Improving Animal Well-Being Through Genetic Selection[1,2]

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ABSTRACT This paper reviews the possibilities of adapting laying hens to cages by means of genetic selection. By selecting separately for rate of lay and longevity using a kin selection method, a strain of laying hen has been developed that shows much less feather pecking and cannibalism than a control strain, and with no decrease in productivity. This experimental strain enjoys a higher level of welfare in cages because it does not require beak trimming.

(*Key words*: beak trimming, cannibalism, feather pecking, genetic selection, welfare)

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INTRODUCTION

The first official committee to specifically address issues related to well-being of animals in intensive production environments was the Brambell (1965) committee in Great Britain. That committee set guidelines for animal care and use in intensive agricultural systems that later influenced legislation affecting the entire European Economic Community (EEC). Animal well-being concerns have forced the poultry industry in the EEC to change or eliminate management practices related to beak trimming, cage design, and bird density (Hurnik, 1990). Two decades later, those same issues were addressed in the U.S. by another committee (Consortium, 1988), which also set standards for care of agricultural animals used in teaching and research. However, except in some research settings, those recommendations remain as guidelines. Nevertheless, there is a growing movement in the U.S. to pressure Congress to legislate standards. Those standards could go well beyond those set by the Consortium (1988) and could have a severe economic impact on consumers. Unfortunately, there has been relatively little funding in this area for research. Even some of the recommendations of the Consortium (1988) committee were based on relatively scant amounts of data. With this lack of critical data, legislative decisions may be made on the basis of emotion rather than data. For an extensive review and history of the poultry welfare movement see Craig and Swanson (1994).

In the egg laying industry, most of the concerns for animal well-being are those related to confined housing in multiple-bird cages and beak trimming. (Craig and Adams, 1984; Appleby and Hughes, 1991; Cunningham, 1992; Craig and Swanson; 1994). Birds may be stressed in multiple-bird cages, and injuries can result from aggression, flightiness, feather loss, and cannibalism (Craig, 1982). To control beak-inflicted injuries, beak trimming of caged layers and birds to be kept in breeding flocks has become a common practice (North and Bell, 1990). The Consortium (1988) concluded that the practice of beak trimming is justified under the special category of standard agricultural practices on the basis that it is necessary to sustain the long term well-being of poultry by reducing cannibalism and feather pecking. However, beak trimming in itself causes pain and suffering. Research by Duncan *et al.* (1989), Craig and Lee (1990), Gentle *et al.* (1990), and Lee and Craig (1990, 1991) indicate that pain associated with beak trimming can last for at least weeks and perhaps longer. Breward and Gentle (1985) found that following partial beak amputation, growth of neuromas occurred in the remaining part of the beak, and that spontaneous firing of afferent neurons associated with pain occurred up to at least 12 wk after amputation. However, neuroma formation may be less likely following beak trimming, at least in turkeys, if carried out within the first 3 wk after hatching (Gentle *et al.*, 1995).

Both The Brambell Committee and the Consortium recognized that there are two alternative approaches to improving animal well-being: management and genetics.

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Abbreviation Key: EEC = European Economic Community; G = generation.

The Consortium (1988:7) acknowledged that stocks and strains of chickens differed in responsiveness to stressors due to prior direct and indirect selection and, citing the research of Gross *et al.* (1984), stated that specific strains may have requirements that differ substantially from those of unadapted or less well-adapted stocks. They therefore concluded that practices to ensure the well-being of special strains should be established independently to those made for the species in general. Thus, certain flighty strains may need more space than recommended, whereas well-adapted birds will need less. The Brambell (1965) committee concluded, with reluctance, that debeaking of birds should be permitted for a limited time to control outbreaks of “vice” (cannibalism). However, within a short period of time, they hoped that suitable strains would be available and in adequate supply so that debeaking was no longer necessary. In a recent conference on Food Animal Well-Being, Moberg and Mench (1993) concluded that a goal of research in this area should be to determine the relative roles that genes and environment play in influencing well-being. This information can then serve as the basis for either modifying management practices or developing genetic selection programs to improve “fit” between animals and their environment where necessary. This paper examines alternative ideas and methods for improving well-being of poultry through genetics.

ADAPTATION: GENETIC SOLUTION TO ANIMAL WELL-BEING?

Craig and Adams (1984) suggest that further selection is needed to improve adaptability of hens to reduce problems associated with crowded conditions, cannibalism, feather pecking, injuries caused by escape and avoidance behavior, excessive pacing prior to egg laying, and the like. However, one of the first questions is: Can genetic selection improve adaptability and well-being of birds in all environments? Appleby and Hughes (1991) claim that welfare problems in cages are less likely to be alleviated by genetic selection than those in alternative systems because, by their definition, and that of the Five Freedoms set forth by Webster and Nicol (1988), welfare is compromised if freedom to exercise normal behavior is absent. However, that argument ignores the possibility that genetic selection can change “normal behavior”. Ash (1990) does “not believe that increased costs legislated solely to allow the animal the right to behave certain ways without improving the health and welfare of the animal can be justified”. If one is willing to accept that a bird can evolve through selection such that it is “comfortable” or even prefers to be in close proximity to a large number of cage mates, such as seen in species with gregarious behavior, then by this definition, its natural behavior is not compromised by intensive management systems. Thus, it should also be possible to solve well-being problems in cages.

Craig and Swanson (1994) questioned why behaviors that are no longer required by the hen should be expressed in production environments as opposed to natural settings. Presumably, almost all such behaviors could be eliminated by genetic selection between or within stocks, so that hens would not be motivated to show them or be frustrated by the absence of environmental conditions allowing their expression. Specific examples of behavioral problems include: susceptibility to hysteria in large groups, amount of time spent pacing before laying, incidence of beak-inflicted feather loss, cannibalistic deaths, fearful or panic responses, cannibalism, feather pecking, and inter-individual aggression (Appleby *et al.* 1992; Craig, 1994). From a sib analysis of birds housed in multiple-bird cages, Craig and Muir (1989) estimated moderate heritabilities for several behavioral traits, indicating that they should respond to selection. In a recent review of welfare issues relative to laying hens, Craig and Swanson (1994) showed that genetic selection for behavioral traits generally produced significant results within a few generations.

TRAITS OF SELECTION

There is one major obstacle to overcome before genetic solutions can be implemented: namely, determining which trait(s) to select in order to truly improve animal well-being. There are at least three possible broad categories to consider: behavior, physiology, and production.

Behavioral Traits

In order to improve animal well-being, Wegner (1990) advised selecting against frustration, restlessness, and stereotyped pacing before laying, and a greater tendency to sit during the prelaying period. However, Craig and Adams (1984) point out that direct selection on behavioral traits could have a negative impact on productivity. Furthermore, the link between behavior and stress is difficult, if not impossible, to establish and can be misinterpreted (Hill, 1983). For example, Duncan and Filshie (1979) showed that a flighty strain of birds that exhibited avoidance and panic behavior following stimulation returned to a normal heart beat sooner than a line of more docile birds, implying that docile birds may be too frightened to move. Therefore, is flightiness good or bad for well-being?

Nevertheless, cannibalism and feather pecking are universally recognized as behaviors that are disadvantageous for the well-being of layers. Appleby *et al.* (1992) reviewed the literature on cannibalism and feather pecking. They concluded that the main cause of feather loss in battery cage systems is not physiological change or abrasion but feather pecking, and that it is painful for the bird to have a feather pulled out. Cannibalism sometimes follows from feather pecking if exposed skin is injured, but more often arises independently. Appleby *et al.* (1992) reported that the most common form of cannibalism was vent pecking with reported losses of 13% in aviaries, and 15% in strawyard and free range systems, which they called disturbingly high. Feather loss can also be an economic problem because birds with few feathers lose heat faster and thus cost more to feed. To reduce harmful aggressive pecking, feather pecking, and cannibalism, beak trimming has been most commonly used. But, as previously noted, beak trimming is itself a cause for concern.

Wegner (1990) concluded that more effort is needed to investigate the origins of feather pecking and cannibalism, including genetic research, with the objective of making it possible to eventually avoid beak trimming completely. Similar views were expressed by Gentle (1986), who stated that if beak trimming is not regarded as an acceptable practice when chickens are to be kept in well-lighted environments, the only alternative is to attempt to breed birds that do not exhibit those damaging traits.

Craig and Lee (1990) compared the benefits of beak trimming in three commercial stocks and found that the benefit differed greatly among genetic stocks. Beak trimming did not further reduce feather loss and mortality from cannibalism in pullets from one line, below their already low levels, indicating that beak trimming could possibly be reduced in severity or abandoned for this stock. However, the selection program and history of this stock is unknown, and it is thus uncertain how other such stocks can be developed. The differences found among stocks in feather pecking and cannibalism could have been due to random genetic drift, as large behavioral differences between lines with similar selection histories have been demonstrated (Craig *et al.* 1983).

Craig and Muir (1993) established that direct selection against cannibalistic pecking can be successful. They selected for hen-days without beak-inflicted injuries for 168 d from 16 to 40 wk of age based on sire family averages. Birds were housed by sire family, 6 per cage in five or six cages, for a total of 30 or 36 pullets per sire family and 18 sire families. Four families were selected and three males from each family were mated. The lines differed significantly after two generations of selection. Base parameter estimates showed that the heritabilities of family means based on six cages of six pullets each exceeded 0.3. Actual selection gave a realized heritability of 0.65 ± 0.13. In the second generation, the mean days without injury of the control and selected lines were 155.3 and 164.8 d, respectively. Because the maximum possible improvement was 12.7 d (168 – 155.3), the selected line achieved 75% of the possible selection differential by the second generation. Rate of lay was not significantly different among lines.

Physiological Traits

H. Siegel (1995) reviewed the interaction of stress and the immune system and concluded that stress has important consequences on the bird's well-being, especially those traits affecting energy and mineral metabolism and interactions with the immune system. Results may manifest themselves in reduced growth in juveniles, diminished reproductive capacity in adults, and increased feed consumption. H. Siegel (1995) emphasizes that the influence of genetics on disease resistance can be viewed from two aspects. The first is a difference in the corticosteroid response to stress and the second is the immunological response. Corticosteroids are produced in response to longer term stressors. Corticosteroids produce many of the outward symptoms associated with long-term stress, including cardiovascular disease, hypercholesteremia, gastrointestinal lesions, and modifications of the immune function. Social environments can also activate stress responses in birds, and like physical stressors, they are capable of depressing the immune system.

Thus, there are at least two broad categories of physiological indicators of stress: the corticosteroid response and the immunological response. On first inspection, one might conclude that animal well-being could be improved by directly selecting on any aspect of these two categories. In the first category, H. Siegel (1981) suggested selection for low responsiveness to nonspecific stress. Such a program was undertaken by Gross and Siegel (1985), who selected on plasma corticosterone in response to social stress rather than nonspecific stressors. However, unexpected results can occur from such programs. For example, the birds of Gross and Siegel (1985) quickly diverged in corticosterone response to social stress, but they did not differ in their corticosterone response to a nonsocial stressor. P. Siegel (1993) therefore concluded that the selection program altered the birds perception of stress rather than involving the general adaptation syndrome itself.

Physiological responses directly involving the immune system include antibody production and disease resistance. Social abuse, low status, and crowding of hens have been shown to be powerful stressors causing changes in resistance (Gross and Siegel 1965, 1973, 1980). H. Siegel (1981) stated that, based on general metabolic effects ascribed to stress, there is a direct link between stress and susceptibility to disease. Increases in social stress reduce antibody levels and thereby lower the resistance of fowl to several important viral infections and to bacterial infections of the respiratory system. Craig and Adams (1984) suggested that selecting for resistance to disease and certain protozoan and parasitic infections could be a useful criterion of well-being because such resistance is altered when stressors are present.

Nevertheless, such selection programs may have drawbacks. Gross and Siegel (1985) found that their line of birds selected for low immune response was more susceptible to infections from endemic bacteria and external parasites when placed in a low stress environment, whereas the high line in a high stress environment was more susceptible to viral infections. Zulkifli and Siegel (1995) thus concluded that general well-being consist of being neither under- nor overstressed. Thus, directional selection toward either extreme could be detrimental to well-being. Also, P. Siegel (1993) states that genetic changes in traits result in reallocation of resources and may preclude compromises. That is, individuals with high genetic potential for immunoresponsiveness may over-respond, resulting in a lack of resources for growth and reproduction.

Productivity Traits

Craig and Adams (1984) advocated direct selection for productivity to improve adaptability. However, Hill (1983) claims that the use of performance as an indicator of well-being has several potential drawbacks due to the conflict with profits. Nevertheless, Craig and Adams (1984) point out this is not necessarily so if productivity is not defined as profitability.

There are at least two situations in which productivity and well-being conflict. The first is disease resistance. P. Siegel (1993) and H. Siegel (1995) both concluded that Individuals with high growth or reproductive potential may divert resources to achieve that potential from immunoresponsiveness and therefore become more vulnerable to pathogens. The second is suffering to achieve greater profits. Eskland (1981) and Craig *et al.* (1992) found that beak trimming was of economic benefit even when cannibalism was not a problem, due to improved feed efficiency.

Hill (1983), Craig and Adams (1984), and Craig and Swanson (1994) concluded that multiple indicators, including physiology, behavior, or performance, are required to make a reliable evaluation of whether husbandry practices and environmental conditions reduce hens welfare significantly, as there is no single measure or type of measure by itself that is likely to be entirely reliable as a criterion of well-being in all situations.

However, Hurnik (1990) and the senior author believe that there is a single indicator of well-being that is time-honored among humans and takes into account all aspects of stress, including cardiovascular disease, hypercholesteremia, gastrointestinal lesions, and disease resistance, as well as behavioral problems such as cannibalism. This all-encompassing indicator is longevity. However, the poultry industry is driven by economics and longevity by itself does not insure profits. As a compromise, the senior author advocates a selection program directed at productivity but with longevity added as one of the important traits of selection regardless of its true economic value. Even if the genetic correlation is negative between some production traits and longevity, it is possible to select against the correlation, but the rate of response will be less (Falconer, 1981).

THE ENVIRONMENT AND THE UNIT OF SELECTION

The Environment of Selection

Equally important to the trait of selection is the environment of selection. Most commercial breeders use individual housing of hens (Hunton, 1990). However, this selection procedure ignores correlated responses of competitive behavior in the multiple-bird cages used by most producers. To determine whether genotypes of birds that produce well in single-bird cages ranked similarly in multiple-bird cages, Muir (1985) split half-sib families and housed pullets in both single and nine-bird colony cages. A significant genotype by cage environment interaction was detected for days of survival, which was later shown by Muir *et al.* (1992) to be mainly due to re-ranking of genotypes, not a change in variance. Further, Muir (1985) showed that the relationship between rate of lay and surviving group size was nonlinear with maximum rate of lay in group sizes of seven. Therefore, to improve overall eggs per hen housed, it is not only necessary to measure production in multiple-bird cages, but to select separately on rate of lay and days survival. This conclusion is consistent with selection for traits that improve well-being while at the same time improving productivity, as discussed in the previous section.

The Unit of Selection

Next in importance in a selection program is the unit of selection. P. Siegel (1989) considered adaptability to be an individual's ability to adapt to its environment. Individuals that adapt have a higher probability of contributing genes to subsequent generations than those that do not. However, this simple conclusion embodies the heart of the problem; it still emphasizes the individual's performance. What if an individual adapts to its environment by eating its cage mates? Survival of the individual would be maximized, along with its productivity, but what of that of the group? Craig (1982) advocated kin selection, in which pullets are housed in cages together as families with mean performance used as the criterion of selection. He hypothesized that families that perform best tend to have those physiological and behavioral characteristics most appropriate for group well-being and productivity. Muir (1985), Craig and Muir (1993), and Muir (1994) hypothesized that kin selection would favor cooperative tolerant behavior and concluded that selection on family means, when families are kept together as family groups, provides a method of improving traits in which behavioral interactions influence overall well-being and productivity.

The theoretical foundation for these conclusions was established by Griffing (1967). Griffing 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. The problem is to optimize production of a given genotype in a competitive environment. Griffing (1967) showed that to optimize productivity in competitive environments, one does not select those individuals that perform the best, rather one selects the group that produces best. In fact, the disturbing conclusion is that if the best performing individuals are chosen, productivity of the group may decline. Further, Griffing (1967) showed that as group size increases, associate effects take on an increasingly dominant role in determining the consequences of selection. This concept implies that even for weakly competitive conditions, a negative response to selection can occur. These results are contrary to the theories advanced by classic quantitative genetic theories and require a rethinking of selection programs by commercial breeding companies.

Griffing (1967) showed that if selection is transferred from the individual to that of the group, a positive response to selection is ensured because group selection operates on both direct and associate components. Of even more interest is that selection only on associate components cannot guarantee a positive response to selection, i.e., selection for reduced aggression will not ensure that production will increase. Although selection of groups composed of random individuals would be expected to improve group performance, it is expected to be slow and decrease as the group size increases. Griffing (1976) showed that if the group is composed of related individuals, efficiency is greatly increased, particularly as group size increases.

Experimental Verification

From the theories of Griffing (1967), one would expect to see a negative effect on well-being under competitive conditions with direct selection for productivity based on performance of the individual. There is abundant evidence to support this conclusion, as indicated below.

Selection Based on Individual Performance

Emsley *et al.* (1977) estimated genetic correlations between egg production and flightiness score, which indicated that greater excitability was mildly associated with higher rates of lay. From these parameters, Kashyap *et al.* (1981) developed a selection index for aggregate economic gain, which includes a number of traits but gives positive weight to egg number and negative to excitability or flightiness, which nevertheless resulted in a positive response in excitability. Further examination of the data collected by Kashyap *et al.* (1981) showed that genetic changes in excitability were greater than what would have been predicted by theory (Bennett *et al.*, 1981). However, their results are in agreement with the theories of Griffing (1967).

Craig and Lee (1989) detected a strong genotype by beak treatment interaction for egg mass per hen housed among three commercial lines. From 32 to 36 wk of age, the genotype that produced the greatest egg mass with beak treatment produced the least with intact beaks. The reranking was shown to be due to mortality from beak-inflicted injuries. Choudary *et al.* (1972) compared four commercial lines of poultry and found that the line with the highest hen-day rate of lay had the lowest hen housed rate of lay due to high mortality. These results tend to confirm Griffing's (1967) theories because productivity and mortality were negatively correlated.

Lee and Craig (1981) found that a stock that was selected for increased productivity had greater feather loss than its unselected control when kept in three-bird cages. Craig *et al.* (1975) compared aggressive behavior among lines of chickens selected for part record egg production under competitive conditions and the unselected control from which the selected lines were derived. Results generally showed that artificial selection had increased aggressiveness and social dominance during adolescence. Results from Lowry and Abplanalp (1970, 1972) showed that strains selected under floor flock conditions became socially dominant to both those selected in single-bird cages and unselected controls. Craig *et al.* (1965) and Craig and Toth (1969) showed that hens of lines selected for social dominance had lower rates of lay than did hens of the same line selected for low social dominance. In addition, Craig (1970) showed that the high social dominance line withstood crowding less well than the low social dominance line. However, in single-bird cages, egg production of the high line was superior to that of the low. Biswas and Craig (1970) also showed that the high strain hens had much lower production than the low line in floor pens or multiple-bird cages but were equally productive in single-bird cages.

Selection Based on Group Performance

The first experiment reported with chickens using kin selection to improve adaptability to social stress was unsuccessful (Craig *et al.* 1982). In retrospect, Craig (1994) concluded that the failure may have been due to the relatively benign environments in which the hens had been kept during selection, i.e., beak trimmed, relatively low density, and part-record egg production. Craig (1982) states that practices such as beak trimming, dim lighting, and declawing should be abandoned when using kin selection so that such tendencies toward feather and cannibalistic pecking and claw-inflicted injuries could be revealed.

A similar group selection experiment was initiated at Purdue University by the senior author in 1981 but with more stringent conditions (Muir and Liggett, 1995a), particularly with respect to duration of stress, beak trimming, and group size. In that experiment, females of each sire family were housed as a group in a multiple-bird cage and selected as a group. In the first two generations (G1 and G2), group size was 9 (413 cm^2 per bird) whereas in the next four generations (G3, G4, G5, and G6) group size was 12 (362 cm^2 per bird). In all generations except G1, birds were not beak-trimmed and lights were at high intensity. Production was measured to at least 60 wk of age and in G1, G5, and G6 to 72 wk. The criterion of selection was initially egg mass, which was computed as the product of eggs per hen housed and egg weight. In later generations an index giving equal weight to eggs per hen per day and days survival was used. An unselected control, with approximately the same number of breeders as the selected line, was maintained for comparison and housed in one-bird cages. Egg weights were collected weekly, biweekly, or monthly in different generations. Egg weights for missing weeks were found by regression. Performance beyond 60 wk of age in generations in which it was not measured was projected by linear regression of postpeak performance.

After four generations of selection, Kuo *et al.* (1991) and Craig and Muir (1991) compared performance of the selected and control lines in six-bird cages with 387 cm^2 floor space per bird from 16 to 36 wk of age with 0, 1/2, or 2/3 of the beak trimmed. Results showed a highly significant beak treatment by genetic stock interaction for hen housed rate of lay, daily egg mass, and mortality. With intact beaks, the selected line had significantly higher egg production, egg mass, and survival. With 2/3 of the beak removed, difference in egg production and egg mass remained significantly different but the magnitude of difference had declined. Further, mortality was not significantly different. Egg weights of the selected line were slightly higher than that of the control but not significantly so.

At the sixth generation, Muir and Liggett (1995a) summarized their results. Because birds were not beak-trimmed in G1, performance of that generation was not comparable to that in subsequent generations. Results based on G2 through G6 showed that rate of lay increased from 52 to 68% whereas percentage mortality decreased from 30.6 to 8.8%. The combination of these factors resulted in an average increase in days survival from 160 to 348 and an increase in total eggs per hen housed from 91 to 237 eggs. In contrast, egg weights decreased from 59.1 to 56.0 g. However, the increase in total eggs more than offset the decline in egg size as egg mass per bird housed increased from 5.3 to 13.3 kg. Performance changes of the control over the same time period were in the opposite direction for mortality, increasing from 3.4 to 9.1%, and days survival, which decrease from 357 to 348 d. These latter results may be due to cumulative inbreeding. The fact that days survival and mortality 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

In the seventh generation, the selected and control lines were compared to a commercial line and were again housed in either single- or 12-bird cages (Muir and Liggett, 1995b). Management conditions were the same as in previous generations, except that birds that died were replaced with extra birds of the same line. Performance was measured from 20 to 58 wk of age. The residual record from 59 to 72 wk of age was again projected by linear regression. In general, annual performances (20 to 72 wk) in single-bird cages in terms of eggs per hen housed, eggs per hen per day, egg weight and egg mass were significantly greater for the commercial than for the selected line, which was in turn greater than the unselected control. Mortality from cannibalism was zero for all three lines. However, in 12-bird cages the reverse was seen, with the selected line superior to the commercial line for eggs per hen housed, egg mass, and eggs per hen per day. The most remarkable difference was for mortality. The commercial line had an 89% mortality at 58 wk of age as compared to the selected line with 20% and the control at 54%. In this same study, Craig and Muir (1996) observed that feather scores did not differ in single bird cages among genetic stocks. However, in 12-bird cages, the selected line had significantly better feather score than the other lines.

At 36 wk of age, half of the birds of each line were subjected to cold stress (Hester *et al.* 1995a), after which, at 47 wk of age, the birds subjected to cold stress were further subjected to heat stress (Hester *et al.* 1995b). Blood samples were taken before, during, and after each stress period. Egg production was also summarized for each of those periods. Packed cell volume immediately after housing indicated that the selected line may have adapted to the new watering system more quickly than the other lines. During cold stress the commercial and control lines showed an increase in heterophil to lymphocyte ratio in 12-bird cages whereas the selected line did not. Egg production before, during, and after cold stress indicated that the selected line withstood social, handling, and environmental stress better than the control and in some cases the commercial line. Similar observations with heat stress showed that the selected line withstood heat stress better as indicated by a lower mortality than the control or commercial lines. Egg production before, during, and after heat stress indicated that the selected line withstood social, handling, and environmental stress better than the control line and in some cases the commercial. Adrenal weights were larger in the selected line than the other lines, suggesting that the line may have a greater capacity to respond to stress than the other lines. Hester *et al.* (1995c) also reported that the lines showed no differences in humoral immune response to sheep red blood cells after either cold or heat stress.

CONCLUSIONS

Taken as a whole, these results present conclusive evidence that group selection on the traits rate of lay and longevity is effective in improving well-being of layers in a relatively short period of time without sacrificing productivity. The way for commercial breeders to develop birds that do not need beak trimming is clear. Further, because group selection is shown to improve well-being in multiple-bird cages, alternatives such as redesigning cage environments, or housing such as floor pens or free ranges, may not be needed.

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