

GENETIC SELECTION FOR POULTRY BEHAVIOUR: BIG BAD WOLF OR FRIEND IN NEED?

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Abstract

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Although genetic selection for certain characteristics has compromised the well-being of domestic animals, selective breeding could and probably should be used to improve welfare. Three of the major behavioural problems facing the poultry industry are fear, feather pecking and social stress. However, these and many other behavioural traits respond readily to genetic selection. The present paper reports the results of selective breeding studies in which underlying fearfulness, sociality, feather pecking, adrenocortical responsiveness, and growth rate were manipulated in Japanese quail, Coturnix japonica, or in chickens, Gallus gallus domesticus. The apparent benefits of selection for appropriate levels of these characteristics are discussed, as are the ethical issues involved. The ultimate aims of the selection programmes and the studies described here are to improve the birds' welfare and productivity by increasing their ability to interact successfully with their physical environment, with one another, and with human beings.

Keywords: *animal welfare, corticosterone, fear, feather pecking, genetic selection, social stress*

Introduction

An animal's ability to adapt to its social and physical environment is a function of its genome as well as its previous experience. Failure to adapt can lead to chronic distress and its myriad harmful consequences. Numerous traits, be they behavioural, physiological or performance-related, can exert profound effects on the adaptability and, hence, on the welfare, health and productivity of farm and other domestic animals (Siegel 1979; Mills & Faure 1990; Jones 1996; Grandin & Deesing 1998). Many of these traits, including fear, dominance ability, socio-sexual behaviour, growth and egg production, are extremely sensitive to genetic selection (Siegel 1993; Craig & Swanson 1994; Jones 1996).

It has been argued, primarily by representatives of the poultry industry, that artificial selection for improved performance implies selection for adaptability to a particular environment and that current high levels of production demonstrate such adaptation. Conversely, it has been proposed that the changes in husbandry practices that have occurred over the last 50 years may have been too rapid to allow the animals' behaviour to evolve sufficiently as a correlate to altered growth and reproductive performance (Faure 1980); and, in addition, that selective breeding has merely modified the threshold of response to stimuli

rather than eliminating old behaviours or introducing new ones (Siegel 1993). Furthermore, performance is generally measured at the level of the group, whereas the harmful effects of stress occur at the level of the individual (Mench 1992). This means that good productivity is not necessarily a good indicator of welfare; indeed the agreement between measures of performance and of physiological stress responses in laying hens are poor (Zulkifli *et al* 1995).

The dangers of overselection for a single trait have been well documented and publicized. Numerous examples have been reported across a wide range of species. These include: the increased excitability and intractability that accompanied selection for rapid growth and high yields of lean meat in pigs and cattle (Grandin 1994); the stereotyped licking that is thought to be linked to selection for high milk production in dairy cattle (Grandin & Deesing 1998); the difficulties in calving experienced by double-muscled cattle (Appleby 1998); the breathing and hip problems caused by overselection for appearance traits in bulldogs and German shepherd dogs, respectively (Ott 1996); the abnormal maternal behaviour and pup killing that followed breeding for tameness in foxes (Belyaev 1979); the leg abnormalities, lameness and cardiovascular problems associated with selection of broiler chickens for rapid growth (Hughes & Curtis 1997); and the increased aggression and proneness to osteoporosis related to selection for early sexual maturity and egg production in laying hens (Craig *et al* 1975; Hughes & Curtis 1997). Clearly, since the majority of these effects could seriously compromise the welfare of domesticated animals, they fuel the controversy concerning the overall desirability of genetic selection. Another concern relates to the loss of biodiversity. However, before we reject the possible role of genetic change, we should consider whether or not selective breeding programmes against undesirable traits or for intuitively desirable characteristics could, perhaps, improve the welfare of farm animals.

A balanced and comprehensive treatment of the impact of genetic selection on the welfare of farm and other captive animals would more than fill the whole of this issue. Therefore, rather than attempting to paint such a broad canvas, we have chosen to present a much tighter consideration of the potential benefits of selective breeding by focusing on studies of three specific behavioural traits in two species of poultry.

Three of the major behavioural problems facing the poultry industry are fear, social stress and injurious pecking (most commonly manifest as feather pecking and cannibalism, which are often erroneously termed 'aggression'). They can all seriously harm the birds' welfare and productivity, particularly if their elicitation is sudden, intense, prolonged or inescapable (Jones 1996; 1997). In this paper, we review some of the deleterious effects that may accompany the elicitation and expression of these behavioural states, we explain why it is imperative that we reduce them, and we describe some ways in which genetic selection might help. More specifically, we focus on the results of selective breeding studies in which fear, adrenocortical stress responses, social motivation, feather pecking, and growth rate were manipulated, either deliberately or coincidentally in quail and chickens. (Unless otherwise stated, any comparisons we report are drawn from between- rather than within-line testing.) We also briefly consider some of the ethical issues surrounding genetic selection and we identify future directions for research.

Because much of the present review describes studies using divergent lines of Japanese quail, *Coturnix japonica*, it is important to emphasize the broader relevance of this species. First, it is an important agricultural animal in many countries (Baumgartner 1994; Jones 1996). For example, more than 2 million birds are bred for the table in France every year and, in Japan, the annual production of quails' eggs exceeds 18 billion. Japanese quail are also becoming an increasingly common sight in the food stores of Britain and North

America. Their small size, rapid growth, high food conversion efficiency and early maturation enable quail enterprises to be established with a low capital outlay; income is also generated rapidly. Second, and of equal importance, is the fact that not only has the Japanese quail assumed worldwide importance as a laboratory animal, but it is also considered to be a particularly useful model for behavioural, physiological and nutritional studies in chickens and other commercially important poultry species (Mills & Faure 1992; Aggrey & Cheng 1994; Jones 1996). Indeed, the Japanese quail and the domestic fowl, *Gallus gallus domesticus*, are genetically close and they can be hybridized (Haley *et al* 1966).

Fear and distress

Harmful consequences

First, the misguided belief that fear and distress are minimized (or even eliminated) by keeping poultry under the invariant and generally uneventful conditions common to most intensive systems must be corrected. Not only is it impossible to eradicate fear and frightening stimuli, but birds kept in environments where external stimulation is low may develop 'behavioural vices' and experience difficulty in coping with subsequent environmental change; indeed, they are likely to overreact even to seemingly innocuous novel stimuli (Jones 1996; 1997). Inappropriate fear responses, like panic or violent escape attempts, can cause injury, pain or even the death of a bird or its companions. For example, chickens often pile on top of and trample one another when they panic; birds at the bottom of the pile may suffocate and others might suffer cuts or broken bones leading to chronic pain, infection and physical debilitation (Mills & Faure 1990; Jones 1996; 1997). Fearfulness (the propensity to be easily frightened by a wide range of potentially alarming stimuli) is also negatively associated with productivity and profitability. For instance, birds characterized as fearful show lower egg production, eggshell quality, hatchability, growth rate, food conversion efficiency, and meat quality than their less fearful counterparts (Mills & Faure 1990; Jones *et al* 1993; Jones 1996; Hemsworth & Coleman 1998).

These negative relationships between fearfulness and productivity may reflect either chronic activation of the hypothalamo-pituitary-adrenocortical system or a series of acute stress responses. In both cases the circulating levels of adrenocorticotrophic hormone, catecholamines and corticosterone would rise. Despite their ideally adaptive role in maintaining bodily homeostasis, the corticosteroids may counter-regulate and result in reduced growth and reproductive capacity, increased fat deposition and immunosuppression (Williams *et al* 1985; Davison & Powell 1987; Zulkifli & Siegel 1995; Jones 1996). Furthermore, underlying fearfulness was increased when circulating corticosterone levels were artificially elevated for up to 11 days in laying hens by implanting them with osmotic infusion mini-pumps releasing the steroid (Jones *et al* 1988). Naturally increased levels of corticosterone are also thought to be positively associated with fear in ducks, rats and pigs and with anxiety in human beings (Schulkin *et al* 1994; Jones 1996). It is conceivable that a vicious circle could develop with fearful birds showing strong neuroendocrine responses to stressors that may, in turn, perpetuate or exaggerate underlying fearfulness.

Genetic modification of fear and distress

Although increased docility has undoubtedly accompanied the domestication process, the scope for further genetic modification of fear is amply illustrated by the considerable diversity still found within and between populations of gallinaceous birds. Indeed, despite the fear-reducing effects of domestication, many chickens, quail, turkeys or ducks still show pronounced fright reactions when they are exposed to unfamiliar objects, noises or people.

Conversely, others show much more phlegmatic responses. Such individual variation means that birds can be bred for contrasting levels of fearfulness. This approach has already met with appreciable success, at least in the laboratory. For example, Gallup (1974) found marked divergence in the tonic immobility (TI) fear reactions of domestic fowl to brief manual restraint after genetic selection for just one generation. Divergent selection of domestic chicks (Faure 1981) and of Japanese quail (Bessei 1979) for high or low locomotor activity in novel test arenas was associated with reduced fear of novelty and shortened TI responses (Faure 1981; Jones *et al* 1982). More recently, important insights into the biology of fear and stress have been gained from our studies of genetic lines of Japanese quail that have been selected in France for long (LTI) or short (STI) durations of tonic immobility (Mills & Faure 1991); and in America for exaggerated (high stress [HS]) or reduced (low stress [LS]) adrenocortical responses to brief mechanical restraint (Satterlee & Johnson 1988). Divergence was rapid and marked in both selection programmes. Quail of the HS line show corticosterone responses that are at least double those of the LS line (Satterlee & Johnson 1988) and there was a 25-fold difference in the duration of TI measured in the STI and LTI birds at the twentieth generation of selection (Faure & Mills 1998).

The manipulation of narrow, stimulus-specific responses would have very limited practical value in terms of improving adaptability. Therefore, it is important to determine whether these selection programmes had exerted only specific effects or more general, non-specific ones. We have now shown that both selection programmes have influenced the birds' overt responses to a wide range of intuitively frightening events. Thus, fear-related behaviour (silence, immobility or withdrawal) was significantly less pronounced in STI and LS quail than in LTI or HS ones when they were observed in a wide variety of alarming test situations. These included manual restraint, mechanical immobilization, an approaching human being, and exposure to an unsheltered area or to novel objects and places (Jones *et al* 1991; 1992a, b; 1994a, b; Satterlee & Jones 1995; Jones 1996; Jones & Satterlee 1996; Faure & Mills 1998). Furthermore, adrenocortical responses were markedly lower in LS than HS quail upon their exposure to a wide range of known stressors, including cold, crating, social disturbance, manual restraint, and food and water deprivation (Satterlee & Johnson 1988; Jones *et al* 1992a; 1994b). Quail of the LS line also showed lower catecholamine responses to brief immobilization than did HS ones (Satterlee & Edens 1987). A mild stressor (dropping a ball into the home cage) also elicited a lower plasma corticosterone response in STI than LTI quail (Launay 1993), but quail of both lines showed similar and very high adrenocortical responses to mechanical restraint (Jones *et al* 1994a). The absence of line differences in the latter study was thought to probably reflect a ceiling effect exerted by this powerful stressor. Indeed, the observed 7- to 20-fold increases in circulating corticosterone levels exceeded those reported when Japanese quail were kept in crates overnight (Jones *et al* 1992a) or when they were subjected to either controlled haemorrhage (Gildersleeve *et al* 1988) or the deprivation of food and water (Scott *et al* 1983). However, a recent observation (Faure & Mills 1998) that restraint elicited a greater adrenocortical response in STI than LTI quail sounds a cautionary note. Genetic drift appears to offer the only explanation for this unexpected finding.

Genetic selection for low levels of dustbathing activity in Japanese quail (Gerken & Petersen 1987) was accompanied by increased fearfulness (Gerken *et al* 1988). It could be argued that this finding illustrates the difficulty of selecting for a particular 'welfare-related'

trait without exerting adverse effects on other traits. However, because novelty is a potent fear-elicitor (Jones 1996) and since the quails' first experience of the dustbathing material occurred only at test, it is likely that the selection programme actually engendered lines of birds showing contrasting levels of novelty induced fear.

Implications for productivity

As well as its positive effects on poultry welfare, the likely economic benefits of selecting for reduced fear or adrenocortical responsiveness to stressors are also becoming increasingly apparent, not only in terms of growth, food conversion efficiency and egg production (Sefton & Crober 1976; Craig *et al* 1983; Mills & Faure 1990; Jones 1996; Jones *et al* 1997; Hemsworth & Coleman 1998), but also in product quality.

First, for example, fearfulness was positively related to the numbers of cracked and body-checked (ie retained in the oviduct) eggs in White Leghorn hens (Ouart & Adams 1982); and medium hybrid layers with a history of laying abnormal eggs were more fearful than 'normal' layers (Jones & Hughes 1986; Mills *et al* 1991). Abnormal table eggs are generally downgraded or rejected at market, with the associated economic loss, and poor eggshell quality can compromise the hatchability of eggs from breeder hens (Jones 1996). Second, stress-induced reductions in meat quality (heightened water loss, lowered pH, increased toughness) were less pronounced in STI than in LTI quail (Faure & Mills 1998). Third, not only are LS quail bigger than HS ones, but their growth rate and bone strength were less severely compromised after their sequential exposure to diverse stressors (Satterlee & Johnson 1985; Satterlee & Roberts 1990). Our suggestion that fearfulness and growth rate are negatively related, was further supported by the findings of two studies which examined the converse association between these traits. Thus, fear was reduced following bi-directional selection of White Plymouth Rock chickens for high, rather than low, body weight at 8 weeks of age (Mauldin & Siegel 1979). Similarly, Japanese quail from genetic lines that had been selected over several generations at the University of Georgia for high (HBW) rather than low (LBW) body weight at 4 weeks of age (Marks 1995) showed less avoidance of a novel object placed at the front of the home cage, less behavioural inhibition during mechanical restraint, and much shorter TI responses (Jones *et al* 1997). The plasma corticosterone response to brief mechanical immobilization was also lower in HBW than LBW quail (Jones *et al* 1997).

Collectively, the above findings are particularly encouraging. Apart from demonstrating the value of model species, they clearly show that selection based on one fear behaviour, one physiological response, or one production index affected the birds' reactions to a wide variety of stressful stimuli. Although all three selection programmes were carried out independently, the general similarities across the resultant lines in the direction of behavioural and physiological divergence suggest that selection may have influenced either a common underlying characteristic, perhaps fearfulness, or a set of closely associated ones. This apparently common genetic link provides a platform for future analysis. For instance, given the current rapid advances in poultry genome mapping (Burt *et al* 1995), it might facilitate the search for the genes regulating fear and distress, particularly if the quail genome is mapped. Potential practical benefits might then include 'the systematic introgression of beneficial genes into commercial lines and marker-assisted selection to either maintain or remove specific gene alleles' (Burt *et al* 1995). The ethical issues surrounding the use of transgenic approaches are briefly discussed below.

Sociality

Contact with their own species is an integral part of all animals' lives at some time or other. However, the amount and type of social contact that an animal seeks, as well as its behavioural and physiological responses to social encounters, are likely to be governed by its underlying levels of sociality (motivation to be with companions). This behavioural characteristic exerts a powerful influence on all aspects of social cognition and interaction, particularly in precocial avian species like chickens and quail. For example, it can affect affiliation, attachment, aggression, sexual behaviour, social stability, and responsiveness to social disturbance (McBride *et al* 1969; Mills *et al* 1993; Jones 1996; Burns *et al* 1998). Chickens and quail would normally live in small family groups or in larger mixed ones with a stable social structure. However, many farming systems impose 'unnatural' conditions on the birds, such as high population densities, confinement in very large single-sex or single-age groups, or the alteration of group membership (Jones 1996). Confinement in inappropriate social environments, or the disruption of established ones, are potent stressors which can damage health and productivity and lead to the development of harmful behavioural states, such as aggression and depression (Mills & Faure 1990; Jones 1996). A mismatch between a bird's underlying sociality and its social environment could cause welfare and performance problems. Therefore, its genetic modification could be beneficial.

Consequences of selection for contrasting sociality

Mills and Faure (1991) describe two genetic lines of quail which have been selected for low (LSR) or high (HSR) levels of social reinstatement (SR) behaviour in a treadmill apparatus when the goal box contains conspecific chicks (Faure & Mills 1998). Each chick was tested individually at approximately 7 days of age and an index of its SR behaviour was calculated by subtracting the time it spent at the end of the treadmill opposite the goal box from the distance it ran to maintain contact with its companions. Tonic immobility was also measured in each chick and, in order to reduce the risk of co-selection for fear and sociality, a further value based on the deviation of each individual SR index from the regression line for TI was used as the selection criterion (Mills & Faure 1991). Selective breeding yielded extremely rapid, significant and asymmetrical changes in SR behaviour. Marked differences were apparent in the first generation, and, after 26 generations of selection, the (mean \pm standard deviation) SR indices were 1092 ± 675 in HSR quail, 134 ± 288 in controls, and -26.9 ± 98 in LSR birds. The absence of any overlap between the standard deviations of the SR index calculated in HSR and LSR birds from the tenth generation onwards suggests that these two lines have become genetically distinct.

We now know that the selection programme has exerted a powerful effect on underlying sociality. For example, whereas sudden isolation caused persistent behavioural agitation (walking, jumping, distress vocalization) for at least 72h, as well as marked, though transient, adrenocortical and leucocytic stress responses in HSR quail, their LSR counterparts were virtually unaffected (Mills *et al* 1993). Furthermore, quail of the HSR line showed greater social proximity when they were observed in both familiar and unfamiliar environments than did LSR ones (Launay *et al* 1991; Francois *et al* 1997), even when the maintenance of social contact compromised their access to food and water (Francois *et al* 1998). Social facilitation of feeding was more pronounced in HSR quail (Faure & Mills 1998) which also showed more socio-sexual behaviour and better copulatory efficiency (higher intromission rates and fewer misdirected mounts) than LSR birds (Burns *et al* 1998). The latter finding is particularly interesting because it demonstrates that selection had

affected a behaviour (mating) which was not even in the birds' repertoire at the time that the selection index was measured.

It was also important to establish that selection for low or high sociality had not compromised the birds' ability to make social discriminations, which might result in inappropriate social encounters and thereby harm the birds' welfare. It now appears that selective breeding has exerted only a weak effect on this characteristic – and then only in LSR quail. First, quail of both genetic lines showed strong species-specificity of social reinstatement behaviour in the treadmill apparatus: they ran to maintain contact with other quail but not with Guinea fowl, *Numida meleagris*, or domestic chicks (Mills *et al* 1995). Second, both LSR and HSR quail were able to discriminate between familiar cage mates and strangers in a two-choice runway test; they showed a clear preference for cage mates (Jones *et al* 1996). Third, regardless of whether stimulus birds were presented singly or in small groups in goal boxes at opposite ends of a runway, HSR quail approached conspecifics from the same rather than a different genetic line sooner and more often and spent longer near them than did LSR birds (Carmichael *et al* 1998). Like HSR quail, more LSR birds moved first towards same-line birds – but they did so only when given a choice between individual birds and they showed no other social preferences in either test situation (Carmichael *et al* 1998).

Implications for welfare and productivity

Because sociality is such a basic motivational system, it is likely that its underlying levels could also be modified by genetic selection in other commercially important species of poultry. Thus, as well as improving our understanding of the biology of social stress and social behaviour, systematic comparisons of the behavioural and physiological responses of LSR and HSR quail could help us to assess the potential value of selection for this characteristic. Conceivably, selecting for the level deemed appropriate for particular housing conditions (eg small or large flocks) might improve welfare by increasing the birds' ability to adapt to that social environment and, thereby, reducing the degree of social disturbance and distress. For example, it has been suggested that high- rather than low-sociality birds might be better suited for housing in the large flocks commonly used in industry (Faure & Mills 1998), although a report of more frequent fighting among HSR than LSR quail (Magnolon 1994) sounded a cautionary note. Of course, the latter observation might merely reflect the greater social proximity maintained by HSR quail, and hence the increased opportunity for fighting, rather than any direct effect of selection on aggressiveness.

Breeding a more socially adaptable bird is also likely to improve productivity by allowing the physical resources that would otherwise be required to cope with social disturbance and other environmental stressors to be used for growth, food conversion or egg production. Encouragingly, 2-day-old broiler chicks from a standard commercial line that negotiated a T-maze rapidly (in < 25s) in order to reinstate social contact, subsequently put on more weight than did their slower (in > 75s) counterparts – both in laboratory conditions (Marin *et al* 1997) and at a commercial farm (Marin *et al* 1999). We have since shown that sociality (measured in terms of runway responses and home-cage proximity) was greater (Jones *et al* 1999), and that adrenocortical responsiveness to a partial water immersion stressor was less pronounced (Marin & Jones 1999), in chicks that negotiated the T-maze quickly than in the slower ones. Thus, better growth in the more sociable 'quick' chicks might reflect the fact that they can devote more of their bodily resources to growth rather than to responding to social stress. This simple, rapid behavioural test may represent a valuable and non-invasive selection criterion for future breeding programmes for meat-type chickens.

Injurious pecking/aggression

Aggression is not thought to be the cause of feather pecking (FP) and cannibalism. However, in line with most industry usage, aggression is defined here as all forms of potentially injurious pecking, particularly feather pecking.

Deleterious consequences of feather pecking

Feather pecking (FP), which consists of pecking, pulling at and removing the feathers of other birds, is a potentially catastrophic phenomenon for several reasons. First, when reared in cool climates, birds with few feathers lose heat faster, have greater energetic needs, and, therefore, cost more to feed (Tauson & Svensson 1980). Second, not only might birds be injured when they are pecked but the associated feather loss increases susceptibility to injury, especially if panic reactions result in trampling and clawing (Mills & Faure 1990; Jones 1996). Third, FP sometimes leads to cannibalism; birds can be literally pecked to death if this occurs (Appleby *et al* 1992). Indeed, one of the main obstacles to the widespread adoption of putative, welfare-friendly, alternative systems, like free-range, is the greater prevalence of cannibalism in such systems than in battery cages.

The remedial measures currently used by the poultry industry have associated welfare problems. For example, although beak trimming is generally effective in reducing feather damage and mortality due to FP and cannibalism, the procedure can cause chronic pain and compromise usage of the chicken's most versatile appendage (Gentle 1986), particularly if carried out on birds older than 10 days (Gentle *et al* 1997). Feather pecking is also reduced by keeping the birds under very low light intensities – but this practice impoverishes the visual environment and it can cause eye abnormalities, such as dim-light bupthalmos¹ (Manser 1996).

Causes of feather pecking

There is no general consensus concerning the precise causal mechanisms underpinning the development of FP, but there is increasing acceptance that the process is likely to be multi-factorial. For example, increased social aggression and FP appear to be correlated responses to selection for accelerated sexual maturity and increased egg production (Craig *et al* 1975). Furthermore, because poultry breeders often measure productivity in individually caged hens, the potential effects of agonistic encounters and of social stress are disregarded (Muir 1996). Thus, in laying hens, increased aggression may at least partly reflect selection in such a non-commercial (non-competitive) environment. The elicitation and expression of FP is also thought to be sensitive to a number of other behavioural traits and states. Damaging pecking has been associated with, or attributed to, fearfulness – because fear was more pronounced in groups of hens showing feather damage (Hughes & Duncan 1972; Quart & Adams 1982; Wechsler *et al* 1998) and because Red Junglefowl, *Gallus gallus spadiceus*, characterized as high feather peckers were more fearful than their low-pecking counterparts (Vestergard *et al* 1993). However, this relationship may be one of effect rather than cause (see below). It has also been suggested that FP is positively related to social status (Hughes & Duncan 1972; Vestergard *et al* 1993) and that it might reflect redirected ground pecking and foraging (Blokhuis 1986) or misdirected dustbathing (Vestergard *et al* 1993). In line with most other researchers in this area we believe that many or all of the above factors, as

¹ An abnormality characterized by loss of corneal convexity. It may be accompanied by varying degrees of cataract and retinal detachment.

well as nutritive ones, may influence the development and expression of FP and cannibalism.

Strain comparisons

The widely recognized existence of individual and strain differences in the incidence of FP implies a strong genetic component and, therefore, a probable sensitivity to selective breeding. However, not only do we need to improve our understanding of the internal factors governing the expression of FP but we must also determine its relationships with other important welfare and production traits before recommending any selection programmes. Comparisons between chickens from two genetic lines of layers that are coincidentally predisposed to show low (LP) or high (HP) levels of feather pecking are already yielding useful insights. For instance, despite the proposed link between FP and fearfulness described above, reports that tonic immobility (TI) durations were lower in LP than HP birds at 14 weeks of age (Blokhuys & Beutler 1992) but not at 68 weeks (Blokhuys & Beuving 1993) suggested that any such relationship was labile. Furthermore, our findings that there were no line differences in timidity at 1 week (Jones, Korte & Blokhuys unpublished data) or in TI at 5 weeks of age (Jones *et al* 1995) suggest that increased fearfulness might be a consequence of FP rather than a cause. Interestingly, whereas LP chicks showed high levels of social reinstatement behaviours, eg running, jumping and peeping, when they were suddenly isolated, HP birds made virtually no attempts to regain contact with their companions (Jones *et al* 1995).

A recent, longitudinal study revealed that LP chickens traversed a runway faster than HP ones in order to reach conspecifics regardless of age at test (Jones, Korte & Blokhuys unpublished data). This finding further supports the suggestion that underlying sociality is greater in LP than in HP birds. Furthermore, HP hens showed active coping responses, such as struggling during manual restraint, whereas LP hens reacted passively and showed a greater adrenocortical response (Korte *et al* 1997). Collectively, these findings suggest that low sociality and an active coping style might be associated with the development of FP, at least in these lines. However, although such associations may provide useful indicators of influential behavioural states, and thereby guide the development of large-scale studies, some caution must be exercised because loose associations found within a line or between two lines may be merely random.

To determine whether the observed correlations among different traits are specific to a particular strain or if they represent more general relationships we clearly have to measure the traits in a number of different lines. Taylor (1976a, b) and Taylor and Hnizdo (1987) formalized this concept and showed that precise estimates of the between-strain phenotypic and genetic correlations could be obtained with relatively small total numbers of observations (100–150) if the number of breeds measured was maximized (to at least 25). Assessing behavioural traits in this number of animals is quite feasible and we are currently pursuing just such an experiment in order to identify the motivations underlying FP and cannibalism.

Large-scale selection programmes are expensive to conduct and commercial poultry breeders generally perform selection in only one type of environment (cages). In many cases this does produce animals which perform well in a number of different production systems – but there is evidence for important genotype x environment interactions in laying hens (Horst 1985). Details of selection programmes are commercially sensitive, but we understand that there has been a trend to emphasize the performance testing of individuals in single-bird cages rather than progeny testing (eg reciprocal recurrent selection) in multiple-

bird cages. While this procedure gives rise to faster annual genetic progress for egg production, it introduces the risk that the birds may be less well adapted to housing in commercial systems of production. For example, competitive pressure on animal breeding companies to maximize egg production per unit time has resulted in earlier sexual maturity in pullets. This may have unwittingly exacerbated at least one of the problems of selection on individual performance: increased social aggressiveness is associated with selection for early sexual maturity (Craig *et al* 1975; Bhagwat & Craig 1977).

Muir (1996) reported that selection based on family performance in multiple-bird cages was ultimately successful in developing a line with high productivity and low mortality (although initial losses were high). The selected line was characterized by an increased resistance to several stressors (Hester *et al* 1996a, b), by a reduction in beak-inflicted injuries, and by improved feathering (Craig & Muir 1996a), although there was little change in other behavioural activities (Craig & Muir 1996b).

Clearly, a greater understanding of correlated behavioural responses to selection for productivity is urgently required, particularly when selection is carried out in non-commercial environments.

Stability of selection responses

Each characteristic of an animal may be affected by different genes throughout ontogeny as well as by environmental variation. For example, dominance rankings do not remain stable in quail during their ontogenetic development (Nol *et al* 1996). Therefore, a potential problem with selection for a particular trait is that the response measured may be specific to the age at test. Encouragingly, line divergence in the duration of TI fear responses was still evident at 10 weeks of age in quail of the STI and LTI lines (Faure & Mills 1998) and as late as 30 weeks in the LS and HS birds (Jones & Satterlee 1997). Furthermore, quail of the HSR line showed consistently higher levels of social reinstatement behaviour on the treadmill than did those of the LSR line regardless of whether they were tested at 1, 2, 4, 6 or 10 weeks of age (Launay *et al* 1993). The fact that line differences in fearfulness and sociality did not disappear with increasing age suggests that the selected traits are stable.

Environment and experience

We wish to emphasize that we do not simply advocate a genetic approach to the solution of welfare problems. Development of the birds' behavioural and physiological capabilities is shaped by their environment and experience as well as their genome. Indeed, manipulation of environmental dynamics can exert profound effects on the organism (Denenberg 1962; Jones 1996). Much of the growing literature concerning the various resources provided in alternative housing systems for laying hens would be relevant here but, for the sake of brevity, we will focus on just two laboratory manipulations.

First, for example, enriching the home environment of young chicks and laying hens with a variety of novel objects, pictures and/or intuitively desirable resources (dustbathing material, pecking devices etc) significantly reduced fearfulness (Broom 1969; Jones & Waddington 1992; Reed *et al* 1993; Jones 1996; Clarke & Jones in press), as well as feather pecking (Vestergaard *et al* 1993), depopulation trauma (Reed *et al* 1993), aggressiveness and mortality (Gvoryahu *et al* 1994) – at least in laboratory studies. It is also interesting to note that environmental enrichment reduced fearfulness in both the STI and LTI lines of quail

(Jones *et al* 1991). The latter finding emphasizes the importance of considering genotype x environment interactions. It also illustrates the scope for the environmental manipulation of fearfulness in genetic lines that have already been subjected to substantial selection pressure for contrasting levels of this characteristic. From an economic viewpoint, other beneficial effects of enrichment include improved growth, food conversion efficiency, and egg production (Gvoryahu *et al* 1990; Nicol 1992; Jones 1996).

Second, handling chickens regularly – or even just allowing them to see people – also reduced their otherwise intense fear of humans (Jones 1993; Eddy & Gallup 1994; Jones 1995) as well as the incidence of aggressive interactions (Collins & Siegel 1987); and it improved egg production (Barnett *et al* 1994). The fact that mere visual contact had such positive effects is particularly encouraging because such an approach is eminently practicable.

Given the above effects, we strongly recommend the adoption of an integrated approach rather than a purely genetic one.

Ethical issues

Many people would question the morality of changing the background genomes of animals to fit them to what they see as the wholly unnatural environment of intensive husbandry systems. However, there are a number of crucial points we must recognize when considering the rights or wrongs of genetic selection. First, the domestication process itself has been one of selective breeding; this point applies equally to farm, laboratory and companion animals. More specifically, domestication must have exerted a substantial effect on behavioural traits in chickens ever since they were first kept by Neolithic man. Second, it is important to make the distinction between selective breeding (where man selects the parents of the next generation and where progress is determined by the duration of inter-generation intervals) on the one hand, and genetic engineering/modification (where development can be much more rapid) on the other. The latter procedure involves techniques such as introduction of embryonic stem cells in blastocysts, pronuclear injection, and retroviral infection, which may themselves have as yet poorly understood implications for animal welfare (Appleby 1998). In this respect, although rapid and intuitively desirable progress could perhaps be made by the introduction or deletion of beneficial and harmful genes, respectively, it would be advisable to carefully monitor the behaviour and physiology of those animals and their progeny. Third, increasing numbers of welfare scientists are recognizing the value of selecting against behavioural traits associated with welfare problems. For example, rearing chickens in 'welfare-friendly' extensive systems, like free-range, has associated problems, such as the increased risk of sudden outbreaks of FP and cannibalism. There is now growing agreement that genetic selection against the predisposition to show FP probably represents the most effective solution to this problem. Finally, we share some of the ethical concerns about genetic selection. Consequently and ideally, we advocate using selection for desirable traits or against undesirable ones as part of an integrated approach that includes environmental enrichment and improved husbandry (see above). The overall aim is not simply to fit the birds to a particular environment but, by increasing their ability to interact successfully with the physical and social environment, to make them better able to adapt to whatever husbandry systems are considered appropriate. This, in turn, is likely to improve their welfare, management and productivity.

Animal welfare implications

Poor welfare can undoubtedly be a consequence of genetic selection for certain characteristics. Equally though, selective breeding could – and probably should – be used to improve animal welfare. We argue that selection for reduced fearfulness, for appropriate levels of sociality, and against feather pecking and cannibalism might provide powerful, welfare-friendly solutions to some of the main behavioural problems currently facing the poultry industry. Such selection is also likely to yield economic benefits.

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