Group Selection for Adaptation to Multiple-Hen Cages: Selection Program and Direct Responses[1,2]

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ABSTRACT A selection experiment was initiated with a synthetic line of White Leghorns in 1982 to improve adaptability and well-being of layers in large multiple-bird cages by use of a selection procedure termed "group selection". With this procedure, each sire family was housed as a group in a multiple-bird cage and selected or rejected as a group. An unselected control, with approximately the same number of breeders as the selected line, was maintained for comparison and housed in one-bird cages.

Annual percentage mortality of the selected line in multiple-bird cages decreased from 68% in Generation (G)2 to 8.8% in G6. Percentage mortality in G6 of the selected line in multiple-bird cages was similar to that of the unselected control in one-bird cages (9.1%). Annual days survival improved from 169 to 348 d, eggs per hen per day (EHD) from 52 to 68%, eggs per hen housed from 91 to 237 eggs, and egg mass (EM) from 5.1 to 13.4 kg, whereas annual egg weight remained unchanged. The dramatic improvement in livability demonstrates that adaptability and well-being of these birds were improved by group selection. The similar survival of the selected line in multiple-bird cages and the control in one-bird cages suggests that beak-trimming of the selected line would not further reduce mortalities, which implies that group selection may have eliminated the need to beak-trim. Corresponding improvements in EHD and EM demonstrate that such changes can also be profitable. The most surprising finding was the rate at which such improvement took place, with the majority of change in survival occurring by the third generation. However, EHD continued to improve at the rate of 4% per generation.

(*Key words*: group selection, well-being, beak-trimming, layer, cannibalism)

INTRODUCTION

During the past half century, changes in management practices of poultry for table egg production have been considerable. Perhaps the greatest change has been from floor pens to multiple-hen cages. The popularity of multiple-hen cages resulted in part because commercial producers found that these cages offered several advantages over floor pens, including improved feed efficiencies (Cunningham, 1982), reduced incidence of some diseases (Cunningham, 1987), and reduced production costs (Craig and Adams, 1984; Craig and Swanson, 1994).

However, conversion to cages has not been without problems. One of the prominent issues has been animal well-being (Craig and Adams, 1984; Cunningham, 1987; Craig and Swanson, 1984). Caging of birds may be stressful in multiple-bird cages, can result in injuries through aggression, flightiness, feather loss, and cannibalism (Craig, 1982). As a result, beak trimming of caged layers has become common practice. However, beak trimming in itself causes pain and suffering (Breward and Gentle, 1985; Gentle *et al.*, 1990; Craig, 1992). Animal well-being concerns have forced the industry in Western Europe to change or eliminate management practices related to beak trimming, cage design, and bird density (Hurnik, 1990). These issues should also be a cause for concern to the poultry industry in general from economic, public relations, and humane perspectives.

From a genetics perspective, stress and behavior are manifestations of how well adapted the bird is to its environment. The environment, in this case, is the multiple-bird cage. A bird that is genetically adapted to cages should not be stressed nor its well-being compromised (Siegel, 1981, 1995). This conclusion results from the observation that through natural selection, species have evolved that not only thrive, but prefer environmental extremes, from the coldest parts of the Antarctic to volcanic fissures on the bottom of the ocean.

The problem for poultry breeders is to utilize a breeding program that adapt layers to multiple-bird cages. This problem is ignored by many commercial

breeders, who use individual housing of hens to measure production (Hunton, 1990; Muir, 1985). As a result, competitive interactions and effects of associated stress in production environments are disregarded. Because the environment of selection and the environment of production are drastically different, the potential for creating a genotype-environment interaction is large (Falconer, 1981). Although two forms of genotype-environment interaction exist, due to scale and relative rankings, it is the later form which is of greatest concern to breeders (Muir et al., 1992). A change in ranking of genotypes across environments is caused by specific adaptation of each genotype to each environment, which implies not only a lack of adaptation to the other environment, but a maladaptation.

The usual solution to eliminate or guard against genotype-environment interactions in production animals is to select the animal in the environment in which it is to perform (Yamada and Bell, 1969), i.e., make the basis of selection performance in multiple-bird cages rather than single bird cages, as suggested by Craig and Adams (1984). However, that solution, if based on individual bird productivity, will not work and could make the problem worse. This conclusion is based on the fact that associate effects of other genotypes in the cage, through behavior, also have environmental effects on the bird being measured and are constantly changing with selection.

To solve this kind of problem, Griffing (1967) recognized that with competition, the usual gene model for a given genotype must be extended to include not only the direct effects of its own genes, but also the associate contributions from other genotypes in the group. To do that, Griffing (1967) extended selection theory to take into consideration interactions of genotypes. In this theory, the conceptual biological model must be first extended to define the group and second the usual gene model must be extended to include not only direct effect of the individuals own genes, but also associate contributions from other genotypes in the group.

Griffing (1967) showed that in the presence of interacting genotypes, the expected change in the mean ($\Delta\mu$) from individual selection of intensity i in a population with a phenotypic standard deviation of σ is

$$\Delta\mu = \left(\frac{i}{\sigma}\right)\left[{}_d\sigma_A^2 + {}_{(da)}\sigma_A\right]$$

where ${}_d\sigma_A^2$ is the additive variance of the direct effects and ${}_{(da)}\sigma_A$ is the additive covariance between direct and associative effects. If the covariance is negative, as occurs when there is competition for a limited resource, then selection based on individual performance can have a reverse effect on the mean, i.e., positive selection will reduce rather than increase the mean. This results because a gene that has a positive direct advantage for the individual has a negative associate effect on the

group. In contrast, if the group is defined as the unit of selection, then

$$\Delta\mu = \left(\frac{i}{\sigma}\right)\left[{}_d\sigma_A^2 + 2\,{}_{(da)}\sigma_A^2 + {}_a\sigma_A^2\right]$$

where ${}_a\sigma_A^2$ is the additive variance for associate effects. In this case $\Delta\mu$ is always positive. Thus, transferring selection from the individual to the group ensures that the population mean will not decrease.

The importance of group selection based on families in understanding the evolution of social behavior was discussed by Hamilton (1964). In particular, Griffing (1976) showed that with group selection, it is possible to select for an allele that has a negative direct effect but positive associative effect, i.e., altruistic or self-sacrificing traits.

Experimental evidence that supports Griffing's (1967) theory was shown by a number of researchers. Goodnight (1985) showed that the leaf area of *Arabidopsis thaliana* would respond to group but not individual selection. Wade (1976, 1977) and Muir (1977) demonstrated with *Tribolium castaneum* that a negative group response could be obtained from positive individual selection for productivity. Craig et al. (1975) demonstrated that stocks selected for part-record egg production on an individual basis exhibited more social dominance and aggressiveness following flock (group) formation during adolescence. Also, Bhagwat and Craig (1977) found that social dominance increased in flocks (groups) assembled during adolescence in response to selection for age at first egg of individual birds.

In contrast, Craig et al. (1982) reported a group selection experiment with egg-strain chickens. In that experiment, two lines were selected for part record egg mass (EM) based on sire family averages. However, in one line, hens of a sire family were housed in separate sire-family groups, whereas in the other hens were intermingled with other sires families, but individual records were recorded so individual sire families could be selected as a group. Thus, both lines represent forms of group selection. However, based on Griffing's (1967, 1976) theories, consequences of the later form are unknown because selection for direct and associate effects were not balanced, i.e., either cooperative (defensive) or aggressive behavior could result. Nevertheless, even if cooperative behavior was selected for with the latter form of group selection, the latter form should have been less efficient than the former. Yet, after seven generations of selection, the lines were not significantly different with respect to productivity in 1- or 18-bird cages. Craig (1994) concluded in retrospect that it appeared likely that absence of differences between the stocks may have occurred because of relatively benign environments. During selection in both environments, hens had been beak trimmed, pens were relatively uncrowded, and part-year records were used so that social stress was minimized and had only a

limited time span in which to affect performance adversely.

Griffing (1967) further notes that as group size increases, associate effects take on an increasingly dominant role in determining the consequences of selection and implies that, even for weakly competitive conditions, a negative response to selection can occur. This result is consistent with the observation that more problems occur in larger multiple-bird cages than small. Muir (1985) observed a significant genotype by cage-environment interaction for days survival in a random bred population of White Leghorns between nine- and one-bird cages but not between four- and one-bird cages, even though birds in the nine- and four-bird cages were housed at the same density. Muir et al. (1992) later showed that this interaction was mainly due to re-ranking of genotypes indicating that the best performers in one cage environment were poorer in the other.

There are some drawbacks to group selection. Griffing (1967) showed that the rate of progress with groups composed of random individuals is slow and decreases as the group size increases. However, Griffing (1976) later showed that if the group is composed of related individuals, the efficiency is greatly increased, particularly as group size increases.

Based on the theories of Griffing (1967, 1976), a group selection experiment was initiated in 1982 with a population of White Leghorns to determine whether the procedure would improve adaptability of layers to multiple-bird cages when stringent competitive conditions were imposed.

MATERIALS AND METHODS

The trait of selection, housing conditions, age at housing, management practices, and duration of the record changed from generation to generation depending on a number of largely uncontrollable factors such as economics, relocation, and lost records, etc. Those differences will be described in detail in what follows. However, the bases of selection was consistently that of the performance of a sire family housed as a group (multiple-bird cage). In all generations, birds were mated using artificial insemination. Starter (19% protein, 3,016 kcal ME/kg), grower (16.9% protein, 2,943 kcal ME/kg), developer (15.84% protein, 2,888 kcal ME/kg), and layer (16.28% protein, 2,870 kcal ME/kg) rations, balanced for all essential nutrients to meet NRC (1985) standards, were fed from 0 to 6, 6 to 14, 14 to 18, and 18 to 72 wk of age, respectively.

Because Hanson (1976) observed that birds placed in multiple-bird cages may exhibit hysterical episodes, which were seldom observed in less than 140 d after housing, selection on the part record to 40 wk of age would miss an important aspect of performance in multiple-bird cages. Therefore, production was always measured to at least 60 wk of age and in three of the generations it was extended to 72 wk. In retrospect, Craig and Milliken (1989) also found compelling evi-dence that the adverse effects of a high-density cage environment became more evident with the passage of time. The control was housed in one-bird cages so as not to allow unintended selection to occur as associated with adaptation to multiple-bird cages.

Generation 1

The genetic material, housing, nutrition, and rearing conditions for this generation was given by Muir (1985). In summary, a randombred population of White Leghorns were obtained from the North Central Regional Poultry Breeding Laboratory (W. Lafayette, IN 47906) in 1982. The line was derived from a cross of six commercial hybrids in 1972 (Garwood et al., 1980) and randomly mated for 10 generations.

In the first replicate, 24 roosters were each mated to six dams. Day-old chicks were beak-trimmed (one half of beak removed), reared in floor pens, and housed at 11 wk of age by sire family in single (20.3 cm wide × 40.6 cm deep) and 48 nine-bird cages (81.3 cm wide × 45.7 cm deep) at a density of 413 cm² per bird. Sire families in nine-bird cages were restricted to three dams each. One cockerel was saved from each dam family and reared in floor pens. A second replicate was also conducted similar to the first except one- and four-bird cages were used. However, because a genotype-environment interaction was only detected between one- and nine-bird cages (Muir, 1985), birds from the four-bird cages were not used further, but data from the one-bird cages were averaged across replicates.

Birds were housed at 11 wk of age so that a social order could be established before sexual maturity. Lighting was restricted to 8 h to avoid premature stimulation. Dead birds were replaced for the next 2 wk. At 14 wk of age, light duration was increased by 1.5 h/wk until 15 h of light/d was provided at 19 wk of age. Pullets were brought into production as early as possible in order to express genetic variation in age at sexual maturity. Eggs were collected and recorded three times a week starting at 20 wk of age. Egg weight (EWT) was measured by cage on all eggs laid from the first collection each week. For cages that did not produce an egg that week, the EWT obtained in the previous week were used. This procedure was continued until the birds were 72 wk of age. Egg mass was calculated weekly for each cage by multiplying EWT by the total number of eggs laid in that week. Mortality was recorded daily. Eggs per hen housed (EHH) was the total number of eggs produced by each cage. Days survival (DS) was the number of days of survival from 20 wk of age to the end of the experiment. Eggs per hen per day (EHD) was computed as the ratio of EHH:DS.

The criteria of selection was EM per nine-bird cage over the 52-wk production period. To maintain consistency with what will be reported later, EM will always be expressed as per hen housed. Because there were two nine-bird cages of pullets housed per sire, an index that combined information over both cages per families was used to make selections:

$$I = P + 0.26\ \overline{P}_f$$

where: P is the EM of the first cage and $\overline{P}_f$ is the average EM over both cages. This index is similar to that which is used to combine information on the individual and the average of its family where the individual is included in that average (Falconer, 1981). Roosters were chosen based on the index of their full- and half-sibs. The top 50 roosters and 150 hens were chosen to mate based on this index. To further increase selection intensity, the top 12 ranking roosters were mated at random to 12 hens each. The next 12 roosters were mated to 4 hens each, and the remaining roosters mated to 2 hens each. However, matings of full and half-sibs were avoided. The control line was reproduced by randomly choosing 150 hens housed in one-bird cages and 50 roosters. Matings were at random.

Generation 2

Two 3-wk egg collections were taken from the selected individuals of Generation 1 (G1) in March and April of 1984. Chicks were vaccinated for Marek's, bronchitis, avian encephalitis, and Newcastle's diseases. The chicks were then placed in floor pens with gas brooders. From this generation forward, chicks were not beak-trimmed in order to more fully express the underlying competitive genotype of the bird that would be hidden if results of aggression were not evident in terms of mortality or morbidity. Further, from this generation forward, birds were housed and light stimulated at a later age, more consistent with commercial egg production. Chicks were fed a starter diet through 6 wk of age. At 7 wk of age, the chicks were fed a grower diet until they were housed. Pullets from each hatch were housed in separate buildings at 17 wk of age and fed a developer diet until 20 wk of age when they were switched to a laying mash for the duration of the experiment. Chicks in floor pens were provided with natural light. Fourteen h of light was provided at the time of transfer to laying cages at 17 wk of age. The light duration was increased by 15 min/wk to a maximum of 16 h/d starting at 18 wk of age. A total of 490 pullets was housed in one-bird cages and 74 sire families in nine-bird cages as described in G1. Because top ranking sires were mated to 12 hens each in G1, several sire families were created from each rooster, however all pullets from a given dam were housed in the same cage. Roosters, one each per dam family, were reared in floor pens. Mortalities were replaced to 20 wk of age. Eggs were collected daily from the first egg produced and EWT were taken weekly per cage. This procedure was continued to 65 wk of age for the first hatch and to 60 wk of age for the second hatch when the facility was closed and selected and unselected control birds were relocated to a new facility.

Because of the relocation, there was not sufficient time to enter the data and make selections based on EM. Instead, the trait of selection was average DS per nine-bird cage, and roosters were selected based on the mean performance of their full- and half-sisters. The prior trait of selection, EM, is the product EHD, EWT, and DS. Therefore, only one of the components was selected in this generation, which placed all of the selection intensity on livability. In retrospect, with few exceptions, the same chickens would have been selected if EM were the criteria of selection because in this generation DS was the major source of variability in EM. Selected birds from each house were treated as replicate lines with matings restricted to birds within that replicate but avoiding full- and half-sib matings (Figure 1). The upper 23% of hens and roosters were chosen as parents of the next generation or 155 hens and 52 roosters over both replicates. The control line was reproduced using 68 roosters and 79 hens mated at random.

Generation 3

Eggs for four hatches were collected from the selected parents for each of the replicate lines starting in November of 1985. Chicks were reared in raised wire cages designed for pullet growing with automatic cup waters and chain feeders. Light was continuous for the first 3 d. Tray paper was placed on the cage floor for the first 10 d. After 3 d, light duration was reduced to 8 h. Heat was provided by central furnace and distributed using fans. The temperature was initially set to approximately 33 C and was reduced by 2.8 C/wk to 21.1 C, where it was maintained until housing at 18 wk. Chicks were fed a starter diet for the first 10 d, a pullet starter to 6 wk, and a developer to 18 wk. After housing, they were fed a prelayer diet for 1 wk and finally switched to a layer diet for the duration of the laying cycle. Upon housing, light duration was increased to 10 h using incandescent lights set to high intensity. The next week, duration of light was increased by 2 h for the next 2 wk after which the duration was increased by 15 min/wk until 16 h was provided, where it was maintained for the duration of the laying cycle.

The laying house consisted of eight light-tight rooms (Rooms 9 to 16) with independent temperature, ventilation, and lighting. Each room contained eight rows of wire cages designed for laying hens. Cages were in four tiers or decks in an overlapping, curtain backed, stair-step like arrangement on both sides that met at the top deck over a dropping pit. Cage floors were sloped with an egg collection tray in front. Water was provided by drip nipples located in the ceiling of each cage. Feed was provided for *ad libitum* consumption and delivered by automatic feeders to a trough in front of each cage. Each row initially contained 48 cages that were 30.5 cm wide, 35.6 cm deep, and 43 cm high. On the two bottom decks partitions were removed from four adjacent cages to form cages that were 122 cm wide for a total of 48 multiple-bird cages per room. The rows were numbered 1 through 4 corresponding to Decks 1 through 4 on the west side of the room and 5 through 8 corresponding to Decks 1 through 4 on the east side of the room, where Deck 1 was the top deck.
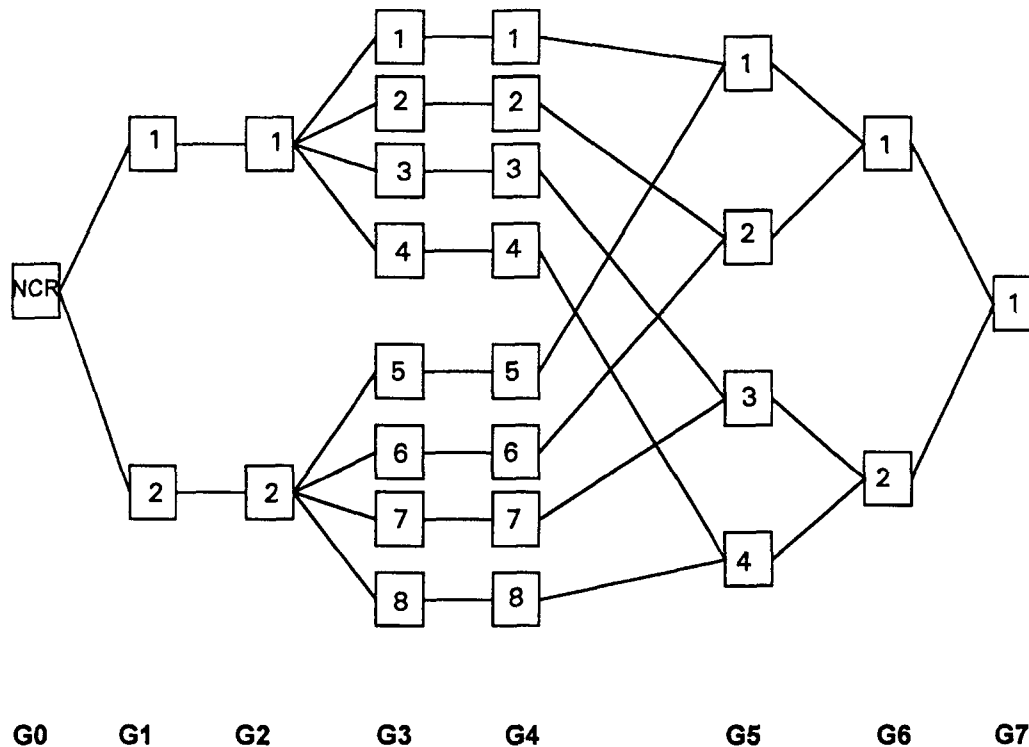
FIGURE 1. History of subdivision and merging of the lines starting with the North Central Regional (NCR) population. Replicate number given within the box and generation (G) number given at the bottom of the figure.

Birds from each of the eight replicate-hatch combinations were housed in a separate room. Pullets from the control line were placed in Rows 1, 2, and 6. Roosters of the control line were placed in Row 5. Pullets of the selected line were placed 12 per cage, by sire family, in Rows 3 and 7. Roosters of the selected line were placed 12 per cage, by sire family, in cages of Rows 4 and 8. This arrangement provided 1,085 cm² per bird in one-bird cages and 362 cm² per bird in multiple-bird cages. Egg production and mortalities were recorded daily by cage and EWT were measured once a week by row from 20 to 61 wk of age.

Because Muir (1985) showed that the mechanisms operating to reduce production in nine-bird cages were curvilinear in nature, which resulted in maximum EM and EHD after one bird had died, it was concluded that selection on EM was not the optimal trait to select upon to improve adaptability. Instead, it was decided to select hens on a nonoptimum linear index of DS and EHD giving equal weight to each and ignoring EWT after first transforming each trait to a mean of 0 and variance of 1. The reasons for this index were threefold. First, genetic parameters did not exist for an optimum index to be constructed. Second, the objective of the breeding program was to improve adaptability of the bird to multiple-bird cages, which is largely manifest in terms of DS and EHD, not maximum aggregate economic return as an optimum index would do. Third, the labor was not available to measure EWT on a per cage basis. Further, to

avoid too rapid an increase in inbreeding, roosters and hens were selected on separate indices. Roosters were selected only on the basis of DS of their sire family cage, which again, as in G2, placed the greatest genetic emphasis on livability. Selection occurred within each room with the top 72 out of 288 hens and 24 out of 288 roosters chosen as parents of the next generation. The control line was reproduced using 24 roosters and 48 hens per room chosen at random from the one-bird cages. Mating was at random but restricted to birds chosen from within a room (Figure 1).

Generation 4

After a forced molt, a 3-wk egg collection was taken from the selected birds of Rooms 13 through 16 in May and Rooms 9 through 12 in June of 1987. Management practices, growing, housing, and selection procedures were the same as in G3 except data were collected to 62 wk of age for Rooms 13 through 16 and to 60 wk of age for the remaining rooms. Also, EWT were measured by row every other week. Birds were again selected within each room with the best 12 roosters and 72 hens chosen. Further, selected and control birds, maintained as separate replicates since G1, were reciprocally crossed to recover from accumulated inbreeding (Figure 1). This resulted in four sets of parental crosses among replicates for a total of 48 roosters and 144 hens per cross. The procedures and number of breeders were the same for the control.

Generation 5

Eggs were set from a 3-wk egg collection from the first cross in December 1988 and continued every 3rd wk until eggs from the fourth cross were set. Rearing conditions were the same as in G4. However, in this generation, roosters were not housed. Instead, birds of the control and selected lines were housed in both cage environments to measure correlated responses. Within each row, equal numbers of selected and control birds were randomized into each cage type by sire family with the restriction that an equal number of each line be present in each row. Further, this generation was intended to be the final generation and only two roosters per sire family were saved to maintain the line. Egg production and mortalities were recorded daily by cage, and EWT were recorded by room for each line cage-type combination every 4th wk.

Unfortunately, within the 1st mo of housing, a power outage at the end of May in 1989 caused a loss of ventilation and death of over 50% of the birds housed in two rooms, one of which was the second replicate of the first hatch and the other was the first replicate of the second hatch. As a result, the experiment was unbalanced with respect to hatch-replicate combinations. It was decided at this time to reassign birds and complete another generation of selection with the next generation being the terminal generation in which correlated responses would be measured. Surviving birds of the two rooms were combined into one room and further testing of the control line in 12-bird cages was discontinued. Results of the heat stress mortality losses will be published in the second paper of this series on correlated responses.

Production in the remaining rooms was measured to 72 wk of age when another mishap occurred. Mortalities were to be recorded in two places, on production records and in a separate notebook. Unfortunately, the notebook was lost and not all mortalities were recorded on the production records. Therefore, data on DS and EHD could not be accurately determined. However, data on eggs per hen housed on a sire family basis (EHH) was accurately recorded and is the same as selecting on the product of DS and EHD because EHD is computed as the ratio of EHH/DS. Therefore, EHH was used as the trait of selection and roosters were chosen based on their full- and half-sib's performance.

Because few roosters were reared from each sire family, the top 40% of males had to be saved whereas the best 17% of females could be retained for breeding. Birds from Rooms 9 through 12 were combined and mated at random as were birds from 13 through 16 to further reduce accumulated inbreeding (Figure 1). This mating resulted in a total of 112 hens and 28 roosters in each of two combined replicates. Controls were reproduced using 110 hens and 25 roosters per combined replicate.

Generation 6

Starting in November of 1991, five 3-wk egg collections were taken from the selected parents from each of the combined replicates. Due to declining egg production, the first three hatches were sufficient to provide pullets for two rooms each, while the last two hatches only provided pullets for one room each. Two cockerels were also saved from each dam family of the first hatch. Birds were reared and housed as initially described in G5. Production was measured to 72 wk of age, at which time body weights of all surviving birds were taken. Correlated responses of the selected line housed in individual cages, controls housed in 12-bird cages, and body weights will be presented in the second paper of this series on correlated responses.

Hens were selected by sire family based on the same index as used in G3 and G4. Roosters were selected based on the sire family index of their sibs. The top 30% of hens and 50% of roosters were saved as breeders for the next generation. However, the two combined replicates were crossed to further reduce accumulated inbreeding (Figure 1).

Summarization of the Data

The data for each generation were reanalyzed to present a consistent format and procedure for presenting the data. First, production data were summarized by cage and week. For generations in which records discontinued before the end of a full record, missing data were projected using linear regression from post-peak production to the end of the production period. McMillan et al. (1986) have shown that the residual record, based on production to 40 wk of age, can accurately be predicted by linear regression of postpeak egg production on age. Because data in this experiment were collected to at least 60 wk of age, these predictions were even more accurate. For EWT data, where weights were taken every other week or every 4th wk, data for intervening weeks were estimated using two regressions. A different regression was used for pre- and postpeak egg production due to a slight curvilinearity in the regression before and after peak production. With all missing data estimated, EM was computed weekly by cage from the product of EHH and EWT. Percentage mortality (MORT) was calculated as (number of dead birds/number of birds housed) × 100.

The data were then summarized into three part records in order to examine how selection was affecting the production curve. Record 1 (R1) was the standard part record to 40 wk of age and consisted of the first 140 d of production. The second record (R2) was from 41 to 60 wk of age or the second 140 d. Sixty-week production has become an industry standard (Bell, 1988) because it represents the time at which a decision will be made as to whether to replace or molt the flock (Larry Issacs, 1994, Manager, Rose Acres Farm, personal communication, Seymore, IN, 47274). The final record (R3) represents that part of the record from 61 to 72 wk of age or the last 85 d. The combination of R1, R2, and R3 is the annual 365 d production. A summary of how the control and selected lines were divided and recombined is given in Figure 1.

Statistical differences for variables that were categorical or count data, including EHH, EHD and mortality

TABLE 1. Performance of pullets in one- and nine-bird cages, Generation 1 (1983 to 1984)[1]

	Time period							
	Annual		R1		R2		R3	
Trait	One-bird	Nine-bird	One-bird	Nine-bird	One-bird	Nine-bird	One-bird	Nine-bird
EHH, no. eggs	222 ± 1	177 ± 3	106 ± 1	94.0 ± 3	81 ± 1	59 ± 3	35 ± 1	24 ± 2
EWT, g	57.9 ± 0.2	58.0 ± 0.3	55.3 ± 0.2	55.6 ± 0.3	58.7 ± 0.2	58.3 ± 0.4	60.8 ± 0.3	61.7 ± 0.6
EM, kg	13.0 ± 0.1	10.4 ± 0.1	5.8 ± 0.1	5.2 ± 0.1	4.8 ± 0.1	3.4 ± 0.2	2.1 ± 0.1	1.49 ± 0.1
DS, d	339 ± 1	292 ± 3	135 ± 1	128 ± 2	130 ± 1	106 ± 5	74 ± 1	58.7 ± 3
MORT, %	12.3 ± 0.8	30.6 ± 2	4.7 ± 0.9	16.0 ± 2.6	5.9 ± 0.9	12.7 ± 2.1	1.7 ± 0.5	1.4 ± 0.5
EHD, %	65.4 ± 0.8	58.4 ± 1.5	78.5 ± 0.8	73.4 ± 1.5	62.8 ± 0.8	55.0 ± 1.6	48.7 ± 0.8	39.4 ± 1.8

[1]Based on 656 single-bird and 48 nine-bird cages, R1 = 20 to 40 wk of age; R2 = 41 to 60 wk of age; R3 = 61 to 72 wk of age, EHH (eggs per hen housed), EWT (egg weight), EM (egg mass), DS (days survival), MORT (percentage mortality), EHD (eggs per hen per day × 100).

(MORT), were determined using chi-square tests as computed by the FREQ procedure of SAS® (SAS Institute, 1989). Statistical differences for continuous variables EWT, EM, and DS were determined by t tests. A t test was used because of the unequal variances that existed between one- and multiple-bird cages.

RESULTS AND DISCUSSION

Because pullets in G1 were beak-trimmed, whereas pullets in G2 through G6 were not, and birds in G1 were housed and photostimulated at an earlier age than those of later generations, the traits in G1 and later generations are different and not directly comparable. Therefore, means for G1 are presented separately (Table 1) from those of later generations. Further, because controls were only maintained in one environment, limitations are placed on interpretation of data. This limitation is particularly true of mortality in the control and may reflect only that due to disease whereas deaths in multiple-bird cages may be due to disease plus other environmental effects not evident in single bird cages, such as heat-related deaths.

Mortality

In G1, even with beak-trimming, MORT was much greater ($P < 0.01$) in nine- than one-bird cages (Table 1). In advanced generations (Figures 2a and 2b) the difference between one- and multiple-bird cages was initially large ($P < 0.01$) but decreased to nonsignificance by G6. The reason for this convergence was a result of changes in both genetic stocks. The trend in the control from G2 to G6 was for MORT to increase ($P < 0.05$) from 3 to 9%. In the same time period, MORT in the selected line declined from 68 to 9%. The pattern of MORT in the part records of the control appears to be random with no discernible trends ($P > 0.05$). In contrast, annual MORT declined rapidly ($P < 0.05$) in the selected line with the majority of the improvement occurring in R1.

Confounded with the major decline in MORT observed in comparison of G2 with G3 for the selected line was the change from 9-bird to 12-bird cages. However, the reverse

effect would have been expected because floor space per bird declined from 413 cm² in 9-bird to 362 cm² in 12-bird cages. Further, larger groups tend to have greater MORT than smaller groups even with the same density as shown by Wilson et al. (1967), Muir (1985), and Cunningham (1987). After this major change, there has been little additional improvement in MORT. This result suggests that a major gene may be involved because genes with

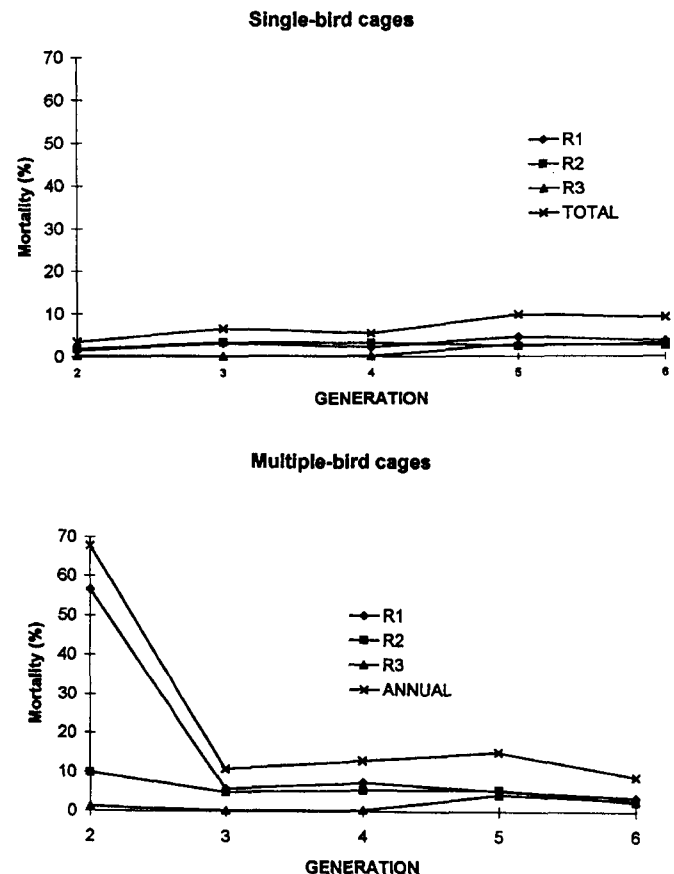**Single-bird cages**

Multiple-bird cages

FIGURE 2. a) Percentage mortality (MORT) for the unselected control in one-bird cages for the total record, from 20 to 40 (R1), 41 to 60 (R2), and 61 to 72 wk of age (R3) for Generations 2 through 6. b) MORT for the selected line in multiple-bird cages for the total record, from 20 to 40 (R1), 41 to 60 (R2), and 61 to 72 wk of age (R3) for Generations 2 through 6.

large effects change in gene frequency faster than those with small effects (Falconer, 1981).
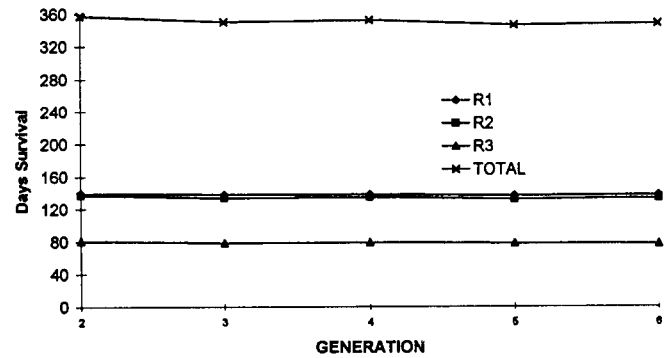
Days Survival

In G1, with beak-trimmed birds, the difference in annual DS between one- and nine-bird cages was 40 d ($P < 0.01$) or 12% fewer DS (Table 1). In G2, in which birds had intact beaks, the difference in DS between cage environments was 188 d or a 53% reduction (Figure 3). By G6, the difference in DS between cage environments had declined to less than 1 d and was not significantly different ($P > 0.25$). As with MORT, the convergence was due to changes in both lines. In the control (Figure 3a) there was a small but significant ($P < 0.05$) decline in annual DS corresponding to the increased mortality observed during that time period. The reason for the decline in DS of the control is unknown but is not likely to be explained as being due to cumulative inbreeding because replicate lines were crossed in G4 and again in G5, as shown in Figure 1, greatly reducing cumulative drift. The decline was also uniform across all part records. In multiple-bird cages (Figure 3b), annual DS of the selected line showed the same general improvement as MORT with the majority of the change occurring between G2 and G3.

Eggs per Hen per Day

In G1 the difference in EHD between cage environments was 6.5% ($P < 0.01$, Table 1). In G2 the difference was 15.9% ($P < 0.01$) but declined to 7.1% ($P < 0.01$) by G6 (Figure 4). During this time period, the selected line improved by 16% ($P < 0.01$) but the control line improved by 5.4% ($P < 0.05$). The reason for the improvement in the control line is unknown. However, one explanation is suggested by examination of the relative increases of the part records. Those increases were 15, 4.5, and 1.7% for R1, R2, and R3, respectively, suggesting that unconscious selection was directed at R1 with correlated effects in R2 and R3 diminishing with greater temporal separation. Because birds were bred after 60 to 72 wk of age, usually with a 6- to 8-wk delay to allow for analysis of the data, moving of birds, trimming, and training of roosters, some birds could have been going out of production and others returning after a natural molt. If the birds in or out of production at the time of breeding were influenced by age at sexual maturity, unconscious selection could have been directed at R1 in the control.

In the selected lines, EHD increased in all records, and in terms of relative increase, the average improved by 31% whereas R1, R2, and R3 increased 47, 14, and 37%. Thus, when selecting on 60- or 72-wk records, the greatest improvements occurred in the early and late records. This improvement in R1 may be due to changes in age at sexual maturity. However, the improved R3 also demonstrates that persistency of lay was improved.

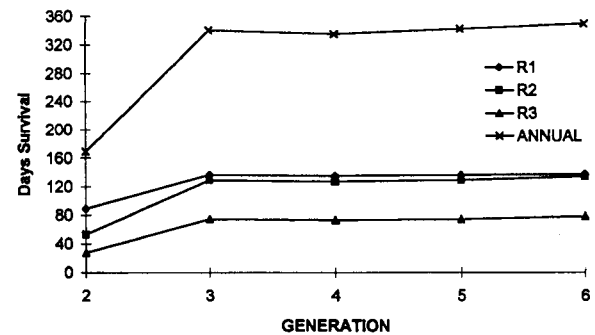**Single-bird cages**

Multiple-bird cages

FIGURE 3. a) Days survival (DS) for the unselected control in 1-bird cages for the total record, from 20 to 40 (R1), 41 to 60 (R2), and 61 to 72 wk of age (R3) for Generations 2 through 6. b) DS for the selected line in multiple-bird cages for the total record, from 20 to 40 (R1), 41 to 60 (R2), and 61 to 72 wk of age (R3) for Generations 2 through 6.

Eggs per Hen Housed

In G1, the difference in annual EHH between one- and nine-bird cages was 43 eggs ($P < 0.01$, Table 1) or a 20% decline. The majority of this reduction was due to the corresponding 40 d decrease in DS and to a lesser extent the 6.5% difference in EHD. In G2, the difference in production between the cage environments was 154 eggs or a 62.5% reduction for birds in the nine-bird cage. By G6 the difference in EHH between the cage environments had reduced to 19 eggs ($P < 0.05$). As with the traits MORT and DS, the convergence of EHH was due to changes in both lines. In the control (Figure 5a) there was a slight but significant ($P < 0.05$) nine egg improvement in annual EHH corresponding to the increased EHD, which offset the higher mortality experienced during that time period. Also, the pattern of change in the part records of the control was similar to that of EHD with relative changes of 11, 3.2, and –4.2% occurring respectively, in R1, R2, and R3.

In multiple-bird cages, performance changes of the selected line were dramatic (Figure 5b), with annual production increasing from 91 eggs in G2 to 237 eggs in G6. The astonishing 160% relative increase in annual egg production was due to improvements ($P < 0.01$) in all part
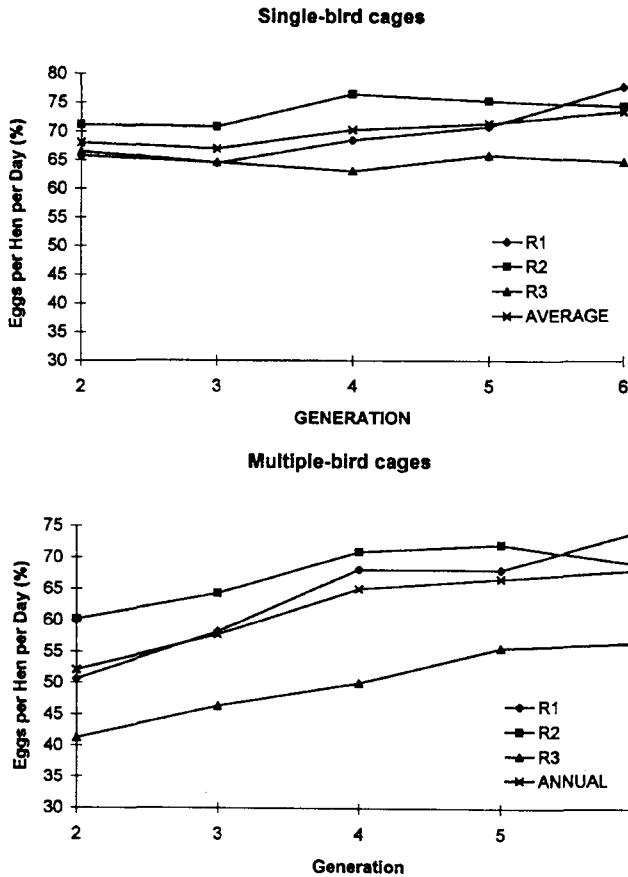
FIGURE 4. a) Eggs per hen per day (EHD) for the unselected control in 1-bird cages for the total record, from 20 to 40 (R1), 41 to 60 (R2), and 61 to 72 wk of age (R3) for Generations 2 through 6. b) EHD for the selected line in multiple-bird cages for the total record, from 20 to 40 (R1), 41 to 60 (R2), and 61 to 72 wk of age (R3) for Generations 2 through 6.

FIGURE 5. a) Eggs per hen housed (EHH) for the unselected control in 1-bird cages for the total record, from 20 to 40 (R1), 41 to 60 (R2), and 61 to 72 wk of age (R3) for Generations 2 through 6. b) EHH for the selected line in multiple-bird cages for the total record, from 20 to 40 (R1), 41 to 60 (R2), and 61 to 72 wk of age (R3) for Generations 2 through 6.

records with the greatest relative increase occurring in R3 (344%), followed by R2 (189%), and the least in R1 (118%). Note that this pattern in the part records is the opposite of changes that occurred in the control. Thus, adjusted for the control, the relative improvement in the part records of the selected line would be even larger. This result further demonstrates the need to go beyond the standard part record (R1) as the basis of selection in breeding programs. In multiple-bird cages the greatest improvements may be experienced in the residual records.

Egg Weight

Annual EWT was not significantly different between cage environments in G1 ($P > 0.01$, Table 1). In contrast, in all advanced generations except G4, EWT of the control was heavier ($P < 0.05$) than that of the selected line (Figure 6). However, the difference between the lines decreased with time because there was a small but significant decline ($P < 0.05$) in annual EWT of the control but response in the selected line was neutral ($P > 0.1$).

Although EWT was selected in G1 as a component of EM, it was subsequently ignored. Thus, a decline in
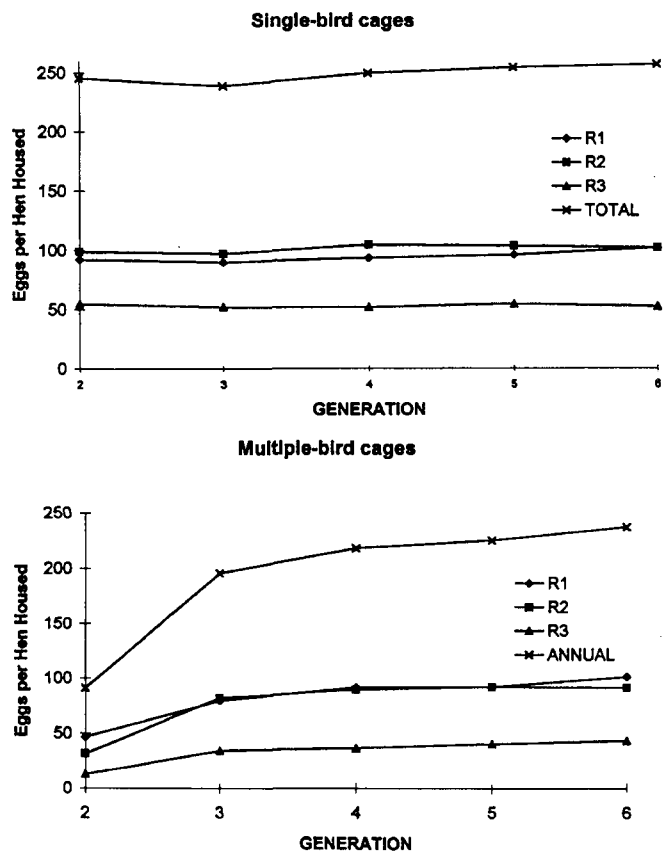
average EWT of the selected line after G2 was expected based on selection for EHD, because these traits have been shown to be negatively correlated (Kinney, 1969). However, the genetic correlation between DS and EWT is unknown. Also, the pattern of responses of the part records of the selected line is curious. The extremely low EWT of R1 in G2 was not consistent with that of other generations. However, R1 of G2 was also the record in which the exceedingly high rate of mortality was recorded. Thus, the low EWT may have been a manifestation of the extreme stress those birds were experiencing in that part record. Also, records R2 and R3 show a significant linear decline, as expected, while R1 first increased for two generations followed by a decrease for two generations. At G4, EWT of the selected line was greater ($P < 0.05$) than that of the control.

Egg Mass

In G1, EM was significantly ($P < 0.05$) greater in one- than nine-bird cages by approximately 25% (Table 1). In advanced generations, there was a small but significant 2.8% increase in annual EM of the control (Figure 7a). This change was associated with a 10 and 3.3% increase in EM,

Single-bird cages
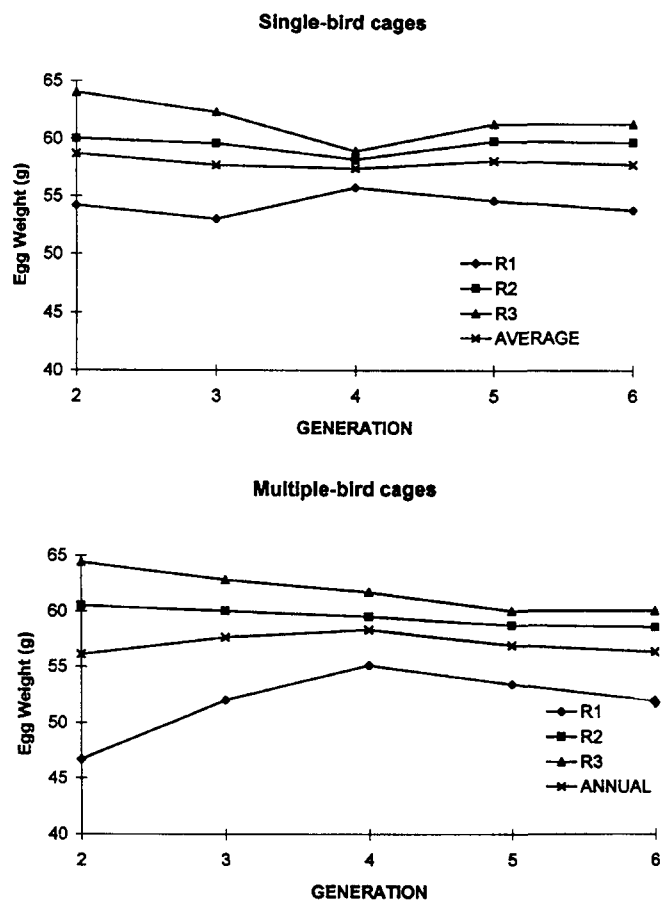

Single-bird cages

Multiple-bird cages

FIGURE 6. a) Egg weight (EWT) for the unselected control in 1-bird cages for the total record, from 20 to 40 (R1), 41 to 60 (R2), and 61 to 72 wk of age (R3) for Generations 2 through 6. b) EWT for the selected line in multiple-bird cages for the total record, from 20 to 40 (R1), 41 to 60 (R2), and 61 to 72 wk of age (R3) for Generations 2 through 6.
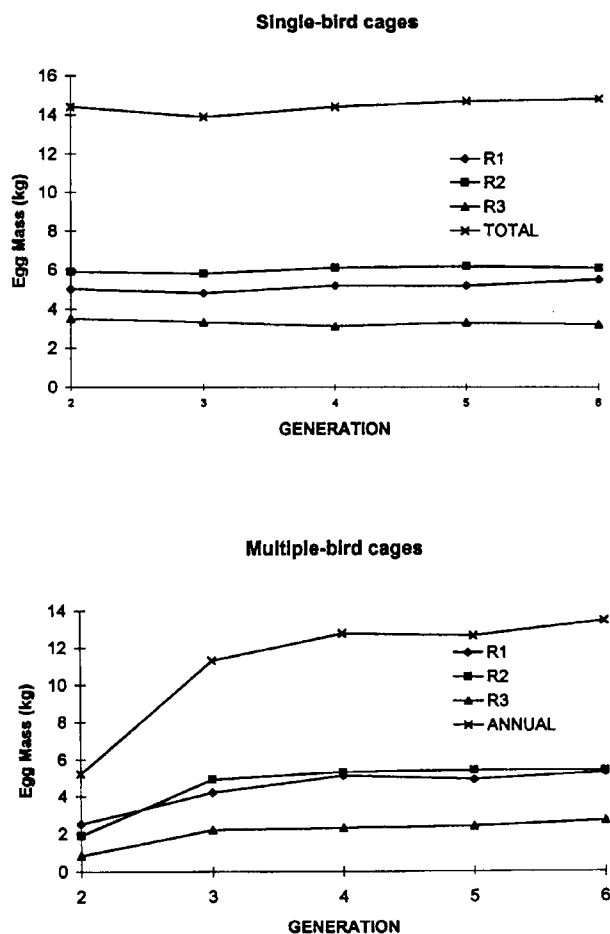
Multiple-bird cages

FIGURE 7. a) Egg mass (EM) for the unselected control in 1-bird cages for the total record, from 20 to 40 (R1), 41 to 60 (R2), and 61 to 72 wk of age (R3) for Generations 2 through 6. b) EM for the selected line in multiple-bird cages for the total record, from 20 to 40 (R1), 41 to 60 (R2), and 61 to 72 wk of age (R3) for Generations 2 through 6.

respectively, in R1 and R2 but a decrease of 8.6% in R3 over the same time interval. These changes were primarily the result of changes in EHD, and to a lesser extent DS and EWT.

In the selected line, a dramatic and continued nonlinear increase ($P < 0.05$) in total EM was observed (Figure 7b). This result corresponded to similar improvements in all of the part records. However, in relative terms, the 157% increase in annual EM was associated with a 112, 184, and 229% increase in R1, R2, and R3, respectively. These results were primarily the consequence of early changes in DS and continued improvements in EHD. Again, the changes in the part records were the reverse of that seen in the control. The observation that the greatest changes occurred in R2 and R3 again strongly suggest the need to select on records beyond R1.

General

Although selection was effective in improving survival to the point where viability of the selected line, in the more perilous 12-bird environment, was the same as the control line in the relatively benign single bird environment, rate

of lay in 12-bird cages remained less than that of the control in one-bird cages. These results may be partially due to the fact that a much greater selection intensity was directed at DS than EHD. In G2, DS was the only trait of selection, moreover in G3 and G4, roosters were selected only on the basis of DS. In other generations, combinations of DS and EHD were selected for. From results presented by Muir (1985), conservative estimates of heritability for DS and EHD, in nine-bird cages, were 0.07 and 0.2, respectively. Unfortunately, it is not possible to compare those estimates with realized heritabilities from these data because multiple traits were selected using an index.

The lower rate of lay of the selected line in 12-bird cages also suggests that the selected line is not fully adapted to that environment in as much as they were still experiencing a decline in production as compared to the control. However, that impediment may be overcome with continued selection as EHD appears to be improving at approximately 4% per generation, even with the relatively mild direct selection for that trait.

Nevertheless, the fact that DS and MORT had improved over the generations in the selected line, housed in

multiple-bird cages, to the point that livability was similar to that of the unselected control line, housed in single-bird cages, is dramatic evidence that group selection is effective in improving animal well-being in competitive environments. However, the experiment does not show that the same results could not have been achieved by individual selection. Had facilities permitted, the optimal experiment would have consisted of an additional line, that of a line selected on family averages of hens housed in individual cages. However, evidence will be presented in a later paper in this series that selection based on individual housing of hens is detrimental to adaptability of birds with intact-beaks.

The ability of the selected line with intact beaks in 12-bird cages to demonstrate the same survival as that of the control housed in 1-bird cages suggests that the practice of beak trimming can be discontinued with proper genetic selection.

ACKNOWLEDGMENTS

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