Genet. Res., Camb. (1962), **3**, *pp.* 210-225
With 3 *text-figures*
Printed in Great Britain

Modification of selection limits for egg number

By HANS ABPLANALP
Department of Poultry Husbandry, University of California, Davis, California

(*Received* 1 *September* 1961)

INTRODUCTION

A number of cases of selection for high egg number in chickens have been reported in which, after several generations, response to selection was either attenuated or came to a practical halt, in spite of continued selection (Yamada *et al.*, 1958; Dickerson, 1955). The present study was conducted with a SCWL population which had been under continuous selection since 1933 at the Department of Poultry Husbandry of the University of California at Berkeley and Davis. The flock's early history in selection response for egg number to about 79 weeks of age has been given by Lerner and Hazel (1947) and by Lerner (1950). Later phases of the project have been summarized by Lerner (1958, chapter 7). Throughout its existence, the Berkeley Production line (P) has been propagated under selection for egg number with a population size of about 12 sires and 10 dams per sire with minor exceptions as noted by Lerner (1958). Up to 1949, selection decisions were based on production of hens to about 79 weeks of age, but from then on increasing numbers of the selected parents were chosen on the basis of January 1 records, when the birds were from 40 to 43 weeks old, depending on the date of hatch (Lerner and Dempster, 1956). Progeny tested parents were used until 1955, after which time only January 1 selections were made. Selection of pullets or hens was based on combined information on individual performance and family averages for egg number; at the same time a lower floor was kept in selection of egg-weight so as to keep it constant. Evidence gathered over the 27-year development of this selected line suggests that response to selection for 79-week egg production may have been greatly reduced by 1951 (Dempster *et al.*, 1952). With the change in the selection criterion from egg production of hens (about 79 weeks old) to that of pullets (42 weeks on the average of 4 hatches) gains were observed, but only for the latter trait (Lerner and Dempster, 1956). Selection response of the P line for 42-week egg production may have approached a plateau sometime after 1953, as shown by comparisons in Table 1 (see also Lerner, 1958, Fig. 72). A diagrammatic summary of the lines in the Berkeley comparisons is given in Fig. 1. They involved, among others, the following lines:

Line P, under continuous selection since 1933; in 1958 this line was divided into two replicates, one tested under floor management as before, the other in cages.

Line PC, derived in 1952 as a randomly selected line from P, but reselected in two replicates after 1958, in a manner comparable to P.

Line PM, derived in 1958 from Line P and propagated in two replicates under random selection.

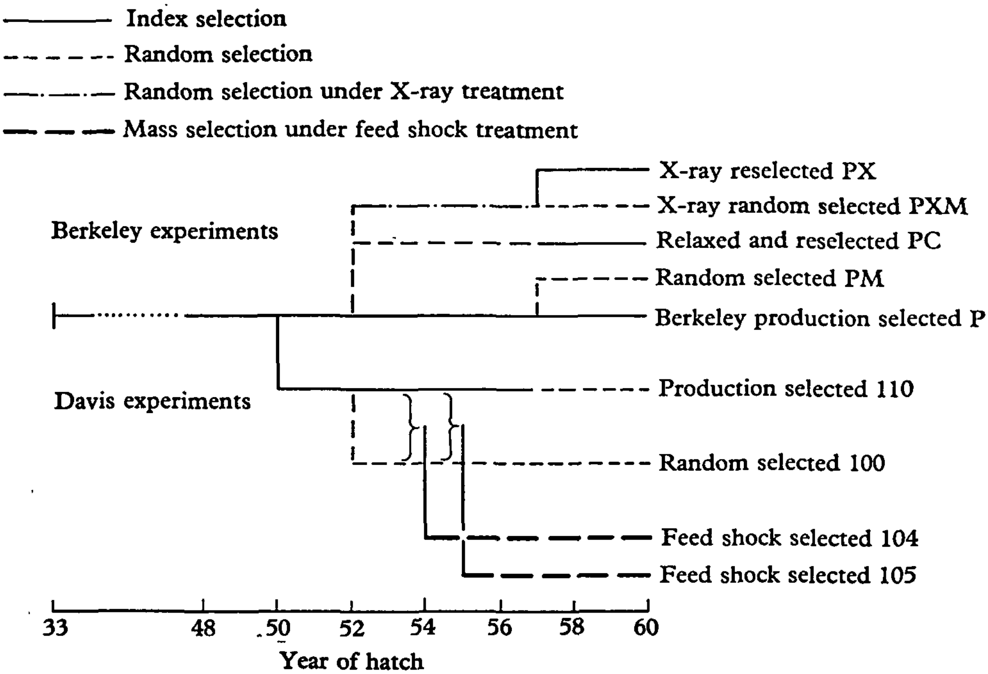

Fig. 1. Graphical representation of populations relevant to the selection experiment for high egg number under feed shock.

A comparison of the last 3 years' data (Table 1) indicates that genetic gains in egg number, at best were small. As usual, in such cases, conclusions about the exact approach to a plateau would be difficult because of inbreeding and possible interactions of lines with annual environments. Concurrently with genetic change in the Berkeley Production line there has been no evidence for drastically reduced heritability over the years (Lerner, 1958), and inbreeding effects counteracting selection

Table 1. *Survivor production to January 1 for Berkeley lines**

Line code	Selection	Management	Year 1951	1952	1953	1958	1959	1960
P	Berkeley production line under continuous selection	Floor	81·2	81·5	88·9	97·1	91·1	97·9
		Cage	60·1	74·8	81·4	96·5	94·2	90·4
PC	Berkeley relaxed (from 1952) and reselected (from 1957) line	Floor	—	—	—	93·3	90·2	91·0
		Cage	—	—	—	98·1	89·7	99·4
PM	Berkeley relaxed (from 1958)	Floor	—	—	—	97·1	89·6	96·2
		Cage	—	—	—	96·6	93·0	96·4

* 1951–53 results have been taken from Lowry *et al.* (1956).

https://doi.org/10.1017/S001667230003500X Published online by Cambridge University Press

could not possibly explain the attenuation of gains (Tebb, 1958). Nor has there been clear-cut evidence for interactions between genotypes and changing environmental conditions of successive generations as suggested by Dickerson (1955). However, such a possibility remains, particularly in view of almost annually diagnosed virus disease conditions at the Berkeley Station of one type or another (Lerner, 1958).

In 1950 a sub-population of the Berkeley Production line was established at Davis (line 110) and was propagated by pullet selection comparable to that practised in the Berkeley flock, but based on production to about 40 weeks of age and without restrictions on egg-size. In 1952 a subline (line 100) was extracted from line 110. It was propagated under random selection without restrictions and a flock size equal to that of line 110 of 8 pens each with 10 mated dams (see Fig. 1).

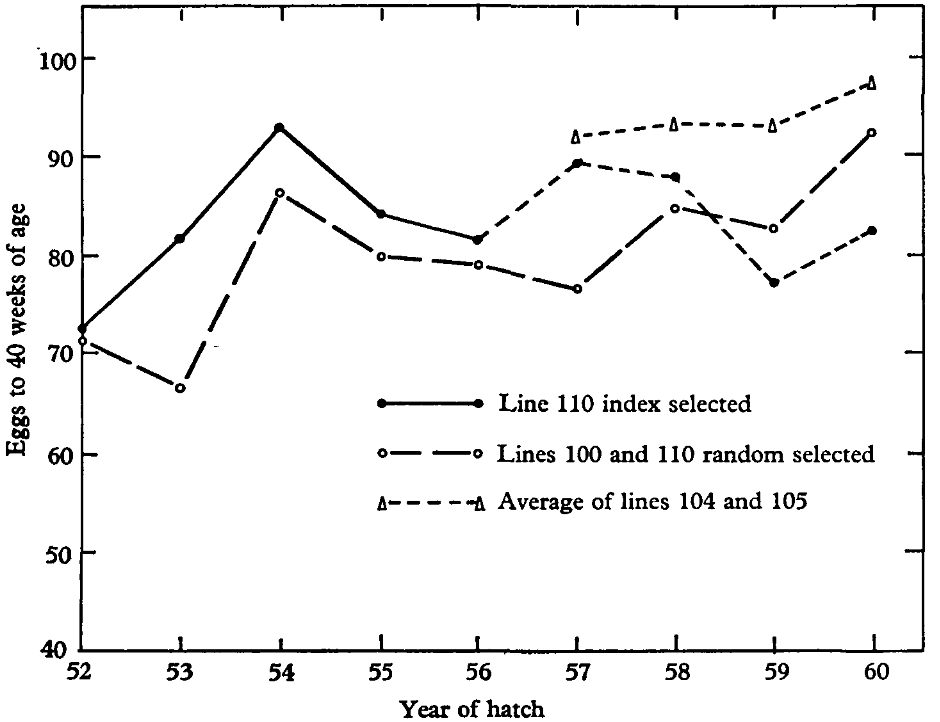

Fig. 2. Number of eggs of survivors to 40 weeks of age, including line 100, selected for egg number from 1933 to 1952 and selected randomly thereafter; line 110, selected for egg number up to 1956 and selected randomly thereafter; averages of lines 104 and 105 which were selected under feed shock since 1954 and 1955 respectively; the hens used in these comparisons were random samples from the respective lines and were tested intermingled in large floor pens under full feeding.

In 1956, 4 years after establishing line 100, selection was also relaxed in the selected line (110). The 2 lines now differed only in 4 generations of selection applied to line 110 between 1952 and 1956. The results of this comparison up to 1960 are shown in Fig. 2. Between 1952 and 1956 the selected line had consistently higher egg production (between 5 and 10 eggs on the average) than the relaxed line, but this

https://doi.org/10.1017/S001667230003500X Published online by Cambridge University Press

difference was established already in the first generation of the comparison. Under relaxation, the advantage of line 110 was later lost and production levels of the 2 lines reversed. Thus by 1952 the Davis production selected line must also have reached a near plateau for 40-week egg production.

Aside from establishing the existence of a plateau in selection response by the method of relaxed selection a number of experiments were initiated between 1952 and 1955 in which a systematic disruption of the presumed selection limits was attempted.

At Berkeley still another population was established and irradiated by X-rays under random reproduction (line PX); in the course of 7 generations it was given a total of 8000 roentgens. Selection for egg number has been resumed for that population in 1957 to test if useful genetic variability was induced by irradiation (Lowry *et al.*, 1960).

At Davis another approach to possible disruption of the existing selection limit was used. Starting in 1954 and 1955 respectively, two replicate populations were extracted from a cross of the Davis random selected line (100) and production selected line (110) and reselected for egg number. In these populations, egg number was determined under a régime of restricted feeding which lasted from 23 to 40 weeks of age (see Fig. 1).

The rationale underlying the experiment was, that new useful genetic variation in egg number might be uncovered by an environment different from normal. If so, the question was whether gains from selection under the artificial environment would cause genetic change under normal conditions. The present report deals primarily with the selection results under feed stress and their implications for the problem of selection limits.

MATERIAL AND METHODS

The choice of a suboptimal environment to be used in connection with selection for egg number was dictated primarily by the objectives of the study. These in turn were formulated on the premise that the plateau in selection response of the original population resulted from a special kind of genotype-environment interaction.

It was assumed that lack of genetic progress was due to a failure to select hens which had the ability to overcome occasional accidents or stresses occurring within generations. This is plausible if one considers that such disturbances, affecting susceptible population members, would tend to reduce their egg production below their potential, while hens unexposed to environmental accidents would lay normally. Thus, artificial selection would favour individuals or families whose ability to withstand minor stresses was never tested. On the other hand, individuals exposed to stress, and capable of yielding information about stress resistance would be discarded because of generally poor lay. In order for such a confounding of accident exposure and selection decisions to occur the former would have to be sufficiently rare so as to allow for a small proportion (perhaps 20%) of virtually undisturbed hens. Unlikely as such a situation might seem in general, it could well have arisen, in this case, as a direct consequence of selection. As indicated by Lerner

(1958) the Berkeley Production flock not only doubled its egg number during the first 10 generations of selection, it also improved in general fitness. This very improvement in viability may have brought about the suggested equilibrium. Perhaps a simpler way of putting it is to say that genetic differences between individuals may become more pronounced under periodic starvation than under normal treatment.

Artificial selection under systematic exposure of all hens to a stress typical of occasional accidents in a hen's environment would be capable of overcoming this type of selection limit. To test this idea repeated starvation periods of 24 hours were chosen for this experiment.

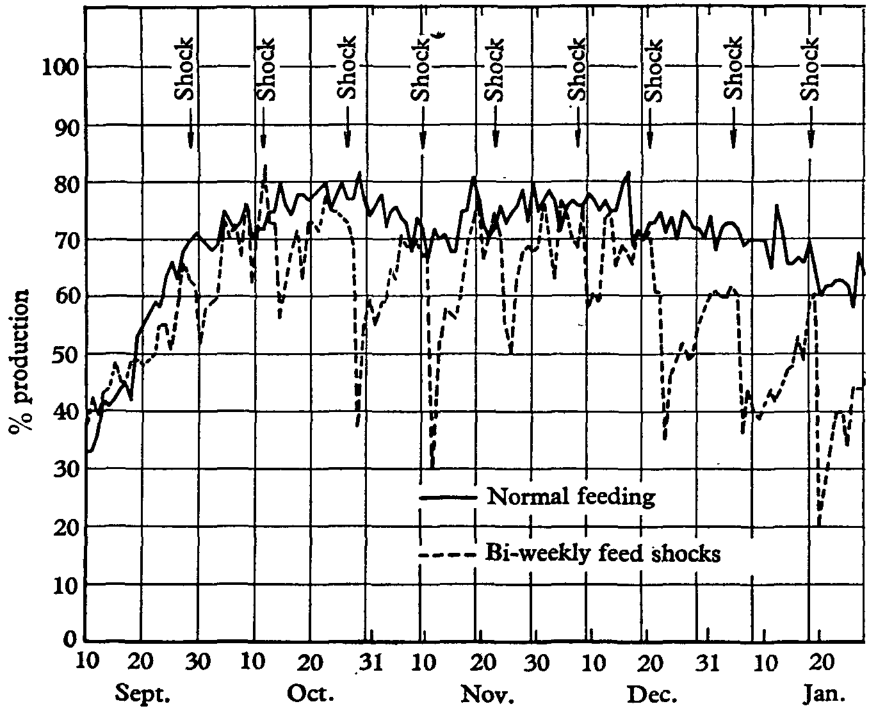

Fig. 3. Production curves of two flocks of hens, one full fed; the other under bi-weekly shocks of one-day starvation. Per cent egg production is computed as the number of eggs per day per 100 living hens.

The average response of the first group of about 160 pullets exposed to periodic starvation is shown in Fig. 3. In this case, hens were stressed every 2 weeks, from 4 p.m. Monday evening to 4 p.m. the following day. Clearly the brief starvation periods were sufficient to throw out of production each time a substantial proportion of hens; but some remained unaffected. The recovery of affected individuals was rapid so that the population laid at a normal rate within a few days after the period of starvation. The treatment, therefore, not only tested the ability of hens to withstand the given stress, but also the ability of the affected individuals to recover; selection in turn would be based on both characteristics. The comparison of production curves of the population under stress and the control group (Fig. 3) also indicates that the overall pattern of decline in lay with age typical of the control line was shown by the population under stress. Thus, the treatment appeared to create no major changes in ageing of hens with respect to lay. Judging from the undiminishing magnitude of successive drops in rate of lay following the application of stress it would appear further that physiological adaptation of hens to the treatment was not occurring. Since they seemed to have no long-range ill effects these treatments appeared to provide a simple, effective, and repeatable method of testing the hens' ability to overcome minor disturbances in their daily environment. The term 'feed shock' seems most appropriate to describe the treatment.

Two replicate lines were established in 1954 and 1955 respectively with selection for egg number from 16 to 40 weeks of age under stress. Both populations were started from a hatch of slightly over 150 pullets from the Davis random line (100). These were reared to 16 weeks, housed in single 12 in. cages and exposed to repeated starvation beginning when the birds were about 23 weeks old. Of the tested hens those with highest egg number were chosen by mass selection; in the first generation the selected pullets were then mated to a random sample of males from the Davis production selected line (110). Afterwards the feed-shock lines were propagated as closed populations. The first matings in line 104 consisted of 30 females selected out of 161, mated in groups of 5 to 6 males of the Davis production line. In subsequent generations, however, it was intended that only 60 pullets be available at housing time; from these, 10 were selected as parents. They, in turn, were mated in 5 groups of two to two shifts of 5 males in succession; thus each pair of females gave 3 weeks' fertile eggs from the first male and after a one-week interruption, was mated to a second male for another hatch of 3 weeks' eggs. The same population size (10 males and 10 females) was used in all generations of line 105 with an attempted selection intensity of one hen out of six. In all generations and both lines the males were selected at random, from 2-day-old cockerels reared from each dam. Table 2 shows the numbers of pullets housed for stress treatment each year. It may be noted from these figures that selection intensity varied between years, based on fluctuations in the rate of reproduction within lines. This variation is due to the fact that in all generations, following the initial tests, reproduction was restricted to two hatches, each from eggs saved over 3 weeks' time. One weeks' eggs were discarded between the two pedigree hatches to allow for changeover of males.

The small size of populations used here was primarily dictated by space, limited to about 200 cages. Family selection of either males or females was avoided for the same reason, and also in order to maintain effective population size as close to the 20 mated parents as possible; in fact, the effective population size varied between 8 and 14 parents. As a consequence inbreeding effects entered the results of this study with an estimated increase in inbreeding coefficients of 14–15%. The present populations were comparable in selection intensity of females of the production lines where plateau conditions had arisen; with respect to selection precision the new lines were at a disadvantage particularly since no family selection was practised. No systematic selection decisions were made for male parents. Without the uncovering of new genetic variation by stress treatment the new lines could thus hardly be expected to yield detectable gains from selection.

The frequency of shock treatments varied in the early generations of the experiment, before both lines were put on identical schedules of shocks at weekly intervals. The schedules used are given in Table 2. These variations in treatment predictably affected average production to 40 weeks of the early generations, but can reasonably be assumed to have produced the same general selection response in egg number.

RESULTS AND DISCUSSION

The average number of eggs laid to 40 weeks by survivors of the two feed-shock selected lines are given in Table 2. By 1960 line 104 had been selected for 6 generations, line 105 for 5. In both populations the average number of eggs laid under stress treatment increased by almost 20 eggs. If anything, the results tend to underestimate actual gains, because in the first generations stress treatments were given only at 2-week intervals, thus permitting only 9 starvation periods before 40 weeks of age. Later generations were given 15 or more treatments before 40 weeks, which would be expected to make for an environmental bias toward lower production compared to the situation with only 9 treatments.

Comparisons of selected lines 104 and 105 with samples of the two Davis control lines (100 and 110) under stress treatment were planned each year beginning in 1957; the performance of control lines is also given in Table 2. It appears that under 15 weekly treatments the control lines laid about 75 eggs, whereas the selected lines had attained production averages of up to 95 eggs by the fifth selected generation. Thus selection under stress was effective, and response in excess of what might have been anticipated from response in the production selected lines (P, PC, 110). Since the cumulative selection differential to 1960 in lines 104 and 105 had been only 55 and 60 eggs respectively, a heritability of over 30% is indicated by the selection response.

The results also indicate that response to selection appeared only after 3 generations of selection. Response thus was first detectable in 1957 for line 104 and in 1958 for line 105. Thereafter, only slight additional improvements are noticeable. No simple explanation can be given for such erratic response to selection; and matters are complicated by the fact that all chicken houses had to be moved 3 miles to a new location in 1957, making it necessary to terminate early the 1956 laying test of line 104. The move of facilities did not, however, involve hens under test so that all birds of the 1957 generation were hatched and reared at the new location and in the same houses the experiment occupied earlier. From then on both lines were reared and tested intermingled, a procedure which had not been possible before because of space limitations. Thus for line 104, at least, response to selection may have taken place as early as 1956. Unfortunately space was not available to test the control lines together with feed-shock lines before 1957.

Egg-weight in the feed-shock selected lines declined by 3 to 4 g. as compared to the average of unselected control lines. Such a result is not surprising, when one considers the fact that egg number and egg-size are negatively correlated, even under normal conditions (Blyth, 1952; Dickerson, 1955; Abplanalp, 1957). Feed-shock treatment might conceivably have accentuated such a negative correlation. It should be noted, however, that index selection over 4 generations in the control line

Table 2. *Production characteristics of feed-shock selected lines and control lines under shock treatments*

Line	Year	Surviving pullets (50 weeks)	Number of shocks	Shock interval (days)	Survivor egg production: 40 weeks	Survivor egg production: 40–50 weeks	40-week egg-weight (g.)	40-week body-weight (kg.)	Age at first egg (days)
104	1954	161	19*	14	75·4	24·0	50·8	1·72	148
	1955	62	18	7	74·2	40·9	53·8	1·66	161
	1956	84	15	3 and 4	—†	—	—	—	166
	1957	53	15	3 and 4	92·5	44·2	54·3	1·74	150
	1958	64	15	7	90·6	40·1	54·0	1·69	145
	1959	27	15	7	95·7	42·0	51·4	1·71	129
	1960	33	15	7	93·3	44·6	52·4	1·77	144
1958–60 avg.		124	15	7	93·2	42·2	52·6	1·72	139
105	1955	154	9	14	83·0	35·5	50·4	1·66	151
	1956	63	9	14	81·1	32·2	52·1	1·58	154
	1957	44	15	7	75·0	42·5	49·1	1·65	157
	1958	87	15	7	96·1	38·3	55·1	1·60	142
	1959	58	15	7	93·5	43·1	52·5	1·59	139
	1960	24	15	7	95·2	40·0	52·6	1·56	140
1958–60 avg.		169	15	7	94·9	40·5	53·4	1·58	140
100	1957	37	15	7	75·9	42·0	47·6	1·69	160
and	1958	46	15	7	76·6	36·1	56·1	1·70	151
110	1959	50	15	7	67·4	37·4	56·8	1·81	148
avg.	1960	42	15	7	84·3	33·8	56·4	1·72	150
1958–60 avg.		138	15	7	76·1	35·8	56·4	1·74	150

* Of 19 shocks applied to 60 weeks of age only the first 9 were used in selection.
† Early termination because of plant relocation.

Q

110 did not result in reduced egg-weight; nor did egg number increase demonstrably. But, where selection for egg number has been practised successfully without restrictions on egg-size (see Shultz (1952) for such selection under inbreeding in the Berkeley production flock) a decline in the latter has been the usual consequence. The gains realized in egg number of lines 104 and 105 under shock treatment were thus made, in part, at the expense of egg-size.

The main conclusion that one can draw from the results of Table 2 in conjunction with those shown in Fig. 2 and Table 1, is that selection response in egg number was possible under feed-shock treatment, in a flock that had probably slowed down considerably with response to selection for egg number under normal conditions.

This raises the question whether gains in egg number realized under shock treatment would also show up under normal feeding. To this end comparisons between bird samples of feed-shock selected lines (104 and 105) or a cross between them (104 × 105), and control lines (100 and 110) were conducted each year beginning in 1957. The results are given in Table 3. A comparison over 3 years of 40-week survivor production for 104 × 105 crosses on one hand, and the average of control lines (100 and 110) on the other, shows an advantage of 20·3 eggs for the former. When compared to results of Table 2 it appears that the gains realized for egg number under stress were also expressed under control conditions. Furthermore, the results in Table 3 for egg-weight indicate that the correlated loss of egg-weight in selected lines was smaller under control conditions than under stress; thus, the difference between control lines and feed-shock selected lines was only 1·9 g. under control conditions in favour of the former, as compared to 3 or 4 g. under shock treatments.

Cross reference between the results in Tables 2 and 3 is somewhat hampered by possible inbreeding effects within selected lines (104 and 105) with negligible inbreeding for the control populations. Using an approximate inbreeding effect of 0·5 eggs for every percent inbreeding (calculated from results obtained by Tebb, 1958), one might estimate an inbreeding depression in selected lines of as many as 7 eggs. Such an estimate agrees roughly with a difference of 7·5 eggs between the 1960 line-crosses (104 × 105) and the average of the pure lines (104 and 105) as shown in Table 3 (101·3 vs. 93·8 eggs).

Another fact that should be noted is that control comparisons were not conducted in the same house as the shock treatments. If anything, the control comparisons were made in a location with a somewhat less favourable environment than the house used for the shock treatments. Thus, for control lines (100 and 110) the data of Tables 2 and 3 show only an average difference, over the last 3 years, of 3·2 eggs in favour of normal feeding (79·3 vs. 76·1); this difference could have been larger under exactly comparable conditions, as shown in Fig. 3 where the age of birds and housing conditions were the same for both treatments.

Also the birds used for comparisons under control conditions (Table 3) were always hatched following reproduction of the lines. With the relatively open houses used in these experiments this meant that the hens used under control treatment were at a disadvantage by being exposed to a longer period of winter weather.

Table 3. *Comparisons of feed-shock and control lines under normal feeding*

Year	Line	Survivors to 50 weeks	Survivor egg production		Egg-weight (g.)		40-week body-weight (kg.)	Age at first egg (days)
			40 weeks	40–50 weeks	40 weeks	50 weeks		
1957	105	51	92·6	40·9	46·5	—	1·73	165
Floor	100; 110 avg.	106	85·3	44·3	46·3	—	1·70	158
1958	104 × 105	45	93·8	38·9	52·4	56·9	1·75	154
Cages	100; 110 avg.	51	78·4	38·4	52·1	56·2	1·84	165
1959	104 × 105	49	100·5	29·5	53·4	55·6	1·67	143
Cages	100; 110 avg.	103	76·0	37·4	55·5	57·7	1·72	152
1960	104 × 105*	24	101·3*	—	52·6*	—	1·73*	148
Cages	104; 105 avg.	31	93·8	35·2	52·7	55·5	1·74	147
	100; 110 avg.	49	83·4	33·1	56·4	59·4	1·75	150
1958–1960	104; 105†	125	96·0	34·5	52·8	56·0	1·72	148
avg.	100; 110	203	79·3	36·3	54·7	57·8	1·77	156
	Difference		+16·7	− 1·9	−1·9	−1·8	−0·05	−8

* Estimated from 39-week measurement as shown in Table 4.
† The 1960 104 × 105 cross data are omitted.

Small samples of 20 to 30 hens of the two feed-shock lines were also reared and tested with the two control lines (110 and 100) under normal feeding in large floor pens, each holding about 110 birds. The results of these comparisons, beginning in 1957, are given in Fig. 2. They agree by and large with the results of Table 3.

While all available evidence thus indicates that selection under feed-shock treatment led to response in egg number under control conditions there is no direct comparison with possible gains from mass selection under normal feeding. Only indirect evidence from similar selections following relaxation in the Berkeley populations (Table 1), and the relative inefficiency of previous selection in the Davis populations (Fig. 2) suggests that the magnitude of response in feed-shock lines was considerably in excess of possible expectations for similar selection under control conditions.

In order to obtain more precise evidence on the relation of shock treatment and selection response, a final comparison of lines was made in 1960. Inbreeding effects were practically excluded from comparisons by contrasting a line-cross of shock selected lines (104 × 105) with back crosses of each shock selected line to each of the two control lines (104 × 100; 105 × 100; 104 × 110; 105 × 110). In addition to normal feeding and repeated weekly shocks of 24 hours two additional stress treatments were used, so as to test the genetic differences under conditions more extreme than provided for previous selection. Accordingly, a treatment series of 15 weekly feed shocks of 33 hours each, and a series consisting of 9 bi-weekly starvation periods of 48 hours each were included in the experiment. From a single hatch of pullets 24 from line-crosses and 8 individuals from each of the four backcrosses were randomly allocated to each treatment, with the exception of somewhat unequal class numbers in the 48-hour treatment. Space limitations made it necessary to terminate this test when the birds were only 39 weeks old; but comparisons of these results (given in Table 4) with the 40-week egg production data used in the preceding tests seem quite reasonable.

Average egg production to 39 weeks under the normal and 24-hour treatments confirm, in principle, the results of the preceding, less accurate comparisons. In order to compare them directly with results presented earlier, it should be noted that the difference between the average of backcrosses on one hand, and the line-crosses of selected shock populations on the other represents only half the genetic difference due to additive gene effects. The differences shown include thus only half the realized additive selection response; possible non-additive gene effects, realized in backcrosses or crosses of selected lines might also be involved, so that an accurate estimate of total additive gains from selection is rendered difficult. Under the circumstances it may be best to consider the differences shown in Table 4 as lower limits of the selection response that might have been observed in large, non-inbred populations; an upper limit might be represented by twice those values.

When egg production results of all four treatments are compared it becomes clear that selection under 24-hour shock treatment had adapted these particular populations to withstand, or overcome, more intensive stresses as well. Thus, differences between selected lines and backcrosses increased as the duration of the shock periods (measured by hours of starvation) was extended in length.

Under normal management the line-crosses exceeded the backcrosses by 9·1 eggs, that is, about half the difference between feed-shock lines and control lines of Table 3, and in agreement with the assumption of only additive gene effects. Under 24-hour feed-shock treatment the difference between line-cross and backcrosses increased to almost 20 eggs; with 36-hour weekly shocks to 22·5 eggs; and under 48-hour bi-weekly stresses to 30·5 eggs. The relative resistance of selected lines to shock thus increased markedly with more severe treatment concurrently with a decrease of total production in backcrosses from 87·3 eggs under normal feeding to

Table 4. *Comparison of feed-shock line crosses with backcrosses of feed shock to control lines*

			Treatment		
Trait	Line	Control	24 hours/ week	33 hours/ week	48 hours every 2 weeks
Eggs to 39 weeks for survivors	Backcrosses	87·3 (32)*	79·4 (31)*	51·4 (32)*	45·8 (23)*
	Feed shock	96·4 (23)*	99·3 (23)*	73·9 (23)*	76·3 (24)*
	Difference	+9·1	+19·9	+22·5	+30·5
Avg. egg-weight (g.) at 39 weeks	Backcrosses	54·3	56·2	48·0	54·1
	Feed shock	52·9	52·5	51·7	53·5
	Difference	−1·4	−3·7	+3·7	−0·6
Body-weight (kg.) at 39 weeks	Backcrosses	1·85	1·72	1·68	1·67
	Feed shock	1·73	1·72	1·67	1·71
	Difference	−0·12	0·00	−0·01	0·04
Gain in body-weight during stress period (23–39 weeks)	Backcrosses	0·26	0·22	0·21	0·13
	Feed shock	0·24	0·25	0·18	0·18
	Difference	−0·02	+0·03	−0·03	+0·05
Kg. of feed per kg of eggs (23–39 weeks)	Backcrosses	2·80	2·78	4·67	—
	Feed shock	2·70	2·89	3·38	—
	Difference	−0·10	+0·11	−1·29	—

* Number of survivors per group that were measured for the traits shown.

45·8 eggs under 48-hour shocks. Average production of the line-crosses showed an increase of 2·9 eggs from normal treatment to 24-hour shocks (96·4 and 99·3 eggs respectively). Adaptation to shock treatment in the selected lines thus appears to have reached the point where possible adverse shock effects on egg production were compensated for, or even over-compensated by subsequent lay.

The shock-selected line-cross had slightly reduced egg-weight under 24-hour shocks, as compared to normal feeding. In contrast, the backcrosses showed a 2-g. increase in egg-weight for the same stress. Similar increase in egg-size under 24-hour shock was also observed for the control lines (11, 110) in earlier experiments (1958–60, Tables 2 and 3). However with the more prolonged weekly shock periods of 33

https://doi.org/10.1017/S001667230003500X Published online by Cambridge University Press

hours the backcrosses had egg-size reduced by perhaps 6 g. while the selected line-cross declined by only 1 g.; making it difficult to generalize on correlated responses in egg-size.

Body-weights at 40 weeks and gains in body-weight during the entire stress treatment (23–39 weeks of age) suggest that feed-shock selection may have resulted in improved homeostasis of the lines involved. In both cases the decrease in body-size of backcrosses due to stress treatment were larger than corresponding changes for the selected line-cross.

Measurements of relative feed consumption (litres of feed for groups of 8 hens of the same line) were made for the first three treatments, while birds of the 48-hour treatment had to be housed in scattered groups of smaller size, so that feed consumption measurements could not conveniently be made for them. Estimates of feed conversion (the amount of feed consumed per kg. of eggs laid) were then made from relative feed consumption measurements, a determination of average specific gravity of the feed used (0·66 kg. per litre), average egg number, and egg-weight at 39 weeks. These feed conversion estimates are also shown in Table 4. The line-cross of selected populations (104 × 105) showed less change in feed conversion from increasingly prolonged shock treatments than the backcrosses to control lines.

Another comparison was made in 1961 between control lines (average of lines 100 and 110), a line-cross between feed-shock lines (104 × 105), and an outcross of feed-shock lines to a population of Jungle Fowl maintained at Davis (Jungle Fowl × lines 104, and 105 respectively). All groups of hens were represented about equally in two hatches taken during the season when lines were normally propagated, since the line-crosses used in the comparison represent the initial generation of a revised selection experiment. The feed shocks used were 33 hours per week and 48 hours per week respectively. The results of this comparison are given in Table 5.

The cross of feed-shock lines was again able to lay eggs at much higher rates than the controls under either treatment. Also the controls showed a stronger relative effect of the more severe starvation treatment (24·5 eggs difference between treatments) than feed-shock lines (13·5 eggs difference). In egg-size feed-shock lines showed a relative decrease under 48-hour treatments while the controls lines maintained egg-size at the same weight. However a detailed interpretation of genetic adaptations of egg-weight in feed-shock lines is rendered difficult by obvious discrepancies in results of the 33-hour treatments in 1960 and 1961. These may have been brought about by extremely favourable climatic conditions in 1961, which resulted in relatively high average production of all birds under the 33-hour treatment. Additional difficulties of interpretation arise from the fact that average egg-weight determination based on about 5 eggs per hen may depend strongly on variation of egg-size within clutches. Thus first and last eggs of clutches tend to be heavier than eggs within clutches. Hens with many interruptions in lay might thus have relatively many first and last eggs included in the sample measured; a fact that may explain a relative increase in egg-size of control lines under 24-hour shocks and their tendency to maintain relatively large average egg-size under 48-hour shocks.

The outcrosses of feed-shock lines to Jungle Fowl showed surprisingly high egg production, considering the fact that normal Jungle Fowl hens lay only about 40 eggs per year under Davis conditions. The ability of the Jungle Fowl crosses to continue laying under feed shock may in part be due to their small egg-size. Also the relative reduction of egg number due to the more severe treatment was less for these outcrosses than either of the other groups (8·6 eggs difference between treatments). The fact that differences between lines become more pronounced under increasingly severe stress confirms the assumption made at the outset that shock treatments give rise to genotype-environment interaction.

Table 5. *Comparison of feed-shock line-crosses with average of control lines and with an outcross of feed-shock lines to Jungle Fowl under feed restriction of 33 hours and 48 hours per week*

		Treatment		
Trait	Line	33 hours/week	48 hours/week	Difference
Eggs to 40 weeks for survivors	104 × 105	88·0 (37)*	74·5 (52)	13·5
	100; 110 avg.	67·0 (26)	42·5 (29)	24·5
	JF × (104; 105)	63·5 (36)	54·9 (54)	8·6
Average egg-weight at 40 weeks (g.)	104 × 105	55·1	52·6	2·5
	100; 110 avg.	55·0	55·2	−0·2
	JF × (104; 105)	47·9	47·7	0·2
Body-weight at 40 weeks (kg.)	104 × 105	1·66	1·57	0·09
	100; 110	1·79	1·67	0·12
	JF × (104; 105)	1·21	1·25	−0·04
Kg. of feed per kg. of eggs	104 × 105	2·56	3·03	−0·47
	100; 110	3·06	4·09	−1·03
	JF × (104; 105)	3·59	4·32	−0·73

* The number of surviving hens are given in brackets.

The combined results of the experiment thus far discussed seem to permit the conclusion that selection for high egg number under shock treatment was successful and imparted to the selected lines increased homeostasis. These findings agree, in principle with those of a similar experiment of selection for rapid growth under restricted feeding (Falconer, 1960). Lerner (1958) has referred to the deliberate exposure of new genetic variance, and its subsequent exploitation by selection as shattering of the canalyzed genotype. In this terminology we may thus be dealing with a case of decanalization.

This is, of course, not the whole picture. Other correlated responses took place which more or less agree with what is known from conventional selection experiments in egg number. Thus, concurrently with selective gain in egg number a reduction of age at first egg by about ten days was observed in both selected lines (Table 2). No simple explanation for such a change can be given when it is remembered that selection under normal feeding in several preceding generations of control line 110 failed to elicit response.

From the average change in body-weight and egg-weight of the two selected lines, it is quite clear that they had achieved their higher egg number under shock with different correlated gains in size. According to the 1958–60 results in Table 2, line 104 established a body-size of 1·72 kg. and an egg-size of 52·6 g. The same kind of selection for line 105, however, resulted in an average body-weight of 1·58 kg. and an egg-size of 53·4 g. These discrepancies, which were clearly representative of the respective lines, can probably be best explained on the basis of genetic drift.

SUMMARY

An attempt was made to modify a near-limit of selection response in the egg production of a closed poultry flock which had been under selection for 31 years; to this end the laying hens were subjected to weekly periods of 24-hour feed deprivation, and selected for egg number under these conditions.

In two replicate populations genetic gains of about 20 eggs were made under shock treatment to 40 weeks of age, over 5 and 6 generations of selection. These gains were also manifest under normal management.

Selection, under 24-hour starvation per week, also improved the ability of the selected populations to lay under weekly starvation periods of 33 and 48 hours respectively. Differences between selected and unselected lines increased with the more severe stress treatments. Also it was found that the difference in average egg production between 33-hour and 48-hour treatments was larger in unselected lines than in the selected ones, indicating the existence of genotype-environment interactions.

Correlated responses of reduced egg-weight and body-weight, and somewhat earlier maturity of selected lines correspond with what might be expected under normally effective selection for egg number. These adaptations however varied considerably between replicate lines.

The author is most grateful to Dr I. M. Lerner for reviewing the manuscript, and to Mrs Dorothy C. Lowry for making available unpublished egg production results of the Berkeley lines for 1958 through 1960. The research at Berkeley is supported by research grant NSF-G18789 of the National Science Foundation.

REFERENCES

ABPLANALP, H. (1957). Genetic and environmental correlations among production traits of poultry. *Poult. Sci.* **36**, 226–228.

BLYTH, J. S. S. (1952). The correlation between egg number and egg weight in the fowl: An investigation of its inconsistency. *Poult. Sci.* **31**, 254–268.

DEMPSTER, E. R., LERNER, I. M. & LOWRY, DOROTHY C. (1952). Continuous selection for egg production in poultry. *Genetics*, **37**, 693–708.

DICKERSON, G. E. (1955). Genetic slippage in response to selection for multiple objectives. *Cold Spr. Harbor Symp. quant. Biol.* **20**, 213–224.

FALCONER, D. S. (1960). Selection of mice for growth on high and low planes of nutrition. *Genet. Res.* **1**, 91–113.

LERNER, I. M. (1954). *Genetic Homeostasis*. vii + 134 pp. London: Oliver & Boyd.

LERNER, I. M. (1958). *The Genetic Basis of Selection*. xvi + 298 pp. New York: John Wiley and Sons.

LERNER, I. M. & DEMPSTER, E. R. (1956). An empirical test of part-record selection for egg production. *Poult. Sci.* **35,** 1349–1355.

LERNER, I. M. & HAZEL, L. N. (1947). Population genetics of a poultry flock under artificial selection. *Genetics*, **32,** 325–339.

LOWRY, D. C., LERNER, I. M. & TAYLOR, L. W. (1956). Intra-flock genetic merit under floor and cage managements. *Poult. Sci.* **35,** 1034–1043.

LOWRY, D. C., LERNER, I. M. & DEMPSTER, E. R. (1960). Report on X-ray induction of variability in polygenic traits of chickens. (Abstract). *Poult. Sci.* **39,** 1270.

SHOFFNER, R. N. & GRANT, R. E. (1960). Relaxed selection in a strain of White Leghorns. *Poult. Sci.* **39,** 63–66.

SHULTZ, F. T. (1953). Concurrent inbreeding and selection in the domestic fowl. *Heredity*, **7,** 1–21.

TEBB, G. (1958). Intra-generation inbreeding effects in a poultry flock selected for egg production. *Heredity*, **12,** 285–299.

YAMADA, Y., BOHREN, B. B. & CRITTENDEN, L. B. (1958). Genetic analysis of a White Leghorn closed flock apparently plateaued for egg production. *Poult. Sci.* **37,** 565–580.