

Genetic Influences on the Behavior of Chickens Associated with Welfare and Productivity

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INTRODUCTION

Behavior is the observable actions, mannerisms, and means by which animals cope with their environment, including other animals in that environment. The environment may be considered in terms of both the internal or physiological environment and the external environment. The latter may be subdivided, with some overlapping, into social and physical aspects. When failure to cope with changes is detected in chickens, the question arises as to whether there should be an attempt to adapt the environment to the bird or the bird to the environment (Muir, 1996, 2003; Muir and Cheng, 2004). Similarly, Cheng (2007) questions “Should we change housing to better accommodate the animal or change the animal to accommodate the housing?” Attention in this chapter is focused on genetic modification to improve the chickens to adaptability to their environments and consequently to enhance their welfare.

In the last half of the 20th Century the greatest change in the layer industry was that from floor pens to batteries of multiple-hen cages. The popularity of multiple-hen cages resulted in part because commercial producers found that multiple-hen cages offered several advantages in both economic and animal welfare aspects, including higher feed efficiencies (Cunningham, 1992), improvement of biosecurity and food safety (De Vylder *et al.*, 2011; Hannah *et al.*, 2011; Holt *et al.*, 2011; Jansson *et al.*, 2010; Jones *et al.*, 2011), and reduced housing and labor costs (Craig, 1982; de Boer and Cornelissen, 2002; Sumner *et al.*, 2011; Van Horne, 1996). Ironically, the biggest change in the 21st century may be away from cages and a return to floor pens or alternative rearing systems (California proposition 2, 2008; United Egg Producers, 2011). Craig and Swanson (1994), Goodwin (2001), Mellor and Stafford (2001), Hemsworth (2007), Swanson (2008), and Mench *et al.* (2011) examined both historical and current ethical perspectives and attitudes towards husbandry

conditions of livestock. Although there is considerable disparity among different social and professional groups, it appears that during the last three decades there has been a definite shift in the direction of greater concern in matters of pain and suffering of farm animals and a tendency to favor protectionist legislation (Mench, 2008; Mench *et al.*, 2011; Millman *et al.*, 2010). Public pressure for increasing the well-being of chickens in Western Europe led to codes of recommendations for “humane” husbandry and, in the extreme, legislation was enacted phasing out the use of conventional cages for layers starting in 2012 in the European Union (CEC, 1999) and some states of the United States (California proposition 2, 2008). It is of special interest that the prohibition of caging hens occurred even though cages have been shown to have some advantages over alternative housing systems (Appleby *et al.*, 1992, p. 207; de Wit, 1992; Lay *et al.* 2011; Mench *et al.*, 2011), for example, cannibalism is more common in non-cage systems than in dimly lit cage houses.

Behavioral problems exist not only among chickens kept in cages but also in alternative systems (Appleby and Hughes, 1991; Craig and Adams, 1984; Lay *et al.*, 2011; Mench, 1992; Siegel, 1989). Recent reviews examined the future of the poultry industry and included issues related to politics, housing, ethical, and well-being concerns (Hester, 2005; Lay *et al.*, 2011; Mench, 2008; Mench *et al.*, 2011; Millman *et al.*, 2010; Newberry and Tarazona, 2011) but perhaps the most striking conclusion given this move away from cages was that of Lay and associates (Lay *et al.*, 2011) who concluded that there is no one clear solution to the housing issue and that no housing system is ideal from a hen-welfare perspective. In floor pens and outdoor systems, hens are exposed to litter and soil, providing a greater opportunity for disease and parasites with similar consequences from adding environmental complexity. Further, the more complex the system, the more difficult it is to manage and with larger group sizes, disease is more likely to spread. Additionally, increasing the space per hen increases incidence of cannibalism and smothering and introduces difficulties in terms of disease and pest control while adding environmental complexity increases undesirable behaviors that are detrimental to welfare (Lay *et al.*, 2011).

A promising resolution was suggested by Muir and associates (Muir, 1996, 2003; Muir and Cheng, 2004) and others (Cheng, 2007, 2010; Laible, 2009; Lay *et al.*, 2011; Newman, 1994; Cheng and Muir, 2005) who concluded that selective breeding for desired traits may help to improve welfare in domesticated settings and decrease or eliminate instances of undesirable behaviors in cages or alternative housing systems. The focus of this chapter is toward changing the nature rather than the nurture of chickens to improve welfare in domestic environments.

ASSESSMENT OF WELFARE

The words welfare and well-being are widely used but connotations vary. Dictionary definitions reflect an anthropomorphic viewpoint, e.g.,

[Merriam-Webster, Inc. \(1983\)](#) defines welfare as “the state of doing well esp. in respect to good fortune, happiness, well-being, or prosperity” and well-being is defined as “the state of being happy, healthy, or prosperous.” To animal researchers, prosperity and happiness are unlikely to be meant, but rather absence of chronic pain and suffering, good health, ability to respond to stressors, and components of fitness (including productivity in some contexts) are likely to be included. There is a tendency, especially among Western Europeans, to place emphasis on mental conditions such as fear, frustration, anxiety, anger, and similar emotional states ([Barnett and Hemsworth, 2003](#); [Duncan and Dawkins, 1983](#); [Duncan and Petherick, 1991](#); [Green and Mellor, 2011](#); [Mellor, 2012](#); [Yeates and Main, 2008](#)). Although most agree that emotional states should be included, it needs to be recognized that certain temporary stressors, likely to be associated with unpleasant mental states, prepare chickens to cope better with more severe stressors later in life ([Gross, 1983](#); [Zulkifli and Siegel, 1995](#)). Life in general is a series of stressors, for humans and animals, in the quest for food, shelter, security, and reproduction. In each of these basic quests, even in natural conditions, most animals experience periods of food deprivation, disease, predation, competition, and stress. Our quest should not be to provide as natural conditions as possible, lest we expose animals to the undesirable aspects of nature as well, but rather to protect animals from such natural stressors, while ensuring a safe healthy food supply, free of disease, for human consumption.

Criteria of Welfare

Having defined, in very general terms, what is meant by well-being, it is then necessary to examine how it may be evaluated. In what follows we adopt the general categories of evidence suggested in the review of [Craig and Adams \(1984\)](#). More detailed descriptions may be found in other reviews ([Craig and Swanson, 1994](#); [Duncan, 2005](#); [Mench, 1992](#); [Webster, 2001](#); [Yeates and Main, 2008](#)).

Overt Signs

Bodily injury, morbidity, extreme weight loss, heavy feather loss (not associated with natural molting), and death of individuals are widely accepted as indicators that welfare is impaired. When the well-being of groups in production settings is considered, longevity, i.e. days’ survival over the production period, can be used as an overt indicator. This measure takes into account all aspects of stress ([Hurnik, 1990](#); [Muir and Craig, 1998](#); [Quinteiro-Filho *et al.*, 2012](#)). Lifetime stress as the result of adverse environments will increase susceptibility to diseases and will result in other physiological manifestations which shorten the life-span. Vices such as feather and cannibalistic pecking also increase exposure to disease or cause death. Thus, longevity, if measured over a long period, is a direct measure of welfare.

Physiological and Immune Responses

The general adaptation syndrome (GAS) can be delineated into short-term fight or flight responses and longer duration accommodation responses involving the hypothalamic–pituitary–adrenal (HPA) and the sympathetic–medullary–adrenal (SMA) axes and is associated with immunocompetence and health. Siegel (1981) stated that, based on general metabolic effects ascribed to stress, there is a direct link between stress and susceptibility to disease and that social stress is an effective initiator of non-specific stress response in fowl. 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. Non-specific environmental stressors can have significant influences on growth, reproduction, and the ability of the bird to resist diseases (Siegel, 1981). Dantzer (1994) indicated that animal response to stressor by changing neurohormonal homeostasis does not depend on the physical nature of the stressor. Corticosteroids, as a final compound, are produced in response to stressors. These produce many of the symptoms associated with long-term stress, including cardiovascular disease, hypercholesteremia, and modifications of the immune function (Siegel, 1995).

Although physiological (including immune) responses frequently reflect the presence of known stressors (Freeman, 1985; Gross, 1983; Hill, 1983; Hoehn-Saric and McLeod, 2000; Piazza *et al.*, 2010; Siegel, 1994; Theorell, 2012; Zulkifli and Siegel, 1995), it has been shown also that such measures can occasionally be misleading or difficult to interpret. For example, plasma corticosteroid concentrations were found to be elevated similarly for hens in high-density cages and spacious floor pens even though other measures indicated that those in high-density cages were under greater stress (Craig and Craig, 1985, Craig *et al.*, 1986).

Functional Genomics

At a recent Poultry Science Keynote Symposium—Tomorrow's Poultry: Genomics, Physiology, and Well-Being (Muir *et al.*, 2010), a novel approach to objectively quantify stress and well-being in animals and to identify management practices that necessarily compromise well-being was discussed. Toward that goal we proposed using the RNA transcriptome as a holistic tool to formulate a metric. The transcriptome represents the expression of all genes in an organism at a given time in response to environmental stimuli. The output from each gene can be quantified on a microarray, or more recently using whole-genome sequencing techniques, commonly termed RNAseq. The methodology for developing this technique was described in a landmark paper by Golub *et al.* (1999) and recently further reviewed by Myers (2011) and Kolpfleisch and Gruber (2012). They demonstrated the power of supervised clustering to diagnose cancer type in humans. In the

first step cancer types were classified by a panel of experts. In the second step the transcriptome was used in a discriminate analysis to predict each cluster. In the third step the transcriptome was sampled on a new set of individuals, and the samples assigned to clusters based on the discriminate function in the previous step. The results were verified by the same team of experts and were found to be extremely accurate. Knowledge of which genes were up- and down-regulated by each cancer type was not needed, only the pattern was important. Transcriptomic profiling has also been used widely in improving human well-being (Chaussabel *et al.*, 2010; Elstner and Turnbull, 2012; Hindmarch and Murphy, 2010; Mestan *et al.*, 2011).

Similarly, application of this novel approach for assessing well-being has the potential to provide common ground and address housing and other issues allowing the animals to speak for themselves through their transcriptome. The approach would include known stressors and animal-friendly environments. Exposure of the animals to those environments for short- and long-term durations, and then collection of their transcriptome from tissues in which emotions are known to be controlled, such as the hippocampus and the HPA axis. The transcriptome would then be isolated and quantified, using the latest technology, such as RNAseq. A supervised cluster analysis would then be performed into known treatments to create a discriminate function. The discriminate function classifies observations by the metric used to create the function. Next, an independent set of animals would be exposed to contentious alternative housing and management practices for short- and long-term duration, the same tissues isolated, the transcriptome quantified, and finally clustered using the previously trained discriminate function. The function will classify questionable housing and management practices into those that are most similar to those recognized as stressors and those that are animal friendly.

Alternatively, if training environments cannot be agreed on by a panel of experts, an unsupervised clustering analysis can be performed on the transcriptome of animals housed in alternative and questionable environments. An unsupervised cluster analysis will at least show if the alternative environments are really different **as perceived by the animals** in the environmental conditions imposed for whatever reason. If two environments do not induce a different transcriptome profile, it would be difficult to argue that the environments are inducing different levels of stress.

Productivity

The use of productivity or performance data as indexes of well-being in chickens has been criticized (Hill, 1983). However, as Craig and Adams (1984) made clear, early comparisons confounded profitability and productivity. When productivity of the individual laying hen is considered in terms of number of eggs, feed efficiency, and mortality, it proves to be a fairly

sensitive indicator of well-being (Adams and Craig, 1985; Appleby and Hughes, 1991, pp. 116–117; Cunningham *et al.*, 1988). Productivity indicators may be useful measures of the continuing effects of stressors when hens have made an adjustment to the “stage of resistance” as defined by physiological criteria. For example, Beuving and Vonder (1978) reported and reviewed by Ruszler (1998): little or no behavior evidence of the stressful conditions of high temperature or water and feed deprivation after the first few days, though their hens stopped laying.

The relationship between stress and production also supports the notion that production is a good indicator of stress. Siegel (1995) and Scheele (1997) pointed out that stress has important consequences on the birds’ well-being, especially those that affect energy and mineral metabolism and interactions with the immune system. Social or behavioral environments can also activate stress responses in birds just as physical stressors do (Cheng *et al.*, 2002, 2003). Results may manifest themselves in reduced growth in juveniles, reproductive capacity in adults and increased food consumption.

When management of broiler breeder stock is considered, a problem with interpretation of their welfare arises. Because of excessive appetites, birds to be kept as broiler breeders are severely restricted in feed intake. This practice prevents obesity of adults which if uncontrolled reduces health, longevity, and reproductive performance, and increases the incidence of leg problems (de Jong *et al.*, 2005; Hocking *et al.*, 2004; Siegel, 1984; Tolkamp *et al.*, 2005). By the criteria cited above, productivity indicates improved well-being with broiler breeders on feed restriction. Nevertheless, feed deprivation has been shown to cause increased aggressive pecking of chickens (Duncan and Wood-Gush, 1971; King, 1965; Mench *et al.*, 1986; Shea *et al.*, 1990). Nevertheless, from the standpoint of physiological indicators, it appears that broiler breeders on feed restriction adjust rapidly (Benyi *et al.*, 2009; Katanbaf *et al.*, 1989).

Behavior

European researchers often use behavioral criteria as the primary, or sometimes the only, indicator of hens’ welfare (Baxter, 1994; Faure and Mills, 1989; Savory and Hughes, 2010; Sorensen, 1981; Wegner, 1985). Dawkins (1983) was critical of such an approach and wrote:

At first sight, the growing awareness that an animal’s behavior may be important evidence to have when assessing its welfare is entirely to be welcomed. But there is, amid the encouraging trend of a greater use of ethological data, also a disturbing one of possible misuse of ethology.

For example, Dawkins (1988) considered the absence of behavior patterns seen in the wild as an invalid criterion of animal suffering although such evidence is frequently used by critics of high-density cage environments.

Assessment of chronic pain by behavioral criteria appears to be a valuable technique. For example, behavioral evidence suggested that pain and heightened beak sensitivity persist for several weeks or even months following beak trimming in hens trimmed at 5 weeks of age or older (Breward and Gentle, 1985; Craig and Lee, 1990; Duncan *et al.*, 1989; Gentle, 1986b, 1989, 1992; Gentle *et al.*, 1990, 1991; Lee and Craig, 1990, 1991; Mench and Duncan, 1998). Nevertheless, interpretations of behavioral evidence can be controversial. Thus, Eskeland (1981) observed that beak-trimmed hens spent more time “resting” and concluded that fearful running by hens of low social rank was almost eliminated by beak trimming. However, Gentle (1986a) suggested that the significant increase in resting behavior among trimmed-beak birds was similar to the inactivity following injury seen in both human beings and animals (Cheng, 2005; Wall, 1979). Because of interpretation difficulties, it is valuable to supplement behavioral observations with other types of evidence as was done by Breward and Gentle (1985) and Gentle (1986a, 1989). They presented evidence that following partial beak amputation, growth of neuromas occurred in the part of the beak remaining and that spontaneous firing of afferent neurons associated with pain occurred up to at least 12 weeks after beaks were trimmed.

Several researchers, including Dawkins (1983) and Faure (1986), have used the willingness of hens to express preferences or “work” for environmental conditions allowing the expression of certain behaviors as evidence of the relative desirability of alternative environments from the hen’s viewpoint. Nevertheless, possible confounding factors must be avoided or compensated for in such tests because previous experience with an environment may have a powerful effect on motivation to choose or work for it so that birds with different experiences choose differently (Byholm and Kekkonen, 2008; Campos *et al.*, 2008; Cornil and Ball, 2010; Mumme *et al.*, 2006; Petherick, *et al.*, 1990).

Behaviors seen as indicating problems with the environment, such as vacuum activities and stereotypies, are frequently cited as indicators that the environment impairs welfare in animals (Mason *et al.*, 2007; Martins *et al.*, 2012). However, Hughes (1980), Dantzer (1993), and Mason and Latham (2004) argue that the occurrence of such activities may allow animals to cope.

General

Difficulties of interpretation of the various criteria of welfare have been discussed (Clark *et al.*, 1997; Consortium, 1988; Craig and Adams, 1984; Craig and Swanson, 1994; Dawkins, 1998; Hetts, 1991; Hill, 1983; Hurnik, 1990; Izzo *et al.*, 2011; Kumar *et al.*, 2012; Mench, 1992; Muir and Craig, 1996), and there is a tendency to agree that, except for overt indicators, no single measure has previously been shown to be adequate, at least when long-term

stressors are involved. Therefore, so far as possible, multiple indicators are preferable. One such multiple indicator is the transcriptome, which includes all expressed genes in the genome and thus includes all physiological responses to the environment.

DOMESTICATION AND BEHAVIOR

Behaviors associated with fitness in a natural environment may not differ greatly from those found in domesticated stock under relatively primitive husbandry conditions. Thus “native fowl” in villages of Southeastern Asia obviously cope with their environment although they may receive only minimal care such as being fed unusable by-products of subsistence farming or leftover food scraps and some protection from predators.

Those behaviors favoring domestication of a species have been described (Cheng, 2010; Hale, 1969), and chickens fit the pattern well. Behaviors that were essential in the wild may be unnecessary or even counterproductive in terms of well-being under modern systems of husbandry. Thus, extreme alertness and flighty behavior may lead to waste of energy and injuries in attempting to escape from otherwise harmless stimuli when predators are not present. Aggressiveness in obtaining desired resources may result in low-status birds’ failure to receive adequate necessities even when enough is supplied for all. Broody behavior, essential to fitness in natural environments, is undesirable in domestic conditions and has been all but eliminated by breeders in egg-production stocks.

GENETIC *VERSUS* ENVIRONMENTAL INFLUENCES

As species-specific activity, behavior is under genetic control through regulating physiological homeostasis. In artificial environments, it may be difficult to know, in the absence of experimental data, whether differences between stocks are of genetic or environmental origin or if both kinds of influence are at work. For example, age at onset of egg laying, egg weight, intensity of egg production, and duration of laying have been under effective genetic selection for many generations but the stimulus of day length and artificial control of photoperiods can also have large effects. Attempts have been made to rule out environmental effects by standardizing environmental conditions, as when stocks are compared for egg production in random sample tests. Even so, stocks being compared may have different requirements for maximum performance or special characteristics which make them superior in some environments and inferior in others.

The existence of genotype by environment interactions for behavioral traits (as for production traits also) complicates the assessment of behavioral problems and possible approaches for improving the welfare of chickens by genetic means. Thus, if a particular egg-laying stock should possess a limited

appetite and therefore require a more concentrated ration for optimal well-being and productivity, it would be penalized if compared with other stocks having greater appetites if all are fed a ration more suitable for the latter stocks.

BEHAVIORAL DIFFERENCES AMONG POPULATIONS

Behavioral differences, usually of a quantitative nature, are found among domesticated stocks of chickens. Most of these can be demonstrated to be of genetic origin. Often it is difficult or impossible to know how these differences arose. Likely contributors consist of genetic differences in foundation populations, random genetic drift in relatively small and isolated populations, adaptation to local environments by natural selection, and different goals under artificial selection. The impact of selection by poultry breeders is clear when comparing breeds developed specifically for beauty, fighting ability, meat production, or table-egg production. As an example of how selection for an economic trait can affect behaviors, [Siegel \(1989\)](#) described how long-term selection for heavy juvenile body weights in broilers resulted in their having more docile behavior, greater appetite, and reduced motor activity when compared with egg-production stock.

Comparisons among stocks are complicated in some cases because of developmental stage effects. Studies by [Tindell and Craig \(1959\)](#) and [Bellah \(1957\)](#) are especially instructive in this regard. Tindell and Craig found differences in peck-order status among hens of four breeds (White Leghorn, Australorp, Rhode Island Red, and White Plymouth Rock) when placed together in intermingled flocks and observed to determine relative peck-order status at about 5 months of age. Bellah used hens of the four breeds from the same experiment that had been kept in separated-strain flocks and determined their relative social dominance ability beginning at about 8 months of age. Strikingly different results were obtained from those of Tindell and Craig when relative social dominance ability of the breeds was compared at the later age. In the most extreme case, Rhode Island Red hens, which ranked lowest among the breeds when compared in intermingled flocks at 5 months, were the most dominant when tested in pair contests at 8 months of age.

Inconsistencies have also been found for social dominance ability among experimental stocks within the White Leghorn breed when compared at different ages. Using two populations subjected to long-term selection for number of eggs laid before 40 weeks of age, mostly in competitive floor-pen environments, and the unselected control from which they were derived, [Craig et al. \(1975\)](#) found that the selected stocks had decreased age at sexual maturity and increased aggressiveness and social dominance ability during the adolescent period. However, for one of the selected strains, rank for the

agonistic traits was reversed relative to the control stock between adolescence and full maturity.

Social inertia can confound accurate determinations of relative social dominance ability after peck orders have become well established (Guhl, 1968). Lee and Craig (1981a) demonstrated this using the same stocks compared in the Craig *et al.* (1975) study. They found that the selected strain had social dominance over the control at 5 months (before egg laying), but the selected stock dominance ability had diminished or disappeared when strangers of the strains were placed together at 17 months of age. Nevertheless, selected strain pullets maintained undiminished dominance over control pullets for the entire laying year when they were kept together from time of housing at 5 months.

Comparisons among breeds, in which a single stock within each breed was used, have revealed behavioral differences of genetic origin. Such differences were found for chicks' open-field activity (Faure, 1979), presence or absence of hysteria among hens in large-group-size cages (Elmslie *et al.*, 1966), duration of tonic immobility (Campo and Alvarez, 1991; Campo *et al.*, 2007; Gallup *et al.*, 1976; Jones and Faure, 1981), and pre-laying behavior of individually caged hens (Mills and Wood-Gush, 1985), and eating (Howie *et al.*, 2011). Such studies are of value in demonstrating whether genetic stock differences exist at all but could be misleading in terms of identifying breeds as having particular characteristics. For example, large strain differences have been shown within the White Leghorn breed for behavioral traits. Thus, Hansen (1976) found hysteria-susceptible and hysteria-resistant strains. Al-Rawi *et al.* (1976) and Buitenhuis *et al.* (2009) detected differences in frequency of agonistic acts; and hens of different stocks were found to differ in feather-loss and mortality from cannibalism when their beaks were left intact (Craig and Lee, 1990).

INBREEDING DEPRESSION AND RANDOM GENETIC DRIFT

Expected general consequences of inbreeding within a population are: there will be subdivision into distinctive lines or subpopulations (because of random genetic drift), uniformity will increase within subpopulations, and there will be a general loss of vigor. Although there are widespread observations over species confirming the consequences of inbreeding in general, the evidence for behavioral traits in chickens is sparse.

A study by Craig and Baruth (1965) examined the effects of inbreeding on vigor as indicated by social dominance ability of cockerels and pullets. Because of small numbers available within each of five partially inbred lines, differences among lines and uniformity within lines were not examined. However, mean performance over the lines when compared with that of a sample of the non-inbred and unselected population from which the lines were derived provided the evidence needed. Partially inbred cockerels were

inferior in ability to win pair contests when matched with non-inbreds, and pullets' peck-order status was negatively associated with their inbreeding coefficients.

McGibbon (1976) observed that the incidence of floor laying in pens increased as inbreeding increased in lines originating from random-bred populations of White Leghorns (Cornell Control) and Rhode Island Reds (Regional Reds). This evidence suggests that homozygous recessive genes were involved. However, environmental conditions during the rearing period were also identified as being influential; floor laying was more prevalent among confinement-reared pullets than in range-reared pullets.

Differentiation associated with keeping relatively small subpopulations isolated over several generations was illustrated for fear-related escape and avoidance behavior by Craig *et al.* (1983). One of two subpopulations selected alike required about 10-times as long to recover from fear as did the other (Craig *et al.*, 1983). Likewise, differences in “righting time” following the induction of tonic immobility were present within some pairs of similarly selected lines (Craig *et al.*, 1984).

MENDELIAN TRAITS

Genes having major effects on morphology and the nervous system are typically deleterious in terms of the well-being of affected individuals and often affect their behavior (Axelsson and Ellegren, 2009; Eyre-Walker and Keightley, 2009; Siegel and Dunnington, 1990). Such genes are usually either sex-linked recessives, which may be expressed in non-inbred stocks, or autosomal recessives, most likely to be seen following inbreeding. Because of the generally deleterious effects of these major genes they are selected against and are not seen in commercial stocks except at very low frequency for homozygous recessive phenotypes.

Some major genes, seemingly having adverse effects, may not be as disadvantageous as they seem at first consideration. For example, results of a study carried out by Ali and Cheng (1985) are relevant. They compared genetically blind hens (*rc/rc*) and sighted hens (*Rc/rc*) segregating from matings of *Rc/rc* × *rc/rc* chickens. During a 2-month experimental period, blind hens were less active, had better feather cover, produced more eggs, required less feed, and did not differ in body weight from sighted hens.

SELECTION INVOLVING BEHAVIORAL TRAITS

Behaviors associated with welfare and productivity in commercial stocks are typically under polygenic control and are measured in quantitative terms. However, some, such as “broody” behavior, are more of an all-or-none nature. Both autosomal and sex-linked genes may be involved. Because selection studies are costly and time consuming, breeders often depend on

heritability estimates in guiding choices as to whether selection is likely to change behaviors of interest. Heritability estimates often have large standard errors and are most relevant to the population in which the data for their estimation are gathered.

Effects of both direct and indirect (genetically correlated) selection responses on several relevant behaviors have been carried out and will be reviewed below. Although selection to improve behaviors associated with well-being has been effective in most experimental studies, commercial breeders are under economic constraints that may prevent their adoption of programs in which behavioral problems are addressed (Faure, 1980, 1981b; Faure *et al.*, 1992; Hocking, 1994). Nevertheless, results of some recent studies (Cheng, 2010; Cheng and Muir, 2005, 2007; Kuo *et al.*, 1991; Muir, 1996) show that major advances may be made within a reasonable number of generations in reducing behavioral problems having an economic impact.

Some behaviors are easily identified and therefore amenable to selection procedures, as in the case of broodiness, or because they leave “traces” (Faure, 1981a), as in the case of feeding behavior which can be measured from feed consumed. However, as Faure (1981a) and Hocking (1994) indicated, selection involving traits such as pre-laying pacing (see below) must be measured by laborious and time-consuming observations that are likely to be impractical for breeders who must evaluate hundreds or thousands of birds. Also, breeders know that each additional trait added to a breeding program reduces the effectiveness of selection for other traits of importance.

Broodiness

Behavior related to incubation of eggs is no longer evident or occurs with very low frequency in major commercial stocks in which broodiness has been selected against. Incubation behavior of hens was a common characteristic in most chicken stocks until a few decades ago. As the need for natural incubation and maternal care of chicks became obsolete, because of artificial incubators and chick brooding equipment, broodiness came under closer scrutiny.

Broodiness is a trait involving sex-linked genes as suggested by Warren (1930) and confirmed by later studies (Dunn *et al.*, 1998; Jiang *et al.*, 2005; Ohkubo *et al.*, 1998; Saeki, 1957). Early on it became evident that within the White Leghorn breed incidence was relatively low whereas other breeds usually had higher levels. Although Saeki (1957) obtained estimates of heritability of less than 20% in the Japanese Nagoya fowl, an early selection study by Goodale *et al.* (1920) indicated that realized selection progress was substantial in the Rhode Island Red stock used. The fact that broodiness was successfully selected against by commercial breeders is not surprising; it appears to be at least moderately heritable (Romanov *et al.*, 1999); most experiments indicated that it is negatively associated with total egg

production; and it is easily identified during the first year of egg production (Saeki, 1957).

Should there be concern about the loss of a previously important behavior from chickens? We believe the absence of a behavior previously expressed is weak evidence that suffering results. Craig and Swanson (1994) discussed this as follows:

With the example of broodiness in mind, one may ask, why should behaviors that are no longer required be expressed? Presumably, most or 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 conditions allowing their expression.

Behavioral exhibition is controlled by both internal and external factors. Internal factors are mainly neuroendocrine factors. Neurons of the central nervous system have the capacity to change structure and functions (neuronal plasticity) to adapt to a given environment (Joseph, 1999; Kolb and Whishaw, 1998; Smith, 1993), which, in turn, affects animals' behavioral exhibition (Rosenzweig and Bennett, 1996; Sausa *et al.*, 2000). Through domestication, farm animals are quite different from their wild counterparts in many ways, including behavior. In addition, the degree of welfare could be dramatically different between strains of a species and individuals of the same strain even housed at the same environment, which is dependent on each individual's behavioral and physiological characteristics (genotypic and phenotypic variations). Adaptation of an individual, but not another, to its surrounding environment can be achieved through environmental stimulation-associated behavioral and physiological plasticity in the animal (a genetic–environmental interaction) and the experiences received during the animal's lifetime (allostasis, i.e. allostatic load or overload) (Clark *et al.*, 2007; McEwen, 2001).

Stereotyped Pacing During the Pre-Laying Period

Breeds, strains within breeds, and individuals within strains vary in stereotyped pre-laying pacing seen in single-hen cages. Such behavior may be interpreted alternatively as indicating frustration (Duncan and Wood-Gush, 1972) or the alleviation of stress (Hughes, 1980; Dantzer, 1993). The absence of nests in single-hen cages is apparently responsible for stereotyped pacing before an egg is laid in some stocks but not in others (Mills and Wood-Gush, 1985). Instead of pacing, some stocks show quiet sitting behavior during the pre-laying period. Thus, it may be conjectured that those stocks showing pacing are frustrated whereas other stocks are not. If convincing evidence becomes available that well-being is compromised in stocks that pace in the absence of nests, then choices need to be made. For example, either cages should be modified by providing nests, stocks should

be used that are not frustrated by the absence of nests, or within-strain selection should be directed towards selecting for quiet sitting behavior rather than stereotyped pre-laying behavior. Mills *et al.* (1985) demonstrated, in a brief selection study, that such selection could be effective.

Increased pacing before egg laying was not seen in high-density, multiple-bird cages, as shown by Ramos and Craig (1988). Crowding in multiple-hen cages reduces the opportunity for increased pacing behavior. Even so, the question arises as to whether the environment in crowded cages differs enough from that in single cages so that results obtained in single-bird cages are relevant. The greater "enclosure" of space which exists among hens in a group may result in less anxiety than would be seen in an individual-hen cage. Therefore, the question arises as to whether selection against stereotyped pre-laying pacing, even if found to reduce stress in that environment, would also reduce stress in multiple-hen environments.

Feather and Cannibalistic Pecking

A behavioral problem occurring especially among hens kept for table-egg production is feather loss and cannibalism. In most production settings these vices are greatly reduced by beak-trimming. However, behavioral and physiological evidence, reviewed earlier, indicated that beak-trimming causes pain which persists for weeks and perhaps even months. The Brambell committee (Bramble, 1965) concluded with reluctance that de-beaking of birds should be permitted for a limited time to control outbreaks of "vice" (feather pecking and cannibalism). However, within a short period of time they hoped that suitable strains would be available and in adequate supply so that de-beaking was no longer necessary.

Craig and Muir (1993) showed that direct selection to reduce beak-inflicted injuries could be rapid when group selection was used. They kept intact-beak hens separately by sire families in multiple-hen cages and selected sire families to produce succeeding generations on the basis of hen-days without beak-inflicted injuries for 168 days from 16 to 40 weeks of age. Selected lines achieved 75% of the possible selection differential by the second generation.

Agonistic Behavior

Gamecock matches frequently terminate in the death of the loser. Selection of winners in game breeds to sire progeny of future generations has without doubt included selection for strength, agility, stamina, and other elements of behavior necessary for that outcome. Game breeds also have accelerated blood prothrombin and coagulation times (Mohapatra and Siegel, 1969) and arteries and veins that are stronger, smaller in diameter, and thicker walled as compared with White Rocks (Steeves and Siegel, 1968). Social dominance

of males was strongly associated with fitness in small flocks of non-game breeds (Guhl and Warren, 1946). However, in somewhat larger flocks with higher densities, Kratzer and Craig (1980) found only a moderate correlation of male social status and completed matings. With even larger flocks and sex ratios similar to those used in commercial breeding flocks, Craig *et al.* (1977) found that social status of White Leghorn cockerels appeared to have little effect on frequency of mating.

Bidirectional selection for high and low social dominance ability, based primarily on the outcomes of initial pair contests in both sexes, was carried out over four generations in White Leghorns by Guhl *et al.* (1960). In a similar study Craig *et al.* (1965) selected on the basis of pair contests between males only over five generations within White Leghorns and Rhode Island Reds. Although realized heritabilities were only moderate, very large differences between high and low strains were produced by the end of the studies in strains derived from each of the three foundation stocks. In the more comprehensive study of Craig *et al.* (1965), there was no obvious decrease in additive genetic variation over generations for the selected trait. The availability of unselected random breeds from the foundation stocks and testing of both males and females by Craig *et al.* (1965) revealed that the responses were essentially symmetrical and were not sex specific. Peck-order status of selected strain hens in intermingled-strain flocks within breeds differed significantly, but the differences appeared to be of reduced magnitude as compared with relative status based on initial pair contests.

McBride (1962), noting the results of Tindell and Craig (1959), postulated that high aggressiveness in a genetic stock would have the same effect on productivity as he had hypothesized for poor husbandry (McBride, 1960). Specifically, he predicted that more aggressive strains would be under greater stress and would have lower mean performance levels and greater variances. Further, he postulated that strains with higher levels of aggressiveness would have a greater negative skew to their frequency distribution curves for productivity traits than found in strains having lower aggressiveness (McBride, 1968).

McBride's hypothesis was tested by Craig and Toth (1969) using hens of the high and low social dominance strains from the White Leghorn and Rhode Island Red strains developed by Craig *et al.* (1965). Strains were kept separately in floor pens and social instability was assured in half of the pens of each strain by randomly redistributing birds among flocks weekly. Although the unstable flocks had more fights, peck-avoidances, and threat-avoidances than the stable flocks (Craig *et al.*, 1969), there was no evidence of loss of productivity in the unstable flocks. A possible explanation advanced was that the greater frequency of agonistic interactions in unstable flocks were not necessarily associated with greater stress for all hens because the frequent changes in group membership would benefit those

individuals that otherwise would have been low in social status over the entire test period if they had been kept in stable organizations.

Mating Behavior of Males

Two bidirectional selection studies for frequency of matings by males (Tindell and Arze, 1965; Wood-Gush, 1960) indicated that large differences could be produced readily. However, a long-term bidirectional study, in which the foundation population was maintained as a control, by Siegel and his colleagues (Dunnington and Siegel, 1983) indicated complex results. It became evident early in the study that results were not symmetrical. Although the initial response to selection in the high line was near zero in the first few generations, responses then began and accumulated until at least 20 generations had elapsed. Realized heritability was 0.18 when calculated over 23 generations. In the low line very different results were obtained; a realized heritability of 0.32 was obtained through generation 11 (Siegel, 1972), but thereafter a very large additional response appeared to be associated with little change in effective selection differentials (Dunnington and Siegel, 1983). Some males failed to mate at all during the test situation. The percentage of non-maters decreased in the high line, was unchanged in the control, and increased dramatically in the low line. During generations 21, 22, and 23 the incidence was 84, 89, and 60%, respectively in the low line.

A surprising lack of correlated responses occurred in Siegel's long-term selection study and an important genotype by rearing interaction was found. Although very large differences were present among the high, control, and low lines for the trait of selection (Dunnington and Siegel, 1983), fertility in natural matings did not differ when males were present for extended periods of time or when artificial insemination was practiced (Bernon and Siegel, 1981). Females of the lines in generations 16 through 23 were tested for mating behavior, and when analyses were carried out within generations no consistent line differences were found (Dunnington and Siegel, 1983).

The question of whether males of the high-, control-, and low-mating frequency lines would respond similarly if reared with females as compared to separate sex rearing after 6 weeks of age was answered by Cook and Siegel (1974). A large genotype by rearing environment interaction was found. Rearing males of the unselected and low lines in heterosexual flocks increased the frequency of maters by about 20% whereas essentially all males of the high line mated regardless of how they were raised.

Appetite

From a controlled five-generation study of single-trait selection on body-weight gain, food consumption, and food conversion ratio (Pym and Nicholls, 1979) it was learned that all three selected lines responded with

realized heritability estimates of 0.37, 0.44, and 0.27, respectively. Of particular interest from the behavioral standpoint is that food consumption and weight gain had a realized genetic correlation of 0.71. In a further study, the similar results were reported from their 10 generations of chickens (Pym *et al.*, 1984). Therefore, selection for weight gain in broilers also involves considerable selection for appetite and *vice versa*. Food consumption records, collected in addition to body weight information, involve considerable expense in data collection but would allow selection for the economic trait of food-conversion ratio also. Presumably because of the extra expense involved and the fact that body weight and food-conversion ratio are correlated in the desired direction (-0.40 in the Pym and Nicholls study), commercial breeders have chosen to select for increased gains in body weight only. Obviously such selection has resulted in increased appetite in broiler stocks. From the considerations above, it comes as no surprise to learn (Nir *et al.*, 1978) that in comparisons of a light and heavy breed to 18 days of age, heavy breed chicks consumed only 11% more feed and failed to gain more weight than *ad libitum* fed controls of their own breed when force-fed to gut capacity as compared to light-breed chicks that consumed 43% more feed and gained 30% more body weight when force-fed to capacity as compared to *ad libitum* fed controls of their breed. Because of their huge appetites, meat-strain birds kept as broiler breeders are severely restricted in feed intake to prevent obesity of adults which would otherwise reduce health, longevity, and reproductive performance, and increase the incidence of leg problems (Decuypere *et al.*, 2010; Sandilands *et al.*, 2005; Siegel, 1984; Su *et al.*, 1999; Yu *et al.*, 1992).

Profound effects of selection for food intake and for body weight to a given age in changing appetite and associated physiological phenomena have been demonstrated by several investigators, and especially by Siegel and his colleagues (Siegel and Dunnington, 1990). The latter selected bidirectionally for 8-week body weight over more than a quarter-century. Their high and low lines diverged dramatically not only for body weight (Dunnington and Siegel, 1985) but also for specific aspects of food intake behavior (Dunnington *et al.*, 1987). Long-term selection for increased body weight apparently resulted in “genetic lesions” of brain satiety centers whereas selection for decreased body weight was offset by electrolytic lesioning of the satiety centers (Burkhart *et al.*, 1983), respectively, involving the melanocortin circuit of the brain (Hen *et al.*, 2006).

Because of poor appetite and associated low feed intake, minimal body weights and fatness required for the onset of egg laying may not be met (Bornstein *et al.*, 1984; Zelenka *et al.*, 1988). In the low-weight line described above, some females are anorexic, eating so little feed *ad libitum* that onset of lay is delayed or prevented (Dunnington *et al.*, 1984); thus over 50% of pullets did not mature in generations 25 and 26 (Siegel and

Dunnington, 1987). Zelenka *et al.* (1988) were able to induce egg production in non-layers of this line by force feeding.

Walking Problems and Tibial Dyschondroplasia

Tibial dyschondroplasia (TD), involving abnormal cartilage development in the proximal end of the tibia, occurs primarily in broiler chickens being fed *ad libitum* and the incidence is higher in males than in females. TD seriously impairs walking ability when present in advanced stages and may reduce weight gains due to the inability of birds to move freely in obtaining feed and water (Yalcin *et al.*, 1995; Whitehead, 1997; Farquharson and Jefferies, 2000; Leach and Monsonego-Ornan, 2007). It has been shown that susceptibility is genetically influenced and that selection procedures are effective in separating lines selected bidirectionally for incidence (Leach and Nesheim, 1965, 1972; Ray *et al.*, 2006; Sheridan *et al.*, 1978; Shirley *et al.*, 2003; Wong-Valle *et al.*, 1993a). Wong-Valle *et al.* (1993a) included an unselected control in their selection study and after seven generations of selection incidences at 7 weeks of age were 92.0, 5.4, and 13.2% in the high selected, low selected, and control lines, respectively.

Primary breeders are concerned about the presence of TD in their stocks as indicated by their use of an instrument which quickly and accurately diagnoses the disease in live broilers (Bartels *et al.*, 1989; Wong-Valle *et al.*, 1993a). Deleterious effects of the disease among prospective broiler breeders are minimized by weight-control management. Although results are not always consistent among studies, it appears from the selection study that body weight at 7 weeks did not differ between the high- and low-incidence lines in three of the first four generations (Wong-Valle *et al.*, 1993b). Kuhlers and McDaniel (1996) and Zhang *et al.* (1998), using data from seven generations of selection in the same stocks, indicated that TD expression and body weights at 4 and 7 weeks of age are genetically and phenotypically independent traits.

Fear-Associated Behavior

Fear is an emotional internal state which can cause physiological indicators of stress (Bronson and Eleftheriou, 1965; Lang and McTeague, 2009; Ohmura and Yoshioka, 2009; Selye, 1956). Reliable behavioral indicators of fear are difficult to establish. For example, Duncan and Filshie (1979) showed that genetic stocks that appeared to be less fearful as indicated by escape and avoidance behavior, exhibited as much fearfulness as another stock when heart rate was used as the criterion of fearfulness. Also, different behavioral indicators may yield inconsistent results when genetic stocks are compared. Murphy (1978) outlined problems in classifying genetic stocks as “flighty” and “docile”. Difficulties in classification of relative fearfulness

were also encountered by [Craig *et al.* \(1983, 1984, 1986\)](#), who found that duration of tonic immobility as a criterion of fearfulness of genetic stocks gave results that were inconsistent with those obtained when the same stocks were compared in terms of escape and avoidance behavior. Therefore, caution is appropriate in interpretation of behaviors associated with fearfulness as indicating welfare problems unless other kinds of evidence are also present.

Nervousness, feather loss, and hysteria are likely to occur in some genetic stocks, but not in others, when group size is “large” and hens have been kept for a period of several months in barren, high-density cages ([Buijs *et al.*, 2009](#); [Craig *et al.*, 1983](#); [Lay *et al.*, 2011](#) [Elmslie *et al.*, 1966](#); [Hansen, 1976](#); [Shimmura *et al.*, 2010](#);). Minimum group size associated with hysteria in susceptible stocks probably varies but the risk appears to rise rapidly when more than 12 are present. Repeated and severe episodes of hysteria are associated with reduced well-being because of resulting scratches, torn skin, feather loss, and reduction in feed consumption and egg production ([Campo *et al.*, 2001](#); [Hansen, 1976](#)).

Open-Field Activity

Open-field activity has been used as a criterion of fearfulness in rodents ([Bellavite *et al.*, 2009](#); [Overstreet, 2012](#)). The test in livestock has been recently reviewed by [Forkman *et al.* \(2007\)](#). [Faure \(1981b\)](#) selected bidirectionally for differences in open-field activity of 2- and 3-day-old chicks. The technique used was highly automated and [Faure \(1980\)](#) estimated that one person could measure between 500 and 1000 chicks per day. Large and significant differences were established between active and inactive lines over an eight-generation study. The inactive or more fearful line had a higher resting level of plasma corticosterone at two weeks and about twice as high a level at five weeks when stressed, but differences were not found at 6 or 25 weeks of age ([Faure, 1981a](#)). Also, hens of the more fearful line consumed less feed for a few days when a different kind of feeder was used.

Tonic Immobility

The phenomenon of induced tonic immobility (TI) has been known for centuries and its duration in chickens is generally interpreted as an indicator of fearfulness ([Campo *et al.*, 2012](#); [Dávila *et al.*, 2011](#); [Gallup, 1974a](#); [Jongren *et al.*, 2010](#)). That TI is influenced genetically was evident from large and moderate realized heritability estimates obtained in single-generation selection studies, respectively, by [Gallup \(1974b\)](#) with 21-day-old “Production Reds”, by [Campo and Carciner \(1993\)](#), and [Anderson and Jones \(2012\)](#) with White Leghorn hens. Also, [Craig and Muir \(1989\)](#) obtained a moderately large heritability estimate on White Leghorn hens which had been kept in

three-bird cages for over 20 weeks. That the housing environment can have a significant effect on the duration of TI has been shown by [Jones and Faure \(1981\)](#), [Kujiyat *et al.* \(1983\)](#), [Campo *et al.* \(2008\)](#), and [Lay *et al.* \(2011\)](#).

Escape and Avoidance (“Flighty”) Behavior

Consistent and significant differences in escape and avoidance behavior of hens from two genetic stocks of White Leghorns were found for each of three stimulus situations believed to cause fear ([Craig *et al.*, 1983](#)). Human observers were involved in two of the tests and a mechanical device was the primary source of stimulation in the third. In addition to stock differences, significant sire family effects, indicative of genetic variation within strains, were also found. Within genetic stocks, negative phenotypic correlations were detected between criteria used as indicators of fearfulness and feather loss; cages with more fearful hens lost more feathers presumably because of abrasion with cages and trampling and scratching. Cages held from 10 to 14 birds each. In a later study, involving hens of a random-bred White Leghorn stock kept in three-hen cages, [Craig and Muir \(1989\)](#) obtained heritability estimates ranging from a nonsignificant value of 0.08 to a significant 0.34.

Potential Problems with Selection on Behavioral Traits

[Wegner \(1990\)](#) suggests that welfare could be improved through adaptation by selecting against frustration, restlessness and stereotyped pacing before laying, and a greater tendency to sit during the pre-laying period. However, direct selection on either behavior or physiological objectives should be viewed with caution. The intended results may not be as expected. For example, [Webster and Hurnik \(1991\)](#) showed that traits associated with non-aggression, such as sitting and resting, were negatively correlated with productivity. Furthermore, the link between behavior and stress is misinterpreted. 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?

An example of problems that can occur if selection is directed at the physiological responses to stress was provided by [Gross and Siegel \(1985\)](#). They were successful in selecting lines of birds for high and low plasma corticosterone in response to social strife. Further testing ([Siegel, 1993](#)) showed that the birds did not differ in their corticosterone response to a non-social stressor. Siegel concluded that genetic selection altered the perception of the animal to stress rather than involving the GAS directly. Even worse, [Siegel \(1993\)](#) noted that the low line in a low-strife environment was more susceptible to infections from endemic bacteria and external parasites while the high

line in a high-stress environment was more susceptible to viral infections. Thus direct selection for low or high immune response would compromise the birds' welfare as measured by longevity. Also, correlated responses on productivity cannot be ignored. Birds with a high genetic potential for immunoresponsiveness must divert energy from growth and reproduction to the immune system.

SELECTION INVOLVING PRODUCTION TRAITS

Antagonisms

There is a natural antagonism between some undesirable behaviors and egg production. Research has shown that selection to improve productivity based on individual bird productivity was associated with increased aggressiveness (Bhagwat and Craig, 1977, 1978; Craig *et al.*, 1975; James and Foenander, 1961; Lowry and Abplanalp, 1972; Lee and Craig, 1981a; Tindel and Craig, 1959). From the reverse perspective, Craig (1994) has shown that selection for social dominance will reduce performance when hens are housed in a large group, but when housed singly, performance is increased. Bhagwat and Craig (1978) found that social dominance increased in response to selection for egg mass. Alternatively, direct selection for social dominance has been shown to reduce performance when hens are housed in groups (Craig, 1994). Craig *et al.*, 1965 and Craig and Toth (1969) showed that hens of White Leghorn lines selected for high social dominance had lower rates of egg production and higher mortality than did hens of the same line selected for low social dominance. In addition, Craig (1970) showed that the high-social-dominance line withstood crowing 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 cage. Craig *et al.* (1975) demonstrated that stocks selected for part record egg production, based on individual performance, exhibited more social dominance and aggressiveness.

Other associations that are relevant include the finding that a stock selected for increased productivity had greater feather loss than its unselected control when kept in three-bird cages (Lee and Craig, 1981b). Also, Choudary *et al.* (1972) compared four commercial lines of poultry and found that the line which had the highest day rate of lay had the lowest hen-housed rate of lay due to high mortality. 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 and Lee (1989) detected a strong genotype by beak-treatment interaction for egg mass per hen housed among three commercial lines. The

genotype that produced the greatest egg mass with beak treatment produced the least with intact beaks. The re-ranking was shown to be due to mortality from beak-inflicted injuries.

Results from [Emsley *et al.* \(1977\)](#) suggest that flightiness is associated with higher productivity. They estimated genetic correlations between egg production and flightiness score which showed that greater excitability was mildly associated with higher rates of lay. [Kashyap *et al.* \(1981\)](#), attempting to break the correlation between production and flightiness, selected layers using a selection index for aggregate economic gain based on genetic parameters estimated by [Emsley *et al.* \(1977\)](#), which gave positive weight to egg number and negative weight to excitability or flightiness. Nevertheless, their results showed a positive response in excitability. [Bennett *et al.* \(1981\)](#) re-analyzed those with retrospective indices and showed that genetic changes in excitability were actually greater than what would have been predicted by theory.

The Environment of Selection

[Biswas and Craig \(1970\)](#) compared White Leghorn hens of lines selected for high- and low-social-dominance strains in single-hen cages and floor pens and in crowded and un-crowded conditions in both cages and floor pens. Significant interactions between genetic stock and environment were present with reversals in ranking between environments. In the first study, high social dominance hens matured earlier and laid more eggs per hen housed when kept in single-hen cages but were later in maturity and laid fewer eggs when kept in within-strain social groups in floor pens. In the second study, changes in rank of performance were also found for age at first egg and hen-housed egg production when the strains were compared in cage and floor pen environments. High-strain hens were lower in performance than low-strain hens when compared in intra-strain groups in floor pens or in multiple-hen cages but were more or equally productive when kept in individual cages.

A significant genotype by cage-environment (single *versus* multiple) interaction for days' survival was observed in a random-bred population of White Leghorns ([Muir, 1985](#)). However, such an interaction can be caused by a change in variance or a change in ranking. [Muir *et al.* \(1992\)](#) showed that the interaction was mainly due to re-ranking of genotypes. Thus, the bird which does the best in one environment is much poorer in the other and *vice versa*.

Although there was no significant interaction for eggs per hen housed, [Muir \(1985\)](#) showed that this result was due to a quadratic relationship of surviving group size with rate of lay, whereby cages with seven surviving birds had a higher rate of lay than those with eight or nine. Estimation of genetic correlations assumes a linear relationship between genotype and

phenotype. 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.

Therefore the problem of adaptation is a joint one: the environment of selection and the traits of selection. The usual solution to eliminate, or guard against, genotype by environment interactions in production animals, is to select the animal in the environment in which it is to perform, i.e. to make the basis of selection performance in multiple-bird cages rather than in single-bird cages. However, that solution will not work in this case and could actually make the situation worse. Selecting the highest performing individual in a group environment will select for the more dominant birds.

From a genetics perspective, the environment is not constant but is constantly changing because the environment is defined not only as that of a group but also of the individuals within that group. Individual genotypes in groups are constantly changing as selection progresses, i.e. the associate effects of other genotypes in the population are involved. Thus, theory predicts that selection based on the individual will be antagonistic to group performance.

Although the studies cited indicated major effects of agonistic behavior on performance in egg-production stocks, most breeders select their elite stocks on the basis of records obtained in single-hen cages (Hunton, 1990). The genotype by housing environment interactions found in these studies emphasize the risk taken by breeders who select for egg production on the basis of hens' performance in single-bird cages for stocks to be housed commercially in social groupings.

MULTI-LEVEL SELECTION

Siegel (1989) considered adaptability to be an individual's ability to adapt to its environment. He concluded that individuals that adapt have a higher probability of contributing genes to subsequent generations than those that do not. This concept emphasizes the individual. What if an individual adapts to its environment by eating its cagemates? Survival of the individual is maximized, but what of that of the group?

There are numerous ways that performance of one individual can influence that of another. Accommodation for such interactions presents an insurmountable dilemma from the point of view of classical (non-interaction) quantitative genetic methodology. 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. The problem is to optimize production of a given genotype in a competitive environment. As a consequence of interacting genotypes, the same genotype can have different expressions in populations having different population structures.

Griffing (1967, 1977) extended selection theory to take into consideration interactions of genotypes. The conceptual biological model was extended to define the group and the usual model was extended to include not only direct effects of its own genes, but also associate contributions from other genotypes in the group. It is also of special note that Griffing (1967) shows 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.

The modern general classification of methods that use group selection or some combination of group and individual selection is now termed multi-level selection. Multi-level selection is the direct analogy of the classical index selection results based on the non-interaction model. Let Y_{kl} be the phenotype of the l th individual in the k th group (or family), then, the between and within group deviations can be combined in an index, $I_{kl} = B_1\tau_k + B_2\gamma_{(k)l}$, where $\tau_k = (\bar{Y}_k - \bar{Y}_{..})$ and $\gamma_{(k)l} = (Y_{kl} - \bar{y}_k)$ are respectively the between- and within-group deviations, and B_1, B_2 are weights. Classical group selection occurs when $B_1 = 1$ and $B_2 = 1$, within group selection results when $B_1 = 0$ and $B_2 = 1$, and multilevel selection results when $B_1 \neq 0$ and $B_2 \neq 0$.

Group Selection Experiments

There is limited, but ample, experimental evidence to support Griffing's (1967) theory. The first experiment was that of Goodnight (1985) who showed that leaf area of *Arabidopsis thaliana* would respond to group but not individual selection. The first experiment to use group selection with chickens was unsuccessful (Craig *et al.*, 1982). Craig (1994) reflected that the reason for lack of response was because he had not provided an environment in which the hidden genetic variability could be expressed, i.e. the beak trimmed hens, density was low, and only a part record was used.

The first successful experiment with group selection in poultry was initiated in 1981 at Purdue University. After four generations of group selection based on half-sister families housed initially in groups of nine, and later in groups of 12, performance was compared between the selected and control lines in six-hen cages with 387 cm² floor space per bird from 16 to 40 and 16 to 36 weeks of age, respectively, by Kuo *et al.* (1991) and Craig and Muir (1991). In the second study a stock derived from a competitive commercial stock by two generations of relaxed selection was included also. In both experiments, hens had their beaks left intact or beaks were trimmed to two different lengths.

Results of the first study showed highly significant beak-treatment by genetic stock by age interactions for hen-housed rate of lay and daily egg mass; as mortality from cannibalism increased dramatically with age in the control, but not in the selected stock, differences between the selected and

control became greater. Somewhat similar results were obtained in the second study; with intact beaks, the selected line had significantly higher egg production, egg mass, and survival than its control. However, with two-thirds of the beak removed, differences in egg production, egg mass, and survival were no longer as evident. Differences in production were presumably due to stress induced by birds with intact beaks. In comparisons between the selected and the commercially derived stock, [Craig and Muir \(1991\)](#) found that egg production was at about the same level with all three levels of beak trimming. However, the selected stock had significantly better survival when beaks were left intact. [Craig and Muir \(1991\)](#) hypothesized that kin selection favored cooperative or at least tolerant behavior as suggested by [Crow and Kimura \(1970\)](#) and concluded that selection on family means when families are reared as family groups provides a method of improving traits in which behavioral interactions influence overall well-being and productivity.

[Muir \(1996\)](#) reported that after six generations, in comparison to the unselected control, annual per cent mortality of the selected line in multiple-bird cages decreased from 68% in the initial generation to 8.8% in the sixth generation. Per cent mortality in the sixth generation of the selected line in multiple-bird cages was similar to that of the non-selected control in single-bird cages (9.1%). Annual days' survival improved from 169 to 348 days and rate of lay improved from 52 to 68%. Annual egg mass improved from 5.1 to 14.4 kg per bird. 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 single-bird cages suggests that beak-trimming of the selected line would not further reduce mortalities which implies that group selection can eliminate the need to beak-trim. An independent study by [Craig and Muir \(1993\)](#), involving different foundation stock, adds confirmatory evidence; kin-selection for days survival of intact-beak hens was dramatically increased relative to the unselected control over a two-generation study. In the [Muir \(1996\)](#) study, corresponding improvements in rate of lay and egg mass demonstrated that such changes can also be profitable.

[Craig and Muir \(1996\)](#) compared the selected and control lines to a commercial line in generation 7. Birds were not beak-trimmed and lights during the laying period were set to high intensity. Birds that died were replaced with extra birds of the same line. In single-bird cages performance, as measured by eggs per hen housed, the commercial line was superior to that of the selected line but in 12-bird cages performances were reversed. The difference in ranking was due to both an improved rate of lay and viability. In the 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.

The lines, described by [Craig and Muir \(1996\)](#), were subjected to the stress of housing at about 17 weeks, to cold stress at 36 weeks, and to heat

stress at 47 weeks of age, with results as reported by [Hester *et al.* \(1996a, 1996b\)](#). Blood physiology and egg production were monitored before, during, and after each of these periods. Packed cell volume immediately after housing indicated that the selected line 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 while the selected line did not. Egg production before, during, and after stress indicated that the selected line withstood social, handling, and environmental stress better than the control and in some case the selected 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. [Cheng *et al.* \(2001a, b\)](#) studied the same line compared with the revised selected line (line with low production and high mortality) housed in single-bird cages. At 21 weeks, the selected line had a higher CD4 to CD8 lymphocyte ratio and lower concentrations of dopamine and epinephrine and lower ratios of epinephrine to norepinephrine and heterophil to lymphocyte ratios. The bidirectional selection has resulted in the change in the immunity and the expression of the neuroendocrine systems. In social stress studies using the same lines plus a commercial line, DeKalb XL, [Cheng *et al.* \(2002, 2003\)](#) and [Cheng and Fahey \(2009\)](#) reported that the selected line has higher resistance to various social stressors than the other two lines. These changes magnify the differences in productivity and survivability observed in the lines under basal and challenged conditions.

Conclusions from Group-Selection Studies

General conclusions were summarized by [Muir \(2003\)](#) and [Muir and Cheng \(2004\)](#). Selection to reduce the major economic and welfare problems of feather pecking and cannibalism among laying hens may be successfully achieved by either direct selection against pecking injuries or by means of correlated responses associated with group (kin) selection for adaptation to multiple-hen cages as indicated by mean hen-day rate of lay and survival.

Multi-Level Selection Experiments

Although ([Griffing 1977](#)) had developed equations to determine optimal weights for between- and within-group deviations, those methods were only published in a conference proceedings and were largely unknown. Further, the results were academic at the time because methods to estimate genetic parameters associated with the model did not exist as [Henderson's \(Henderson 1975, 1984; Henderson & Quaas, 1976\)](#) mixed model methods

were just being developed and was limited to models with one random effect.

In order to estimate genetic parameters associated with the model, Muir and colleagues (Muir 2005; Muir & Schinckel 2002) recast Griffing's model in terms of a mixed model methodology, with two random effects, one for direct effect of the allele on the phenotype and another for effects on associates. Griffing termed the social or competitive effects, as "associative effects", which are now commonly referred to as indirect genetic effects (IGEs) (Agrawal *et al.*, 2001; Bijma 2010a, b; Bijma and Wade, 2008; McGlothlin and Brodie, 2009; Wade *et al.*, 2010). An important result of the mixed model approach of Muir (2005) and later (Bijma *et al.* 2007a) is that genetic variances and covariances associated with direct (σ_D^2) indirect (σ_A^2), and their covariance (σ_{DA}) could be estimated by use of REML (Patterson and Thompson, 1971). These genetic parameters, in combination with weights for the between- and within-group deviations, unified the concepts of multilevel (kin and non-kin), group, and within group selection (Bijma *et al.*, 2007a, b; Griffing, 1977). Bijma *et al.* (2007a, b) used the term g to define the strength of multi-level selection, ranging from 0 to 1 corresponding respectively to within and between group selections.

As a result of the two-component model of Muir (2005), the direct and IGEs can be directly estimated for each individual using best linear unbiased prediction (BLUP) (Henderson, 1975, 1984; Henderson and Quaas, 1976). As a result, any combination of weights could be placed on those effects resulting in optimal selection (Bijma *et al.* 2007b). Muir and colleagues (Muir, 2005; Muir and Schinckel, 2002) used this approach, in comparison with individual selection, to select for increased 6-week weight in Japanese quail housed in multiple random groups of size 16. We used a base index in which the IGEs were summed over all ($n - 1$) interacting genotypes in a group of size n , plus the direct effect known as the total breeding value [TBV, (Bijma *et al.*, 2007a, b)]. We demonstrated that selection for TBV was effective in increasing 6 week weight while reducing mortality. In contrast, individual selection did not increase 6 wk wt while having the negative effect of increasing the rate of mortality.

An interesting consequence of defining the index as the trait of selection, in terms of the TBV, is that the total heritable variance can exceed the observed phenotypic variance (Bijma *et al.*, 2007a) indicating that the response to selection can be greater than the selection differential, and explains the results we observed with poultry where the realized heritability in the initial generations were >1 . Basically the response to selection includes the heritable social environment, not just the direct effects

Muir and Schinckel (2012) examined multi-level selection for quail housed in kin groups for 43 days weight and survival in Japanese quail. We showed that multi-level selection occurs whenever BLUP selection is applied if quail are housed in groups because BLUP weights all information from

relatives, in addition to that of the individual. If families are housed in kin groups, then BLUP selection has elements of both kin and group selection. We showed that multi-level selection in kin groups was effective in reducing detrimental social interactions, and reduced mortality, which contributed to improved weight gain. Simple multi-level selection using standard animal model BLUP was easy to implement, only requiring that animals be housed in kin groups.

GENERAL CONCLUSIONS

The wild progenitors of domesticated chickens possessed a number of traits, including absence of highly specific environmental requirements that pre-adapted them to domestication. They continue to show adaptability and have responded to man's selection as seen by wide diversity among breeds and types. Nevertheless, because of large and rapid changes in housing systems and husbandry practices during the last 50 years, questions arise as to whether their welfare is compromised and whether genetic adaptation has been adequate. Criteria used in assessment of chickens' well-being include overt indicators (bodily injury, morbidity, weight loss, non-molt feather loss, death, and mean days survival of groups), physiological and immune responses, productivity, and behavior. With the exception of overt indicators, difficulties of interpretation of the various criteria lead to the conclusion that, so far as possible, multiple indicators should be used. Nevertheless, because behavior is the means by which animals attempt to cope with their environments, behavioral observations can yield valuable clues as to what is causing impaired welfare, and it is clear that behavior-related problems can themselves have major adverse consequences.

Most behavioral differences found among domesticated stocks of chickens can be shown to be determined genetically and are under polygenic influence. However, it is often difficult to know whether those differences arose because of foundation population differences, random genetic drift, adaptation to local environments, or different goals under artificial selection. The tendency to assign behavioral differences to breeds needs to be moderated when only a single strain within a breed has been used for characterization. Long-term selection studies for behavioral or economic traits that succeed have shown that profound correlated responses are likely to accompany the primary responses.

Although selection to improve behaviors associated with well-being has been effective in most experimental studies, commercial breeders are under economic constraints that may prevent their ready adoption of programs to address those problems. Behaviors that are easily identified (such as broodiness) or that leave traces (such as feed consumed) are more amenable to selection than those that must be measured by time-consuming observations (e.g., pre-lay pacing, fear-related and aggressive behavior). It has also been

noted that direct selection could be disappointing if such selection reduced efficiency of production. It has been shown that kin selection was effective in reducing a major social-behavior problem when the consequences were readily evident. Thus, cannibalistic behavior by quail was reduced by selecting individuals on the basis of weight when kin were caged together. This method is easy to implement and does not require behavior to be directly measured. The impacts of behavior are evident in performance traits. An alternative approach, also utilizing kin selection for improvement of well-being of birds in multiple-hen cages, was based on the hypothesis that when productivity is high, behavioral stresses must be reduced or absent. Thus, increased adaptation of layers to multiple-hen cages was attained by selecting families that had high egg production and survival even when kept together under conditions that would stress less-well-adapted stocks (hens with intact beaks in high-density, larger-group-size cages). That an impressive response was obtained within a few generations indicates that this approach deserves further attention commercial conditions and that eventually management practices such as peak trimming will no longer be necessary.

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