Department of Physics, Chemistry and Biology

Introductory essay

# Early experiences in the chicken production and its long-term effects on behaviour

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# 1. Introduction and aim

What you experience as young have long term effects on the physiology and behaviour of the organism. Stress early in life can permanently alter the behaviour of an individual which is connected to a certain degree of plasticity in young individuals. The development of stress viewed from an evolutionary perspective indicates that it functions as the body's security system which reacts to a stimulus, consequently leading to a promoted fitness if a beneficial coping strategy is adopted. Mild forms of stress has been proven to somewhat preadapt the individual to stressful events in adulthood, while severe early stress seems to have deleterious consequences later in life on behaviour, immunology and the cardiovascular system. Proximate studies show that the HPA-axis display developmental plasticity also during the prenatal stage and is sensitive to changes in the mother's homeostasis, thereby there is an adaptability to stress already within the fetus. In poultry production, the long-term effects of stress is an important factor to consider or at least be familiar with, since behaviour and HPA-axis sensitivity can be modified both in a positive and in a negative direction due to early treatment and experience.

The aim of this essay is to discuss the stress concept and identify stressors in the chicken industry with emphasis on stressors during the perinatal phase and what the consequences early stress can have on adult behaviour and physiology. But firstly one needs to understand the physiology of stress and the difficulties to find a universal definition of stress. The Swedish production system is also described, for identifications of potential stressors.

# 2. Stress definitions

"*Everybody knows what stress is and nobody knows what it is."* These are the words of Hans Selye (Selye, 1973), by many regarded as the inventor of the stress concept. By this quote, Selye is addressing the problem in finding a universal definition of stress; there seems to exist as many definitions of stress as there are scientists working with the topic. He himself defines stress as *"a nonspecific response of the body to any demand made upon it"*. He means that the nonspecific response can be for example exposure to extreme temperatures, exercise and metabolic challenges, meaning that stress also include things we experience as positive and further claims that complete release from stress means death. In other stress definitions, you often encounter concepts in line with: "*threat to homeostasis*" (Moberg and Mench, 2000) or "*state of disharmony*" (Chrousos and Gold, 1992), and one can also see that the definition of stress varies depending on which field it is used in (ethology, biomedicine, physiology etc.). Some also defines stress without adding either positive nor negative value to it, for example *''stress is a state when the hypothalamo-pituitary-adrenal (HPA) axis is activated with increased secretion of glucocorticoids in response to a stressor''* (Cockrem, 2007).

In many of the examples of definitions above, stress have a negative sound to it and indicates or focuses at its deleterious nature. But also a stimulus we perceive as positive (exercise, arousal, excitement) activates the HPA-axis and some mean that is therefore to be interpreted as stress. Due to the many definitions (and in many cases - lack of definitions) a fairly recent attempt has been made to redefine and clarify the concept of stress and its definition. Koolhaas et al. (2011) mean that negative events where responses that exceed the adaptive capacity in the organism should be regarded as a stressor.

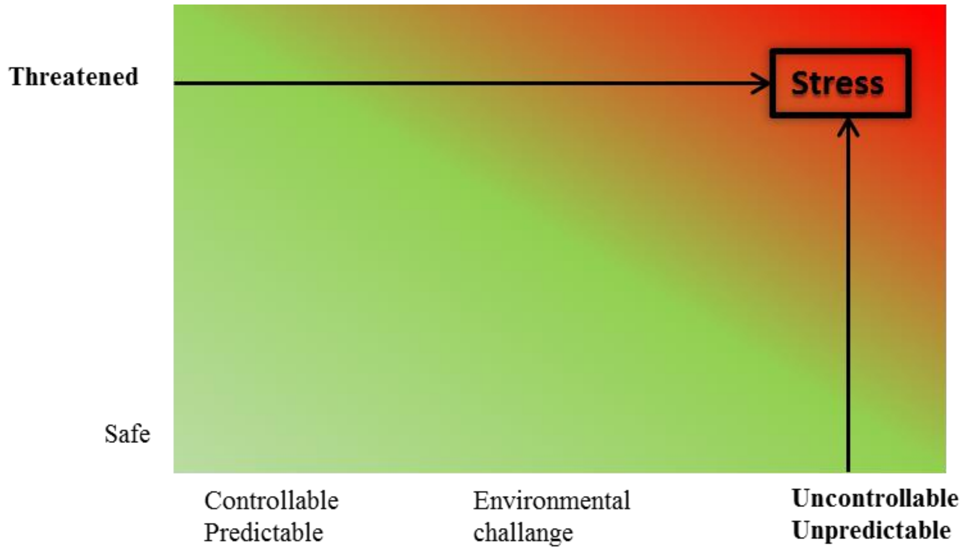


Figure. 1. Suggestion of stress definition restrictions inspired by Koolhaas et al. (2011). During controlled and safe circumstances (low left corner), the stress concept should not be used because the state belongs to normal support of behaviour. Stress as a term should rather be used during uncontrollable/unpredictable and life threatening situations (right top corner).

Further the authors state that *"demands that fall within the adaptive capacity belong to the realm of the normal physiology of behaviour and therefore should not be regarded as stressors".* The authors thereby suggest that the negative sound to stress remains, and that changes in the homeostasis due to for example positive events or emotions should not be regarded as stressors but rather as normal physiological mechanisms (fig. 1). A background to this suggested redefinition was, amongst other, work performed by Fish et al. (2005). In a resident intruder test in male mice, both the winning and the loosing mouse had the similar heart rates and levels of cortisol in the blood, however heart rate decreased faster and the cortisol was metabolized at a higher rate in the dominant mouse (Fish et al., 2005).Viewing physiological variables, both mice were clearly stressed, however the dominant mouse regarded the attack as a reward and thereby, according to de refinement of the stress definition above, not considered a stressor.

## 3. Stress physiology and behaviour

The main neurohormonal pathway that is activated in response to a stressor is the hypothalamic-pituitary-adrenal-axis (HPA-axis, fig. 2), causing a cascade of hormonal responses, releasing glucocorticoids, adrenaline and noradrenalin to the blood. The glucocorticoid cortisol (or its equivalent corticosterone) is a steroid hormone produced by the adrenal glands. When exposed to stress, (but also to for example physical exercise, arousal or illness), the hypothalamus releases corticotropine-releasing-hormone (CRH) to the pituitary gland, which in turn excretes adrenocorticotropic hormone (ACTH), signaling to the adrenal glands to release cortisol.

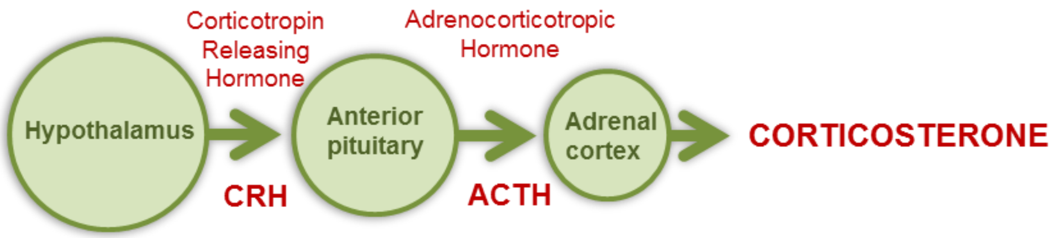


Figure 2. The hormonal pathway constructing the HPA-axis. A perceived stimulus initiates the secretion corticotropine releasing hormone (CRH) from the hypothalamus, stimulating the anterior pituitary to release adrenocorticotopic hormone (ACTH). This induces corticosterone/cortisol release from the adrenal cortex into the blood stream.

The stress concept is sometimes also classified in order to specify and pinpoint the stressors' severity. It can be classifications as mild, moderate and severe stress. Further discriminations within the stress levels have been introduced, such as the terms "distress" (Lay Jr, 2000), which indicates the harmfulness of stress. As explained by Moberg (Moberg & Mench 2000), "distress" can be induced by both a brief but acute event and long-term stress. Distress arises when the stress affects the animals' well-being to such a critical point that functions like growth and reproduction are impaired. He uses ovulation as an example, which can be interrupted by severe stressors like restraint, transportation and isolation.

The consequences of negative stress have deleterious effects on the organism. Examples are impaired immune function (O'Mahony et al., 2009; Solomon et al., 1968), deteriorated growth (Satterlee et al., 2000) reproduction (Shini et al., 2009), altered foraging behaviour (Lindqvist and Jensen, 2009), cognitive functions (see for example Lindqvist et al. (2007)and behavioural abnormalities (Jones et al., 2010). Also alterations in physiology can appear, visualized for example during extensive breeding for altered plasma corticosterone response during restraint in Japanese quail. Quail with high corticosterone response displayed fluctuating asymmetry in normally bilateral symmetric characteristics (Satterlee et al., 2000), and Japanese quail with low plasma corticosterone response reaches puberty earlier than birds with high response (Satterlee et al., 2002).

Research has also been performed where different breeding lines has been exposed to stressful situations. By doing this, one can investigate connections between different traits and the stress response. Changes in stress response has been observed when breeding for altered physiological measurements (Satterlee and Marin, 2006; Veenema et al., 2003) or behavioural responses (Agnvall et al., 2012; Trut, 1999). Veenema et al. (2003) saw that the cortisol levels in wild house mice selected for short or long attack latency were associated with the coping style in a forced swimming test, where the animals bred for long attack latency were significantly more immobile and did less climbing and swimming compared to the mice bred for short attack latency. We thereby see numerous physiological and behavioural changes connected to stress response.

Fear is often connected to danger and a subsequent stress response, and is considered a powerful stressor (Jones, 1996). Fear and the response to a fearful situation are necessary for the survival of the individual and thereby beneficial for the fitness. It has a wide range of definitions, for example, a reaction to the perception of actual danger (Forkman et al., 2007) and some also suggests a connection to an undesirable state of suffering (Jones, 1996). In relation to its biological significance however, Jones suggests a refined definition: *"fear is regarded as an adaptive state with fear behaviour functioning to protect the animal from injury."* Taken together, fear could be defined as a stimulus which, depending on the intensity, gives rise to defensive behavior, avoidance, flight or escape and can thereby be connected to stress and its response.

## 3.1. Long-term effects on early stress

Early experiences of various kinds influence the behavioural development on different levels within the individual. Experiments on early experience and its effects on behaviour later in life have often involved various stressful treatments which induce a stress response in the animal (McEwen, 2007). Several papers with emphasis on early experience points at behavioural effects in adulthood on cognitive performance (Calandreau et al., 2011), parenting behaviour (Stone and Bales, 2010), and sexual behaviour (Sachser and Kaiser, 1996). Alongside with behaviour, also immunology (Solomon et al., 1968) can be affected. The HPA-axis can also be modulated during the postnatal stage in response to for instance human handling (Fraisse and Cockrem, 2006) or other types of stressors. Early experiences are therefore often connected- directly or indirectly- to stress and its consequences which sometimes have detrimental effects on the individual.

There are contradicting results on how stress during the perinatal stage affects the ability to cope with stress later in life. It appears however that certain types or degrees of postnatal stress can result in a greater stress coping ability later in life (see for example Goerlich et al. (2012).

Levine (1957) investigated the effects of physiological stress by handling infant rat pups (1-20 days of age). At 21 days of age, handles pups were significantly heavier than unhandled pups and the significance remained also during adulthood (70 days of age). At the same age, unhandled animals had significantly heavier adrenal glands, implying a lower degree of stress adaptation. Also Michel et al. (2007) found positive consequences of early negative stress. Adult rats preadapted to heat stressed had higher levels of circulating corticosterone and ATCH but displayed an improved physiological adaptation to the heat stimulus, such as reduced levels of dehydration and decreased metabolic activity, whereas the opposite were seen in the non-heat adapted rats; they had lower levels of corticosterone and ACTH but were physiologically more affected by the heat. Seemingly, an increase of ACTH and corticosterone does not necessary affect certain physiological functions if the individual is preadapted to stressors.

Maternal separation is considered a powerful stressor on the offspring and numerous studies, mainly in primates and rodents has been conducted to evaluate the long-term stress consequences of maternal separation (see for example review by Parker and Maestripieri (2011)). Univocal studies in mammals point at the deleterious consequences on both behaviour and physiology in maternally deprived young. Male rat pups exposed to daily maternal separation for 10 days were at 7-8 weeks of age tested, and displayed visceral hypersensitivity and functional bowel disorders compared to the control group (O'Mahony et al., 2009). Matsumoto et al. (2006) found that early maternal separation led to impaired growth and altered response in the HPA-axis during immobilization. Maternal deprivation can also lead to abnormal behaviour (reviewed in Latham and Mason, 2008) and mental dissordes, such as depression (Réus et al., 2011). This is an issue to address when it comes to chick production, since the chicks never come in contact with adult individuals during rearing. In chickens, the maternal presence has ben show to play a signifincant part in the development of natural behaviours. Riber et al. (2007) observed earlier onset of perching and more ground pecks compared with chicks without maternal presence, and connect the increase of natural behaviour with decreased stress and thus resulting in fewer abormal behaviours later in life. Also, brooded chicks displayded a smaller degree of hippocampal lateralization compared to chicks raised without a hen (Nordquist et al., 2012). Seemingly, not only mamals but also birds are behaviourally and physiologically affected by maternal separation. Taken together, we can conclude that there is substantial plasticity in the stress response in young individuals, and that early experiences may give lasting effects.

## 3.2. Maternal- and transgenerational effects

Early experiences can cause phenotypic changes that affect adult behaviour and physiology. The behavioural development of an individual is controlled by genetic mechanisms alongside with environmental factors, and early experiences can also cause transgenerational effects in an epigenetic fashion (Goerlich et al., 2012). It has been demonstrated that rat pups from mothers with high levels of nursing behaviour had alterations in the epigenome compared to pups whose mothers performed decreased levels nursing behaviour. The differences rose during the pups' first week after birth. A significant increase of methylation was seen in the exon $1_7$ glucocorticoid receptor promoter sequence of the low nursing dames. Evidence were strengthened by a cross-fostering test where pups of high nursing dames displayed increased methylation in the promoter sequence in question, when fostered by a low-nursing dame. The effect remained also during adulthood (Weaver et al., 2004). Also in the domestic chicken, stress related plasticity in the offspring can be induced not only by means of genetic mechanisms but also by epigenetic mechanisms. This was seen when adult individuals were exposed to unpredictable light rhythm. The adults developed a "better safe than sorry"- foraging strategy, favoring easy accessible feed over highly desirable but hidden food. The conservative foraging behaviour was transferred to the offspring (Nätt et al., 2009). Also in quail, maternal behaviour characteristics have been shown to transmit to the offspring, with emphasis on social reinstatement behaviour (Formanek et al., 2008), further proving potential transgenerational effects of stress.

Phenotypic changes can also occur due to maternal effects, which are the direct effects transferred from parent to offspring (Bernardo, 1996). Plenty of work on maternal effects has been performed on mammals, mainly in primates and rodents. Female Rhesus Macaques were exposed to sound stress during pregnancy and the offspring were tested at 18 months of age. The prenatally stressed animals showed signs of increased stress sensitivity by displaying higher rates of abnormal social behaviour and generalized disturbance behaviour (Clarke and Schneider, 1993). Similar behaviour consequences were seen in 24 months old Rhesus Macaques born from mothers given moderate amounts of alcohol during pregnancy (Schneider et al., 2001).

Alterations in sexual behaviour has also been observed in prenatally stressed animals, for example in Guinea pigs (Sachser and Kaiser, 1996), where prenatally stressed females display male courtship behaviour. In birds, it has been shown that maternal effects such as elevated levels of maternal steroid hormones can be transferred to the egg and gives rise to long-term, and often deleterious phenotypic and behavioural effects in the chick. To simulate maternal stress, yellow-legged gull (Larus michahellis) eggs were injected with corticosterone. Results showed that maternal stress can affect both behavior and immunity. The chicks displayed a reduced rate and loudness of late embryonic vocalizations and reduced begging display when hatched. Also the T-cell mediated immunity was depressed (Rubolini et al., 2005). Similar results were found in barn swallows (Hirundo rustica) where the eggs from nesting females were injected with corticosterone. Compared to the unmanipulated eggs, the nestlings hatched from the corticosterone injected eggs had lower hatchability, smaller body size and slower plumage development (Saino et al., 2005). Unpredictable mild stressors on laying female quail gave rise to earlier hatching, alterations in egg composition and also altered the phenotype of the offspring, however partly on the contrary to the barn swallows, the quail chicks originating from stressed mothers were heavier (Guibert et al., 2011). One can thereby conclude that maternal stress results in alterations in hatchability and egg composition which gives rise to diverse phenotypic traits in the offspring, and that some studies also show that prenatally stressed offspring display lower degrees of plasticity, compared to postnatally stressed animals.

## 4. Swedish production and housing systems

The Swedish commercial poultry production consists of the breeding of meat-producing Broilers and egg-producing breeds. Viewing numbers from 2010, more than 78.5 million chickens were slaughtered for consumption in Sweden (Svenskfagel.se), and the consumption is steadily increasing. Concerning eggs, the Swedish production was 103.700 tons during 2009 and has been increasing during the last years (http://www.svenskaagg.se). There are three types of housing systems of egg-producing chickens in Sweden, cage-systems, free-ranging one-or-multilevel systems and organic systems. The legislations for numbers of birds per $m^2$ vary in Sweden with housing system and age of the birds. For adult birds in free-range systems, the allowed number of birds is 7-9 per $m^2$, and it is common that the numbers of birds exceeds 10.000 in one stable. In organic production, a maximum of 6 individuals per $m^2$ is allowed. In cage systems, only breeds with a mean weight on less than 2.4 kg are allowed to be kept in cages. The permitted number of animals varies depending on cage size, but the space is more restricted compared to the free-range systems. The expanding numbers of birds in the large scale production may contribute to welfare issues, and it is obvious that the modern production systems have few similarities to main wild ancestor to the domestic breeds, the Red Junglefowl (Fumihito et al., 1996), originating from the tropical forests of south-east Asia. According to the Swedish law animas must have the ability to behave naturally. In systems for laying hens, both free-range and cage systems have their pros and cons. If focusing on natural behaviour, the free-range system is to prefer, as reviewed by Appleby and Hughes (1991). The authors however note that abnormal behaviours are less common in cage systems were fewer animals are kept together, and suggest that the best solution would be small groups of chickens housed in free-range systems. It is however also suggested that feather pecking is a misdirected ground peck, wherefore floor substrate that encourages ground pecking is of high significance (Blokhuis and Wiepkema, 1998; El-Lethey et al., 2000). It has further been observed that the free-range housing systems increase the risk for disease and parasites spreading in the flock (Esquenet et al., 2003; Fossum et al., 2009; Permin et al., 1999). Thereby, depending on what welfare parameter we measure, the best housing system can be debated.

## 4.1. Human-animal interaction

In modern intensive farming, close contact between humans and animals are regular. There are some seemingly obvious benefits for animals living under human care. For example, feed and water is provided and often unlimited, the animals have shelter and are protected from predators and other threats. If they get sick caretakers can provide medical care and prevention from disease is also possible through vaccinations. However, human presence can still be stressful. As reviewed by Hemsworth (2003), interactions between stockpeople and stock animals may result in decreased production and welfare in the animals. Chickens are per definition domesticated, but seem however affected by humans and often display fearful behaviours like crouching or flight in human presence (Jones et al., 1981). By interpreting the behavioural responses, human presence affects the chicken behaviour, but potentially also triggers complex hormonal activities in the female which can be transferred to the eggs, wherefore possible actions could be taken to reduce the fear levels. Habituation to humans is an effective way of reducing fearfulness and thereby stress. Differences were seen when comparing female quail habituated and non-habituated humans. Habituated individuals produced eggs containing more yolk, less immunoreactive progesterone and surprisingly also more androgens. The chicks hatched earlier but were larger. Strangely though, chicks of non-habituated mothers required more TI-induction attempts and seem thereby less fearful, which the authors connect to the levels of androgens in the eggs (Bertin et al., 2008). By habituating the mother to humans, reduced fearfulness in the offspring is possible to achieve, as seen in Japanese Quail (Bertin and Richard-Yris, 2004). Unfortunately, this is impossible to implement in the poultry production since the bids are raised without mothers.

## 4.2. Production and stress

As seen in the examples above, adult chicken behaviour can be affected both by transgenerational mechanisms, maternal effects, or direct effects on the chick at an early age.
Domestic chickens in the production industry live under what can be regarded as extreme conditions. As identified by Morgan and Tromborg (2007), artificial habitats contain a wide range of potential stressors for animals in captivity, such as sound, light, odors, temperature, confinement, lack of retreat space, restricted feeding and foraging, forced human proximity and abnormal social groups. The

stressful environment applies a hard pressure on the individual and its coping ability, but in the long run, increased tolerance to the above mentioned stressors are likely to spread in the population, since it can be expected that the best suited individuals have a higher survival rate. However, stress in the production environment can also be regarded as a negative spiral where stress in the chicken can result in delayed onset of the laying cycle and decrease the egg production (Shini et al., 2009), and as mentioned in previous section, stress in the mother can induce negative consequences in the offspring. Repeated cortisol administration has been used for experimental mimicking of chronic stress. In adult chickens, chronic corticosterone administration resulted in several physiological changes, such as a significant change in body weight, relative organ weights and an increase of blood glucose, cholesterol and triglyceride (Shini et al., 2009) and increased feather pecking (El-lethey et al., 2001). Elevated levels of corticosterone thereby have negative consequences both on physiology and behaviour in the animals and may therefore be regarded as a welfare issue, as well as a production issue.

Common management procedures in the chicken industry can be identified as potentially stressful for the animals, especially during the first day of the chicks' life. Exposure to painful treatments (vaccination, wing-tagging, sex-sorting), regroupings, transportations on conveyer belts and in trucks, artificial light and extreme group sizes are common practice. We should also take into consideration that chicks are not reared by a hen, which with support from the literature mentioned in previous sections could potentially be a severe stressor.

Abnormal behaviour like feather pecking, cannibalism and vent pecking are problems that occur in populations of domestic birds, and can be originating from early stress. The consequences for the victimized individuals can be severe suffering, painful wounds and eventually death. In an experiment comparing chicks raised under standard conditions with chicks raiser with a simulated brooder hen (a heating block hanging close to the floor draped with material to provide darkness and warmth), almost no occurrences of feather pecking and cannibalism were seen in the dark brooder chicks (Jensen et al., 2006), further indicating the function of a present hen during chick rearing. Viewing feather pecking more closely, certain individuals are more prone to feather peck due to genetic factors (Buitenhuis et al., 2003). In combination with poorly enriched environment (such as straw and sand for dust bathing) which decrease natural exploratory and foraging behaviour (El-Lethey et al., 2000), these individuals may be even more prone to develop abnormal behaviours.

## 5. Discussion

There is no doubt that there is an appreciable plasticity in the neurohormonal pathway in perinatal animals which can be modified by negative stress. It seems however like the intensity, time slot and duration of the stressor plays a significant role in weather the stress has deleterious effects on the individual or not. Behaviour plasticity early in life could prepare the individual for upcoming events later in life and the individual is then somewhat preadapted. There are seemingly different effects depending on if the stress is prenatal or postnatal. As stated previously, exposure to stressors early in life after birth/hatch, the individual cope better with stress as adult. Prenatal stress however seem to evoke dysfunction in the HPA-axis with rather deleterious effects as a consequence in adulthood (reviewed by Weinstock (1997)), implying lower degrees of plasticity in the fetus compared to the young individual.

In Sweden, a preventive act to minimize stress was taken by the Swedish Board of Agriculture. It is recommended (DFS 2007:5, saknr. L100) that chicks are to be raised in an environment that prepares them for the system they are to be kept in as adults, meaning that free range hens should be raised as free range chicks and the same accounts for caged hens. This is to prevent major changes in the chickens' environment which can cause abnormal behaviour. If measures to improve the welfare are taken already from an early age in the chick, it is possible to reduce the potential problems occurring in adulthood. Cannibalism is an example of a behavioural problem seen as a consequence of poor environment already at an early age (Gunnarsson, 1999; Riber et al., 2007). There are however certain events in the chick production that we simply cannot skip. In the large-scale production, birds are vaccinated against Marek's disease during their first day in life. The vaccination requires an intramuscular injection. Painful events such as vaccination are crucial partly due to the animals' future welfare, i.e. it won't suffer from disease later in life, and wing tagging is also essential due to legislations and the importance of identification. However the stress provoked by sex sorting, transports on conveyer belts, and social regroupings could be possible perhaps not to eliminate – but to minimize. Swedish production industry has currently the following organization: When the chicks are hatched they are either transported to the egg producer the day after hatching or stays at the hatchery until 15 weeks of age and are then transported to the egg producer (svenskaagg.se). A possibility would be that the transportation on day one could be eliminated if the chicks were hatched and raised on the same location. This would require reestablishment of large parts of the production industry, and it would also require larger farms, which now days are something many regard as negative both for an environmental and a welfare perspective (Appleby and Hughes, 1991).

It has further been seen that aggression is reduced in larger groups of chickens compared to small groups (D'Eath and Keeling, 2003). The dominant animals displayed aggression towards the stimulus bird regardless it was an unknown bird or an individual from the same flock. It was suggested that the individual recognition in a large group is harder and therefore the chickens' social strategies shift (D'Eath and Keeling, 2003). Viewed from a stress reduction perspective, larger groups would be beneficial for minimizing aggression. There are also possibilities to reduce stress not by alterations in the environment but through conscious breeding for increased stress tolerance or reduced fearfulness. Successful results have been seen in fish (Pottinger and Carrick, 1999; Pottinger et al., 1994). In poultry, successful results have been seen in several species. In turkeys selected for high or low adrenal corticosterone response to cold stress, it was seen that after six generations, the line selected for high cort response had almost twice as high cort levels after cold stress compared to the low response group (Brown and Nestor, 1973) It was also seen that ACTH injections in both selected group gave a higher an almost double response in the group selected for high cort response to cold stress, indicating the possibility for selection towards decreased stress response. The same authors also found a better over-all reproductive performance in the birds selected for low corticosterone response (Brown and Nestor, 1973). In Japanese Quail, animals bred for low plasma corticosterone response displayed higher ambulation rate and shorter freeze in open field test, indicating a lower stress response, compared to high stress selected birds (Satterlee and Marin, 2006). Also environmental enrichment has been shown to be an effective method to reduce stress. Morley-Fletcher et al. (2003) investigated the reversibility of prenatal stress during adolescence in rat pups. The prenatally stressed rat pups displayed reduced play behaviour, and had a prolonged corticosterone secretion after a short period of restraint during adolescence, while adolescent rats increased play behaviour in an enriched environment. The corticosterone response however had followed the same pattern as in the rat that did not have access to enrichment. As reviewed by Rodenburg et al. (2008) both the brooding period of the hen and the early-life history can influence the behaviour of chickens. Maternal presence has been seen to enhance natural behaviours, such as ground peck and earlier perch use (Riber et al., 2007) with a reduced risk of developing abnormal behaviours later in life.

By further investigating the perinatal experiences in chicks and the long-term and transgenerational effects on behaviour and physiology, negative welfare issues can be minimized in adulthood and we might take a step closer to improve the chicken welfare.

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