doi:10.1017/S0043933917000812

The welfare of layer hens in cage and cage-free housing systems

K.M. HARTCHER[1,2]* and B. JONES[1,2]

[1]RSPCA Australia, PO Box 265, Deakin West ACT 2600 Australia; [2]Sydney School of Veterinary Science, University of Sydney, Sydney NSW 2006 Australia
*Corresponding author: khartcher@rspca.org.au

Historically, animal welfare has been defined by the absence of negative states such as disease, hunger and thirst. However, a shift in animal welfare science has led to the understanding that good animal welfare cannot be achieved without the experience of positive states. Unequivocally, the housing environment has significant impacts on animal welfare. This review summarises how cage and cage-free housing systems impact some of the key welfare issues for layer hens: musculoskeletal health, disease, severe feather pecking, and behavioural expression. Welfare in cage-free systems is currently highly variable, and needs to be addressed by management practices, genetic selection, further research, and appropriate design and maintenance of the housing environment. Conventional cages lack adequate space for movement, and do not include features to allow behavioural expression. Hens therefore experience extreme behavioural restriction, musculoskeletal weakness and an inability to experience positive affective states. Furnished cages retain the benefits of conventional cages in terms of production efficiency and hygiene, and offer some benefits of cage-free systems in terms of an increased behavioural repertoire, but do not allow full behavioural expression. In Australia, while the retail market share of free-range eggs has been increasing in recent years, the majority of hens (approximately 70%) remain housed in conventional cages, and furnished cages are not in use. Unlike many other countries including New Zealand, Canada, and all those within the European Union (where a legislated phase-out commenced in 1999 and was completed in 2012) a legislative phase-out of conventional cages has not been announced in Australia. This review came about in light of the current development of the Australian Animal Welfare Standards and Guidelines for Poultry in Australia. These standards are intended to provide nationally consistent legislation for the welfare of all poultry species in all Australian states and territories. While it is purported that the standards will reflect contemporary scientific knowledge, there is no scientific review, nor scientific committee to inform the development of these

World's Poultry Science Journal, Vol. 73, December 2017
Received for publication April 7, 2017
Accepted for publication July 18, 2017

standards, and conventional cages are permitted in the standards with no phase-out proposed.

Keywords: cage-free; cages; free-range; housing system; layer hen; welfare; welfare standards; legislation

Introduction

There are three main science-based frameworks which have been used to understand animal welfare (Fraser, 2003; Hemsworth *et al.,* 2015). These include: 1) biological functioning; an animal's ability to cope with its environment and whether its needs are met; 2) affective state; an animal's subjective experiences, and 3) natural living; the ability for an animal to live according to its nature and perform normal behaviours (Broom, 1986; EFSA, 2005; Fraser, 2003; Hemsworth *et al.*, 2015).

Historically, animal welfare has been defined by the absence of negative experiences such as disease, hunger, thirst, stress or reduced fitness (Bracke and Hopster, 2006). Indeed, the majority of animal welfare research in the last 40 years has focused on the avoidance of negative states. However, there is increasing interest and research in the experience of positive welfare states in animals (Hemsworth *et al.*, 2015). This shift in welfare science has led to the understanding that good animal welfare cannot be achieved without the experience of positive affective states such as feeling comfort, pleasure, and a sense of control (Mellor and Beausoleil, 2015).

The Five Freedoms were developed by the United Kingdom Farm Animal Welfare Council and released in 1979. The principles form a basic qualitative framework on which welfare schemes and welfare assessment tools have been based. The Five Freedoms have been highly influential in the development and scope of animal welfare standards internationally. While they do not prescribe specific conditions, they were the first to include subjective experiences, health status and behaviour in one framework (Mellor, 2016). Over time, they have resulted in a shift in animal welfare assessment away from a focus on biological functioning towards a focus on the animal's experiences.

The Five Domains of Potential Welfare Compromise (commonly referred to as the Five Domains) model was originally developed as a framework with which to assess the welfare of animals used in research in 1994 (Mellor and Reid, 1994). It was subsequently adopted in 1997 as part of regulatory requirements for assessing the welfare of animals used for scientific purposes in New Zealand. The model integrates biological functioning and affective states by considering internally regulated, as well as externally generated inputs (Mellor and Beausoleil, 2015). The physical considerations of the model comprise nutrition, the environment, health and behaviour, while the fifth domain considers mental state, or affective experiences. A compromise in any of the physical domains also influences the emotional experience directly. For example, food deprivation leads to the affective experience of hunger, which in turn may lead to further negative mental states, such as frustration or stress (Hemsworth *et al.*, 2015; Mellor and Beausoleil, 2015).

Thus, good welfare involves a combination of adequate nutrition, an appropriate environment, optimal health, the expression of normal behaviours, and positive mental experiences. The Five Domains model has recently been adapted to allow the assessment of positive as well as negative experiences to encourage more opportunities for animals to experience positive states whilst minimising negative states (Mellor, 2013; Mellor and

Beausoleil, 2015). Assessment of animal welfare and the management of animals in the future will require an emphasis on the experience of positive affective states (Hemsworth *et al.*, 2015).

Innate, or 'normal' behaviours are those which are inherent to animals, and typically, which animals are motivated to carry out. The performance of these behaviours is thought to be a component of biological functioning, is pleasurable, and necessary to avoid stress (Bracke and Hopster, 2006). In layer hens, innate behaviours include dustbathing, perching, foraging, and nesting. These behaviours are often driven by internal factors, and are internally and physiologically regulated (Hughes and Duncan, 1988). The need to express normal behaviours, the level of satisfaction these behaviours provide, and the amount of frustration caused by their inhibition, can be scientifically assessed. This may be done by measuring the intensity, duration, and incidence of particular behaviours (Bracke and Hopster, 2006). Frustration is an aversive state which arises when animals are prevented from performing a behaviour that they are strongly motivated to perform (Fraser *et al.*, 2013). Housing can create welfare problems when it causes frustration. The opportunity for hens to perform behaviours which they are motivated to perform is central in achieving positive welfare states (Mellor and Webster, 2014).

In Australia, the market share of free-range eggs sold at retail has been increasing in recent years. However, the majority of layer hens (approximately 70%) are housed in conventional cages. Furnished cages are currently not in use. Unlike several other countries including New Zealand, Canada, and all those within the European Union, where a legislated phase-out commenced in 1999 and was completed in 2012, a legislative phase-out of conventional cages has not been announced in Australia.

While conventional cages are more hygienic, contribute to a lower incidence of infectious diseases, allow easier management, and are cheaper to operate, they do not provide adequate space per hen, hens experience extreme behavioural restriction, and the lack of movement causes metabolic disorders, high rates of disuse osteoporosis, and the birds experience severe frustration due to the prevention of normal behaviours such as nesting (Duncan, 2001).

This review is in light of the current development of the *Australian Animal Welfare Standards and Guidelines for Poultry* in Australia. The Standards and Guidelines are intended to streamline poultry welfare legislation across Australia and improve welfare outcomes for all poultry species. This process is funded by the poultry industries as well as state and federal Governments. It is purported that the development came about in recognition of 'significant advances in husbandry practices, technology, and in available science, since the current code was endorsed in 2002', and that the standards will 'aim to reflect contemporary scientific knowledge, provide competent animal husbandry advice, meet mainstream community expectations, and that can be maintained and enforced in a consistent, cost-effective manner' (Animal Health Australia, 2016).

Indeed, while there are a number of factors which influence societal use of animals and determining acceptable animal use, including human health, economic, social, and environmental factors, science provides the means to understand the impact of animal use on the animal. Therefore, science has a very prominent role in underpinning decisions on animal use, and the conditions under which animals are kept (Hemsworth *et al.,* 2015).

However, unlike in many other countries, there is no scientific review conducted to inform the development of farm animal welfare standards in Australia, and no scientific advisory committee, making it impossible for the standards to reflect contemporary scientific knowledge. The Australian Government Productivity Commission conducts independent research and acts as an advisory body. In late 2016, the Productivity Commission produced a report on the Regulation of Australian Agriculture which includes animal welfare policy governance in Australia. The report highlights concerns with the lack of national leadership and flaws in national standard-setting. Key points in the report include that the current approach to developing national standards and guidelines for farm animal welfare needs to be improved by relying more on rigorous science and evidence of community values. They proposed that an independent statutory agency be stablished to develop the standards (Australian Government Productivity Commission, 2016).

Evaluation of contemporary scientific knowledge is necessary to understand what is known about how different housing environments may be affecting hen welfare, inform decision-making, and identify important areas for future research. There is a need for comprehensive, independent scientific literature reviews to cover all welfare aspects for the housing and husbandry of all poultry species.

This review aims to summarise scientific literature on the welfare of layer hens housed in the various housing systems: conventional cages, furnished cages, and cage-free, in relation to four key areas: musculoskeletal health, disease, severe feather pecking, and behavioural expression. There are many more factors which can affect hen welfare including nutrition, the environment (air quality, lighting, environmental enrichment, access to resources), genetics, group size, predation, social environment, stocking density and space allowance, management practices, and husbandry and the human-animal relationship which are not covered in this review.

Skeletal health

Commercial layer hens have been genetically selected for production characteristics, including rate of lay. Their ancestors, the red jungle fowl, lay approximately 10 to 15 eggs per year (Romanov and Weigend, 2001). In comparison, the modern-day layer hen can lay over 350 eggs per year. They also have a higher growth rate, heavier adult body weight, earlier sexual maturity, and larger egg sizes than the red jungle fowl. The formation of egg shells requires the deposition of calcium. The high rate at which eggs are laid therefore leads to a loss of bone calcium and consequently high rates of osteoporosis, skeletal fragility, and susceptibility to fractures.

Bone fragility and muscle weakness are exacerbated when birds are unable to move and exercise sufficiently (Webster, 2004; Widowski *et al.,* 2013). The extreme behavioural restriction hens experience in conventional cages therefore further contributes to bone weakness, and hens often suffer from disuse osteoporosis (LayWel, 2006). Hens in conventional cages suffer the poorest bone strength, and the highest rate of fractures at depopulation than in all other housing systems (Widowski *et al.,* 2013).

By contrast, hens in cage-free systems experience the best musculoskeletal health. A study by Rodenburg *et al.* (2008) comparing cage-free and furnished cages found that hens in cage-free systems had stronger wing and keel bones than hens in furnished cages. An increased behavioural repertoire and the ability to exercise, including walking, running, perching, wing-flapping, and flying increases musculoskeletal strength, and decreases the incidence of osteoporosis and fractures which occur during depopulation. However, bone fractures are a risk when hens fall or sustain injuries during flight on objects such as perches, feeders, drinkers, or nest boxes within the shed (Lay *et al.,* 2011; Fraser *et al.,* 2013). Therefore, hens in cage-free systems can experience more fractures during the laying period than those in cage systems (Lay *et al.,* 2011; Widowski *et al.,* 2013).

Furnished cages typically allow hens to perch, which contributes to improved bone strength (Lay *et al.,* 2011). Hester (2014) suggested that the addition of perches to cages may be a compromise that allows the benefits of cages to be retained (improved liveability and lower respiratory disease), while better meeting the behavioural needs of layer hens. Hens in furnished cages exhibit the lowest number of total fractures compared with both cage-free and conventional cage systems. This is probably due to improved musculoskeletal health due to the use of perches when compared to conventional cages, and an absence of the environmental complexity which can be present in cage-free systems (Widowski *et al.,* 2013).

Rodenburg *et al.* (2008) compared keel bone fractures in furnished cages, floor housing, and aviary systems and found that there were significantly fewer hens with keel bone fractures in furnished cages compared with the cage-free systems (62%, 82% and 97% of birds with fractures, respectively). Hester (2014) stated that although perches contribute to the incidence of keel fractures, hens should have access to perches due to the high motivation to perch, improved bone strength, improved feather quality, and improved foot pad, toe, and nail health. Further, there is no deleterious effect of perches on production besides dirty and cracked eggs (Hester, 2014).

Bone strength has been found to be heritable. Genetic selection is extremely effective in improving bone strength and resistance to osteoporosis (Fleming *et al.,* 2006), with bone strength improving over just one or two generations (LayWel, 2006). A study by Fleming *et al.* (2005) found that hens selected for improved bone strength also had significantly higher egg production.

The number of fractures sustained by hens in cage-free systems should be addressed through a combination of selective breeding, optimised diets, the provision of perches, plus improvements in the design, placement, and maintenance of structures in the shed, including perches (LayWel, 2006; Widowski *et al.,* 2013). Further research is required into optimal perch design and placement, the effect on keel bone damage, and how chicks and pullets learn to use perches (Hester, 2014).

Disease

Generally, there is a reportedly higher incidence of bacterial infections, viral diseases, coccidiosis, and red mites in litter-based and free-range systems than in cage systems (Rodenburg *et al.,* 2008; Fossum *et al.*, 2009; Widowski *et al.*, 2013). Contact with soil, litter, faeces, and other vectors including rodents and insects increases the risk of infectious diseases. Birds with access to the outdoors may have a higher risk of contracting diseases such as avian influenza, Newcastle disease, and ectoparasites from wild birds (Lay *et al.*, 2011; Widowski *et al.*, 2013), while red mites often reside in the environment (Chauve, 1998; Lay *et al.*, 2011; Fraser *et al.*, 2013).

The risk of infectious diseases can be significantly lowered by proactive approaches such as biosecurity and vaccination programmes (Martin, 2011; Fraser *et al.,* 2013). Health and hygiene practices have led to a decline in the proportion of birds with viral, parasitic, and non-infectious diseases in cage-free systems in Switzerland (Kaufman-Bart and Hoop 2009). Four approaches to infectious disease control have been suggested by Fraser *et al.* (2013). These include: 1) protecting individual animals through hygiene, vaccination, and anti-parasite treatments, 2) preventing disease spread within a farm, 3) preventing the entry of diseases onto farm, and 4) eliminating diseases over large areas.

Hens in conventional cages may experience metabolic disorders due to lack of exercise. Caged hens can show paralysis around peak production, termed 'cage layer fatigue' which is due to bone weakness, fractures of the thoracic vertebrae, and compression of the spinal cord (Duncan, 2001). Other non-infectious diseases including fatty litter and disuse osteoporosis are more prevalent in conventional cages compared with systems that allow greater opportunities for behavioural expression and movement (Weitzenbürger *et al.,* 2005; Kaufman-Bart, 2009; Lay *et al.,* 2011; Widowski *et al.,* 2013). Fatty liver is a metabolic disease typically seen in conventional cages (EFSA, 2005; Jiang *et al.,* 2014) which can cause rupture of the liver and sudden death. The main factors which are thought to contribute to the development of fatty liver include lack of exercise and restricted locomotion, high environmental temperatures, and a high level of stress (EFSA, 2005). Non-infectious diseases such as disuse osteoporosis and fatty liver which are associated with lack of movement and exercise are difficult to treat or manage in conventional cages due to the inherent behavioural restriction in these systems.

Severe feather pecking and cannibalism

Severe feather pecking, whereby hens vigorously peck at and pull out the feathers of other birds, is a significant welfare concern in the layer industry. It has been documented in all types of housing systems including cage, litter-based, free-range, and aviary (Appleby and Hughes, 1991; Huber-Eicher and Sebö, 2001; Bestman *et al.,* 2009). Research suggests that there is a small proportion of birds which initiate severe feather pecking, and that the behaviour may then spread throughout a flock (Bessei and Kjaer, 2015). Therefore, housing birds in large groups, as commonly occurs in cage-free systems, may contribute to an increased prevalence of severe feather pecking (Hughes, 1995; McAdie and Keeling, 2000; Potzsch *et al.,* 2001).

Mitigating the risk and spread of severe feather pecking is critical for hen welfare. Management practices which may minimise the risk of severe feather pecking include the provision of adequate nutrition, appropriate feed form, high-fibre diets, suitable litter from an early age onwards, no sudden changes in diet or environmental conditions, minimising stress and fear in the birds, provision of environmental enrichment, appropriate rearing conditions, good husbandry and matching the rearing and laying environments (Kjaer and Bessei, 2013; Rodenburg *et al.,* 2013; Hartcher *et al.,* 2016).

Severe feather pecking is heritable (Savory, 1995; Kjaer and Bessei, 2013; Bessei and Kjaer, 2015), and current studies are investigating traits which may predispose particular birds to initiate the behaviour, to enable genetic selection against these traits. Management practices should therefore be paired with genetic selection programmes. This approach, as well as further research into this area, has the potential to reduce the prevalence of severe feather pecking (LayWel, 2006; Rodenburg *et al.,* 2013; Bessei and Kjaer, 2015; Hartcher *et al.,* 2016).

Movement

Animals require an absolute amount of physical space to extend their limbs and perform basic movements including changing posture and turning around. The amount of space required for a hen to turn around and stretch its wings is greater than the space which is provided in most conventional cages (Widowski *et al.,* 2016). Hens have been found to perform 'rebound' levels of wing-flapping, tail wagging, and stretching when they are moved to a larger space after weeks of confinement in a small area, with some behaviours correlated to the duration of confinement. This indicates that hens do not adjust to prolonged spatial restriction (Nicol, 1987; Lay *et al.,* 2011).

Furnished cages generally allow more movement than conventional cages. They typically provide more space, perches, enclosed nests, substrate, and an area to scratch. Behaviour is therefore more unrestricted and varied than in conventional cages, hens are able to perform some of their most highly motivated behaviours, and physical condition is better (Appleby *et al.,* 2002). However, the extent to which behaviours are able to be expressed in furnished cages has been questioned (Cronin *et al.,* 2012). Litter is often delivered in insufficient quantities, and locomotion, ground-scratching, wing-flapping and flying are inherently limited or prevented in caged environments (Appleby *et al.,* 2002; Lay *et al.,* 2011).

Cage-free systems generally allow greater opportunities for locomotion and basic movements than in cages. Locomotion is increased because resources are spread out horizontally and sometimes vertically. However, stocking densities may be inhibitive, and must be low enough to facilitate movement and behavioural expression (Leone and Estevez, 2008; Lay *et al.,* 2011).

Studies have demonstrated that hens are highly motivated to perform a number of innate behaviours including perching and finding a nesting site, and when housing constraints prevent hens from performing these behaviours, they can experience frustration and emotional distress which may be exhibited by stereotypic back-and-forward pacing behaviour (Fraser *et al.,* 2013). There may also be physical consequences including compromised biological function or harmful variants of the restricted behaviour such as feather pecking or hysteria (Lay *et al.,* 2011). Correspondingly, studies have reported lower levels of frustration in systems where hens are able to express behaviours such as nesting and dustbathing (Zimmerman *et al.,* 2000; Widowski *et al.,* 2013).

Perching

The provision of perches allows hens to perform their normal perching behaviour, therefore satisfying a behavioural demand (Lay *et al.,* 2011). Hens have demonstrated a strong motivation to access perches in behavioural tests, for example by pushing through weighted doors (Olsson and Keeling, 2002), and almost all hens use perches at night if adequate perch space is provided (Blokhuis, 1983; 1984; Appleby *et al.,* 2002; Lay *et al.,* 2011; Fraser *et al.,* 2013). Hens show signs of unrest when they are deprived of the opportunity to perch at night, and experience frustration and reduced welfare if perching is not possible (Olsson and Keeling, 2002; Fraser *et al.,* 2013).

The use of perches can reduce fearfulness and aggression (Donaldson and O'Connell, 2012), reduce bird density on the floor (Cordiner and Savory, 2001), lower the risks of piling and smothering (Lay *et al.,* 2011), improve motor activity, and provide resting locations and places of refuge from aggressors (Cordiner and Savory, 2001; Lay *et al.,* 2011; Yan *et al.,* 2014). The provision of perches within the first four weeks of life has also been shown to reduce the risk of cloacal cannibalism in adulthood (Gunnarsson *et al.,* 1999).

The use of perches has been shown to improve bone strength (Lay *et al.,* 2011) and musculoskeletal health due to exercise (Yan *et al.,* 2014). Enneking *et al.* (2012) provided pullets with perches from one day to 17 weeks of age. Birds with perch access had greater bone mineral content of the tibia, sternum and humerus, as well as greater muscle deposition at 12 and 71 weeks of age compared to birds without access to perches (Enneking *et al.,* 2012; Yan *et al.,* 2014). In cages, perches also give reprieve from standing on a sloped wire floor (Hester, 2014).

While there are welfare benefits to providing perches, their use can also present risks to welfare. Perches and other structural features within the housing environment such as tiers in aviary systems can cause keel bone deformities and foot pad lesions, and there is risk of fractures if birds do not land successfully when jumping or flying between perches or tiers in cage-free systems (Lay *et al.,* 2011; Heerkens *et al.,* 2016). Perches installed in cages can also cause keel bone fractures and deformities, although at a lower rate than in cage-free systems (Hester, 2014).

Poorly designed and maintained perches have been associated with bumblefoot due to an accumulation of droppings and litter (Lay *et al.,* 2011), and perches in furnished cages have been associated with an increased risk of cloacal cannibalism. Pickel *et al.* (2011) investigated perch shape and type and the effects on hens' keel bones and foot pads. Certain designs, such as those with a soft surface, larger surface area, and a hygienic surface may be important in minimising risks to keel bones, foot health, and subsequently hen welfare (Pickel *et al.,* 2011).

Management practices can have an effect on perch use. In particular, the rearing environment and whether pullets are provided with perches during rearing, the stocking density during the laying period, and the lighting programme all affect how hens utilise perches. Rearing without early access to perches appears to cause low muscle strength, a lack of motor skills, an inability to keep balance, and impaired cognitive spatial skills, with long-lasting effects on welfare (EFSA, 2015). Therefore, providing perches during the rearing period enhances the ability to utilise them in the laying period, and also reduces the incidence of floor eggs (Gunnarsson *et al.,* 1999; Lay *et al.,* 2011). A recent review by Janczak and Riber (2015) recommended that the rearing system should provide constant access to perches.

The welfare issues associated with perches may be partly addressed by good management, and perch placement, type and design. For example, the risk of unsuccessful landings, and therefore bone deformities and fractures, may be reduced by perch type and placement (Scott *et al.,* 1997; Lay *et al.,* 2011). Heerkens *et al.* (2016) found that the provision of ramps was effective in reducing keel bone and foot pad problems, and suggested that the adaptation of housing systems combined with genetic selection programmes may offer effective methods to improve hen welfare (Heerkens *et al.,* 2016).

Nesting

Nesting behaviour is a priority for hens (Weeks and Nicol, 2006; Lay *et al.,* 2011), and is important for their welfare (Cooper and Albentosa, 2003; Weeks and Nicol, 2006; Cronin *et al.,* 2012; Widowski *et al.,* 2013). The need for layer hens to perform pre-laying behaviour and utilise a nest has been assessed by motivation tests, which have consistently demonstrated that it is a high priority (Widowski *et al.,* 2013).

The majority of layer hens prefer to lay their eggs in a discrete nest site (Appleby *et al.,* 2002; Weeks and Nicol, 2006; Cronin *et al.,* 2012), and the strength of the motivation to access a nest box has been demonstrated in a number of different ways. Cooper and Appleby (2003) concluded that hens' work-rate to access a nest 20 minutes prior to egg-laying, as measured by the extent to which they were willing to work by pushing a push-door for resources, was twice the work-rate to access food after four hours of confinement without feed. Similarly, Zimmerman *et al.* (2000) found that hens exhibited greater frustration when a nest was denied than feed and water deprivation. Hens which were denied an appropriate nest site at oviposition expressed frustration through specific, gakel-call vocalisations.

In conventional cages, where there are no secluded nest sites, hens have expressed frustration in the form of repetitive, stereotyped pacing (Yue and Duncan, 2003; Lay *et al.,* 2011), and the retention of eggs beyond the expected time of lay (Yue and Duncan, 2003; Widowski *et al.,* 2013). Hens prefer to lay eggs in a nest rather than on a sloping wire floor, and the lack of a nest may reduce welfare (Hughes *et al.,* 1989; Lay *et al.,* 2011). In addition to satisfying a behavioural demand, a closed nest area can reduce cloacal cannibalism. (Newberry, 2004; Lay *et al.,* 2011).

While there have been a number of studies which assessed the behavioural motivation for hens to access nest boxes, taking physiological measurements is not as straightforward, and there is a lack of information on the physiological stress responses of hens when nest boxes are denied. Complications associated with taking physiological measurements of stress include the highly variable peak in plasma corticosterone prior to egg-laying which may confound measurements (Cronin *et al.,* 2012). Some studies have investigated the correlation between the concentration of corticosterone in plasma and egg albumen, although there have been conflicting findings, and there is a need to investigate this relationship and how corticosterone may be used as part of welfare assessments. Downing and Bryden (2008) found a positive correlation, which suggested that corticosterone in egg albumen may provide a non-invasive measure of stress. However, Engel *et al.* (2011) found few correlations between corticosterone concentrations in plasma, albumen, yolk, and faeces. Corticosterone may be deposited into egg albumen over an 8-hour period each day, while hens typically display pre-laying behaviours 1-2 hours prior to egg laying. Corticosterone in albumen may therefore not be a useful indicator of stress associated with nesting. Research on the stress physiology of hens in relation to egg-laying behaviour is very limited, and the correlation between corticosterone concentrations in plasma and egg albumen needs further validation (Cronin *et al.,* 2012).

Dustbathing

Functionally, dustbathing is performed to clean the feathers (Lay *et al.,* 2011). It acts to remove skin parasites, regulate the amount of feather lipids, and maintain plumage condition (Olsson and Keeling, 2005). Hens have been found to work to obtain a dustbathing substrate, and after deprivation of dustbathing, are more motivated to dustbathe, indicating that it is a high priority (Widowski and Duncan, 2000). However, the evidence on the motivation to access substrate for dustbathing is not as conclusive as the motivation to access other resources, and some some sstudies have not found any evidence of a motivation to dustbathe. It has been suggested that the methodology used, for example, whether or not hens can see the litter in the experiments, may affect differences between studies (Olsson and Keeling, 2005).

Conventional cages have no provisions for dustbathing. Sham dustbathing can occur, where hens perform dustbathing movements on the wire floor, which would normally include scooping dust into the plumage. However, the dustbathing sequence cannot be completed, as there is no substrate, nor shaking off lipid-saturated dust. Sham dustbathing lacks positive feedback (Widowski and Duncan, 2000), does not satisfy birds' motivation for dustbathing (Olsson and Keeling, 2005), and indicates a reduced state of welfare (Lay *et al.,* 2011). Further, when birds are unable to dustbathe, plumage is in a poorer condition as it is dirtier, less waterproof and less insulative (Scholz *et al.,* 2014).

Furnished cages have some provisions for dustbathing (Appleby *et al.,* 2002; Lay *et al.,* 2011). However, the extent to which dustbathing is accommodated in furnished cages is variable, and significant variation has been found in the use of dustbaths between different types of furnished cages (Tauson, 2005). Typically, hens in furnished cages only receive very small amounts of feed as litter material once per day onto an Astroturf mat in the main area of the cage to allow foraging and dustbathing. The hens' propensity to forage keeps the mat relatively clean and minimises its use for egg laying (Lay *et al.,* 2011). However, since litter is provided in small quantities, it is often quickly depleted. Restricted access to litter, and the small amounts provided, can cause stress (Lay *et al.,* 2011), and subordinate hens may be excluded from the litter area by more dominant hens (Shimmura *et al.,* 2008).

Cage-free systems have the ability to provide adequate materials to facilitate dustbathing. However, not all systems provide dustbathing material. It is possible for cage-free systems to have plastic or wire flooring. If dustbathing material is provided, regular monitoring and maintenance is often required to keep the litter from becoming wet and avoiding associated conditions including high concentrations of atmospheric ammonia and contact dermatitis (Widowski *et al.,* 2013), or too dusty, and avoiding negative health implications associated with high levels of dust in the air (Rodenburg *et al.,* 2005).

Foraging and exploration

Foraging is a key part of the normal behavioural repertoire of chickens (LayWel, 2006). Litter is an important element of the birds' environment, and caged hens have a high demand for a litter substrate (Gunnarsson *et al.,* 2000). It is preferred over wire mesh by hens, and is necessary for the normal expression of some behaviour patterns (Dawkins, 1981). When litter is available, it is used extensively by hens for scratching and pecking (Ekesbo, 2011; Hartcher *et al.,* 2015). Further, hens perform foraging behaviours even when feed is provided *ad libitum* (Lay *et al.,* 2011; Widowski *et al.,* 2013), a phenomenon termed 'contrafreeloading', demonstrating an innate behavioural motivation to forage for food.

Foraging behaviour is not possible in conventional cages, and is only partially accommodated in furnished cages, where substrate may be insufficient, or quickly depleted. Environmental complexity is extremely limited in both conventional and furnished cage systems, which limits the hens' ability to explore their environment and forage (LayWel, 2006).

Allowing hens to access an outdoor area improves opportunities for behavioural expression including foraging, exercising, and exploring. If the range area is well-maintained, easily accessible from the shed, offers shade and shelter, and is attractive to birds, this will enhance its use. When birds utilise outdoor areas, this lowers the stocking density inside the shed, and can result in increased locomotion and exercise, and improve inter-individual distances and normal social behaviours (Knierim, 2006).

Hens are motivated to forage. Access to good quality, well-maintained litter is critical to their welfare to maintain good plumage condition, improve the feeling of satisfaction, and potentially reduce adverse behaviours such as severe feather pecking (Rodenburg *et al.,* 2013).

Conclusions

Hens in cage systems have the lowest risk of contracting and transmitting infectious diseases and severe feather pecking. They also suffer fewer fractures during the laying period, which is likely due to the lack of environmental complexity in these systems. However, hens in conventional cages experience extreme behavioural restriction, suffer the poorest musculoskeletal strength of all housing systems, and the highest number of fractures at depopulation. They also experience the highest rate of some non-infectious diseases, including fatty liver and disuse osteoporosis, compared with housing systems which allow greater opportunities for behavioural expression and exercise.

Furnished cages retain the benefits of conventional cages in terms of hygiene and efficiency of production, and offer some benefits of cage-free systems. Behavioural expression is increased due to the provision of perches, claw-shortening devices, enclosed nest sites, and, to a certain extent, substrate. Hens in furnished cages have improved musculoskeletal health compared with those in conventional cages, and suffer the fewest number of fractures over their lifetimes compared to both cage-free and conventional cage systems. While furnished cages offer some provisions for dustbathing, their use varies between different types of furnished cages, and hens are often unable to dustbathe satisfactorily due to the depletion or inadequate provision of dustbathing materials. There is also a very limited ability for hens to forage and ground-scratch. Therefore, while there are some provisions to allow greater behavioural expression than in conventional cages, the hens' full behavioural repertoire is not able to be expressed in furnished cages.

Cage-free systems have the potential to allow hens to express their full behavioural repertoire. This is dependent on stocking densities, flooring material and maintenance, as well as the provision of adequate resources including suitable enclosed nesting sites and ample perch space. Foraging, ground-scratching and dustbathing in particular are able to be fully expressed in cage-free systems: these activities are impossible for hens to perform in conventional cages, and are very limited in furnished cages. Hens in cage-free systems have the best musculoskeletal health, a decreased incidence of osteoporosis, and fewer fractures which occur during depopulation. However, the larger group sizes and ability to perform a greater variety of behaviours also contribute to the shortcomings of cage-free housing systems. Two of the biggest welfare concerns in cage-free systems is the extent to which infectious diseases and severe feather pecking can occur. Another factor which affects welfare is the higher incidence of fractures incurred during the laying period.

The incidence of fractures may be addressed by good design, placement and management of structures in the shed. Genetic selection programmes should also be utilised to decrease the sensitivity of hens to osteoporosis and fractures. Similarly, the risk of severe feather pecking may be mitigated by good management practices including adequate diets, suitable environmental enrichment, minimising stress, matching the rearing and laying environments, and pairing this with genetic selection. The risk of infectious diseases may be mitigated by health management practices encompassing biosecurity, vaccination and hygiene programmes.

The main risks to hen welfare in cage-free systems are, at present, highly variable, and need to be addressed by management practices, robust welfare standards, genetic selection, and further research. Conversely, the extreme behavioural restriction that hens experience in conventional cages cannot be mitigated. Since the introduction of conventional cages, the scientific assessment of animal welfare has advanced. A major focus for animal welfare science in the future will be the promotion of positive affective experiences while avoiding negative experiences. While cages can allow greater control over the environment and bird health, the full impact on the welfare of the hens needs to be considered. The opportunity to perform behaviours which hens are motivated to perform is central to the experience of positive welfare states.

Science should have a very prominent role in underpinning decisions on animal use and the conditions under which animals are kept. Many countries have established scientific committees and independent animal welfare advisory bodies to ensure that the development of animal welfare standards are science-based, and many have instituted legislated phase-outs of conventional cages. The Australian Productivity Commission concluded that the current standards-setting process is not adequate and recommended that an independent body be established to develop farm animal welfare standards. However, while it is purported that the standards reflect contemporary scientific knowledge, there is no scientific review, nor scientific committee to inform the development of these standards, and conventional cages are permitted with no phase-out proposed.

References

ANIMAL HEALTH AUSTRALIA (2016) Poultry Standards and Guidelines Q&A Poultry Australian Animal Welfare Standards and Guidelines Questions and Answers. http://www.animalwelfarestandards.net.au/poultry, accessed 4 July 2017.

APPLEBY, M.C. and HUGHES, B.O. (1991) Welfare of laying hens in cages and alternative systems: environmental, physical and behavioural aspects. *World's Poultry Science Journal* **47**: 109-128.

APPLEBY, M.C., WALKER, A.W., NICOL, C.J., LINDBERG, A.C., FREIRE, R., HUGHES, B.O. and ELSON, H.A. (2002) Development of furnished cages for laying hens. *British Poultry Science* **43**: 489-500.

AUSTRALIAN GOVERNMENT PRODUCTIVITY COMMISSION (2016) Regulation of Australian Agriculture, Productivity Commission Inquiry Report. http://www.pc.gov.au/inquiries/completed/agriculture/report, accessed 11 July 2017.

BESSEI, W. and KJAER, J. (2015) Feather pecking in layers - State of research and implications, in: *26th Annual Australian Poultry Science Symposium* **26**: 214-221.

BESTMAN, M., KOENE, P. and WAGENAAR, J.P. (2009) Influence of farm factors on the occurrence of feather pecking in organic reared hens and their predictability for feather pecking in the laying period. *Applied Animal Behaviour Science* **121**: 120-125.

BLOKHUIS, H.J. (1983) The relevance of sleep in poultry. *World's Poultry Science Journal* **39**: 32-37.

BLOKHUIS, H.J. (1984) Rest in poultry. *Applied Animal Behaviour Science* **12**: 289-303.

BRACKE, M.B.M. and HOPSTER, H. (2006) Assessing the importance of natural behavior for animal welfare. *Journal of Agricultural and Environmental Ethics* **19**: 77-89.

BROOM, D.M. (1986) Indicators of poor welfare. *British Veterinary Journal* **142**: 524-526.

CHAUVE, C. (1998) The poultry red mite *Dermanyssus gallinae* (De Geer, 1778): current situation and future prospects for control. *Veterinary Parasitology* **79**: 239-245.

COOPER, J.J. and ALBENTOSA, M.J. (2003) Behavioural priorities of laying hens. *Avian and Poultry Biology Reviews* **14**: 127-149.

COOPER, J.J. and APPLEBY, M.C. (2003) The value of environmental resources to domestic hens. A comparison of the work rate for food and for a nest as a function of time. *Animal Welfare* **12**: 39-52.

CORDINER, L.S. and SAVORY, C.J. (2001) Use of perches and nestboxes by laying hens in relation to social status, based on examination of consistency of ranking orders and frequency of interaction. *Applied Animal Behaviour Science* **71**: 305-317.

CRONIN, G.M., BARNETT, J.L. and HEMSWORTH, P.H. (2012) The importance of pre-laying behaviour and nest boxes for laying hen welfare: a review. *Animal Production Science* **52**: 398-405.

DAWKINS, M.S. (1981) Priorities in the cage size and flooring preferences of domestic hens. *British Poultry Science* **22**: 255-263.

DONALDSON, C.J. and O'CONNELL, N.E. (2012) The influence of access to aerial perches on fearfulness, social behaviour and production parameters in free-range laying hens. *Applied Animal Behaviour Science* **142**: 51-60.

DOWNING, J.A. and BRYDEN, W.L. (2008) Determination of corticosterone concentrations in egg albumen: A non-invasive indicator of stress in laying hens. *Physiology & Behaviour* **95**: 381-387.

DUNCAN, I.J.H. (2001) The pros and cons of cages. *World's Poultry Science Journal* **57**: 381-390.

EFSA (2005) Welfare aspects of various systems for keeping laying hens. *EFSA Journal* **197**: 1-23.

EFSA (2015) Scientific Opinion on welfare aspects of the use of perches for laying hens. *EFSA Journal* **13**: 1-70.

EKESBO, I. (2011) Domestic Fowl (Gallus gallus domesticus). In: Farm animal behaviour, characteristics for assessment of health and welfare CABI, Wallingford, England, UK, pp.105-112.

ENGEL, J., WIDOWSKI, T., TILBROOK, A. and HEMSWORTH, P. (2011) Further investigation of non-invasive measures of stress in laying hens. Proceedings of the 22nd Annual Australian Poultry Science Symposium, Sydney, New South Wales, 14-16th February, **22**: 126-129.

ENNEKING, S.A., CHENG, H.W., JEFFERSON-MOORE, K.Y., EINSTEIN, M.E., RUBIN, D.A. and HESTER, P.Y. (2012) Early access to perches in caged White Leghorn pullets. *Poultry Science* **91**: 2114-2120.

FLEMING, R.H., MCCORMACK, H.A., MCTEIR, L. and WHITEHEAD, C.C. (2005) Nutritional and genetic interactions in avian osteoporosis. *Proceedings of the 15th European Symposium on Poultry Nutrition*, Balatonfured, Hungary, 25-29 September, 2005, p.45.

FLEMING, R.H., MCCORMACK, H.A., MCTEIR, L. and WHITEHEAD, C.C. (2006) Relationships between genetic, environmental and nutritional factors influencing osteoporosis in laying hens. *British Poultry Science* **47**: 742-755.

FOSSUM, O., JANSSON, D.S., ETTERLIN, P.E. and VÅGSHOLM, I. (2009) Causes of mortality in laying hens in different housing systems in 2001 to 2004. *Acta Veterinaria Scandinavica* **51**: 1-9.

FRASER, D. (2003) Assessing animal welfare at the farm and group level: the interplay of science and values. *Animal Welfare* **12**: 433-443.

FRASER, D., DUNCAN, I.J.H., EDWARDS, S.A., GRANDIN, T., GREGORY, N.G., GUYONNET, V., HEMSWORTH, P.H., HUERTAS, S.M., HUZZEY, J.M., MELLOR, D.J., MENCH, J.A., SPINKA, M. and WHAY, H.R. (2013) General Principles for the welfare of animals in production systems: The underlying science and its application. *Veterinary Journal* **198**: 19-27.

GUNNARSSON, S., KEELING, L. and SVEDBERG, J. (1999) Effect of rearing factors on the prevalence of floor eggs, cloacal cannibalism and feather pecking in commercial flocks of loose housed laying hens. *British Poultry Science* **40**: 12-18.

GUNNARSSON, S., MATTHEWS, L., FOSTER, T. and TEMPLE, W. (2000) The demand for straw and feathers as litter substrates by laying hens. *Applied Animal Behaviour Science* **65**: 321-330.

HARTCHER, K.M., TRAN, K.T.N., WILKINSON, S.J., HEMSWORTH, P.H., THOMSON, P.C. and CRONIN, G.M. (2015) The effects of environmental enrichment and beak-trimming during the rearing period on subsequent feather damage due to feather-pecking in laying hens. *Poultry Science* **94**: 852-859.

HARTCHER, K., WILKINSON, S., HEMSWORTH, P. and CRONIN, G. (2016) Severe feather-pecking in non-cage laying hens and some associated and predisposing factors: a review. *World's Poultry Science Journal* **72**: 103-114.

HEERKENS, J.L.T., DELEZIE, E., RODENBURG, T.B., KEMPEN, I., ZOONS, J., AMPE, B. and TUYTTENS, F.A.M. (2016) Risk factors associated with keel bone and foot pad disorders in laying hens housed in aviary systems. *Poultry Science* **95**: 482-488.

HEMSWORTH, P.H., MELLOR, D.J., CRONIN, G.M. and TILBROOK, A.J. (2015) Scientific assessment of animal welfare. *New Zealand Veterinary Journal* **63**: 24-30.

HESTER, P.Y. (2014) The effect of perches installed in cages on laying hens. *World's Poultry Science Journal* **70**: 247-264.

HUBER-EICHER, B. and SEBÖ, F. (2001) Reducing feather pecking when raising laying hen chicks in aviary systems. *Applied Animal Behaviour Science* **73**: 59-68.

HUGHES, B.O. and DUNCAN, I.J.H. (1988) The notion of ethological 'need', models of motivation and animal welfare. *Animal Behaviour* **36**: 1696-1707.

HUGHES, B.O., DUNCAN, I.J.H. and BROWN, M.F. (1989) The performance of nest building by domestic hens: is it more important than the construction of a nest? *Animal Behaviour* **37**: 210-214.

HUGHES, B.O. and GENTLE, M.J. (1995) Beak trimming of poultry: its implications for welfare. *World's Poultry Science Journal* **51**: 51-61.

JANCZAK, A.M. and RIBER, A.B. (2015) Review of rearing-related factors affecting the welfare of laying hens. *Poultry Science* **94**: 1454-1469.

JIANG, S., HESTER, P.Y., HU, J.Y., YAN, F.F., DENNIS, R.L. and CHENG, H.W. (2014) Effect of perches on liver health of hens. *Poultry Science* **93**:1618-1622.

KAUFMAN-BART, M.H. and HOOP, R.K. (2009) Diseases in chicks and laying hens during the first 12 years after battery cages were banned in Switzerland. *The Veterinary Record* **164**: 203-207.

KJAER, J.B. and BESSEI, W. (2013) The interrelationships of nutrition and feather pecking in the domestic fowl - a review. *Archiv für Geflügelkunde* **77**: 1-9.

KNIERIM, U. (2006) Animal welfare aspects of outdoor runs for laying hens: a review. *NJAS - Wageningen Journal of Life Sciences* **54**: 133-145.

LAY, D.C., FULTON, R.M., HESTER, P.Y., KARCHER, D.M., KJAER, J.B., MENCH, J., MULLENS, B.A., NEWBERRY, R.C., NICOL, C.J., O'SULLIVAN, N.P. and PORTER, R.E. (2011) Hen welfare in different housing systems. *Poultry Science* **90**: 278-294.

LAYWEL (2006) LayWel - Overall strengths and weaknesses of each defined housing system for laying hens, and detailing the overall welfare impact of each housing system.

LEONE, E.H. and ESTEVEZ, I. (2008) Use of space in the domestic fowl: separating the effects of enclosure size, group size and density. *Animal Behaviour* **76**: 1673-1682.

MARTIN, M. (2011) Biosecurity and disease control - the problems defined, in: OWEN, R.L. (Ed.) *A Practical Guide for Managing Risk in Poultry Production*, pp.1-11 (American Association of Avian Pathologists, Jacksonville, North Carolina, USA).

MCADIE, T. and KEELING, L. (2000) Effect of manipulating feathers of laying hens on the incidence of feather pecking and cannibalism. *Applied Animal Behaviour Science* **68**: 215-229.

MELLOR, D. (2013) Setting the scene: When coping is not enough: promoting positive welfare states in animals. Proceedings of the 2013 RSPCA Australia Scientific Seminar. When coping is not enough: promoting positive welfare states in animals, Canberra, ACT, Australia, 26 February 2013, pp.2-13.

MELLOR, D.J. (2016) Updating animal welfare thinking: moving beyond the "Five Freedoms" towards "a life worth living". *Animals* **6**: 1-20.

MELLOR, D. and BEAUSOLEIL, N. (2015) Extending the 'Five Domains' model for animal welfare assessment to incorporate positive welfare states. *Animal Welfare* **24**: 241-253.

MELLOR, D.J. and REID, C.S.W. (1994) Concepts of animal well-being and predicting the impact of procedures on experimental animals, in: BAKER, R., JENKIN, G. & MELLOR, D.J. (Eds) *Improving the well-being of animals in the research environment*, pp. 3-18 (Australian and New Zealand Council for the Care of Animals in Research and Teaching: Glen Osmond, SA, Australia).

MELLOR, D.J. and WEBSTER, J.R. (2014) Development of animal welfare understanding drives change in minimum welfare standards. *Revue Scientifique et Technique (International Office of Epizootics)* **33**: 121-130.

NEWBERRY, R.C. (2004) Cannibalism, in: PERRY, G.C. (Ed.) *Welfare of the Laying Hen*, pp. 239-259 (CABI Publishing, Wallingford, UK).

NICOL, C.J. (1987) Behavioural responses of laying hens following a period of spatial restriction. *Animal Behaviour* **35**: 1709-1719.

OLSSON, I.A.S. and KEELING, L.J. (2002) The push-door for measuring motivation in hens: Laying hens are motivated to perch at night. *Animal Welfare* **11**: 11-19.

OLSSON, I.A.S. and KEELING, L.J. (2005) Why in earth? Dustbathing behaviour in jungle and domestic fowl reviewed from a Tinbergian and animal welfare perspective. *Applied Animal Behaviour Science* **93**: 259-282.

PICKEL, T., SCHRADER, L. and SCHOLZ, B. (2011) Pressure load on keel bone and foot pads in perching laying hens in relation to perch design. *Poultry Science* **90**: 715-724.

POTZSCH, C.J., LEWIS, K., NICOL, C.J. and GREEN, L.E. (2001) A cross-sectional study of the prevalence of vent pecking in laying hens in alternative systems and its associations with feather pecking, management and disease. *Applied Animal Behaviour Science* **74**: 259-272.

RODENBURG, T.B., TUYTTENS, F.A.M., DE REU, K., HERMAN, L., ZOONS, J. and SONCK, B. (2008) Welfare assessment of laying hens in furnished cages and non-cage systems: an on-farm comparison. *Animal Welfare* **17**: 363-373.

RODENBURG, T.B., TUYTTENS, F.A.M., SONCK, B., DE REU, K., HERMAN, L., and ZOONS, J. (2005) Welfare, health, and hygiene of laying hens housed in furnished cages and in alternative housing systems. *Journal of Applied Animal Welfare Science* **8**: 211-226.

RODENBURG, T.B., VAN KRIMPEN, M.M., DE JONG, I.C., DE HAAS, E.N., KOPS, M.S., RIEDSTRA, B.J., NORDQUIST, R.E., WAGENAAR, J.P., BESTMAN, M. and NICOL, C.J. (2013) The prevention and control of feather pecking in laying hens: identifying the underlying principles. *World's Poultry Science Journal* **69**: 361-374.

ROMANOV, M.N. and WEIGEND, S. (2001) Analysis of genetic relationships between various populations of domestic and jungle fowl using microsatellite markers. *Poultry Science* **80**: 1057-1063.

SAVORY, C. (1995) Feather pecking and cannibalism. *World's Poultry Science Journal* **51**: 215-219.

SCHOLZ, B., KJAER, J.B., PETOW, S. and SCHRADER, L. (2014) Dustbathing in food particles does not remove feather lipids. *Poultry Science* **93**: 1877-1882.

SCOTT, G.B., LAMBE, N.R. and HITCHCOCK, D. (1997) Ability of laying hens to negotiate horizontal perches at different heights, separated by different angles. *British Poultry Science* **38**: 48-54.

SHIMMURA, T., EGUCHI, Y., UETAKE, K. and TANAKA, T. (2008) Comparison of behavior, physical condition and performance of laying hens in four molting methods. *Animal Science Journal* **79**: 129-138.

TAUSON, R. (2005) Management and housing systems for layers-effects on welfare and production. *Proceedings of the Nutrition Society* **61**: 477-490.

WEBSTER, A.B. (2004) Welfare implications of avian osteoporosis. *Poultry science* **83**: 184-192.

WEEKS, C.A. and NICOL, C.J. (2006) Behavioural needs, priorities and preferences of laying hens. *World's Poultry Science Journal* **62**: 296-307.

WEITZENBÜRGER, D., VITS, A., HAMANN, H. and DISTL, O. (2005) Effect of furnished small group housing systems and furnished cages on mortality and causes of death in two layer strains. *British Poultry Science* **46**: 553-559.

WIDOWSKI, T., CLASSEN, H., NEWBERRY, R., PETRIK, M., SCHWEAN-LARDNER, K., COTTEE, S. and COX, B. (2013) Code of practice for the care and handling of pullets, layers and spent fowl: Poultry (layers). Review of scientific research on priority areas.

WIDOWSKI, T.M. and DUNCAN, I.J. (2000) Working for a dustbath: are hens increasing pleasure rather than reducing suffering? *Applied Animal Behaviour Science* **68**: 39-53.

WIDOWSKI, T.M., HEMSWORTH, P.H., BARNETT, J.L. and RAULT, J.-L. (2016) Laying hen welfare I. Social environment and space. *World's Poultry Science Journal* **72**: 333-342.

YAN, F.F., HESTER, P.Y. and CHENG, H.W. (2014) The effect of perch access during pullet rearing and egg laying on physiological measures of stress in White Leghorns at 71 weeks of age. *Poultry Science* **93**: 1318-1326.

YUE, S. and DUNCAN, I.J.H. (2003) Frustrated nesting behaviour: relation to extra-cuticular shell calcium and bone strength in White Leghorn hens. *British Poultry Science* **44**: 175-181.

ZIMMERMAN, P.H., KOENE, P. and VAN HOOFF, J.A. (2000) Thwarting of behaviour in different contexts and the gakel-call in the laying hen. *Applied Animal behaviour Science* **69**: 255-264.