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Domestication, selection, behaviour and welfare of animals — genetic mechanisms for rapid responses

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Abstract

Increased production has been the major goal of animal breeding for many decades, and the correlated side-effects have grown to become a major issue in animal welfare. In this paper, the main genetic mechanisms in which such side-effects may occur are reviewed with examples from our own research in chickens. Pleiotropy, linkage and regulatory pathways are the most important means by which a number of traits may be affected simultaneously by the same selection pressure. Pleiotropy can be exemplified by the gene PMEL17 which causes a lack of black pigmentation in chickens and, simultaneously, predisposes them to become the victims of feather pecking. Linkage is a probable reason why a limited region on chicken chromosome 1 affects many different traits, such as growth, reproduction and fear-related behaviour. Gene regulation is affected by stress, and may cause modifications in behaviour and phenotype which are transferred from parents to offspring by means of epigenetic modifications. Insights into phenomena, such as these, may increase our understanding not only of how artificial selection works, but also evolution at large.

Keywords: *animal welfare, chicken, gene expression, linkage, pleiotropy, tameness*

Introduction

During the previous decades, breeding for increased production has been the chief goal for animal agriculture. It has been estimated that average production levels have increased by more than 85% since 1960 and, in conjunction with this, many production-related diseases and disorders have increased; for example, leg problems in fattening pigs, mastitis and lameness in dairy cattle, and locomotory and circulatory problems in fast-growing broilers (Rauw *et al* 1998). Hence, breeding animals with a large emphasis on increasing production may be associated with risks for animal welfare. To be able to maintain, and even increase, production levels in farm animals in the future, without jeopardising welfare, there is a need for increased biological knowledge concerning the mechanisms behind side-effects on traits which have not been explicitly selected for. For example, increasing the frequency of alleles which cause faster growth may, at the same time, cause a modification in developmental, behavioural, physiological or immunological traits under the influence of the same genes.

Behaviour is a central part of the mechanisms allowing animals to adapt to their social and physical environments (for example, through learning and forming social systems). Therefore, selection side-effects on behaviour may have serious effects on the welfare of animals. If genes that are under selection pressure during breeding for increased production simultaneously affect behaviour, the adaptive capacity of the selected animals may be affected.

Mechanisms of correlated responses

Selection for desirable traits in animals has been ongoing for several thousand years, and the process of domestication offers a model for evolution which makes it of general biological interest to investigate correlated mechanisms. There is limited experimental research on the evolution of different traits, including behaviour, during domestication. However, there is sufficient evidence, based on comparative studies of domestic stocks and their wild ancestors, to identify a number of typical domestication changes, which can be summarised under the concept of 'the domesticated phenotype' (Belyaev *et al* 1984; Vasilyeva 1995). This includes external morphological changes, such as altered fur and plumage colours (mainly an increased frequency of white and spotted colour morphs), changes in body size and growth pattern, and changes in relative size of different body parts (including brachycephaly; the shortening of skulls, and chondrodystrophy; the shortening of legs) (Clutton-Brock 1999). Furthermore, there are usually internal morphological changes, such as an overall decrease in brain size, and modified relative sizes of other internal organs, for example intestines (Jackson & Diamond 1996; Kruska 1996), and physiological changes, such as changes in endocrine responses and reproductive cycles (Setchell 1992; Kuenzl & Sachser 1999). Of course, there are also behavioural changes, such as reduced fear, increased sociability, and reduced anti-predator responses (Hedenskog 1995; Johnsson *et al* 1996; Price 1997). These cascades of selection responses have led some researchers to suggest that domestication may actually be a single-gene process (Stricklin 2001).

Behavioural differences between laying hens and red junglefowl (*Gallus gallus*)

Chickens are excellent models for studying these aspects of behaviour. In semi-natural enclosures and in a variety of controlled behaviour test situations, several aspects of behaviour would appear to differ between laying hens and their ancestors (Schütz & Jensen 2001; Schütz *et al* 2001). Firstly, layers are generally less active, showing a reduced foraging and exploratory behaviour. Secondly, they have a less intense social behaviour, expressed as a lower frequency of social interactions. Thirdly, they have a modified and less intense anti-predatory behaviour in tests where they are exposed to predator models and, fourthly, there is a modified foraging strategy, where layers are less inclined to explore unknown food sources. Junglefowl (*Gallus gallus*) are also generally more exploratory and appeared to adapt better to sudden changes in environmental conditions (Lindqvist *et al* 2002). Furthermore, we found indications that layers may have greater difficulty forming and remembering social relationships (dominance-subordinance) than junglefowl, since the aggression level after regrouping is generally higher in layers and persists for a longer period of time (Väisänen *et al* 2005). Together, the results indicate an adaptation to the domesticated environment on the part of laying hens, and signs of a negative effect on social adaptability.

Gene localisation and animal welfare

QTL (Quantitative Trait Locus) studies have enabled us to identify, amongst others, genes involved in plumage colouration variation in fowl. Unexpectedly, this had an important bearing on chicken welfare. Feather-pecking is one of the most important welfare-related behavioural problems in modern egg production, where birds peck at and pull out the feathers of other individuals in the same group, and it is common in junglefowl, as well as being more frequent in females than in males (Jensen *et al* 2005). Examining both the performance of feather pecking and the resulting plumage condition in F2 birds of a cross between red junglefowl and White Leghorn layers, we found a significant QTL for plumage condition, indicating the risk of being the victim of the behaviour (Keeling *et al* 2004). This QTL coincided perfectly with the PMEL17-locus, and homozygotes for the wild genotype were significantly more vulnerable to being victims, whereas heterozygotes were almost as protected from the behaviour as the homozygous mutant (both heterozygote and homozygote mutants were largely white). Furthermore, the risk of being victimised apparently increased when the wild-types were more common in a cohort. Social behaviour may partly explain why they are more vulnerable to pecking (Nätt *et al* 2007). It remains to be investigated how this gene and its mutation may affect the brain and behaviour of chickens, since it is not thought to be expressed in the brain.

Gene expression

The orchestration of gene expression during development may be an important part of developmental biology and domestication (Saetre *et al* 2004), and such patterns of expression differences may be affected by mutations in regulatory genes (Andersson & Georges 2004). In such a scenario, a single nucleotide mutation may have huge effects on a variety of phenotypic traits, and such mutations may therefore underlie the rapid and complex phenotypic changes observed during domestication. To analyse effects caused by changes in gene expression, we have used a cDNA (cDNA = complementary DNA, ie the gene sequence without introns) microarray containing over 13,000 expressed sequence tags (EST; roughly corresponding to genes).

Using this microarray, we recently demonstrated that stress-induced phenotypic effects in one generation may be both phenotypically and genetically transmitted to the next generation (Lindqvist *et al* 2007). Domestic chickens raised under mildly stressful conditions (unpredictable light-rhythm) had an impaired spatial learning capacity which was inherited by their unstressed offspring. Furthermore, the stress-induced changes in gene expression pattern in parents' hypothalamus was also transferred to the chicks. This indicates that previously unknown mechanisms may speed up adaptation to stressful environments. Since the effects were not seen in red junglefowl, the results further suggest that there may have been a selection for adaptability during domestication.

Animal welfare implications

The results discussed in this paper indicate that three different mechanisms may act simultaneously in creating correlated responses to selection: pleiotropy, linkage and common regulatory pathways. When animals are selected for production traits mainly, this may cause unwanted side-effects, of which many have been extensively documented in several species (Rauw *et al* 1998). Some of these side-effects affect production, such as reduced fertility in fast-growing broilers (Rauw *et al* 1998), and are likely to be the target of counter-selection. In other cases, the side-effects may be related to less-obvious traits which may nevertheless have a strong welfare aspect. Our own studies indicate that selection for increased production in leghorns may have influenced the general coping capacity of the birds (Väisänen *et al* 2005). Furthermore, we found that feather pecking individuals in an F2 generation of a junglefowl × Leghorn intercross grew faster, had weaker bones and became sexually mature earlier (Jensen *et al* 2005). Since selection in chickens has been strong on early onset of laying and on utilising calcium for egg production, this may have caused an unintentional selection for increased feather-pecking.

Further understanding of mechanisms such as these may help us in the future to select animals with genotypes which are not only high producing, but also associated with traits which are beneficial for animal welfare.

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