lines in 894 and 743 housed pullets, respectively (P < 0,05). Finally, in 20 hens per line dissected in 1983, the R⁻ line appeared to be slightly fatter than the R⁺: 6,7 vs 5,9 % of live weight for abdominal fat measured according to RICARD and ROUVIER (1975) and 12,9 vs 11,5 % for intermuscular plus subcutaneous

fat of the eviscerated carcass.

Responses on wattle length, rectal temperature and percentage of cracked eggs and abdominal fat were in agreement with the direction of the observed phenotypic correlations (BORDAS and MERAT 1981) between these traits and residual feed consumption. The lack of correlation of adult body weight of hens and albumen height with the R variable did not lead to expect divergence observed between lines for the former trait.

Practically, breeding for more efficient birds by reducing the R term shows favorable correlated responses (as compared to selection in the opposite direction) for egg shell strength and hatching rate. The associated reduction of body weight is probably more economically important than the concomitant depression in egg weight. The only obviously unfavorable effect is mortality after 18 weeks which, however, has to be confirmed in further studies.

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Manuscript received October 1984

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SELECTION FOR IMPROVED FEED EFFICIENCY IN BROILERS

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SØRENSEN, P. 1984. Selection for improved feed efficiency in broilers. *Ann. Agric. Fenn.* 23: 238—246. (Nat. Inst. Anim. Sci., DK-1958 Copenhagen, Denmark.)

In a 4-generation-selection experiment, using a fast growing White Cornish as the base population, two lines were selected for better food conversion ratio (FCR) in the interval of 18—39 days and a third for higher weight at 40 days. Each line was reproduced by 20 males and 110 females. In generation 4 the weight line exceeded the FCR lines by 204 g; at a fixed weight the feed efficiency of the FCR lines was better than that of the weight line; in terms of kg food/kg chick, the FCR lines decreased per generation 0,02 more than the weight line.

Decreased fatness, bending of growth curves, and a better efficiency as to the metabolism of food are thought to be the main reasons why the FRC lines performed that good with regard to feed efficiency.

Diminishing profit from a selection programme with growth rate as main selection criterion is considered.

Index words: selection, broilers, growth rate, feed efficiency, fatness, bending of growth curve, selection experiments, diminishing returns.

INTRODUCTION

In an intensive broiler operation the cost of the food for the growing of chickens is amounting to about 70 % of the total cost of the raising of the chickens; no doubt, therefore, an increase of feed efficiency will always be of importance in maximizing the profit.

Since the beginning of the fifties the chicken breeders have been aware that an increased growth capacity will reduce the amount of food needed to obtain a certain market weight and that is most likely the explanation of the situation, in which we are placed to-day, and in which we are left with chickens having a daily

gain of 2,5 to 3 times higher than that of the original chicken breed, as you may find them at the fancy breeders' (JENSEN et al. 1984).

The law of Diminishing Return plays a role regarding the amount of profit obtained from a generation of selection for growth rate, and in such a way that even if the same progress per generation is obtained over a long range of generations still less is gained with regard to feed efficiency.

That phenomenon is further considered in a short paragraph in the paper.

Until recently selection for feed efficiency

has not been seriously considered by the commercial breeding firms. The most important reasons are:

- a) Weight is much easier to record, not only for the breeder himself, but also for the chicken producer.
- b) High body weight is positively correlated to carcass conformation.
- c) The equipment developed at research farms for the measuring of feed efficiency may not always look attractive to the breeder who has to measure 10 000 chickens or more at one time.

Even if no limits to selection for growth seem ahead of us, and even if the breeders have a strong feeling against turning the breeding goal from growth to something else, they are or they will be facing serious problems arising from the many generations of strong selection for increased growth rate of which can be mentioned: Leg disorders and fatness.

So far, few selection experiments including feed efficiency have been reported concerning broilers. GULL and WASHBURN (1974) presented the results of a divergent selection for FCR in which body weight was kept constant using a random-bred population previously selected for growth rate, and they found realised heritabilities for FCR on ,4 for the random-bred chickens and ,25 for the weight selected population. Later Pym and his group gave thoroughly analysed results of a selection experiment in which selection for growth, food intake, and efficiency were compared (PYM and NICHOLLS 1979, PYM and SOLVYNS 1979) and they found a realised heritability for FCR on ,21.

The growth potential of chickens from the two experiments was somewhat below that of the commercial broilers we have nowadays.

The aim of this paper is to present results from 4 generations of a selection experiment comparing growth and food conversion ratio (FCR) as the selection objective on lines originating from a fast growing White Cornish stock.

The diminishing profit from genetic improvement

The physiologists claim that the need for energy to maintenance can be described by the equation:

$$E_M = k W^{0,75}$$

for which the daily energy requirement (E_M) is dependent on the metabolic weight ($W^{0,75}$) in kg, and THORBEC and HENKEL (1976) found that $k = 460$ kJ in fasting chickens kept in cages. Under practical conditions with a maximal utilization of the growth capacity of the chickens the k -value is considered to be higher. A comparison of broiler stocks over the times indicates that the actual k -value is about 25 % higher ($k' = 580$ kJ) (SØRENSEN 1977).

To a fixed market weight the energy (or feed) required for maintenance might be stated as:

$$F_M = \sum_{i=1}^n k' W_i^{0,75n}$$

where n = the day on which the market weight is obtained

The growth curve of the considered interval is concave and can be described by means of a second degree polynomium: ($W_i = 0,04 + b_1 i + b_2 i^2$). The matching curve for metabolic weight will be less curved and in fact, the area below this curve is close to a rectangular triangle, and that is the reason why the need for energy to maintain the body with approximation can be rewritten to a simpler form:

$$F_M = k' (1/2 W^{0,75} n)$$

From this approximation it is easily realized that if the market weight was obtained one day earlier the saving of food to maintenance would be half a part of the feed needed for that purpose on the day the market weight is obtained. The approximation is very robust as to the particular purpose of calculating $F_{M(n)}$ and $F_{M(n-1)}$ over a wide range of growth

capacities as the two growth curves are close to one another.

Assuming a market weight of 1,5 kg and a diet having a density of 13,4 kJ/g corresponding to: $k'' = 43,3$ g from which follows that the need for maintenance on the n^{th} day will be: $43,3 \times 1,5^{0,75} = 58,7$ g. It means that over a wide range of growth capacities a one-day reduction to obtain the market weight of 1,5 kg reduces the need for food by 29 g per chick corresponding to a reduction of the FCR of 0,019.

Looking at the results of the Danish National Random Sample Test for broilers in Denmark over the past 10 years (= 10 generations) an increase of 50 g/generation can be seen as a very firm pattern. Ten years ago the market weight of 1,5 kg was obtained at the age of 46 days, and a generation of selection

caused a reduction of 1,18 d assuming that the daily gain at the time when the market weight was obtained was 30 % higher than the average of daily gain during the rearing period. At the present time the same weight is obtained at 36 days and the reduction is 0,92 days. For a further generation of selection for growth a progress of 50 g at 1,5 kg is presumed.

To summarize this paragraph: assuming the same progress of gain per generation at the same market weight, the resulting profit in terms of a better FCR and a less rent for accommodation is now reduced to 78 % of the amount 10 years ago. In other words the law of diminishing return plays a role, and a comparison of various selection criteria to obtain maximum profit from the genetic improvement at a certain time may some generations later lead to another choice of selection criteria.

MATERIAL AND METHODS

The experiment was started up in 1980 at the Breeding Station STRYNØ situated on a small island south of Funen.

Establishment of the experimental lines

A fast growing stock of White Cornish origin was used as base population of three experimental lines designated as follows:

<u>Line</u>	<u>Selected for:</u>
86	better FCR on normal diet
87	better FCR on low protein diet
88	higher weight at 40 days.

A total of 200 females and 40 males was used as parents for generation 0 in such a way that each full sib group was distributed to all three lines.

No control line was run due to the fact that it proved impossible to keep them constant as to growth capacity, even if all precautions were

taken to eliminate the effect of the natural selection. SØRENSEN (1984) suggested that epistatic effects on linked loci may play a role.

Technical equipment to measure feed consumption

The cages used were designed to contain one chick from the age of 18 d to 40 d. The dimension of the individual cages built together in sections of 20 cages was $21 \times 40 \times 37$ cm (width \times depth \times height) with an installed water supplier at the back wall and a feeding system in front of the cage made up by two 2-litre-milk cartons as a combined trough and silo, the idea of which was adapted from GUILL and WASHBURN (1972). The capacity of the cage system amounts to 1056 chickens at a time and is used twice per generation.

The day old chickens are placed on ordinary floor conditions.

Selection and reproduction procedure

At the age of 40 days the chickens of line 88 were weighed and that measure was the selection criterion; chickens of the lines 86 and 87 were selected according to the following:

$$\text{Eff} = \frac{(W_2 - W_1)}{\text{FI}}$$

where W_1 = Weight at 18 days when placed in cages

W_2 = Weight at 39 days.

FI = Food consumed between the two points of weighing.

Chickens with leg disorder were culled in advance.

Own performance was used as the source of information to estimate the breeding value, and at the age of 42 d the flock was selected down to about twice the number required as parents for the next generation.

At the onset of laying the final selection was carried out in such a way that birds with bad legs were culled, and among the rest selection regarding the primary goal was used to reduce the number to 22 males and 110 females per line.

The breeders of the experimental lines had to follow the general procedure prevailing at the breeding station; therefore, eggs for hatching were not collected until an average hen age of 9 months leaving a generation interval of 11 months. All the breeders were kept in individual cages and artificial insemination was carried through by routine during the period of reproduction.

A number of 5 hatches was produced at an interval of 1 to 2 weeks between each. The FCR lines were reproduced in the first and the fifth hatches to the cage system for the purpose of selection. Chickens of the third hatch were used to the comparative test of the three lines. Line 88 was reproduced through hatches 1—2 and 4—5.

Diets

During the rearing period 0—42 d the diets shown in Table 1 were used. Chickens of lines 88 and 86 got the diet_I and line 87 the diet_{II}. After 6 weeks of age the birds follow the general programme for keeping breeder hens including also the use of commercial diets.

Table 1. Composition of diets used for chickens during the period: 0—6 weeks.

Ingredients g/kg	Diet _I	Diet _{II}
Corn	624,2	734,0
Oats	—	10,7
Soya bean meal	273,3	163,7
Meat and bone meal	21,9	13,1
Fish meal	32,8	19,6
Animal fat	5,0	—
Vitamine premix	10,0	10,0
Chalk	5,0	8,5
Dicalciumphosphat	16,6	26,4
Mineral mix	5,0	5,0
Methionine (10 %)	6,2	—

Carcase quality and fat content

The National Random Sample Test of broilers includes a cutting procedure in which 50—60 chickens are cut into the following 5 parts: Wings, breast meat with skin, but without bone, drumsticks, thighs, and a rest. The procedure used is adapted at Research Institute of Poultry and Fishing, Hillerød, and the trained staff of this research plant is performing the cutting. After weighing the parts, the results are related to the weight of the carcase without neck and neck skin. Content of fat is estimated as an amount of abdominal fat related to live weight; abdominal fat includes leaf fat at the abdominal wall as well as the fat surrounding the gizzard. Usually 30—40 chicks of one sex from each entry are included.

RESULTS

The presentation of results obtained at this early stage is concentrated on the selection intensities obtained, analysis of: Weight, food intake, and food conversion ratio as regressed on generations, and investigation of content of fat.

Selection intensities

In Table 2 the number of chickens at 6 weeks of age is presented. As an overall average 28 % of the females and 6 % of the males were used as parents for the next generation.

The average of a direct and indirect selection during four generations is shown in Table 3. The direct selection intensity was 1,02 for the FCR lines and ,94 for the weight line; the difference is due to a poorer reproduction capacity of weight line in the later generations.

For the FCR lines the indirect selection on weight and food intake shows a very firm

Table 2. No. of chickens with a complete recording for each line and generation.

Generation	Lines		
	86 Nos.	87 Nos.	88 Nos.
0	590	596	580
1	861	950	1069
2	901	812	917
3	684	724	398
4	791	838	561

pattern of a selection for a decreased early weight and an increased finishing weight and a weak indication of reducing the food intake. The opposite selection for weight at 18 and 39 d is the same as a selection for a bending of the growth curve.

Weight at 18 and 39 days of the FCR lines

To study the influence of a possible effect of bending the growth curve on weight at 18 and 39 d, the Table 4 was set up. For each line, sex

Table 3. Selection intensity (i) of direct, selected traits as well as part in traits.

Average of generation: 0-4	Line 86		Line 87		Line 88	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
Weight at 40 d } Efficiency } direct	—	—	—	—	1,17	0,71
	1,26	0,77	1,30	0,74	—	—
Weight at 18 d } Weight at 38 d } Food intake } indirect	-0,20	-0,13	-0,41	-0,20	—	—
	0,33	0,14	0,23	0,13	—	—
	-0,06	-0,07	-0,04	-0,03	—	—

Table 4. Weight at 18 and 39 d of the FCR lines.

Generation	Lines	♂♂			♀♀		
		W ₁₈	W ₃₉	W ₁₈ /W ₃₉	W ₁₈	W ₃₉	W ₁₈ /W ₃₉
0	86	476	1691	0.282	429	1450	0.296
	87	408	1537	0.266	389	1373	0.283
1	86	470	1605	0.293	428	1411	0.303
	87	415	1498	0.277	389	1341	0.290
2	86	461	1684	0.274	429	1479	0.290
	87	418	1559	0.268	388	1397	0.278
3	86	433	1692	0.256	397	1480	0.268
	87	350	1466	0.239	336	1339	0.251
4	86	445	1688	0.263	404	1454	0.278
	87	328	1389	0.236	318	1259	0.253

and generation, weights, and the proportion are given. Line 86 is almost constant as to 39 d weight throughout the experiment whereas a significant decrease of weight at 18 d is recognized (regression on generation was for male $-9,9 \text{ g} \pm 3,1$ and for female $-8,2 \text{ g} \pm 3,3$). The proportion (W_{18}/W_{39}) shows correspondingly a decrease as should be expected.

For line 87 a fluctuating pattern is seen for the W_{39} variable which gives an insignificant indication that the weight at 39 d has decreased, the weight at 18 d decreased by 20 g per generation. The proportion (W_{18}/W_{39}) showed as for line 86 a decrease indicating that the growth curves have changed their shape during the course of the experiment, keeping the market weight constant or perhaps somewhat decreased.

Gain ($W_{39} - W_{18}$) increased for line 86 (male: $18 \text{ g} \pm 14,1$ per generation and female: $15,8 \text{ g} \pm 10,2$), but not statistically significant. For line 87 the W_{39} weight decreased more than the W_{18} , as the gain was negative (male: $-10,3 \text{ g} \pm 10,6$ per generation and female $-3,5 \text{ g} \pm 10,9$).

Feed intake and food conversion ratio of the FCR lines

In Table 5 the amount of food consumed in the interval of 18 to 39 d as well as the food conversion ratio are represented for the 5 generations. Obviously there is a reduction in both traits. Regressed with No. of generation and eliminating the effect of sex, the food intake was per generation reduced by $28 \text{ g} \pm 2,9$ for line 86 and $53 \text{ g} \pm 2,8$ for line 87; the corresponding values for FCR were $0,056 \pm 0,002$ and $0,038 \pm 0,002$. For both of the lines there is a significant decrease in feed intake of 1 % and 2 % respectively per generation; and as the gain increased 1,5 % in line 86 and decreased by less than 1 % for line 87 the resulting proportion of feed intake and gain

Table 5. Food intake 18—39 d and FCR of the FCR lines.

Generation	Lines	$\sigma\sigma$		♀♀	
		FI	FCR	FI	FCR
0	86	2412	2,00	2140	2,11
	87	2299	2,04	2096	2,14
1	86	2363	2,09	2139	2,19
	87	2341	2,18	2139	2,26
2	86	2272	1,87	2065	1,98
	87	2293	2,02	2109	2,10
3	86	2348	1,88	2105	1,95
	87	2249	2,02	2095	2,09
4	86	2290	1,85	2038	1,95
	87	2069	1,96	1918	2,04

(the FCR) decreased significantly for both of the lines during the 4 generations of selection.

Test of experimental lines for growth and FCR

The second and third generations were tested at the National Random Sample Test for broilers at FAVRHOLM and the subsequent generation was tested at the experimental station. In Table 6 comparisons of weight at 40 d can be seen; particularly the difference between the FCR lines and the weight line demonstrates that the distance between the two groups has increased by $51,4 \text{ g} \pm 8,5$ per generation.

Table 6. Weight at 40 d of experimental lines fed on normal diet and reared on floor

Generation	Nos.per. line	Lines			Difference, L88 - (L86 + L87)
		86	87	88	
2	400	1572	1576	1701	127
3	160	1686	1552	1750	131
4	160	1678	1739	1928	219

Assuming that the same market weight irrespective of the growth capacity of the lines, the comparison of their FCR ought to be at a fixed weight. In experimental work with chickens it is often impossible to run chickens to various ages, and that was the case with the test in question. To overcome this inconve-

nience, the FCR is corrected to a fixed weight in the following manner:

$$x = (W_f - W_{obs}) \frac{1}{DG_s}$$

where x = No. of days between observed weight (W_{obs}) and the fixed weight (W_f)

DG_s = daily gain at the W_f .

From observations (SØRENSEN, unpublished) it is found that broilers increase their FCR by 0,019 per day in the area of 1500—2000 g live weight. By using this correction the FCR to a fixed weight was calculated as presented in Table 7. The food intake of the weight line exceeded that of the FCR lines by almost 15 % in generation 4 whereas the weight difference was 12—13 % (Table 6); that is why there is space left also for a difference in FCR, even at a fixed weight, in favour of the FCR lines.

The observation done on the base of Table 5 that line 86 seems to develop a better FCR than line 87 is confirmed when chickens are reared on floor. Contrary to the observation in the preceding paragraph that line 86 had a higher growth potential than line 87 is not confirmed; in fact they seem to have the same average over the 3 generations (Table 5) even if large variations occurred.

Table 7. Food intake (0—40 d) and FCR at 40 d and at a fixed weight for the experimental lines fed on normal diet and reared on floor.

Gener- ation	Parameter	Lines			Difference L88 — (L86 + L87)
		86	87	88	
2	Food Intake, kg	2,58	2,63	2,92	0,315
	FCR, 40 d	1,70	1,73	1,78	0,065
	FCR; 1600 g	1,72	1,76	1,77	0,030
3	Food Intake, kg	2,70	2,37	2,86	0,325
	FCR, 40 d	1,60	1,53	1,64	0,075
	FCR; 1600 g	1,57	1,54	1,59	0,035
4	Food Intake, kg	2,87	3,05	3,40	0,440
	FCR, 40 d	1,70	1,74	1,88	0,160
	FCR; 1650 g	1,69	1,71	1,79	0,090

Fat content of chickens from the experimental lines at the 1984-test

Already at an early phase of the experiment it was obvious that chickens of the FCR lines had a lower fat content than the weight line; on the other hand excessive fatness has never been seen in line 88. Female chickens from test of the fourth generation were examined for abdominal fat, and to give a greater width data from chickens fed on a low protein diet are supplied. The excuse for the use of these "low protein" data for fatness is that they contribute to the postulate that the origin-stock was not predisposed to excessive fatness, even if fed on diets which are known to provoke fatness. The "low protein" part of the experiment has not been commented earlier and will not be discussed further in the present paper.

Table 8 gives the amount of abdominal fat found in 40 d old female chickens raised on floor, and they confirm the earlier observations that the FCR lines are leaner than the weight line. On both of the diets the FCR lines had a statistically significantly lower content of fat than the weight line.

Table 8. Amount of abdominal fat and as percentage of live weight of 40 d old female chickens from generation 4, fed on diet I and diet II respectively (Table 1).

Line	Diet	Nos. of ♀♀	Weight, g	Abdominal fat	
				Amount, g	%
86	I	33	1554	13,3	0,85
	II	33	1377	17,8	1,29
87	I	34	1620	12,3	0,77
	II	33	1378	26,3	1,80
88	I	35	1808	19,4	1,11
	II	30	1615	33,3	2,05
F-test for line effect				P < 0,0001	P < 0,0001
F-test for diet effect				P < 0,0001	P < 1,0001

Carcase quality of the experimental lines at the 1983-test

In any change of selection it is very important to follow the possible way in which carcase quality may change. In the previous paragraph

Table 9. Carcase composition by cutting into 5 pieces. Results from the 1983-test on generation 3.

Line	Nos.	Part as percentage of carcase				
		Wing	Breast meat	Drumstick	Thigh	Rest
86	51	11,90	21,84	14,46	20,69	31,11
87	50	11,79	21,79	15,00	20,43	30,99
88	50	11,73	22,02	14,81	20,71	30,73
F-test for difference		P = 0,40	P = 0,80	P = 0,005	P = 0,40	P = 0,027

it was shown that selection for better FCR reduced fatness compared to selection for weight. Another important way to look at the quality is the distribution of meat. In Table 9 it is shown that by cutting the carcase into 5 pieces no statistic difference could be seen

between the lines with regard to the wing, breast meat, and thigh; the significant variance for drumstick is difficult to believe should be due to the effect of selection as the weight line is intermediately placed between the two FCR lines.

DISCUSSION

In evaluating realized genetic parameters from experiments like the one presented, it is important to know the environmentally based fluctuations over generations. The best way of having such a control with these fluctuations is to keep a control line. As already mentioned, a conflicting situation arises from the fact that use of stock as base population, which already has been selected for many generations for the trait in question, often caused a relapse in the control line. Experiences at the breeding station STRYNØ showed that even if all precautions are taken to eliminate the effect of the natural selection, a decrease of 20–30 g/generation was seen for several generations (SØRENSEN et al. 1980). Under these conditions it was thought more efficient to make an evaluation of environmentally based fluctuations from the contemporary lines under development at the station, and particularly the line used as base population for the experiment. In a future publication, considering the genetic parameters from the experiment, that way of eliminating environmental effect will be used.

The manner in which selection for a better feed efficiency has responded in the present

experiment is obvious by:

- a) Reduction of fatness
- b) Bending of the growth curve.

As to fatness: In spite of the very low level of abdominal fat found for chickens fed on a normal diet, line differences are found. SØRENSEN (unpublished results) did find — in a White Plymouth Rock stock varying from 9 to 20 % total fat — that the regression of percentage of total fat on percentage of abdominal fat followed a second degree polynomium ($R^2 = 0,85$), and using that equation the prediction of total fat would be 8,5 and 10,1 for the lines 86 and 88 respectively when fed on Diet₁. PETERSEN (1969) reported that the costs of depositing one gram of fat and one gram of protein were 51 kJ and 47 kJ respectively, but depositing a gram of protein is accompanied by three grams water without any energy expenditure whereas deposited fat is almost pure; therefore, the difference of 16 g more fat/kg chick in line 88 requires about 50 g extra food/kg chick. Referring to Table 7 the differences in FCR at a fixed age were found to be 160 g in the fourth generation or regressed 140 g; in other words about one third of the

differences between FCR lines and the weight line are due to a less fat content of the FCR lines.

It is with the present knowledges, not possible to give any idea of how much the obvious change of the growth curve influences the maintenance requirement. At the fourth generation — after correcting for fatness — the difference between the two groups is about 100 g food/kg chick; the maintenance expenditure is close to 1000 g/kg chick, therefore it is difficult to believe that the bending of the growth curve will be able to save 10 % of the energy for maintenance. Among other traits which may have been influenced by selection for FCR is the rate of the metabolizability shown by Pym and colleagues to be increased in their experiment, but also the activity of the chickens may have changed.

In a dynamic process, as f.ex. breeding with broilers, the evaluation of which selection

criterion will be the one given maximum profit, in a programme of genetic improvement, is just an evaluation for the moment. The present experiments demonstrate that the gain obtained from direct selection for FCR is per generation 0,02 higher than was obtained by selection for weight which in return increased by the same amount. In other words, the FCR lines have over the four generations had about the double in response with regard to feed efficiency. Other relations may play a role in favour of a continuous selection for higher growth rate. One of these is a psychological one and comes from the fact that growth rate for that long time has been the major criterion for selection that everyone engaged in the broiler business connects good quality stock with the rate of growth and considers feed efficiency as a second parameter which directly originates from growth rate.

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Manuscript received August 1984

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FEEDING BEHAVIOUR AND FEED CONSUMPTION IN CHICKENS SELECTED FOR BODY WEIGHT

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SIEGEL, P. B., CHERRY, J. A. & DUNNINGTON, E. A. 1984. Feeding behaviour and feed consumption in chickens selected for body weight. *Ann. Agric. Fenn.* 23: 247—252. (Virginia Polytechn. Inst. and State Univ., Poul. Sci. Dept., Blacksburg, VA 24061, U.S.A.)

Effects of continued selection for high and low juvenile body weight on food intake and feeding behaviour were studied during a long-term selection experiment. Correlated behavioural and physiological responses to selection were due to quantitative, but not qualitative, changes in control and regulatory mechanisms. Altered thresholds reduced sensitivity for controlling feed intake with resulting overconsumption in high-weight and underconsumption in the low-weight line. Consequences include obesity or undernutrition, both of which reduce fitness unless corrected by nongenetic procedures.

Index words: chickens, body weight, feed intake, feeding behaviour, selection experiment, feed efficiency.

INTRODUCTION

Domestic animals may be larger or smaller than their wild progenitors (PRICE 1984), with an important aspect of the domestication process being adaptation to artificial selection and changes in the environment (SIEGEL 1975). In chickens, selection away from an optimum body weight alters mechanisms which affect food intake (BURKHART et al. 1983), carcass composition (SIEGEL 1984), and reproductive capabilities (SIEGEL and DUNNINGTON 1984, DUNNINGTON et al. 1984). Antagonistic relationships between growth and reproductive

traits, which are well documented (KINNEY 1969), justify development of egg-type and meat-type rather than dual purpose commercial chickens.

Meat-type chickens are larger than those bred for egg production, and their *ad libitum* feed consumption is near the capacity of the gastrointestinal system (NIR et al. 1978). This overconsumption contributes to obesity (MCCARTHY and SIEGEL 1983) and restriction of feed intake has become routine in the husbandry of meat-type breeders. Environ-

mental influences also cause variation both within and among populations in allocation of food resources (e.g., GROSS and SIEGEL 1981, SIEGEL et al. 1984). This paper discusses

relationships among growth, efficiency of feed utilization, and feeding behaviour during long-term selection for high and low juvenile body weight in chickens.

MATERIAL AND METHODS

The selected trait

Two lines, one selected for high and the other for low body weight at 56 days of age, were derived from a population consisting of progeny from crosses of seven inbred lines of White Plymouth Rocks. Since details concerning population sizes, selection procedures, husbandry practices, and environmental controls have been reported (SIEGEL 1962, 1970, 1978), only a few general comments are presented. In the initial parental generation, individuals with heavier and lighter 56-day body

weights were selected to be parents for the high (H) and low (L) lines, respectively. Thereafter, each line was closed and truncation selection was made for high and low 56-day body weight within the H and L lines, respectively. Through 20 selected generations, cumulative selection differentials were 16,85 and 19,40 standard deviations in the H and L lines, respectively. Corresponding responses were 4,68 and 3,53 standard deviations. Realized heritabilities (gain/reach) were 0,28 for the H and 0,18 for the L line.

RESULTS AND DISCUSSION

Changes in efficiency of feed utilization

Efficiency of feed utilization may be influenced by under and/or overconsumption of feed (TITUS 1949), and is variable depending on whether growth is measured to a fixed weight or specific age. During early generations of selection, feed efficiency of embryos was measured. Growth of the developing embryo may be restricted by finite resources available from the egg. Using successive eggs from S₅ generation line H and L dams, LEPORE et al. (1963) conducted chemical analysis of some freshly laid eggs and incubated others to obtain comparable data for the chick at hatch. H-line embryos were more efficient in the utilization

of energy and certain amino acids (particularly the sulfur-containing ones) than those from the L line. These results indicated that genetic alterations in growth potential implemented by selection for 56-day body weight modified efficiency of food utilization by embryos.

A different pattern emerged when comparisons between lines involved chicks after hatch (SIEGEL and WISMAN 1966). Under *ad libitum* feeding, H chicks consumed more feed and grew faster than those from the L line, but there was no difference between lines in feed efficiency to a fixed age. When the feed intake of line H chicks was limited to that of their L-line counterparts in pairfeeding trials, they utilized feed more efficiently than L chicks. These

results were consistent across several rations and inferred that correlated responses for feed consumption masked those for feed efficiency. They also suggested that improvements of feed efficiency in growth selected lines marketed at a fixed weight could be attributed, in part, to their earlier market age (i.e., reduced maintenance). Additional generations of selection resulted in differences between lines in feed efficiency to a fixed age that were sufficiently large to override increased consumption (OWENS et al. 1971, BARBATO et al. 1983 a, 1983 b). The superior feed efficiency of the H to L line chickens may be associated with several factors including changes in oxygen consumption (OWENS et al. 1971), rate of feed passage (CHERRY and SIEGEL 1978), intestinal glucose absorption capabilities (WALKER et al. 1981), and temperature regulation (DUNNINGTON and SIEGEL 1984).

Feed intake

Selection for increased juvenile body weight increased feed consumption (e.g. LEPORE 1965, PYM and NICHOLLS 1979) and contributed to obesity (SIEGEL 1984). Correlated responses for food consumption, as well as shifts in feed: water consumption ratios, were observed within a few days post-hatch (MARKS, 1980, BARBATO et al. 1983 b).

Although many physiological and behavioural factors are involved in feed consumption (see the excellent volume edited by BOORMAN and FREEMAN 1979), the gastrointestinal tract sets a maximum limit on feed intake. Feed intake behaviour should be viewed in a temporal context (JENSEN et al. 1962, DUNCAN et al. 1970, SAVORY 1974), with a distinction made between volume consumed and feeding activity. MASIC et al. (1974) observed different patterns in feed consumption and feeding activity in meat- and egg-type chickens. Subsequently, BARBATO et al. (1980) measured feeding traits

in *ad libitum*-fed H and L line cockerels at several ages. Although meal sizes were the same (6,7 g) for both lines, the number of meals per day of H males was almost twice that of L males (14,0 vs 7,7). Feeding bouts were longer for H than for L birds (13,3 vs 8,7 min), while time spent per day in nonconsummatory feeding activities were less for H than for L males (297 vs 450 min). Correlations of meal size with pre- and post-meal intervals indicated involvement of both meal activation and termination mechanisms.

Hypothalamic lesioning increased feed consumption and induced obesity in egg-type chickens (e.g., LEPKOVSKY and YASUDA 1966, YASUDA 1983). Electrolytic lesions of the ventromedial hypothalamus of S₂₂ generation hens from the H and L lines produced the expected obesity syndrome in L- but not H-line hens (BURKHART et al. 1983). The lack of response by line H birds suggested absence or improper functioning of satiety mechanisms.

NIR et al. (1978) reported that feed consumption of meat-, but not egg-type, chickens approached gut capacity. When S₂₃ generation H and L line chicks were force-fed, the latter could be overfed at an earlier age and to a greater extent than the former (BARBATO et al. 1984). They noted that the degree of overfeeding appeared to be associated with the relative size of certain gastrointestinal components, particularly the anterior ones. If selection for increased body weight resulted in "genetic lesions" of the higher neural centers involved with satiety, and consumptive limits were set mainly by gastrointestinal capacity, then the suggestion by DROR et al. (1977) that intestinal capacity should be considered in selection programs has merit for meat-type chickens.

Food preferences

Domestication has reduced the chicken's sensitivity to sucrose solutions and subsequent

caloric intake regulation (KARE and MALLER 1967). Although meat-type chickens are over-eaters, their ability to discriminate among food sources and balance their diet has received little attention. S₂₃ generation line H and L cockerels were allowed to exhibit a preference between water and dextrose or quinine sulfate solutions (BARBATO et al. 1982). Trials were designed to measure a preference between water and one of the test solutions -- a two choice comparison, with the measure being volume of water to test solution consumed. No preferences were noted between 1,25 % dextrose and water by cockerels from either line. Line L males preferred a 2,5 % dextrose solution to water, while H males did not exhibit a preference until the choice involved 5 % dextrose. Although at 10 % dextrose, L males were still exhibiting a stronger preference than H males, the line difference disappeared when the choice involved 15 % dextrose and water. The pattern for quinine sulfate mirrored that observed for dextrose in that more of an aversion to it was expressed at lower concentrations by L- than H-line males. Thus, while discrimination was observed in both lines, chickens selected for high juvenile body weight had higher thresholds for the response than those selected for low weight.

In a concurrent experiment, GIDLEWSKI et al. (1982) provided S₂₂ generation pullets with 10 and 20 % glucose solutions *in lieu* of water. H-line pullets required twice as long as L-line pullets to adjust caloric intake to control levels (30 vs 15 days). These results provided further evidence that selection for body weight modified sensory mechanisms associated with regulation of caloric intake necessary for energy

balance which, in turn, may contribute to obesity.

Performance of meat and egg-type chickens under dietary self-selection feeding regimes is similar to that of their genetic counterparts fed single complete diets (KAUFMANN et al. 1977, SUMMERS and LEESON 1978). To determine whether nutrient drives were similar, S₂₁ generation H and L-line males were fasted and then given simultaneous access to high protein and high energy diets (HUEY et al. 1982). Total feed intake plus protein and energy consumption were compared to those obtained from birds fed a single complete diet. Within a line, total feed intake was similar regardless of whether the birds were provided a single complete or split diet. Comparisons of protein and energy consumption, however, varied with line. H-line males consumed 24 % more protein and 4 % less energy on split than on complete diets. In contrast, L-line males consumed 25 % less protein and 2 % more energy on the split than complete diet. These data while confirming that chickens selected for high and low juvenile body weight discriminate between diets, inferred a response to body needs. A higher dietary preference for protein in the H-line and a higher energy preference by the L-line post-fast may be due to relative rates of accretion and depletion of body stores in these lines. This hypothesis is based on the observations by CALABOTTA et al. (1983) of higher lipogenic enzyme activity and increased mobilization of free fatty acids from adipose tissue in L- than H-line birds. This increased lipolysis by L-line birds plus the greater growth potential of H-line birds could influence dietary preferences.

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Manuscript received August 1984

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EIGHT GENERATIONS OF SELECTION FOR DUSTBATHING ACTIVITY IN JAPANESE QUAIL

MARTINA GERKEN and J. PETERSEN

GERKEN, MARTINA & PETERSEN, J. 1984. Eight generations of selection for dustbathing activity in Japanese quail. *Ann. Agric. Fenn.* 23: 253—254. (Inst. für Tierzuchtwiss., Eendenicher Allee 15, D-5300 Bonn 1, FRG.)

The inheritance of dustbathing behaviour and its relationship with unselected traits were studied in Japanese quail (*Cot. cot. jap.*). Results are reported on the first eight generations of selection.

Two lines were divergently selected to develop one high (H) and one low (N) line, in addition line K served as randombred control. Selection was restricted to males only. Within each selected line about 135 birds were tested and the 24 males with the highest and lowest dustbathing activity were chosen to reproduce their respective lines. Dustbathing activity was measured as frequency of dust tosses during one dustbath. Birds that did not start dustbathing within 20 minutes were observed again. Males not completing one dustbath were classified as nonbathers and were excluded from selection.

In all generations several unselected traits were measured: latency to begin dustbathing, duration of dustbathing and ratio of frequency of dust tosses to duration (intensity-index). In addition in generation S7 about 120 females from each line were evaluated for dustbathing activity.

By the S1 generation the difference between the selected lines became significant. After 8 generations the mean value for the K line was 10,6 while those of the N and H lines were 5,4 and 21,4 dust tosses, respectively. Regressions of control-adjusted means on generations were similar for each selected line, suggesting a symmetrical response to selection.

Correlated responses to selection were observed in several unselected traits. After 8 generations males of the N, K and H lines bathed 2,1, 3,4 and 6,2 minutes and exhibited 2,8, 3,5 and 4,0 times dust tosses per minute dustbathing. There was no persistent difference between the selected lines with regard to latency.

Although nonbathers had been excluded from selection, the incidence of such males increased in the low line and decreased in the high line. In generation S8 the percentage of nonbathers in the high line was significantly lower than in the low line (1,9 vs. 16,9 %). This result is discussed in the context of a threshold trait.

In generation S7 female dustbathing activity values for the N, K and H lines were 8,6, 13,7 and 21,0 dust tosses, respectively, the differences between the lines being highly significant. Although selection had been restricted to males only, the selection caused parallel genetic changes in female dustbathing displays.

The heritability estimates for all lines and generations based on fullsib correlations for the frequency of dust tosses, latency, duration and intensity index were $,28 \pm ,04$, $,13 \pm ,04$, $,32 \pm ,04$ and $,27 \pm ,04$, respectively. Through the 8 generations the realized heritabilities were $,26 \pm ,02$ (H line) and $,22 \pm ,02$ (N line).

The exerted selection may be considered a suitable method to cause genetic changes in the overall dustbathing behaviour.

Index words: selection, dustbathing activity, dustbathing behaviour, Japanese quail, nonbathers, genetic changes.

The full paper published in Proceedings of XVII World's Poultry Congress and Exhibition, Helsinki, Finland August 8.—12.1984.

Manuscript received August 1984

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SELECTION FOR IMMUNE RESPONSE AS RELATED TO THE MAJOR HISTOCOMPATIBILITY COMPLEX (MHC)

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NORDSKOG, A. W. 1984. Selection for immune response as related to the major histocompatibility complex (MHC). *Ann. Agric. Fenn.* 23: 255—259. (Dept. of Anim. Sci., Iowa State Univ., Ames, Iowa 50011, U.S.A.)

A summary of 10 years of research at Iowa State University relating the major histocompatibility complex (MHC) of the chicken to disease resistance shows that the immune response region of the B complex exerts genetic control over total mortality, resistance to Marek's disease, and to regression of Rous sarcoma-induced tumors. From backcross experiments, recombinants have been produced between the histocompatibility region and the immune response region of the MHC. A wide difference was found between B¹ and B¹⁹ haplotypes in disease resistance. In the main, this was attributed to a "defective" immune response region carried by the original B¹ haplotype. A 4-generation selection experiment for high and low response to immunization with *Salmonella pullorum* gave a maximum response difference in the 3rd generation, but the difference was not related to the MHC.

Index words: selection, immune response, MHC, *Salmonella pullorum*, disease resistance.

Journal paper No. J-11554 of
the Iowa Agriculture and Home Economics
Experiment Station, Ames.
Project 2237. Supported in part by
USPHS Grant AI 12746

The major histocompatibility complex (MHC) is a gene cluster recognized by strong transplantation reactions (H). The acceptance or rejection of a skin graft, for example, is dependent on antigenic structures present on tissue cells of both a donor and recipient, which, if they differ, causes the recipient to destroy the graft. DOHERTY and ZINKER-NAGEL (1975) demonstrated that the products of the MHC also control cellular or cytotoxic reactions to virus-infected tissue.

The MHC represents the most highly polymorphic system known in mammals. All species that have been adequately studied have an MHC system. The best known are the H-2 in mice and the HLA in humans. Because it is identified with the Ea-B blood group system in chickens (BRILES et al. 1982) it is known as the "B complex". Its role in determining genetic resistance to Marek's disease and to Rous sarcoma virus (RSC) induced tumor regression is now well-recognized (BRILES et al. 1977,

COLLINS et al. 1977, PEVZNER et al. 1981 a, 1981 b).

Three classes of MHC genes are now recognized: Class I genes are involved in immune response to cell-bound antigens as virus-infected cells. Class II, or Ir genes, produce "H" cell surface antigens and react to soluble substances. Class III genes control the expression of certain components of the complement system.

Binding of antigens foreign to an animal is due to immunoglobulin receptors on the surface of B and T lymphocytes. The MHC, in cooperation with T cells, recognizes foreign antigens and triggers an immune response. A cellular immune response accommodated by cytotoxic T cells recognizes foreign antigen only if bound with their own MHC products; this requires the identity of MHC Class I loci between effector T cells and foreign antigenic cells. For a humoral response, the antigens must be accompanied by a Class II Ir gene product, which permits the activation of helper (or suppressor) T cells and leads to the ultimate differentiation of a B cell into an immunoglobulin-producing plasma cell.

Serologically, the B complex and the Ea-B blood group locus in the chicken are one and the same (ALTMAN and KATZ 1979). The cell-surface antigens on both erythrocytes and leukocytes identified with Ea-B are controlled by at least 3 loci: B-F, B-G, and B-L (PINK et al. 1977). The former codes for histocompatibility (H) antigens. The latter contains genes involved in the regulation and control of B cell-T cell lymphocyte and macrophage cooperation directed to destruction of body-invading pathogens.

The present communication focuses on the B-L region of the B complex (PINK et al. 1977) as it relates to disease resistance. We have identified B-L with immune response to the amino acid polymer, GAT (PEVZNER et al. 1978).

Relating the MHC to disease resistance

In 1965 the S¹ Leghorn population was derived from crosses of 2 commercial inbred lines identified by different Ea-B blood group markers. Matings were set up to produce all combinations of B¹, B², B¹⁹, and B²¹ alleles, giving 4 homozygous and 6 heterozygous genotypes among the progeny in each of 10 successive year-generations from 1965 to 1975. The laying-house performance of two of these groups is presented in Fig. 1. In particular the B¹B¹ homozygous group (B¹B¹) is contrasted with the B¹ heterozygous group (B¹B², B¹B¹⁹, and B¹B²¹). In each year, adult mortality was highest and egg production was lowest among the B¹ homozygotes. We first interpreted these results in terms of linkage of the B¹ allele to a major "fitness" locus (NORDSKOG et al. 1973). Separate experiments showed that B¹B¹ pullets had lower antibody titers after being immunized with *Salmonella pullorum* bacterium as well as with other test substances. We then decided to set up a selection experiment for serum antibody titer to *S. pullorum* bacterium.

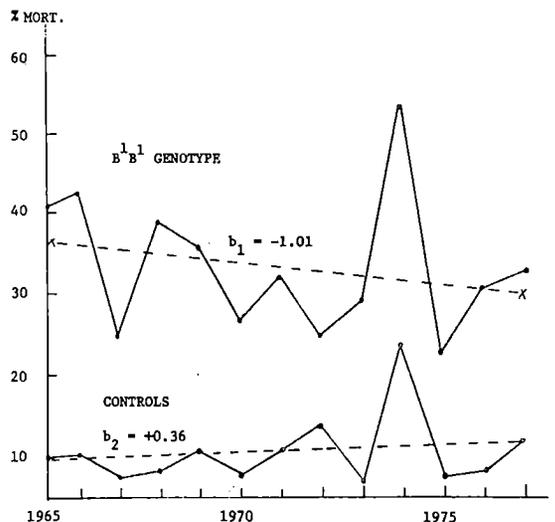


Fig. 1. Adult mortality from all causes of B¹B¹ females of the S¹ Leghorn line. The b's are regression coefficients of mortality on years. (From NORDSKOG et al. 1977. Avian Immunology p. 245. Ed. Benedict. With permission.)

Selection for immune response to *S. pullorum*

A selection experiment for high and low *anti S. pullorum* antibody titer carried out over 4 generations within the B¹B¹ blood group population (PEVZNER et al. 1981 b) was aimed primarily at identifying different response patterns controlled by the B-L immune response genes of the B complex. Maximum divergence was obtained in the third generation (Fig. 2) of the selection experiment, immune response was deduced to be controlled by polygenes. We were surprised, however, to find that the B¹B¹ subline, selected for high immune response, had consistently greater total mortality (Figs. 3 and 4) and greater susceptibility to challenge with Marek's disease virus (Fig. 5) as opposed to the B¹B¹ subpopulation selected for low response.

In the 3rd and 4th generations, the high and low subline breeders were immunized with the synthetic polypeptide, Glu-Ala-Tyr (GAT) (NORDSKOG et al. 1977). In progeny samples of both the *S. pullorum* selected sublines, we found high and low GAT responders in each. The results, presented in Figs. 3, 4, and 5, show that total mortality as well as susceptibility to Marek's disease was consistently greater in the GAT-low than in the GAT-high responders. We, therefore, deduced that a locus in the B-L region of the B complex, identified by response to GAT immunization, exerted genetic control, at least in part, over disease resistance.

Finally, the data suggested that response to *S. pullorum* antigen is mainly a function of non-B complex genes operating independently of the MHC. The greater incidence of both Marek's and total mortality in the B¹B¹ subline selected for high response to *S. pullorum* is thought to have been a chance consequence of a higher frequency of GAT-low genes resulting from random gene drift between generations. This could well happen because the initial subline populations, being small, are likely not to have been representative.

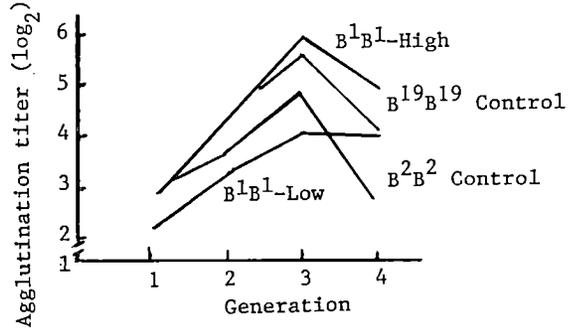


Fig. 2. Agglutination titers to *S. pullorum* of the B¹B¹ selected groups and of the B²B² controls. (From PEVZNER et al. 1981a. *Poult. Sci.* 60: 923. With permission.)

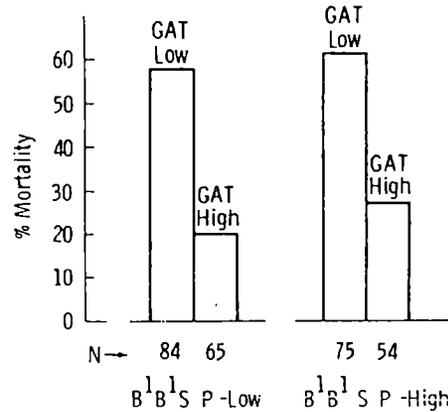


Fig. 3. Total mortality of B¹B¹ birds of the 2nd generation (8 weeks to 10 months). (From PEVZNER et al. 1981a. *Poult. Sci.* 60: 929. With permission.)

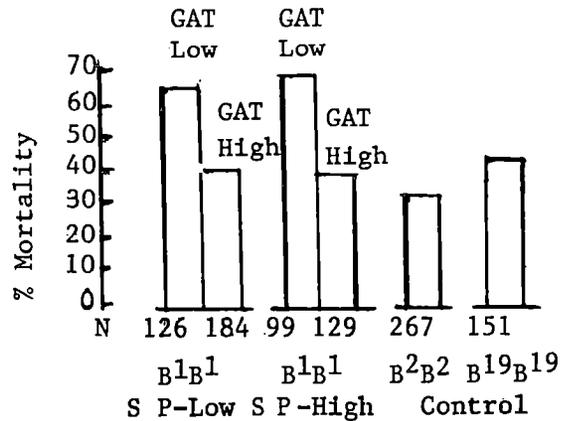


Fig. 4. Total mortality of the 3rd generation (8 wks. to 10 mo.). (From PEVZNER et al. 1981a. *Poult. Sci.* 60: 930. With permission.)

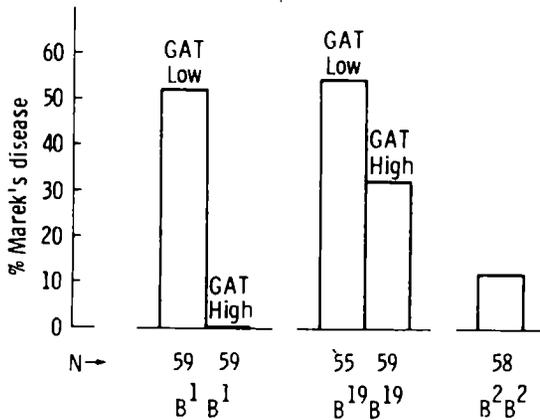


Fig. 5. Incidence of Marek's disease in B¹B¹ and B¹⁹B¹⁹ high and low GAT responders and B²B² controls of the 4th generation. (From PEVZNER et al. 1981b. Poul. Sci. 60: 930. With permission.)

Genetic linkage of resistance to Marek's disease to the B complex is now well established (STONE et al. 1977, LONGENECKER et al. 1976, and PEVZNER et al. 1981). Genetic control of Rous sarcoma-induced tumors has also been associated with immune response to GAT (GEBRIEL et al. 1979). GAT-high birds were better able to regress RSV-induced tumors than were GAT-low birds. Table 1

demonstrates a strong association of GAT response to RSV-induced tumor expression: GAT high birds had 33,3 % regressors versus 6,0 % for GAT low. In contrast, no relationship could be detected between *S. pullorum* high and low from the selection experiment.

In 1978 we performed a backcross experiment (PEVZNER et al. 1978) using B¹B¹⁹ mated to B¹B¹ and to B¹⁹B¹⁹. Prior observations showed that the B¹B¹ birds were low GAT responders and the B¹⁹B¹⁹ birds were high responders. One B¹B¹ male (No. 11 000), identified as a high responder, was judged to be a recombinant within the B complex because backcross and F₂ progeny tests indicated strong linkage between the B complex and immune response to GAT. A successful search for other B-complex segregating recombinants made possible the expansion of four recombinant haplotypes, B¹B¹ GAT-high and low and B¹⁹B¹⁹ GAT-high and low, into sizable numbers which now have on hand.

Finally, it seems that the close correspondence of RSV-induced tumor regression to the findings for Marek's disease resistance in our S1 line suggests the possibility of a single pleiotropic gene controlling resistance to these pathogens. Further work, however, would be required to establish this contention.

Table 1. Summary of tumor response from inoculation of RSV of B¹B¹ birds classified according to immune response to GAT and to *S. pullorum* titer.

Classification of breeder population	No. progeny inoculated	Regressor		Progressor		χ ²	d.f.	P
		No.	%	No.	%			
GAT-low	67	4	6.0	63	94,0	16,71	1	≤0,01
GAT-high	84	28	33.3	56	66,7			
<i>S. pull.</i> -low	151	32		119		0,025	1	N.S.
<i>S. pull.</i> -high	83	18	21.7	65	78,3			
	68	14	20.6	54	79,4			
	151	32		119				

From GEBRIEL et al. 1979. Immunogenetics 9: 329, with permission.

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Manuscript received August 1984

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BREEDING FOR ANTIBODY PRODUCIBILITY TO NEWCASTLE DISEASE VIRUS AND DISEASE RESISTANCE IN JAPANESE QUAIL

S. TAKAHASHI, H. TAKAHASHI, S. INOOKA and Y. MIZUMA

TAKAHASHI, S., TAKAHASHI, H., INOOKA, S. & MIZUMA, Y. 1984. **Breeding for antibody producibility to Newcastle disease virus and disease resistance in Japanese quail.** *Ann. Agric. Fenn.* 23: 260. (Nat. Inst. for Environmental Studies, Tsukuba, Ibaraki 305, Japan.)

The selection for high (H) and low (L) antibody response to inactivated Newcastle disease virus (NDV) vaccine was carried out over 22 generations using Japanese Quail. The significant difference between the H and L lines was continued throughout 22 generations. The maximal divergence between the two lines was obtained in the 18th generation, when the antibody titres were 8,54 and 1,85 (log₂) in the H and L lines respectively. From the analysis of regression formula, the divergent rate (y) for generation (x) through 22 generations was estimated as $y = 0,29x + 0,29$ (log₂, r:0,9).

When these quails were challenged with virulent NDV (Q-strain) at the 7th — 8th and 18th generations, the high responder quails showed greater resistance than the low responder quails in comparison such as the mean survival time and the mortality (in Exp. 1, the mean survival time was $7,2 \pm 1,7$ days and $6,1 \pm 1,6$ days, and the mortality was 65 % and 92 % in the H and L lines respectively; in Exp.2, $6,1 \pm 1,8$ v.s. $4,2 \pm 0,8$ days, and 83 % v.s. 100 % respec.).

These facts showed that the selection for high and low antibody producibility to inactivated NDV vaccine was effective to the NDV infection in Japanese Quail. In addition, reproductive traits such as egg weight, egg production rate, fertility, hatchability, viability, and fitness index were almost same in both two lines through all the generations. The discriminant analysis of the quail's skeleton structure succeeded in separating the H or L line at high probability (male: 97 % and female: 100 %).

Index words: selective breeding, antibody producibility, Japanese quail, heritability, Newcastle disease virus, disease resistance, reproductive traits, body weights, skeleton shape.

The full paper published in Proceedings of XVII World's Poultry Congress and Exhibition, Helsinki, Finland August. 8.—12.1984.

Manuscript received August 1984,

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GENETIC ASPECTS OF TWISTED LEGS IN A BROILER SIRE STRAIN

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LEENSTRA, F. R., van VOORST, A. & HAYE, U. 1984. Genetic aspects of twisted legs in a broiler sire strain. *Ann. Agric. Fenn.* 23: 261—270. (Spelderholt Centre for Poultr. Res. and Ext., 7361 Da Beekbergen, The Netherlands).

Genetic aspects of twisted legs in a broiler sire strain were studied in a selection experiment. Three lines were selected: the R-line, individual selection for six week body weight; the AD-line, sib selection against twisted legs after rearing in cages at four weeks of age; and the K-line, individual selection after rearing in cages against twisted legs, followed by individual selection for six week body weight among unaffected birds. After three generations of selection the lines were compared for frequency of twisted legs and body weight after rearing on litter at six weeks of age and after rearing in cages at four weeks of age.

The average frequency of twisted legs was in cages 38 %, 9 % and 19 % for R-, AD- and K-line respectively, and after rearing on litter 15 %, 3 % and 6 %. In all three lines about 50 % of the chickens with twisted legs were seriously affected and thus retarded in growth.

Body weight at four weeks was 947 g, 902 g and 945 g for R-, AD- and K-chickens. Body weights at six weeks were 1838 g (R), 1682 g (AD) and 1809 g (K). Although the realized selection pressure for body weight in the K-line was only about two-third of that in the R-line, K-line cockerels were heavier when reared in cages due to a lower frequency of severely twisted legs. In the AD-line body weight did not change during the selection experiment.

From these results it can be concluded, that selection against twisted legs after rearing in cages is effective, and that it reduces growth retardation and mortality due to twisted legs among progeny reared on litter.

Index words: chickens, broiler sire strain, genetics, selection, leg weakness, skeletal abnormalities, twisted legs, body weight.

INTRODUCTION

One of the common leg abnormalities in broilers is the twisted leg. This abnormality is characterized by bending and twisting of tibia and metatarsus (DÄMMRICH and RODENHOFF 1970, WISE 1979, HAYE and SIMONS 1978). In severe cases the gastrocnemius tendon slips off

the hock. The bones of affected birds are not shortened and their chemical composition is unchanged (WISE 1979, HAYE and SIMONS 1978). Twisted legs can be observed in chickens from ten days of age onwards. Between ten days and four weeks of age the frequency of twisted

legs increases, but after four weeks new cases seldom develop (HAYE and SIMONS 1978).

There are considerable differences between broiler strains in the frequency of twisted legs (HAYE and SIMONS 1978, HARTMANN and FLOCK 1979). This strongly suggests, that the frequency of twisted legs is heritable to some extent.

To determine if and how selection against twisted legs will influence the performance of chickens, three selection lines were created from a practical like broiler sire strain. Broiler sires were chosen because of the high incidence of twisted legs and because of the fact that in

commercial selection programs the choice of the sire strain is most obvious, when selection against twisted legs is considered.

Twisted legs can only be measured as a categorical trait. Selection is thus most efficient when the frequency of twisted legs is high (FALCONER 1981). When rearing in cages, under continuous light and feeding *ad libitum* a high density diet, the frequency of twisted legs is high compared to litter housing, intermittent lighting and restricted feeding (HAYE and SIMONS 1978, SIMONS 1982). Thus, as selection environment cages, continuous light and *ad libitum* feeding of a broiler ration were chosen.

MATERIAL AND METHODS

Base population and breeding methods

The starting population (fifty males and hundred females) was obtained after two generations of crossing between three commercial broiler sire strains. After these two generations each chicken had grand parents of each of the three strains.

All adult stock was housed individually and breeding was so arranged, that all chickens were fully pedigreed. Within a selection line matings were assigned at random, but full sib matings were avoided.

Selection lines and selection methods

Three selection lines were created. The lines and their selection parameters were:

- ★ R-line: individual selection for six week body weight after rearing on litter and *ad libitum* feeding. Against twisted legs only natural selection was permitted.
- ★ AD-line: full sib selection against frequency of twisted legs at four weeks of age after rearing in cages with *ad libitum* feeding. The frequency of twisted legs was counted on an

all or none basis. In order to correct for unequal number of progeny per dam the frequency of twisted legs per dam, sex and hatch was transformed with the Freeman-Tukey arcsinus transformation (MOSTELLER and YOUTZ 1961). The transformed frequencies gave a ranking of full sib families per sex and hatch. The average of these rank numbers over sexes and hatches was used as selection criterion. This family mean was based on the results of about five chickens in the first and eight in the second and third generation. Chickens destined to be parents of the next generation, with a maximum of four sons and four daughters per dam, were reared on litter. Among them only natural selection against twisted legs was permitted.

- ★ K-line: individual selection against twisted legs followed by selection for six week body weight among chickens without twisted legs. The birds were reared in cages and fed *ad libitum*.

At the start of the experiment three hatches of the same parents were bred. The first was used to select the first generation of the R-line and the second to select the AD-line on the

Table 1. Number of breeders per generation (n) and percentage of the flock to which they, according to their selection criterion, belong (%).

R-line: individual selection for body weight at six weeks of age.

AD-line: sib selection against twisted legs.

K-line: tandem selection, first parameter twisted legs, second parameter body weight at six weeks of age.

Generation	R-line				AD-line				K-line			
	♂♂		♀♀		♂♂		♀♀		♂♂		♀♀	
	n	%	n	%	n	%	n	%	n	%	n	%
1	50	18	100	41	50	23	100	45	20	53,36	60	69,64
2	50	21	100	53	50	28	100	42	20	70,28	90	85,67
3	25	30-10 ¹⁾	100	26	25	38	100	38	25	80,42	100	90,45

1) In the third generation the 10 % heaviest cockerels of the R-line were used for other purposes.

Table 2. Number of chickens used per generation, type of housing, sex and line (see for abbreviations table 1).

Generation	Cages						Litter					
	R-line		AD-line		K-line		R-line		AD-line		K-line	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
1	—	—	—	—	247	260	323	304	292	268	—	—
2	408	408	408	408	256	206	425	416	273	287	—	—
3	492	492	492	492	240	240	476	470	282	311	—	—
4	408	408	408	408	408	408	408	389	405	408	361	294

twisted leg score of their full sibs of the third hatch. The K-line was selected from the third hatch.

Selection was carried out for three generations. The number of breeders and the selection intensity per line and generation are summarized in Table 1. Table 2 gives the number of chickens used per generation, sex, hatch, line and type of housing.

Housing and management

Until six weeks of age two types of housing were used: cages with a wire mesh floor (galvanized 2 mm gauge, square opening of 18 × 18 mm) and floor pens with wood shavings or straw as litter material. The 48 cages, divided over two tiers, measured 100 × 45 × 40 cm and were equipped with a feeder on one

long side and two drinking cups on the other. Until four weeks of age a maximum of 17 chickens was kept per cage (38/m²), until six weeks of age of 11 chickens (24/m²).

In earlier experiments the frequency of twisted legs was lower at the upper tier (HAYE and SIMONS 1978).

It was decided to confound this possible tier effect with the clearly existing sex effect. All males were reared on the lower tier, all females on the upper tier.

Up to the third generation floor pens of about 60 m² were used to rear sexes and lines intermingled. The chickens were housed to a maximum density of 15/m². In the fourth generation floor pens of about 6 m² were used, in which, by adjusting the size, exactly 11 chicks per m² were kept. In the fourth generation lines and sexes were reared separately.

All floor pens were equipped with feeders and automatic drinkers, providing *ad libitum* feed and water.

The environmental temperature for one day old chickens was kept at 32 °C in the cages and 30 °C in the floor pens and decreased gradually to 22 °C at four and 18 °C at six weeks of age.

The cage housed birds and the ones in the floor pens of the fourth generation were kept under continuous light, all others received 14 hours light per day.

All chickens of the third and fourth generation and the birds housed in cages in the first and second generation received a pelleted broiler diet (13,4 MJ metabolizable energy and 21,5 % crude protein). The others were fed a mash diet of 11,8 MJ ME and 20 % crude protein.

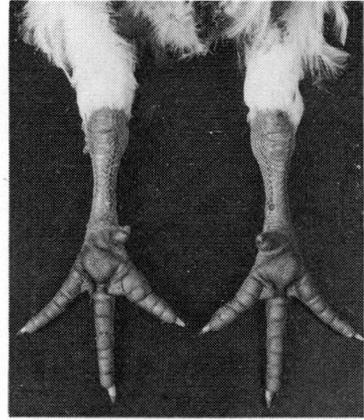
Between 9 and 11 days of age the chickens were vaccinated against NCD (La Sota). Those chickens, that might be used for further breeding, were also vaccinated against Marek's disease and at four weeks of age again against NCD.

Coding for twisted legs

The chickens reared in cages and those of the fourth generation reared on litter were checked by one person for incidence of twisted legs at four weeks of age. The chickens were classified as (1) normal: no visible bending or twisting of tibia and metatarsus, (2) slightly abnormal: tibia and/or metatarsus of one or both legs are slightly bent or twisted, but the bird can walk on the affected leg(s), (3) severely abnormal: the bones of one or both legs are severely bent or twisted — often the tendon has slipped from the hock — and the bird cannot use the leg(s) in a normal way. Fig. 1 illustrates the classification. Both inside and outside bending occurred, but no distinction in classification has been made between inside and outside bending.

All chickens that died during the experiment were autopsied. When they had slightly or

Figure 1. Coding for twisted legs:



a. normal



b. slightly twisted



c. seriously twisted.

severely twisted legs, they were classified accordingly.

Comparison of the lines

In the second and third generation R- and AD-lines were reared together in cages and on litter. In the fourth generation three hatches of all three lines were reared together on litter and in cages. Per sex, line and hatch eight cages were used, each accommodating 17 chickens. On litter there were two pens per sex, line and hatch with 34 to 68 chickens per pen.

Data collected and statistical evaluation

All chickens reared in cages and the ones of the

fourth generation reared on litter were coded for twisted legs. Individual body weight (full fed) was recorded in all generations at four or six weeks of age.

The data on twisted legs of the fourth generation were examined with a log linear model for influence of line, sex and hatch (FIENBERG 1977). Specific differences between pairs of observations were tested with the χ^2 -test.

Body weight in the fourth generation was examined by analysis of variance with cage or pen means as observations. Differences between pairs of observations were tested with the Duncan test.

The level of significance was set as $P < 5\%$.

RESULTS

Selection intensity

Table 1 shows — per line and generation — the percentage of the flock to which, according to the selection criterion, the parents of the next generation belong. The percentage of chickens selected is dependent on the selection method used. In the case of individual selection against twisted legs (K-line), the percentage selected was equal to the percentage of chickens without twisted legs. In the case of sib selection the percentage of families selected can never be less than the percentage of families without twisted legs. Thus, already after one generation, selection against twisted legs in the K-line became rather inefficient due to the low frequency of twisted legs in this line. In the third generation of the AD-line it was possible to select parents for the fourth generation from families in which no twisted legs occurred. Therefore, after three generations selection pressure in the AD-line could not be increased.

Selection pressure in the K-line for body weight is less compared to the R-line, both, due to the smaller number of chickens at the start and due to the tandem selection in the K-line. The selection differentials for body weight show this (Table 3).

Frequency of twisted legs

The frequency of chickens with twisted legs at four weeks of age after rearing in cages is given per generation, hatch and sex in Fig. 2. Both the total percentage of chickens with twisted

Table 3. Selection differential for six week body weight in grams per generation, sex and line (see for abbreviations Table 1).

Generation	R-line		AD-line		K-line	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
1	209	80	35	4	179	61
2	195	70	- 9	-36	171	59
3	128	144	- 9	- 5	112	75

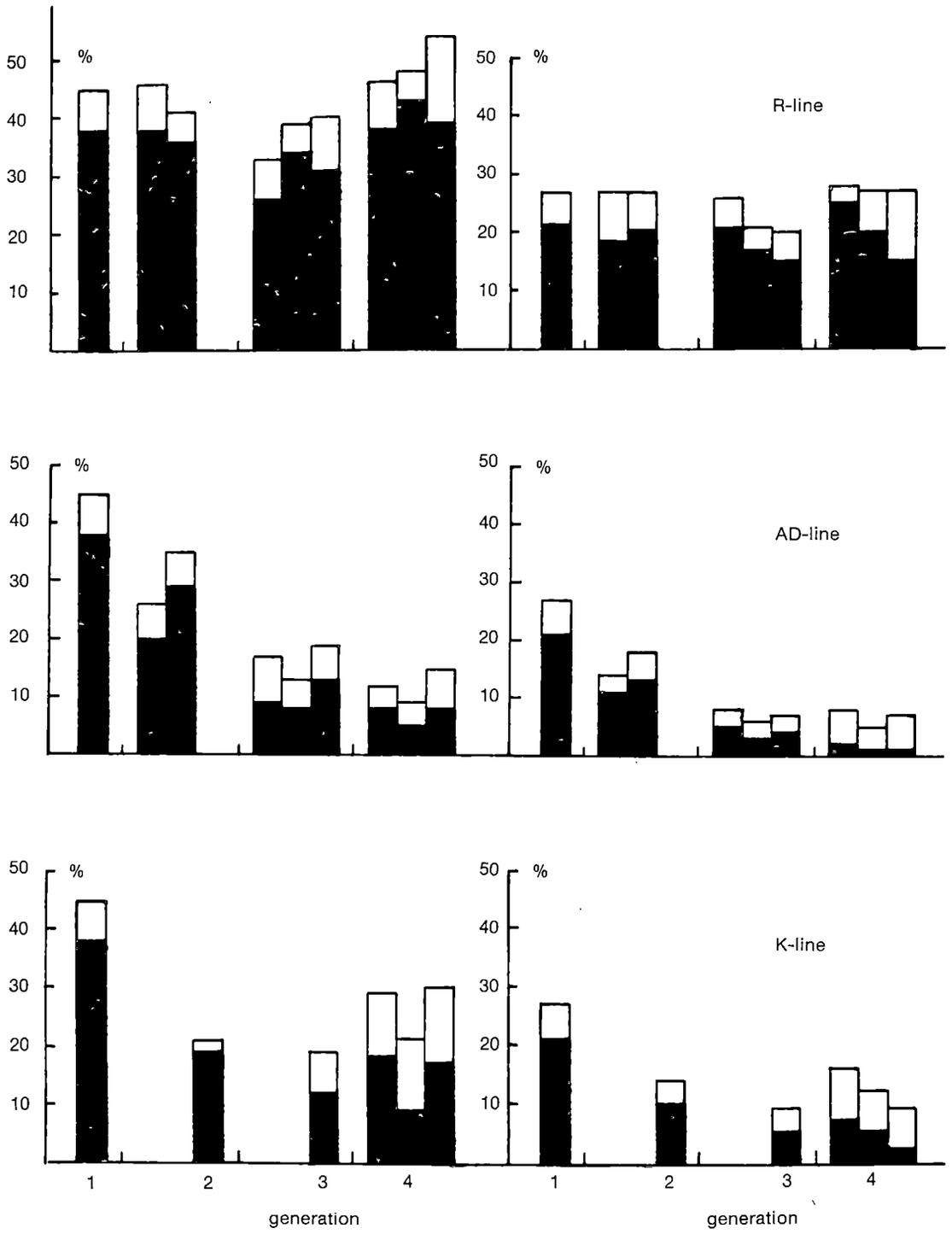


Figure 2. Frequency of chickens with twisted (total bar) or severely twisted (black bar) legs per line, sex, hatch and generation. (See for abbreviations Table 1.)

Table 4. Frequency (%) of chickens with twisted legs and with severely twisted legs (between brackets) in generation four after rearing in cages and after rearing on litter per sex, hatch and line (see for abbreviations Table 1).

Housing Line	Hatch 1		Hatch 2		Hatch 3	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
R	46(38)	28(25)	48(43)	27(20)	54(39)	27(15)
Cages AD	12(8)	8(2)	9(5)	5(1)	15(8)	7(1)
K	29(18)	16(7)	21(9)	12(5)	30(17)	9(2)
R	18(12)	10(3)	10(5)	9(3)	27(14)	16(4)
Litter AD	5(3)	1(0)	4(2)	1(0)	7(0)	3(0)
K	8(4)	6(1)	7(2)	5(0)	8(2)	4(0)

legs and the percentage with severely twisted legs is diminished by selection. It is obvious, that males are more susceptible to twisted legs than females, although the sex effect is probably increased by the effect of the tier of the cages, which was confounded with sexes.

Table 4 gives the frequency of twisted legs among chickens of the fourth generation after rearing in cages and on litter. Also on litter males show a higher incidence of twisted legs

compared to females. After rearing in cages and compared per sex, the AD-line has a lower frequency of twisted and severely twisted legs than the K-line, which had in turn a lower frequency than the R-line. On litter there were no significant differences between AD- and K-line cockerels in total and severely twisted leg frequencies, but both had lower frequencies than R-line cockerels. In females differences in incidence of severely twisted legs could not be tested due to the low frequencies of severely twisted legs among females reared on litter. AD- and K-pullets did not differ in total frequency of twisted legs, but both had a lower frequency compared to the R-line. Differences in the frequency of twisted legs between the lines that are significant at the 5 % level are summarized in Table 7.

For most variables hatch effects were present. There was, however, never an interaction between hatch and line performance.

In the fourth generation of the selection

Table 5. Mean body weight in grams at four weeks of age after rearing in cages of all chickens and of chickens without twisted legs (between brackets) per generation, hatch, sex and line (see for abbreviations Table 1).

Generation	Line	Hatch 1		Hatch 2		Hatch 3	
		♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
2	R	935(1017)	904(930)	907(975)	887(917)	—	—
	AD	921(954)	870(871)	888(929)	860(871)	—	—
	K	—	—	—	—	1041(1078)	952(957)
3	R	985(1042)	881(927)	1004(1052)	936(956)	1050(1079)	953(971)
	AD	959(963)	871(877)	969(970)	900(901)	992(1005)	906(916)
	K	—	—	—	—	1051(1060)	960(962)
4	R	944(1024)	908(948)	962(1050)	950(985)	963(1028)	958(985)
	AD	907(916)	870(869)	945(949)	876(872)	951(954)	861(861)
	K	959(994)	910(928)	998(1006)	926(930)	971(986)	907(908)

Table 6. Mean body weight in grams at six weeks of age after rearing on litter of all chickens and of chickens without twisted legs (between brackets) of generation four per sex and line (see for abbreviations Table 1).

Line	Hatch 1		Hatch 2		Hatch 3	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
R	1938(1978)	1702(1706)	2002(2043)	1717(1726)	1966(2002)	1704(1717)
AD	1751(1761)	1546(1542)	1829(1843)	1574(1566)	1845(1834)	1544(1540)
K	1908(1917)	1686(1683)	1957(1972)	1706(1698)	1959(1957)	1639(1641)

lines, both housing systems combined, 63 chickens died due to twisted legs. Among them were 50 (3,1 %) of the R-line, 11 (0,7 %) of the K-line and 2 (0,1 %) of the AD-line.

Body weight

Mean body weights after rearing in cages at four weeks of age and after rearing on litter at six weeks of age are given per hatch, sex and generation in Table 5 and 6. Differences in body weight between R- and K-line on one hand and the AD-line on the other, increased per generation. As in each generation within the AD-line there were no differences in body weight between the selected and not selected AD-line birds (Table 3), it is not probable, that the growth potential of the AD-line decreased. The increasing differences between AD- and R- and K-line should thus be attributed to an increasing growth potential of the R- and K-line due to the selection of the R- and K-line for body weight.

The frequency of severely twisted legs did influence the mean body weight of the group (Tables 5 and 6). In practically all groups the mean body weight of the whole group was lower than the mean body weight of the chickens without twisted legs. Differences in body weight between normal birds and those with slightly twisted legs were small and in most cases not significant. When lines, sexes

and hatches of the fourth generation are taken together, the cage housed chickens without twisted legs were 22 g heavier than those with slightly twisted legs; on litter the ones with slightly twisted legs weighed 15 g more.

In the fourth generation, in cages and on litter, for males and females, there was a significant line effect on four respectively six week body weight. R- and AD-males reared in cages did not differ, but both had a lower body weight compared to the K-line. In females the AD-line had a lower body weight than K- and R-line, which did not differ significantly. On litter at six weeks of age, AD-line males and females had a lower body weight than R- and K-line birds. There were no significant differences between K- and R-line.

When only the body weight of chickens without twisted legs is considered, the rank-order for birds reared in cages for body weight was: AD lower than K, K lower than R. After rearing on litter and at six weeks of age there were no significant differences between R- and K-line, but AD-line chickens had a lower body weight. Differences in body weight between the lines that are significant at the 5 % level are summarized in Table 7. In general R-line chickens showed the largest difference between the body weight of all birds and those without twisted legs, as the R-line had the highest frequency of severely twisted legs.

Table 7. Differences, that are significant at the 5 % level, between the lines in generation four, tested with the χ^2 or the Duncan test (see for abbreviations Table 1).

Variate	Cages		Litter	
	♂♂	♀♀	♂♂	♀♀
Twisted legs	AD < K < R	AD < K < R	AD, K < R	AD < K, R
Severely twisted legs	AD < K < R	AD < K < R	AD, K < R	1)
Body weight all birds	R, AD < K	AD < R, K	AD < R, K	AD < R, K
Body weight normal birds	AD < K < R	AD < R, K	AD < R, K	AD < K < R

1) Due to low frequencies of severely twisted legs this variate could not be tested.

DISCUSSION

From the results obtained it is evident, that selection against twisted legs can give positive results. Selection against the frequency of twisted legs when rearing in cages, does reduce the frequency of twisted legs when rearing on litter to the same extent. The changes in twisted leg frequencies are dependent on the way of selection. Three generations of single trait sib selection reduced the twisted leg frequencies to 25 % of the original level. One generation of individual selection already reduced the frequency to less than half the original level. The second and third generation of individual selection did not reduce the frequency any further. The fact, that selection reduces the frequency of twisted legs, proves that the frequency of twisted legs is to some extent genetically determined.

HARTMANN and FLOCK (1979) and SOMES (1969) also found genetic variation in the frequency of twisted legs within a line. SOMES (1969) found an autosomal recessive major gene with minor modifier genes responsible for the development of twisted legs, while the results of HARTMANN and FLOCK (1979) indicated sex-linked inheritance.

Our results do not contradict directly both possibilities, although the threshold model (FALCONER 1981) (quantitatively inherited sensitivity, while environment and sex determine the frequency at which sensitivity twisted legs occur) seems more appropriate to explain the consistent differences in twisted leg frequencies between litter and cage rearing and between males and females.

Severely twisted legs have a direct effect on body weight; chickens with one or two severely twisted legs have in general a lower body weight than birds with normal or slightly twisted legs. This is in agreement with the results of HARTMANN and FLOCK (1979). They found, however, that birds with slightly twisted legs had a 3 % higher body weight than

normal birds, while in our birds there was no clear difference between the body weight of normal and slightly affected birds. On the other hand COOK et al. (1984) could not increase the severity of leg problems in broilers by artificially increasing the body weight starting at one day of age. The phenotypic correlation between twisted legs and body weight is therefore not clear, but seems to be close to zero.

However, for selection purposes the genetic correlation between twisted legs and body weight is more important. HARTMANN and FLOCK (1979) do expect this correlation to be rather low. The same conclusion can be drawn from our results. Only with a genetic correlation close to zero it will be possible to obtain non significant differences in body weight between selected AD-line chickens and their not selected hatch mates. Also the results of the K-line compared to those of the R-line do not suggest a strong genetic correlation between sensitivity for twisted legs and body weight.

From comparison of the selection results of the K-and the AD-line it can be concluded, that for practical purposes, i.e. increasing genetically the resistance of broilers against twisted legs, a family selection combining own performance with that of siblings, is most effective. The environment in which the chickens are tested, should increase the frequency of twisted legs as much as possible in order to increase selection pressure.

Acknowledgements — The authors are grateful to P.C.M. Simons and J.H. van Middelkoop for their comments during the experiments; to R. Pit for his technical assistance, and to C.A. Kan for critically reading the manuscript.

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Manuscript received August 1984

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SELOSTUS

Siipikarjan valintakokeita käsitellyt kansainvälinen konferenssi Helsingissä 7.8.1984

KALLE MAIJALA

Maatalouden tutkimuskeskus

Maailman XVII siipikarjakongressin edellä järjestettiin yksipäiväinen konferenssi täydentämään ja syventämään itse kongressin perinnöllisyystieteellisessä jaostossa käytäviä keskusteluja. Konferenssin esitelmät jaettiin tutkittujen ominaisuuksien perusteella neljään ryhmään: munantuotanto, lihantuotanto, käyttäytyminen ja terveys. Lisäksi oli

katsaus Pohjoismaissa käynnissä oleviin valintakokeisiin. Esitelmistä neljä oli myös itse maailmankongressin ohjelmassa, ja ne on julkaistu kokonaan kongressijulkaisussa, minkä vuoksi niistä tässä kongressivihossa on vain lyhennelmät.

YLEISTÄ

Avauspuheenvuorossaan K. Maijala esitteli eri maiden käytännön jalostuksessa eri ominaisuuksien suhteen saavutettuja edistymisnopeuksia, jotka oli arvioitu mittaripopulaation avulla. Keskimääräinen vuotuinen edistyminen oli vuoden munatuotoksissa 2 munaa, munintaprosentissa yksi prosenttiyksikkö ja vuoden munamassatuotoksessa 0,2 kg. Kanojen sukukypsyyssikä oli alentunut päivän vuotta kohti ja rehunkulutus munakiloa kohti 0,04 kg vuodessa. Munan koko oli yleensä vielä kasvanut ja kanojen eloonjäänti pysynyt suunnilleen muuttumattomana tai hieman heikentynyt.

N. KOLSTAD (Norja) selosti Pohjoismaiden valintakokeita. Kokeissa on vertailtu erikoistunutta valintaa indeksivalintaan sekä kudosten vasta-aineominaisuuksiltaan erilaisten linjojen tuotanto- ja elinvoima-ominaisuuksia. Edelleen on

tutkittu munijakanojen valintaa rehuhyötysuhteen mukaan sekä broilereiden valintaa rehuhyötysuhteen ja jalkavikojen perusteella. Munijakanojen rehunkulutuksen muuntelusta elopaino ja sen muutokset sekä munamassatuotos selittävät yhteensä vain noin 80 %, joten näistä riippumatonta muuntelua on. Rehuhyötysuhteen periytymisaste oli munintakauden alussa yli 40 % ja kauden lopussa noin 25 %. Rehunkulutuksen lisääntyminen munakiloa kohti oli yhteydessä kanojen höyhenpeitteen häviämiseen ja paljaiden ruumiinosien, kuten säärten ja harjan, kokoon. Broilereiden rehuhyötysuhteeseen perustunut valinta johti hitaampaan kasvuun mutta parempaan rehuhyötysuhteeseen kuin kasvunopeuteen perustunut valinta. Jalkavikojen vähentämiseen tähdännyt valinta oli tuloksellista.

MUNANTUOTANTO

R. S. GOWE (Kanada) kertoi noin 30 vuotta jatkuneen munijakanojen valintakokeen tuloksista. Jos valintaperusteena pidettiin munämäärää, jonka kana oli tuottanut yhdeksän kuukauden ikään ehdittyään, koko vuoden tuotos parani 0,8 kpl/v. Vastaavan ajan munintaprosenttiin perustunut valinta taas lisäsi vuosituotosta noin 2 kappaleella. Edellinen menetelmä alensi sukukypsyyssikää selvästi enemmän kuin jälkimmäinen. Eloonjääneisydessä sekä kanojen ja munien painoissa ei valintalinjojen välillä ollut eroa, mutta munintaprosenttiin perustuvalla valinnalla oli edullisempi vaikutus munien kuoren paksuuteen, valkuaisen kiinteyteen ja veripilkkujen esiintymiseen kuin osavuoden munatuotokseen perustuvalla valinnalla.

L. E. LILJEDAHL esitti yhteispohjoismaisen valintakokeen Ruotsin osakoikeissa 9 sukupolven aikana saatuja tuloksia. Kokeen tarkoituksena oli verrata munatuotoksiin (N) tai munanpainoon (E) yksipuolisesti kohdistunutta valintaa indeksivalintaan (I), joka ottaa munatuotokset ja munanpainon samanaikaisesti huomioon. Valinta tapahtui energian, valkuaisen ja välttämättömien aminohappojen suhteen niukalla ruokinnalla. Valinta oli kaikissa linjoissa tuloksellista, mutta N-linjassa parani munatuotos ja E-linjassa munanpaino nopeammin kuin I-linjassa. Ominaisuuksien välinen vierova perinnöllinen vuorosuhde ilmeni selvästi siinä, että munanpaino pieneni N-linjassa ja munatuotos E-linjassa. Aluksi munatuotoksen ja munanpainon välinen

perinnöllinen vierova vuorosuhde oli lähellä nollaa, mutta se voimistui valintakokeen aikana sukupolveista toiseen. Munatuotoksen periytymisaste siis pieneni N-linjassa, sukukypsyyksiän periytymisaste taas N- ja I-linjoissa, munanpainon periytymisaste E-linjassa ja munamassatuotoksen periytymisaste kaikissa linjoissa.

H. ABPLANALP (Kalifornia, USA) oli harjoittanut 18 sukupolven ajan valintaa leghornkanojen monikeltuaisuusmuiden lisäämiseksi. Kaksi keltuaista sisältävien munien osuus kasvoi alle 1 %:sta noin 40 %:iin. Enimmillään keltuaisia oli yhdessä munassa kuusi, ja eräs kana tuotti 40 viikon ikään mennessä yli 200 keltuaista. Keltuaiden lisääntyessä myös kanojen paino nousi. Kääpiögeenin tuonti monikeltuaislinjaan vähensi ratkaisevasti keltuaiden määrää ja ruhon rasvaisuutta.

B. SHELDON (Australia) oli työtovereineen valinnut 25 vuoden ajan munijakanoja munintavälin perusteella ja yhtämittaisen valon vallitessa. Kahdessa valintalinjassa munintaväli aleni 22,2 tuntiin ja 22,7 tuntiin, joten normaali 24 tunnin vuorokausirytmistä saatiin rikotuksi. Munintavälin lyhentymisen näytti johtuvan siitä, että muna kulutti vähemmän aikaa munatieteessä. Se ei siis johtunut munan aikaisemmasta irtoamisesta edellisen munan munintaan verrattuna. Välien lyheneminen oli osittain tehotonta siinä

mielessä, että äärimmäisen lyhyitä välejä seurasi usein pitkä väli, jopa sarjan katkeaminen.

T. KOMIYAMA (Japani) oli pyrkinyt yksipuolisen valinnan avulla alentamaan sukukypsyyksiä. Perusaineistossa, jona käytettiin neljän linjan risteytyspopulaatiota, muninnan aloitusikä oli 196 päivää. Huomattavimmin edistettiin sukupolvien 4 ja 15 välillä, jolloin aloitusikä aleni 179 päivästä 126 päivään. Tämän jälkeen ei juuri edistytty. Toteutunut periytymisaste oli mainitulla välillä 48 %. Sukukypsyyksiän alenemista seurasi ensimmäisen munan painon ja tällöin mitatun elopainon aleneminen, mutta muninnan 90 ensimmäisen päivän munatuotos ei muuttunut. Nopeasti sukukypsäksi tulevan linjan aloitusikä nousi päivänpituuden säätelyn avulla 157 päivään, jolloin myös munanpaino nousi 30 %, kananpaino 12 % ja munintaprosentti 28 %. Valintalinjojen väliset risteytyskokeet osoittavat, että sukukypsyyksiä alenee myös heteroosin ansiosta.

A. W. NORDSKOG (Iowa, USA) oli valinnut neljän sukupolven ajan neljää linjaa sellaisen indeksin perusteella, johon sisältyi elopaino, munakiloto tuotos ja rehunkulutus, sekä neljää linjaa sellaisen indeksin perusteella, johon rehunkulutus ei sisällynyt. Edellinen indeksi paransi rehuhyötysuhdetta tehokkaammin kuin jälkimmäinen, mutta sukukypsyyksiä piteni sitä käytettäessä noin 6 päivää.

LIHANTUOTANTO

P. MERAT (Ranska) oli tutkinut, mitä sivuvaikutuksia seurasi valinnasta, joka oli tehty ns. jäännösyöntimäärän perusteella. Jäännösyöntimäärä on havaittu syöntimäärä miinus elopainon ja kasvu- tai munatuotoksen perusteella enustettu syöntimäärä. Jäännösyöntimäärä oli keskimääräisestä syöntimäärästä kukoilla yli 15 % ja kanoilla 6–8 %. Pieneen jäännösyöntimäärään perustunut valinta pienensi kummankin sukupuolen harjan ja helkkojen kokoa, alensi peräsuolen lämpötilaa ja paransi haudontatulosta. Naarailla se lisäsi jossakin määrin pienensi munanpainoa ja elopainoa sekä paransi munankuoren lujutta.

P. SØRENSEN (Tanska) oli valinnut kahta broilerilinjaa rehuhyötysuhteen perusteella 18.—39. ikäpäivänä ja kolmatta linjaa niin, että hän tähtäsi suureen 40. ikäpäivän painoon. Neljännessä sukupolvessa painon mukaan valittu linja oli 204 g painavampi kuin rehuhyötysuhdelinjat. Tiettyssä elopainossa hyötysuhdelinjojen hyötysuhde oli parempi kuin painolinjan: niiden rehunkulutus kasvukiloa

kohti pieneni sukupolvessa 0,02 kg enemmän kuin painolinjan. Tämä hyötysuhdelinjojen tulosten paremmuus näytti perustuvan rasvoittumisen vähenemiseen, kasvukäyrien taantumiseen ja rasva-aineenvaihdunnan tehostumiseen. Myös kasvunopeuteen perustuvan valintaohjelman hyödyn vähenemistä tarkasteltiin.

P. B. SIEGEL (Virginia, USA) oli työtovereineen valinnut kanoja elopainon mukaan pitkän ajan sekä painavaan että kevyeen suuntaan ja tutkinut tämän valinnan vaikutusta rehunsyöntiin ja syöntikäyttäytymiseen. Käyttäytymis- ja fysiologiset sivuvaikutukset näyttivät johtuvan säätelymekanismien määrän mutta ei laadun muutoksista. Kynnysten muuttuminen vähensi rehunsyönnin säätelyherkkyyttä, minkä vuoksi painavat kanat söivät liikaa ja kevyet kanat liian vähän. Rehunsyönnin säätelyherkkyyden vähenemistä seurasi toisaalta ylilihavuutta ja aliravitsemusta, jotka molemmat vähentävät elinvoimaa, ellei niitä korjata hoitotoimin.

KÄYTTÄYTYMINEN

Martina GERKEN (Saksan liittotasavalta) kertoi kahdeksan sukupolvea kestäneen viiriäisillä tehdyn valintakokeen tuloksista. Kokeissa uroksen valinnan perusteena oli ollut pehkukylpykäyttäytyminen. Yhtä linjaa oli valittu aktiivi-

seen, yhtä passiiviseen suuntaan, ja yksi linja pidettiin vertailulinjana. Kylpemisaktiivisuutta mitattiin valintaa varten sillä, montako pehkupotkaisua oli yhden kyllyn aikana. Lisäksi tehtiin havaintoja muista kylpemisominaisuuksista.

Kahdeksan sukupolven kuluttua oli aktiivisen linjan potkaisu luku 21,4, passiivisen 5,4 ja vertailulinjan 10,6. Sivuvaikutuksena kylpyjen pituudet muuttuivat (6,2, 2,1 ja 3,4 min), samoin kuin potkujen tiheydet (4,0, 2,8 ja 3,5 potkaisua minuutissa). Kylpemättömien osuus väheni aktii-

visessa linjassa ja kasvoi passiivisessa linjassa. Myös naaraiden kylpemiskäyttäytymisessä ilmeni eroja; niitä tutkittiin seitsemännessä sukupolvessa. Pehkupertkaisu luvun toteutunut periytymisaste oli aktiivisessa linjassa 26 % ja passiivisessa linjassa 22 %.

TERVEYS

A. W. NORDSKOG (Iowa, USA) selosti 10 vuoden aikana tehtyjä valintakokeita, joissa on pyritty lisäämään munijakanoiden taudinvastustuskykyä ja selvittämään taudinvastustuskyvyn yhteyksiä MHC-verityyppijärjestelmään (MHC = major histocompatibility complex eli solujen yhteensopivuusyhdistemä). Tutkimusten mukaan B-yhdistelmän vastustuskykyalue kromosomistossa säätelee kokonaiskuolleisuutta sekä Marekin kanahalvauksen ja erään kasvaintyyppin vastustuskykyä. Takaisinristeytyskokeissa on voitu tuottaa MHC:n yhteensopivuusalueen ja vastustuskykyalueen uudelleen ryhmittymisiä. B1- ja B19-haplotyyppien havaittiin poikkeavan toisistaan suuresti vastustuskyvyltään. Tämä johtui pääasiassa alkuperäisen B1-haplotyyppin sisältämästä vajeatehoisesta vastustuskykyalueesta. Neljä sukupolvea kestänyt valinta, joka kohdistui vahvaan ja heikkoon vastuuteen *Salmonella pullorum* -immunitaatiota vastaan, aiheutti suurimman eron kolmannessa sukupolvessa, mutta ero ei ollut yhteydessä MHC-yhdistelmiin.

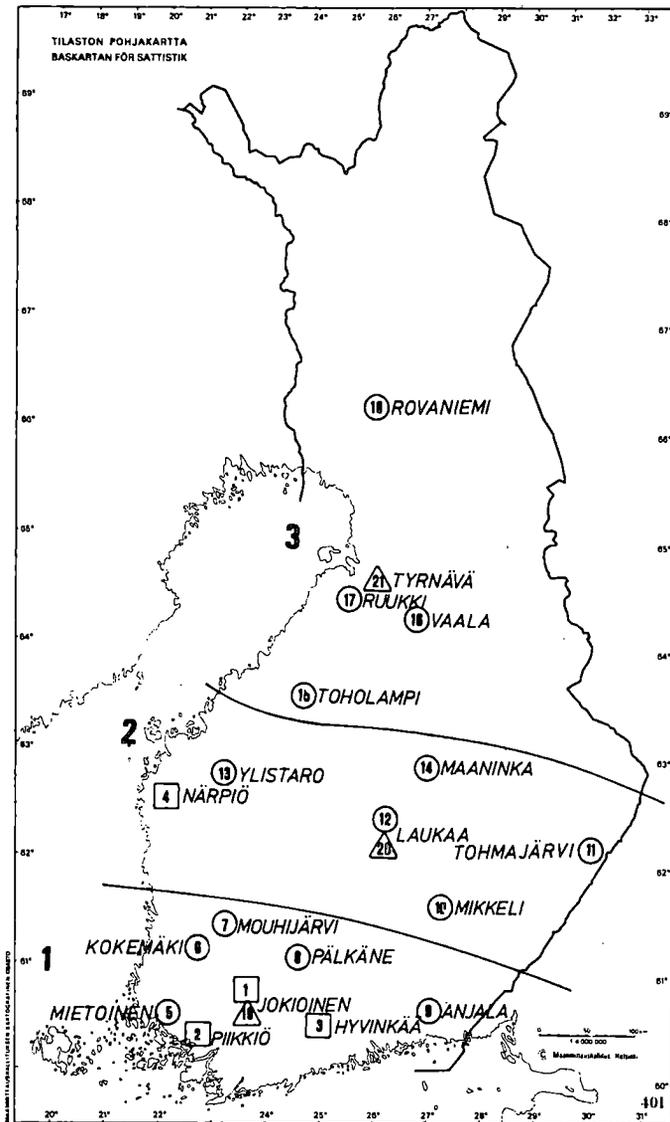
S. TAKAHASHI (Japani) oli työtovereineen valinnut 22 sukupolven ajan japanilaisia viiriäisiä sekä korkean (K) että alhaisen (A) vasta-ainereaktion mukaan, kun eläimet oli rokotettu passivoidulla Newcastle'n tauti-virus (NDV) rokotteella. K- ja A-linjojen väliset erot olivat koko ajan tilastollisesti merkitseviä. Suurin eroavuus todettiin 18.

sukupolvessa, jolloin vasta-ainetitterit olivat 8,54 ja 1,85 (log 2). Koko kokeen aikana ero kasvoi 0,29 yksikköä sukupolvessa. Kun eläimet saastutettiin elävällä NDV-kannalla 7., 8. ja 18. sukupolvessa, K-linjan eläimillä oli suurempi vastustuskyky kuin A-linjan eläimillä, esim. keskimääräisen elinajan ja kuolleisuuden suhteen. Valinnan välittömän vaikutuksen ohella ei ollut havaittavissa, että valinta olisi vaikuttanut merkittävästi muihin ominaisuuksiin kuin luuston rakenteeseen.

Ferry LEENSTRA (Alankomaat) oli tutkinut työtovereineen broilerinpoikasten jalkojen vääntymiseen vaikuttavia perinnöllisiä tekijöitä. R-linjassa oli kysymys yksilövalinnasta 6 viikon painon mukaan, AD-linjassa sisarusvalinnasta jalkojen vääntyneisyyden vähentämiseksi sekä K-linjassa yksilövalinnasta samoin kuin AD-linjassakin, mutta täydennettynä tervejalcaisten eläinten yksilövalinnalla 6 viikon painon mukaan. Linjoja verrattiin toisiinsa 3 sukupolven valinnan jälkeen, jolloin R-linjassa oli vääntyneitä jalkoja häkkikasvatuksessa 38 %, AD-linjassa 9 % ja K-linjassa 19 %, lattiakasvatuksessa vastaavasti 15 %, 3 % ja 6 %. Elopainot 6 viikon iässä olivat vastaavasti 1838 g, 1682 g ja 1809 g. AD-linjassa elopaino ei valinnan aikana muuttunut. Jalkojen vääntymisen vähentäminen valinnan avulla näyttää siten tulokselliselta.

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