# MEASURES OF DEVELOPMENTAL INSTABILITY AS INTEGRATED, *A POSTERIORI* INDICATORS OF FARM ANIMAL WELFARE: A REVIEW

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**Abstract** *Animal Welfare 2003,* ***12***: 535-540

*Developmental instability, of which fluctuating asymmetry is the most commonly used and recommended measure, has recently been claimed to be an objective, integrated and retrospective indicator of animal welfare. The theoretical and empirical grounds for these claims are reviewed. In theory, carefully selected composite indices of fluctuating asymmetry are valid indicators of animal welfare in the sense that they reflect the ability of the developmental processes of an animal, with a given genetic constitution, to cope with environmental stressors. Relevant scientific experiments are scant and are mainly restricted to poultry, but they are on the increase and they largely support the application of developmental instability for assessing animal welfare. A scheme for monitoring farm animal welfare based purely on measures of developmental instability would have important advantages, but cannot be recommended yet. It cannot be ruled out that certain factors are clearly relevant to the welfare status of an animal but do not notably/proportionally affect its morphogenesis. Moreover, such a monitoring scheme would not be appropriate for applications with an emphasis on problem analysis/management.*

**Keywords**: *animal welfare, developmental instability, developmental stability, farm animal, fluctuating asymmetry, poultry*

## Introduction

Developmental instability refers to the inability of developmental pathways to resist accidents and perturbations during growth processes such that the intended phenotype is not realised. Stressors that give rise to elevated levels of developmental instability can be genetic (eg inbreeding, hybridisations, mutations) and/or environmental (eg nutritional stress, chemical pollution, parasitic infections).

There are several indices of developmental instability, such as the frequency of phenodeviants (ie unusual expressions of a trait) or the phenotypic coefficients of variation. Møller and Swaddle (1997), however, recommend the use of indices based on comparison of measurements taken from repeated elements of the same trait in the same individual in order to avoid the problem of genotypic differences. For example, one could measure deformations in the circuli in the scale morphology of fish. Measuring deformations, however, is tedious. It is usually easier to measure the right and left elements of a bilaterally symmetric trait; in other words, fluctuating asymmetry (Ludwig 1932). Moreover, as both sides of these traits develop simultaneously in the same environment, the left and right sides experience identical environmental influences. Other repeated-formation measures may not experience identical environmental conditions because of the sequential development of traits. These arguments explain why fluctuating asymmetry is the most commonly used, and the recommended, index of developmental instability (Palmer & Strobeck 1986; Møller & Swaddle 1997).

### *Fluctuating asymmetry*

Fluctuating asymmetry is defined as small, randomly directed deviations from perfect symmetrical development in bilateral traits, resulting from the inability of individuals to undergo identical development on both sides of the plane of symmetry. The frequency distributions of signed left–right character values are useful for distinguishing fluctuating asymmetry from two other types of asymmetry: directional asymmetry and antisymmetry. In the case of fluctuating asymmetry, the frequency plots centre around zero (symmetry) and are near normal — predominantly leptokurtic, in fact (Gangestad & Thornhill 1999). Directional asymmetry, however, is typified by a skewed distribution to either the left or the right side, while antisymmetry is typified by a platykurtic or bimodal distribution. Fluctuating asymmetry provides a useful measure of how well development processes cope with internal genetic and external environmental stresses during morphogenesis. It is not clear, however, whether or not the latter two types of asymmetry could also be used as indicators of developmental instability, as they have traditionally been thought of as adaptive and functional asymmetries (Palmer & Strobeck 1986, 1992).

The development of a single trait may be affected by a large number of (random) factors (Gangestad & Thornhill 1999). The correlation between fluctuating asymmetry of different traits is consistently positive but low (Polak *et al* 2002). Consequently, composite indices of asymmetry based on pooled measurements from several traits often provide a more precise estimate of developmental instability than asymmetry in a single trait (Leung *et al* 2000).

The number of applications of developmental instability in the life sciences is manifold, ranging from human medicine to pollution monitoring (Møller & Swaddle 1997). During the last decade it has increasingly been suggested that developmental instability may also be a useful indicator of animal welfare.

## Developmental instability as a measure of farm animal welfare

### *Assessing farm animal welfare*

Society puts increasing pressure on livestock producers to improve the welfare of their animals. In order to achieve this it is of paramount importance to be able to measure and monitor animal welfare accurately and objectively. Most researchers stress the importance of using a wide variety of welfare indicators, but there is no consensus about exactly which or how many parameters should be measured. These indicators may include measures of behaviour, physiology, immunology, pathology and performance. This implies that accurate assessments of animal welfare are likely to be time-consuming and expensive. Moreover, most of these parameters are influenced by a multitude of environmental factors (time of day, season, weather). In the case of on-farm welfare monitoring, it is almost impossible to account for all of these confounding factors. Finally, most of these parameters are scored in different units, so they are not easily integrated in an overall 'welfare-index'. Indeed, there is no completely objective method for determining the relative weights of the various parameters that have been measured/scored (see Spoolder *et al* 2003, pp 529–534, this issue). Using measures of developmental instability as integrated indicators of animal welfare might overcome some of these difficulties. Below we review the empirical and theoretical grounds for this claim.

### *Empirical basis*

It is only during the last decade that studies have been published in which the use of measures of developmental instability for the assessment of farm animal welfare is evaluated. Forkman and Corr (1996) noted a positive effect of wattle asymmetry of roosters and the number of eggs laid by hens mated with them. More relevantly, fluctuating asymmetry in broiler chickens is positively related to rearing density and duration of tonic immobility — a measure of fearfulness (Møller *et al* 1995). Møller *et al* (1999) have also reported positive correlations between asymmetry and leg/gait problems and greater asymmetry in chickens reared under continuous instead of changing light regimes. Chickens provided with 8 h darkness, sand, and zinc bacitracin (an antibiotic growth promoter) have lower levels of asymmetry than chickens reared under 24 h light and no sand (Stub & Vestergaard 2001). Sanotra (1999; cited by Møller & Manning 2003) found weak negative relationships between asymmetry level and the percentage of chickens that died or that were discarded at slaughter. Yngvesson and Keeling (2001) reported that both victims and cannibalistic hens are more asymmetrical than control birds. Lower levels of fluctuating asymmetry were found in a line of quail selected for increased stress resistance, as reflected by small plasma corticosterone response to restraint, than in a line selected for exaggerated corticosterone response (Satterlee *et al* 2000). Campo *et al* (2000, 2002), however, questioned the use of fluctuating asymmetry as a general tool to assess fear and stress susceptibility in chickens that have not been deliberately disturbed because asymmetry levels are not consistently associated with, respectively, tonic immobility duration and leukocyte ratio across breeds or traits. Studies on farm animals other than poultry are extremely scant and relate more to performance than to welfare.

### *Theoretical basis and issues to be resolved*

The level of developmental instability has been advocated as an objective, potentially non-invasive, animal-based measure of animal welfare (Møller *et al* 1995, 1999). Other advantages that have been reported include the predefined, inbuilt optimum (symmetry) and the negative correlations with performance traits and profitability (growth, survival, fecundity) (Møller 1999). Because of these negative correlations, taking actions to reduce asymmetry is likely to benefit both the producer (in terms of increased profit) and the animals (in terms of increased welfare) (Møller & Manning 2003).

Møller *et al* (1995, 1999) also claim that it is an integrated measure of animal welfare. Although they do not explain what they mean by this, it could be interpreted to imply that animal welfare may be measured solely on the basis of this single indicator in which the different stressors have already been integrated as they are perceived by the individual. The above-mentioned problems associated with the traditional multi-parameter approach would no longer apply and the logistic advantages would be huge. Hence, it would soon become the method of choice for most applications of on-farm welfare monitoring except, perhaps, for those that emphasise problem analysis/management (see Main *et al* 2003, pp 523–528, this issue). It is important, therefore, to investigate whether animal welfare can be determined solely by measuring the level of developmental instability.

As explained above, measures of developmental stability indicate a growing organism's ability to cope with its environment given its genetic constitution. Indeed, this is strikingly similar to the more operational definitions of animal welfare which negatively relate welfare to the effort an animal is putting into coping with environmental stressors or to the biological cost of responding (Wiepkema 1982; Broom 1986; Moberg 1996). But as well as these 'functioning-based' conceptions of animal welfare there is also the 'feelings-based' approach (Duncan & Fraser 1997). According to the latter approach, the welfare of sentient beings primarily relates to their subjective states. Consequently, measurements of welfare should be based on the animal's feelings or emotions rather than the presence or absence of indicators of reduced biological function (Duncan 1996). There are some indications that the degree of developmental stability might be affected by these more subjective states as well. Unpredictable feed restriction, for example, has a greater effect on the degree of fluctuating asymmetry in starlings than predictable feed restriction (Swaddle & Witter 1994), and fluctuating asymmetry appears to be positively related to depression in men (Martin *et al* 1999). However, the empirical evidence is far too scant at present to contend that all factors that affect welfare according to the feelings-based approach also notably (let alone proportionally) affect the degree of developmental instability, and *vice versa*. For example, acute pain is very relevant to the welfare status of an animal, but a notable (let alone a proportionate) effect of acute pain on the stability of an organism's development has not yet been demonstrated.

Another important question is whether the level of developmental instability would be a sensitive indicator of animal welfare. One might expect that relatively severe stress is required to induce notable asymmetries under farm conditions where animals often are provided with food and water *ad libitum* and have excess energy available for homeostatic buffering. However, farm animals may be particularly susceptible to the negative effects of stress on their phenotypic development for two reasons. First, domestication may relax natural selection against asymmetric individuals. Second, in order to increase productivity, farm animals have been subjected to intense directional selection which is believed to increase the level of developmental instability (Møller & Swaddle 1997). The lower level of asymmetry found in free-living junglefowl compared with domesticated chickens raised on *ad libitum* food, and in a slow-growing strain compared with two fast-growing strains, is in agreement with the above hypothesis (Møller & Swaddle 1997; Yalçin *et al* 2001). The sensitivity also depends on the growth curves of the morphological traits measured. It is conceivable that sensitivity is greatest during maximal growth and nil when the traits are fully developed. This implies that this method has little promise for measuring the welfare of farm animals once the growth processes have been completed.

Finally, I wish to note that a solid methodological framework for optimal measurement of the degree of fluctuating asymmetry in an individual or a population is still lacking. Such a framework should detail (1) how, which, and how many morphological traits should be measured in which species/strains of farm animal, (2) the 'normal' variation of fluctuating asymmetry in the population studied, and (3) the influence of 'welfare-related factors' versus 'other factors' (eg age, season) on this variation in fluctuating asymmetry.

## Conclusions and animal welfare implications

Carefully selected measures of developmental instability appear to be valid indicators of farm animal welfare in the sense that they precisely reflect the ability of the developmental processes of an animal, with a given genetic constitution, to cope with environmental stressors. This is largely supported by a limited but increasing number of studies on poultry, although some concerns about consistency across breeds and traits remain. A scheme for monitoring farm animal welfare based purely on measures of developmental instability would have important (logistic) advantages, but cannot be recommended yet. Indeed, with the evidence available at present, it cannot be ruled out that certain factors are clearly relevant to the welfare status of an animal but do not notably/proportionally affect its morphogenesis. Moreover, such a monitoring scheme would not be appropriate for applications with an emphasis on problem analysis/management.

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