

A review of environmental enrichment for laying hens during rearing in relation to their behavioral and physiological development

D. L. M. Campbell,^{*,†,1} E. N. de Haas,[‡] and C. Lee^{*,†}

^{*}Commonwealth Scientific and Industrial Research Organisation (CSIRO), Agriculture and Food, Armidale, NSW 2350, Australia; [†]Adjunct to School of Environmental and Rural Science, University of New England, Armidale, NSW 2350, Australia; and [‡]Behavioural Ecology Group and Adaptation Physiology Group, Department of Animal Science, Wageningen University and Research, 6700 AH, Wageningen, the Netherlands

ABSTRACT Globally, laying hen production systems are a focus of concern for animal welfare. Recently, the impacts of rearing environments have attracted attention, particularly with the trend toward more complex production systems including aviaries, furnished cages, barn, and free-range. Enriching the rearing environments with physical, sensory, and stimulatory additions can optimize the bird's development but commercial-scale research is limited. In this review, "enrichment" is defined as anything additional added to the bird's environment including structurally complex rearing systems. The impacts of enrichments on visual development, neurobehavioral development, auditory stimulation, skeletal development, immune function, behavioral development of fear and pecking, and specifically pullets destined for free-range systems are summarized and areas for future research identified. Visual enrichment and auditory stimulation may enhance neural development but specific mechanisms of impact and suitable commercial enrichments still need eluci-

dating. Enrichments that target left/right brain hemispheres/behavioral traits may prepare birds for specific types of adult housing environments (caged, indoor, outdoor). Similarly, structural enrichments are needed to optimize skeletal development depending on the adult layer system, but specific physiological processes resulting from different types of exercise are poorly understood. Stimulating appropriate pecking behavior from hatch is critical but producers will need to adapt to different flock preferences to provide enrichments that are utilized by each rearing group. Enrichments have potential to enhance immune function through the application of mild stressors that promote adaptability, and this same principle applies to free-range pullets destined for variable outdoor environments. Complex rearing systems may have multiple benefits, including reducing fear, that improve the transition to the layer facility. Overall, there is a need to commercially validate positive impacts of cost-effective enrichments on bird behavior and physiology.

Key words: neuro, pecking, fear, immune, free-range, skeletal

2019 Poultry Science 98:9–28
<http://dx.doi.org/10.3382/ps/pey319>

INTRODUCTION

Laying hen production systems are a global focus of concern for animal welfare. Conventional caging systems can, for example, restrict behavioral expression and increase risks of skeletal degradation (Whitehead and Fleming, 2000), whereas newer non-cage (aviaries, barns, free-range) or furnished cage systems (all collectively termed "alternative housing systems") may, for

example, increase feather pecking, incidences of skeletal injuries, and mortality (Lay et al., 2011; Weeks et al., 2016). Thus, much research has focused on how birds behave and perform in different housing systems and what modifications in system design and management can be made to improve hen welfare. Recently, there has been increasing focus on the impacts of the rearing environment on long-term behavior, health, and welfare of layers. Stress experienced during the rearing period can have short-term as well as long-term and transgenerational negative impacts (Ericsson et al., 2016). Janczak and Riber (2015) reviewed varying management modifications and environmental parameters during rearing such as beak trimming, lighting, perches, stocking density, feed, and air quality, recognizing the long-term impacts of rearing conditions through lay. The importance of optimizing rearing periods, particularly for birds going into alternative housing systems, has been similarly highlighted previously (Häne et al., 2000;

© The Author(s) 2018. Published by Oxford University Press on behalf of Poultry Science Association. This is an Open Access article distributed under the terms of the Creative Commons Attribution Non-Commercial License (<http://creativecommons.org/licenses/by-nc/4.0/>), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is properly cited. For commercial re-use, please contact journals.permissions@oup.com

Received February 22, 2018.

Accepted June 28, 2018.

¹Corresponding author: dana.campbell@csiro.au

Staack et al., 2007; Colson et al., 2008; Leenstra et al., 2014). Data indicate that for optimal welfare and productivity of layers, it is best to match the rearing housing system with the layer housing system (Janczak and Riber, 2015). Modifications can also be made during rearing to best prepare birds for an optimal laying cycle.

Environmental enrichment is a potential method for improving bird development. A frequently used definition of enrichment stated by Newberry (1995) is “improvement in the biological functioning of captive animals resulting from modifications to their environment”. This definition highlights the important distinction between environmental enrichment that has a demonstrable impact on the animals versus environmental change—modifications that lead to no quantifiable improvements but are anthropomorphically included (Newberry, 1995). Enrichments should have impact by increasing the performance of natural behavior, reducing the incidences of abnormal and damaging behavior, reducing negative emotional states, improving physical health, and improving the use of the provided environmental resources (Newberry, 1995). To further build on this, and important for commercial poultry production, enrichments must also be economically and practically feasible. This includes having no adverse impacts on the animals, such as increasing rates of injury, posing hygiene risks (Van de Weerd and Day, 2009) or reducing consumption of formulated feed (e.g., a consumable pecking toy is eaten instead) which is needed to maintain high levels of production. Some types of “enrichment” for layers may be considered as a basic necessity, such as litter to forage in, perches to roost on, and nest boxes to lay in. But these are not always present in all housing systems, and the conventional system for laying hens is a cage with no additional provisions. Thus, in comparison to a simple cage environment, even provisions of basic items could be considered as “enrichments” in poultry production. Newberry (1995) also highlighted the importance of experiences during rearing periods, where modifications of certain behavioral traits may be more difficult, and enrichments less relevant, if applied after the ontogenetic periods in which certain behaviors may develop and mature (Rogers, 1993; Johnsen et al., 1998; Gunnarsson et al., 2000). Similarly, physiological benefits such as improved musculoskeletal strength are likely to be greater when environmental modifications are applied during growth and physical development.

Laying hens are descendants of the red junglefowl, and although the domestication process has both differentiated the modern laying hen from its ancestors and differentiated between strains of modern layers, the basic biology and behavior of the fowl remains similar. Behaviorally, the needs, priorities, and preferences of the modern hen are to perch, nest, forage, and dust bathe (reviewed in Weeks and Nicol, 2006). Time engaged in some behaviors within commercial strains,

such as foraging (Campbell et al., 2017a), is different to what has been documented in semi-wild populations of junglefowl, potentially resulting from different energetic investments by the high-producing modern layer (Dawkins, 1989; Schütz and Jensen, 2001). High levels of damaging behaviors such as feather pecking and cannibalism are also seen in alternative housing systems (Fossum et al., 2009; Weeks et al., 2016; Singh et al., 2017). This suggests the current environments are not meeting the needs of the birds, exacerbating the prevalence of undesirable behavior. Similarly, the high rates of injuries such as keel fractures suggest that the modern hen is not physically suited to structurally complex housing, or that the artificial environment is not suitably designed based on the modern hens locomotor and flying skills (Wilkins et al., 2011; Campbell et al., 2016a), and that hens are potentially inadequately reared for such environments.

Currently, pullets are reared in all types of housing systems including conventional cages, furnished cages, aviaries, and floor-based systems. The latter 2 systems may include covered or uncovered outdoor access and floor-based system may use litter, slats, and perches in varying configurations. Typically, day-old chicks are transferred from the hatchery to a rearing farm, and then transferred around 16 wk to a similar variety of layer housing systems. Generally producers will try to match type of rearing facility with the type of layer facility (Janczak and Riber, 2015) but this is not always possible. Complex rearing systems are commercially available which are designed to stimulate navigation and locomotor skills of the birds, and thereby improve muscle and bone strength of pullets by having different levels of height in the rearing system. However, cost of these systems may restrict their wide use and simple cost-effective enrichments could be particularly valuable to smaller scale producers. Several countries have banned the use of conventional cages (e.g., Switzerland from 1992, Austria from 2009, European Union from 2012), and producers are phasing out cages to meet consumer demands for perceived more welfare-friendly eggs. Thus, there is an increasing use of alternative rearing and layer systems that both allow and require more from the birds in terms of physical effort and/or behavioral capabilities than a conventional caged system. Improving animal welfare is a key focus for both quality of life for the birds and for improvements in their health and productivity. Enrichments during rearing offer the potential to enhance bird development to suit alternative systems. Some current welfare standards such as the Australian and UK RSPCA pullet rearing standards (RSPCA Australia 2015; RSPCA UK 2016) require pecking enrichments, perches and litter, or accessible ground area and many producers may already implement enrichments that they have found to be or are believed to be beneficial to the birds. A critical evaluation of tested enrichments within the literature and identification of gaps in knowledge for future research is necessary to identify enrichment schemes which have

quantifiable impact on bird behavior and health for improved welfare.

This review expands on the recent review by Janczak and Riber (2015) that detailed effects of some enrichments by focusing on the sensory, physical, and behavioral development of laying hen pullets and how enrichments can impact in these areas of biology. Enrichments are classed as any environmental modifications that have demonstrable impacts on the birds including perches, toys, furnishings, and more complex alternative rearing systems. Although the genetic selection processes continually modify the characteristics of current layers and thus enrichments may impact new strains in different ways, dated research is included if there are a lack of recent studies. References to broiler studies are included in some cases where the general biological functioning is also applicable to layers. The first section details visual capabilities as this is a critical sense for chickens.

Visual Development

Chickens are prey animals and thus vision is a critical sense that is necessary for optimal navigation within commercial housing systems. Briefly, chickens have excellent color vision including the ultraviolet spectrum (Olsson et al., 2015), limited depth perception (Dawkins, 1995, 1996), and moving objects are perceived easier than stationary objects (Broom, 1969). Their visual capabilities extend beyond that of humans with a more detailed overview of abilities and preferences provided by Nicol (2015) and Prescott et al. (2004). Lighting conditions during rearing play a key role for visual development. Dim light, very short, or very long continuous photoperiods can hamper the ability of chicks to focus (Lewis and Gous, 2009) and low illuminance can also cause myopia (short-sightedness) (Cohen et al., 2008, 2011). However, high light intensity is also strongly correlated with development of feather pecking, confounding use of higher intensities in commercial systems (Janczak and Riber, 2015).

The use of other visual stimuli during rearing to stimulate neural development and adult visual capabilities is less well studied. Chicks have an innate attraction for objects or stimuli which move in a biological motion (Regolin et al., 2000) both as they appear in real-life (Broom, 1969) and from a display (Vallortigara et al. 2005; Vallortigara and Regolin, 2006). In young chicks, exposure to visual objects that spontaneously change speed increased neuronal activity compared to chicks shown objects of constant speed (Lorenzi et al., 2017). Visual pattern stimulation in the first week of life also increased GABA receptor density in the optic lobe when compared to no pattern stimulation (Fischer de Plazas et al., 1991). Thus, visual stimulation during rearing for laying hens likely has consequences for neural development, including lateralization (discussed in *Neurobehavioral development*) but feasible implemen-

tation within a commercial system needs to be determined.

Chickens are able to perceive images from video, such as food items, conspecifics, predators, and moving vs. static images. At day 1 after hatch, chicks peck at insect-like features from a video screen with preferences for sideways-moving over forward-moving insects (Clara et al., 2009). Chicks alter their feeding behavior when viewing video showing conspecifics feeding from a specific food dish or a predator-like stimulus (Keeling and Hurnik, 1993; Dharmaretnam and Rogers, 2005). Chicks are also able to recognize conspecifics on video by approaching the screen over an image of a goal box (Clarke and Jones, 2001). Video images such as screensaver programs displayed within the home environment attract chicks attention over periods of several days where mild to moderate novelty is preferred (Jones et al., 1996). However, optimal discrimination of images occurs at a distance of 5 to 25 cm and not beyond 120 cm (Dawkins and Woodington, 1997). Video imaging could be suitable as environmental enrichment acting to improve welfare and reduce damaging behavior (Jones, 2004), but this method is still yet to be validated for any positive impacts on a commercial scale.

Overall, the research on commercial application of visual enrichment is limited. Visual objects would need to be accessible in close proximity to the birds, with moving images likely preferred over static images. The scope for use of robotic birds in rearing facilities is increasing and represents a fascinating opportunity for behavioral research. The use of stimulatory color and patterns (painted static) which are relatively simple to implement within commercial facilities and any subsequent impacts on visual abilities and neural development do warrant further investigation. Visual stimulation during rearing may be particularly beneficial for birds destined for free-range access (see the section *Free-range hens: indoor rearing for outdoor access*). Visual stimulation is also inextricably linked to neurobehavioral development and brain lateralization as detailed in the following section.

Neurobehavioral Development

Scientific evidence is accumulating that chickens have far greater cognitive capacity than previously assumed (Marino, 2017; Garnham and Løvlie, 2018). The domestic fowl has shown cognitive, social, and emotional intelligence on par with many other bird or mammalian species (reviewed in Marino, 2017; Garnham and Løvlie, 2018). In evolutionary terms, this may be expected given that junglefowl ancestors live in spatially complex environments with established territories and social hierarchies (Collias et al., 1966; Collias and Collias, 1967). Environments with simple rearing systems such as floor litter barns or cages are likely not cognitively stimulating or spatially complex enough to adapt pullets to navigate in aviary or outdoor laying systems.

Recent evidence shows that birds that roost far from pop holes that provide entry to the outdoor area are less likely to access the range during the day (Pettersson et al., 2017a). These results could indicate that these birds lack spatial cognitive skills which helps them to navigate through different areas indoors and outdoors, or that they require greater cognitive skills because of their location within the shed. This suggestion is supported by studies which show that range use is correlated with individual performance in spatial tasks (Campbell et al., 2018a). Additionally, accurate navigation of elevated tiers requires well-developed spatial skills, acquired during early rearing experience with perches (Gunnarsson et al., 2000). A general lack of competence may contribute to the high levels of abnormal behavior, injuries, and mortality seen within alternative housing systems.

Domestic fowl, as many other bird species, have a lateralized brain (reviewed in Rogers, 2008). Different hemispheres are able to function relatively independently to confer advantages such as being able to forage for food and be vigilant for predators simultaneously (Rogers et al., 2004; Dharmaretnam and Rogers, 2005), with most neurobehavioral research focused specifically on visual processing. The asymmetry of the thalamofugal visual system is transient, and no longer present after the first 3 wk post-hatch (Rogers, 2008) and is markedly more prominent in male chicks (Rogers, 1997). However, the same basic pattern of hemispheric asymmetry is similarly present in adults as in chicks (McKenzie et al., 1998; Dharmaretnam et al., 2002). The left hemisphere processes visual cues such as landmarks and categorizes stimuli to distinguish objects and focus attention (Della Chiesa et al., 2006a,b; Vallortigara et al., 1996; Tommasi and Vallortigara, 2001, 2004; Rogers 2012). The right hemisphere is important for recognition of individual conspecifics, responses to environmental or sensory novelty, paying attention to the unexpected, and environmental stimuli on a broad level (Vallortigara and Andrew, 1994; Regolin and Vallortigara, 1996; Daisley et al., 2009; Rogers, 2012). Therefore, the right hemisphere is predominant in fear responses (Daisley et al., 2009). Table 1 in Rogers (2014) provides a good summary of the hemispheric differences.

Chicks show distinct behavioral changes within the first few weeks of life, which correspond to the developmental time course of which eye/hemisphere is used in their lateralized brain (summarized in table 2 of Rogers, 2014). On day 8, there is a bias for the left hemisphere to control responses, with a change to the right hemisphere by day 10/11 (Andrew, 1988; Regolin and Vallortigara, 1996). There are sex differences between male and female chicks with typically reduced lateralization in female chicks, but with consistency in responses between strains (Workman and Andrew, 1989; Vallortigara et al., 1997). However, visual lateralization differences are, to some degree, more distinct in birds that are incubated with exposure to light in the final

days of development. This reflects the process in nature where the mother hen periodically leaves her eggs during the final stages of incubation. Light can enter the egg through the right eye into the left hemisphere only, resulting in asymmetry of the thalamofugal visual projections (Koshihara et al., 2003). Dark-incubated layer chicks do not display the same degree of lateralization (Rogers, 1990) which can result in poorer task performance (Rogers et al., 2004; Dharmaretnam and Rogers, 2005; Chiandetti et al., 2017). However, the timing of when and for how many hours that light should be present during incubation (many hatcheries dark-incubate), and the subsequent long-term effects in commercial rearing situations for layers are unknown. Some positive effects of light during incubation on health and responses to stress and fear have been demonstrated in broiler chicks (Archer et al., 2009; Huth and Archer, 2015; Archer and Mench, 2017).

Brain lateralization can play a direct role in animal welfare, and neurological measures could be used for welfare assessment (Rogers, 2010; Nordquist et al., 2013). Rogers (2010) hypothesized that stressed animals may rely more on the right hemisphere that attends to novelty and fear, and that lateralization differences could be the cause of differences in cognitive biases. Rogers (2010) also discussed the potential for early developmental experience to play a long-term role in the development of hemispheric control. Greater lateralization in the hippocampus was detected in adult hens at 52 wk of age, following rearing for the first 7 wk of life without a foster hen, compared to birds reared with a foster hen (Nordquist et al., 2013). A left-hemispheric dominance is proposed to be beneficial for animals in captivity (Rogers, 2010). The role of the left hemisphere in positive cognitive bias may specifically suit chronically stressful environments (Rogers, 2010). Early environmental enrichment may be an option for modulating hemispheric control.

Environmental enrichment can enhance neural development of animals (e.g., van Praag et al., 2000). For example, free-range housing with weekly provision of straw from 16 to 48 wk of age increased hippocampal lateralization in adult hens, in comparison with conventional caged or small littered floor pen housing (Patzke et al., 2009). The detected neurological differences resulting from the housing treatments were small but the adult hens' brain remained susceptible to surrounding conditions (Patzke et al., 2009). Housing impacts on brain plasticity would likely be stronger when modifications are present during neuronal and structural formation in early life. The first 3 wk post-hatch are critical periods for hemispheric development in chickens and synapses continue to mature up to 8 to 10 wk post-hatch (Rogers, 1995). Therefore, rearing and provision of enrichments have the potential for long-term neurophysiological impacts. Broiler chicks which could explore in the presence of opaque or transparent screens in the home pen to simulate moving "out of sight" of a mother hen had improved spatial abilities

and orientation toward a visually occluded goal than those chicks reared without visual occlusion experience (Freire et al., 2004). Rearing with or without visual barriers also produced neural changes in the hippocampus (Freire and Cheng, 2004). Day 11 of age is a specific critical period for chicks in visual processing as it coincides with the shift in hemispheric dominance (Freire and Rogers, 2007). Recent evidence showed that exposure to 2 different geometric-shaped environments resulted in increased hippocampal activation in broiler chicks in comparison to control chicks (Mayer et al., 2017).

Spatially complex rearing environments may also improve overall adult fitness as found in other avian species (Lazic et al., 2007; Whiteside et al., 2016). Only a few long-term laying hen studies have looked at the impacts of rearing environments on subsequent cognitive performance and brain plasticity, particularly in commercial settings. Tahamtani et al., (2015) showed that birds reared in an aviary system from 4 to 16 wk compared to rearing in a conventional cage system from 0 to 16 wk had improved spatial performance and short-term spatial memory as adults. However, there were no immunohistological differences in tyrosine hydroxylase intensity (the rate-limiting biosynthesis enzyme for dopamine) detected between cage-reared and aviary-reared birds at adult age in the hippocampus and caudolateral nidopallium (Tahamtani et al., 2016a). All birds were cage-housed in the first 4 wk of life, the period where structural formation takes place. This could have contributed to the lack of neuronal differences. However, the improved spatial performance in aviary-reared hens stipulates that early-life environmental complexity can have long-lasting effects on spatial skills.

Overall, chickens have a demonstrated cognitive capacity above what is often commonly accepted, but current rearing conditions may not be conducive to neural development reaching natural capacity. Controlled studies assessing the impacts of early environmental spatial complexity on subsequent adaptation to and navigation in free-range or aviary housing systems are warranted. Enrichments aimed at targeting different brain hemispheres may enable birds to be better suited to or have improved welfare specifically in different types of outdoor and/or indoor alternative systems. Future studies would aim at assessing the degree of lateralization present in adult birds resulting from dark or light incubation and/or different types of rearing conditions and the positive/negative impacts of hemispheric specializations.

Auditory Development and Stimulation

The majority of the chicken auditory system development occurs in ovo and matures earlier than other sensory systems (Gao and Lu, 2008). Chicks will exhibit responses to sound around embryonic days 11/12 (Saunders et al., 1973). Being a precocial species

(hatched with relative independence and ability to self-feed), chicks hatch with adult-like auditory capabilities. At a level of 60 dB sound pressure, the hearing range for adult chickens is between 9.1 and 7.2 kHz, with optimal sensitivity at 2.6 dB/2 kHz (Hill et al., 2014). In comparison with humans, chickens have better sensitivity for frequencies below 64 Hz. This ability of chickens to detect low frequency sounds may relate to the importance of low-frequency communication between the hen and chicks as these sounds are generally below 800 Hz (Nicol, 2015).

Whether the effects of auditory stimulation on chicken behavior are beneficial or detrimental will depend on the nature of the sound and timing of exposure. Auditory enrichment by means of classical music played to chicks up to 8 wk of age (5 h per day on 3 d per week; maximum 75 dB) altered the heterophil to lymphocyte (H/L) ratio compared to control chicks (no music; 65 dB), which is indicative of reduced stress (Dávila et al., 2011). The same auditory enrichment provided by playing music to adult laying hens did not alter hens' H/L ratio, indicating the importance of timing the enrichment to occur during the rearing period (Campo et al., 2005 but also see Cotter, 2015 for a review on the H/L ratio as an indicator of stress). Fluctuating asymmetry (differences in bilateral skeletal anatomy), used as an indicator of developmental stress (Knierim et al., 2007), was also reduced by rearing chicks post-hatch with music when compared to a control treatment which further supports the positive impacts of classical music during rearing. The effects of auditory enrichments on fear as measured by tonic immobility tests (catatonic state to reduce predation, Forkman et al., 2007) are inconclusive. In the experiments by Dávila et al., (2011) described earlier, no consistent effects of classical music during rearing on tonic immobility were reported. However, Campo et al. (2005) found increased tonic immobility duration in 36-wk-old hens when exposed to classical music in addition to background noise (75 dB) for 5 h/d for 3 d during the laying period, compared to hens just exposed to background noise (65 dB).

Similar to humans and other species, chicks prefer harmonic consonant sound over dissonant sound intervals (Chiandetti and Vallortigara, 2011). This preference has been proposed to be related to the occurrence of harmonic spectra in natural environments (Chiandetti and Vallortigara, 2011). There is evidence from studies in humans that auditory stimulation such as maternal sounds and music can improve learning and memory later in life (Chaudhury et al., 2013). In domestic chicks, exposure to rhythmic maternal hen calls increased memory ability through the release of norepinephrine in the brain (Field et al., 2007). Auditory enrichments can modify neural connectivity in the early period of life leading to enhanced cognitive function. There is evidence that playing specific maternal cluck calls to 15 to 16-day-old chicks reduced their stress response (Edgar et al., 2015). The playback of hen

vocalizations has also been found to increase feed conversion and body weight for the first 9 d of life in broiler chicks (Woodcock et al., 2004). Specific maternal sounds aid chicks in finding food and act to alert others to the presence of threats (Collias and Joos, 1953). Thus, further studies would determine if exposure to auditory stimulation during rearing can have beneficial effects on birds during lay through reducing stress and fearfulness and improving learning and memory, particularly in relation to critical periods of exposure.

While there are beneficial effects of playing some forms of music to chickens (Dávila et al., 2011; Chaudhury et al., 2013), there can be detrimental effects of exposure to high sound levels for poultry in general. A longitudinal study of 22 free-range organic laying farms in the UK found that higher sound levels during rearing (up to 20 wk of age; mean 59.4 dB, range 14.3 to 80.0 dB) were associated with earlier onset of severe feather pecking in laying hens (Drake et al., 2010). It was not clear as to whether the causal effect was related to the noise made by the birds, as birds that vocalize more frequently have a tendency to feather peck (Bright, 2008), or by the environmental noise. Another study of 29 laying hen farms in the UK found that exposure to high sound levels (mean 58.3 dB, range 32 to 66 dB) during rearing was linked to an increased probability of severe feather pecking during lay (Gilani et al., 2013). In this study, the birds themselves were not thought to be the cause of the high sound levels as feather pecking had not developed during rearing. Therefore, it was proposed that the sound was most likely mechanical noise, generated from ventilation fans, mechanical feeder lines, and manure belts. High ambient noise level exposure (90 vs. 65 dB) increased the H: L ratio and tonic immobility in chickens indicating increased stress and fearfulness (Campo et al., 2005). Sound, particularly when loud, has been shown in numerous species including rats, mice, and humans to have detrimental effects on brain connectivity by disrupting neural activity and disturbing functional development of the brain (Chaudhury et al., 2013). During incubation, developing chick embryos can be exposed to loud sounds from the ventilation fans. This extensive sound exposure may have a strong impact on brain development. Noise during incubation has been shown to increase pessimistic judgment in adult hens (Rodenburg et al., 2017). Additionally, thousands of birds reared in enclosed areas may create high noise pollution which could lead to increased stress, or impaired vocal communication in these chicks (Ortega, 2012). While it has been proposed that music may mask background noise and reduce stress in chickens, this was not evident when comparing 65 dB background noise with background noise plus classical music (75 dB) (Campo et al., 2005). Commercial producers have reported using radio playback to mask sudden noises during rearing (e.g., from nearby road traffic) and observe that birds will preferentially congregate around the radio (personal communication to DLMC 2017). But the pre-

cise mechanism of whether auditory enrichment operates by adapting birds to environmental noise, masking environmental noise, or stimulating changes in neural development and/or neurochemical release is not yet clear (Wells, 2009).

Overall, reduced noise (particularly reduced mechanical noise) during rearing appears to be beneficial to birds later in life. Preference testing for sound-attenuated areas within noisy rearing facilities may determine the adaptability of young birds to noise, or if areas of reduced noise could be beneficial. In contrast, exposure to certain forms of music during rearing may be beneficial by reducing stress and possibly reducing fearfulness during lay. Playbacks of sounds that jungle fowl might naturally be exposed to in their forest habitat are a potential sound enrichment to be tested during domestic pullet rearing. However, precise critical periods for exposure are not known. As well, it is not known if the detrimental effects of continuous high sound exposure are due to the impacts of the exposure per se or are related to being less able to detect species-specific sounds. Further studies investigating maternal vocalizations or “clucks” as a form of auditory enrichment during rearing are recommended. These species-specific sounds are used to obtain information about their environment and it is possible that high sound levels may disturb sensory information processes in chicks. Practically, auditory playbacks may be challenging to provide in a commercial environment. Sound from speakers will be masked by the mechanical and bird noise within the facility and will likely only reach birds at a short distance from the speakers. However, intermittent exposure as birds move around the shed (floor-based systems) may still have impacts. Speakers placed within dark brooders may optimize the number of birds exposed to playbacks. Greater investment in speakers may be required for sheds where birds remain in more fixed locations (e.g., caged).

Skeletal Development

There is abundant evidence that laying hens suffer from skeletal issues such as brittle, broken, fractured, or deformed bones (e.g., Whitehead and Fleming, 2000; Lay et al., 2011; Wilkins et al., 2011). The long duration of egg production can deplete calcium from keel, tibial, and humeral bones during the lay cycle reducing bone strength (Whitehead and Fleming, 2000; Whitehead, 2004). These effects appear particularly strong for hens in cages where they have restricted movement opportunities (Webster, 2004). Additionally, hens have higher wing loading (body mass relative to wing area) than their ancestors making them less agile during aerial locomotion (Moinard et al., 2004), which could, in turn, make them more susceptible to injuries. In particular, hens are prone to keel bone fractures, likely resulting from collisions within alternative housing systems (Campbell et al., 2016a; Gebhardt-Henrich et al., 2017).

These fractures are significant welfare and production concerns (Casey-Trott and Widowski, 2016) as they are associated with pain (Nasr et al., 2012, 2013). Bone development occurs throughout the rearing period with a dramatic change in bone structuring during the onset of sexual maturity and beginning of egg production (a detailed description of bone biology can be found in Whitehead, 2004). Activity within alternative housing systems that increases the loading on bones (mechanical stress that stimulates bone formation) will improve bone breaking strength in adult laying hens at the end of lay in comparison to caged hens (Knowles and Broom, 1990; Fleming et al., 1994; Leyendecker et al., 2005; Jendral et al., 2008; Regmi et al., 2016). But birds can also suffer from a higher prevalence of and more severe keel damage at the end of lay in non-cage systems (Wilkins et al., 2011). Perches for adult birds improve bone strength and bone volume during lay compared to cages without perches (Hughes and Wilson, 1993; Barnett et al., 1997 but see Moinard et al., 1998) and fulfill a behavioral need (Weeks and Nicol, 2006). But perches can also be a source of health problems and skeletal injury themselves (Sandilands et al., 2009; Hester, 2014; European Food Safety Authority Animal Health and Welfare Panel (EFSA AHAW), 2015), potentially exacerbated if hens are not competent in navigating them (Gunnarsson et al., 2000; Campbell et al., 2016a).

Perching behavior in domestic laying chicks is observed to begin after 1 wk of age (Kozak et al., 2016). Chicks that perch earlier will also show earlier use of perches for night-time roosting (Heikkilä et al., 2006). Observations of space use in small groups of domestic chicks in an aviary system showed chicks preferred to remain on the ground during the first week of life with minimal use of areas above 70 cm in height (Kozak et al., 2016), typical of a chick's motivation to stay with their mother. Movement and perching on inclined surfaces (ramp/ladder) was observed to peak in wk 2 of age and cease after wk 5 of age across the 9-wk observation period (Kozak et al., 2016). Movement and perching on elevated surfaces (up to 69 cm in height) steadily increased across time (Kozak et al., 2016). Thus, use of structural enrichments such as elevated surfaces during the rearing period is likely critical for young birds to develop appropriate perching behavior resulting in use of provided structural resources that improve bone strength and reduce the risk of later injury.

In conventional cages, the lack of space for movement does reduce the loading on bones, but within such an environment, perches could be a beneficial addition. Enneking et al., (2012) found positive effects of perches in conventional cages on bone mineral content of the tibia, sternum, and humerus in birds aged 12 wk (Enneking et al., 2012). Cage-reared birds with perches showed greater shank width (indicating improved skeletal development) when sampled at 71 wk of age compared to cage-reared birds without perches, even if they were subsequently housed with perches during lay (Yan

et al., 2014). Cage and perch-reared end-of-lay birds showed some increases in keel bone (only) mineralization density compared to cage-reared birds without perches (Hester et al., 2013). However, the presence of perches as adults increased rates of keel damage with no reduction in keel damage for those birds that had perch access during rearing (Hester et al., 2013). Comparisons between cages and non-cage systems showed birds reared on the floor up to 17 wk of age and then transferred to varying furnished cage designs had reduced bone breaking strength of the humerus and tibia as assessed in different birds at 3 different ages across the lay cycle (Vits et al., 2005). The authors noted that floor-reared birds were reluctant to move on the novel wire floor at the beginning of lay which may have resulted in reduced loading on the bones. However, lower bone breaking strength of birds reared on the floor was also reported previously (Gregory et al., 1991). The birds reared on the floor did show lower incidence of keel bone deformities (visual assessment of damage following dissection; Vits et al., 2005). Floor rearing with perches did not lead to keel bone injuries at the end of rear, but also did not prevent a high proportion (56 to 68%) of birds having keel fractures at the end of the lay when housed in single-tier aviaries (Wilkins et al., 2005).

With the increase in birds being housed in alternative layer systems, rearing in alternative systems similar to those used during lay may better physically prepare birds for jumping, flying, and accurate navigation of the system complexities compared to floor or cage rearing. Michel and Huonnic (2003) found higher strength in tibias and humeri of birds reared and housed in aviaries compared to being reared on the floor with perches, and aviary-reared birds used more tiers during lay. Similarly, recent comparisons between multiple structural bone properties and serum markers of bone formation and absorption periodically throughout rearing of pullets from cages and aviaries showed positive effects of aviary-housing on skeletal structure (Regmi et al., 2015). Birds from caged housing were given floor access at 6 wk of age for the aviary-reared group (only) and overall, the load-bearing exercise permitted within the aviary system produced structural and material changes that improved skeletal structure. However, the complexities of the measurements and interactions between housing system and age indicate that more studies are needed to understand the physiological mechanisms behind the impact of exercise on skeletal development for pullets across the rearing period (Regmi et al., 2015). Assessment of skeletal structure of cage-reared and aviary-reared hens from the same flocks after being placed into cage, aviary or furnished systems during lay, indicated the improved bone mass and density acquired during aviary rearing was best maintained in aviary housing that permitted continued exercise opportunities (Regmi et al., 2016). Future study also needs to focus on the differing skeletal developmental impacts as exercise/housing system affects bones in

different ways (Regmi et al., 2015, 2016). For example, tiered systems that require wing-assisted jumping or allow for flight will likely enhance wing bone development more than floor-based systems. Pullets from the same aviary-reared flocks as described in Regmi et al. (2015, 2016) showed more keel abnormalities (injuries and deformities) than those from conventional caged rearing, which continued to increase in greater proportions throughout the lay cycle (Blatchford et al., 2016). These data support recent evidence that keel bone damage and structural bone properties are poorly related (Gebhardt-Henrich et al., 2017).

Recent research across the flock-cycle length highlights the impacts of rearing on incidences of keel bone damage into the production phase. Birds reared in an aviary system or conventional cages were assessed for muscle development at rear and keel bone damage at lay (Casey-Trott et al., 2017a). At 16 wk of age, aviary-reared pullets had higher wing and breast muscle weights compared to cage-reared pullets, but leg muscles were heavier in the cage-reared pullets. The aviary-reared pullets showed improved bone growth factors including total bone density, total bone mineral content, and breaking strength compared to cage-reared pullets (Casey-Trott et al., 2017b). At lay, palpation at 30, 50, and 70 wk of age found significantly lower percentages of keel bone fractures in aviary-reared birds compared to cage-reared birds, irrespective of adult housing system (Casey-Trott et al., 2017a). Rearing system or adult housing system did not impact the prevalence of keel bone deviations (Casey-Trott et al., 2017a). Improved bone quality as a result of aviary rearing was still present at the end of lay with additional impacts of the adult housing system on bone properties (Casey-Trott et al., 2017c).

Perches and the structural elements in furnished and aviary rearing systems are shown to provide benefits to pullets for greater bone strength and mineral content and may protect against later injury in layer housing. Research approaches and practical applications should look to provide structural enrichments in a way that minimizes injury through, for example, soft materials (Pickel et al., 2011; Stratmann et al., 2015), ramp access, and specific ramp design (Heerkens et al., 2016; LeBlanc et al., 2017; Pettersson et al., 2017b). New designs to be used during rearing such as swinging perches or flexible perches may both improve balance and coordination and reduce impact injuries at lay (LeBlanc et al., 2016). More research that focuses on developmental timelines of skeletal changes, including differing impacts on varying bone types and use of alternative rearing systems, or floor-based structural enrichments (e.g., perches, platforms) is needed. These data would help evaluate the most effective system and enrichment designs for protection against skeletal degradation and injury. The impacts of structural elements on the development of spatial cognition and opportunities for birds to rest and escape from other birds on elevated areas should be considered.

Immune Function

Stress can play a pivotal role in the optimal development of the immune system. The complex neuroendocrine response to stressors can reduce the immune response to a pathogen (El-Lethey et al., 2003; Kaiser et al., 2009; Hoerr, 2010) leading to vaccination failure or increased disease during production (Hoerr, 2010; Shini et al., 2010). The precise mechanisms by which this occurs are highly complex by nature and require continuing elucidation (Kaiser et al., 2009; Shini et al., 2010). Chronic experimentally elevated corticosterone during the rearing period can have detrimental effects on multiple aspects of hen physiology including reducing body weight and immune organ weight (spleen and bursa of Fabricius) relative to control birds (Shini et al., 2008, 2009), thus modeling the potential impacts of a stressful rearing phase. However, acute or moderate (dis) stress can be positive (Zulkifli and Siegel, 1995) and may actually benefit immune function by encouraging adaptation and survival mechanisms (Shini et al., 2008, 2010; Dhabhar, 2009). Enrichment thus could be considered as reducing chronic stress by providing resources ethologically favored by chickens (e.g., foraging material, perches), as well as initiating acute stress, perhaps in the form of novel objects or complex spatial environments to learn to navigate. Enrichment could also act to reduce fear (see section on *Behavioral development – Fear*), demonstrably linked to stress (Jones et al., 1988; Fraise and Cockrem, 2006). Conversely, enrichments may not be required to reduce stress, but might instead function to enhance well-being and thus act to augment immune function through positive affective states (humans: Barak, 2006; Jenkins et al., 2018), or increased moderate exercise (reviewed in Walsh et al., 2011).

Experimental evidence for the benefits of enrichments during rearing on immune function comes from comparisons between conventional and furnished cage rearing. Matur et al. (2015, 2016) reared birds from 3 to 17 wk of age in either conventional cages or furnished cages (Matur et al., 2015, 2016). At 17 wk of age, some birds from each rearing condition were subject to stress via social remixing and antigenic stimulation (Matur et al., 2015). Measurements of immune system blood parameters showed, as predicted, the furnished housing reduced the heterophil percentage, H/L ratio, and increased antibody production (Matur et al., 2015). However, liver and spleen weights were not affected by rearing conditions. Hens in the furnished cages also showed higher innate immune responses compared to stressed cage-reared and unstressed furnished-reared hens (Matur et al., 2015) indicating the improved adaptability of these birds. Similarly, transport stress including antigenic stimulation (Matur et al., 2016) showed the enriched birds had higher antibody responses but body or relative immune organ weights (spleen, thymus, and bursa) were not affected. There were also significant interactions between rearing

treatment and transport stress on multiple molecular measures of immune function indicating positive impacts of enrichment on innate and adaptive immune responses (Matur et al., 2016). Housing pullets from 11 wk of age in floor pens with slats or with part coverage of litter or foraging material (long-cut straw, wood shavings, chaff) until 19 wk of age also modified responses to antigenic stimulation (El-Lethey et al., 2003). Birds housed with slats had poorer immune responses, comparable to birds supplemented with dietary corticosterone, although surprisingly, not equally across all injected antigens (El-Lethey et al., 2003). The slats condition thus appeared to be stressful for the birds, downgrading immunocompetence but no specific observations were made of how time budgets and behavior of the birds in the slats or litter condition differed.

The behavioral changes in response to enrichment and the precise physiological mechanisms by which enrichment modifies immune function need to be better understood. Enriched rearing conditions may act to increase physical activity, improve the overall affective state, affect molecular function via increased bacterial load in enriched conditions, or a combination thereof. Moe et al. (2010) compared conventional cage rearing to floor litter rearing from 0 to 16 wk of age. At 16 wk birds were transferred to either conventional caged layer housing or furnished cage housing that contained a litter bath, nest box, and a perch with 4 combinations of rearing and layer housing groups. At 62 wk of age, the floor-reared hens showed a higher response to one antigen challenge and the floor-reared, furnished-housed hens showed a higher response to a different antigen (Moe et al., 2010). However, the floor-reared, furnished-housed birds showed the highest H/L ratio. The authors thus concluded that immune function may have been affected by pathogenic load in the more environmentally complex housing rather than as a direct consequence of stress within different systems (Moe et al., 2010).

The timing of application of enrichments may also be critical for maximal impact. Newly hatched chicks are particularly vulnerable, but pullets throughout rear are subject to multiple vaccination periods until transfer to the layer facilities which all put strain on the developing bird. In ovo and hatch conditions can also have long-term impact on the bird's immunocompetence. Walstra et al. (2010) compared suboptimal (inconsistent) incubation temperatures and standard commercial post-hatch conditions with optimized (consistent) incubation temperatures and access to feed, water, and foraging material directly following hatch. Birds from both incubation/hatch treatments were then transported to either conventional cages for the first 7 wk or floor litter pens with perches. From week 7 to 16, birds were then all housed in floor pens with perches. Responses to infectious challenges at 7 and 13 wk of age showed birds with optimized incubation/hatch and enriched-rearing conditions showed the most adaptive response to the pathogens including positive effects of the optimized incubation/hatch treatment alone (Walstra et al., 2010).

The prevalence of alternative housing systems is increasing, including outdoor and organic systems which present greater pathogen risk in comparison to conventional caged systems and place different environmental stressors on the birds (Salamano et al., 2010). This, in combination with reduced use of antibiotics and increases in antibiotic resistance, sees a need for methods to naturally enhance bird immunity for industry optimization; the rearing phase is a critical time period. Certainly enriched conditions in comparison to caged housing have positive impacts on immunocompetence and benefits result from exposure at week 0 onwards. But more research into understanding the mechanisms for improving immune function through early environmental enrichment is warranted. The current research indicates environments that may allow greater expression of natural behaviors or provide higher environmental complexity are beneficial. Chronic stress can be detrimental to immunocompetence, but potential benefits of acute stress are not well documented. Research into the potential for novel enrichment stimulation across development (e.g., replenishing novel objects) or system change throughout the rearing period (e.g., moveable tiers, access to new areas) to stimulate acute corticosterone responses that may enhance adaptive immune responses warrants future attention. Additionally, the relationship between positive affective states and immunocompetence is an avenue to be explored. Enrichment can lead to optimistic cognitive biases (e.g., rats: Brydges et al., 2011; pigs: Douglas et al., 2012) with developmental stress showing continued cognitive impacts through adulthood (rats: Brydges et al., 2012). Birds will show behavioral change in anticipation of a rewarding versus aversive or neutral stimulus (Zimmerman et al., 2011) suggesting they do experience positive emotional states. Thus, enrichments that are highly valued by hens may result in positive affective states which may enhance natural and adaptive immunity. With potential life-long consequences of early immune challenge experiences (Parmentier et al., 2009; Grindstaff, 2016), enrichment, rearing, and immunocompetence should be an area of research focus. Fear is also linked to stress and thus methods to reduce fear as detailed in the following section may result in enhanced immunocompetence.

Behavioral Development—Fear

Chickens are a prey species and thus fear is evolutionarily adaptive. However, high levels of fearfulness identified during rearing can lead to welfare problems in lay (de Haas et al., 2014a). Red junglefowl chicks will show fear responses and escape behavior from a few days of age (Kruijt, 1964). Early peaks in fear responses within the first 10 d may be related to visual development and assessment of novelty (Andrew and Brennan, 1983). In semi-natural conditions, chicks remain with the mother hen up to 12 wk of age (Collias

et al., 1966). In contrast, domestic chicks in commercial production systems are never in contact with their mother (for logistical and health reasons). This may have negative implications for the development of appropriate fear responses where chicks could either have increased fear to non-threatening stimuli or inappropriate reactions to potential threats (Campo et al., 2014; Edgar et al., 2016). Some positive effects of the mother hen can be simulated with dark brooders which are warm, enclosed, dark areas for chicks to access in the absence of adult hens (Gilani et al., 2012; Riber and Guzman, 2016, 2017). But longer-term commercial impacts of dark brooders on hen behavior and welfare still need to be established.

A positive association with stockpeople will benefit production in hens (Hemsworth, 2003). Increased human contact by handling in the first few weeks of life will reduce fear toward humans (Jones and Waddington, 1993; Jones, 1994, 1995), as will regular visual contact (Jones, 1993) which could be implemented commercially by multiple walks through the house by staff. But reduced fear responses toward humans may not always translate to other fear-inducing situations. Alternatively (or concurrently), objects/manipulable stimuli placed in pens may enhance environmental complexity, increase exploration, and reduce neophobia (Newberry, 1999). Chicks may, however, show an initial fear reaction toward novel stimuli (Jones and Carmichael, 1999a); thus, object presence likely requires an initial period of adaptation before positive effects may result. Research in the area of object placement within rearing facilities is limited. Early experiments showed a variety of manipulable, brightly colored, and stimulating objects such as balls, buttons, thimbles, and drawings taped to the walls provided from day 1 and changed every 3 d, reduced fear in chicks tested at 3 wk of age more than regular handling or no enrichment (Jones and Waddington, 1992). A similar enrichment strategy had noticeable effects as early as 7 d of age (Jones, 1982). However, chicks reared from day 1 to 6 wk with physical enrichment in the form of plastic colored strings and barley grains distributed on the ground by hand daily in floor litter pens showed no reduction in fearfulness at 6 wk of age (Dávila et al., 2011). Similarly, Hartcher et al. (2015a) found no evidence that pecking strings, grain provision, and increased litter depth reduced fearfulness in pullets tested at 9 wk of age. However, a combination of both novel objects (plastic bottles, balls, and rattles), human handling, human presence, and human voice via radio for the first 5 wk of life, followed by housing in an area of high human activity until 24 wk of age did reduce fear reactions in response to human catching procedures and fewer injuries during depopulation early in the lay cycle (Reed et al., 1993). In this case, it was not possible to tease out the differential effects of the additional cage objects, versus handling, versus human presence. Accumulative positive effects may result from application of multiple stimuli, regardless of their specific nature (see

Lambton et al., 2013 for an example related to prevention of feather pecking). Overall, additional objects in cages or floor pens on a commercial scale are poorly researched in terms of the extent of enrichment needed to have long-term impacts on fear. However, more recently, with the increase in alternative housing systems, attention has been drawn to the impacts of rearing birds in more complex housing, similar to the environments they would be transferred to at lay.

Day-old chicks reared in either aviary systems or conventional cage systems (all birds kept on paper in cages up to 4 wk of age before aviary doors opened) were transferred to furnished cage systems at 16 wk of age (Brantsæter et al., 2016a,b). Fear of novel objects and humans was reduced in the aviary-reared birds when tested up to 5 wk following transfer compared to the cage-reared birds (Brantsæter et al., 2016a,b). These results suggest the complexity of the aviary rearing environment had positive impacts on fear, measured across more than one dimension but effects may not be detectable further into the production cycle (Brantsæter et al., 2016a,b). Comparisons between open (floor-based with levels), closed, and partially open aviary systems found reduced fear of a novel object at 1 and 5 wk in those birds housed in the open system (de Haas et al., 2014a). Complex rearing systems may improve adaptation to a new environment, but long-term benefits of a specific rearing system are unclear. Conversely, Anderson and Adams (1994) found higher fear in floor-reared compared to cage-reared pullets. Floor-reared birds have greater ability to move away from personnel during rearing, thereby decreasing human interaction. The natural response of moving away could be confounded by housing system. De Haas et al. (2014a) found no effect of housing type in the first 4 wk of life (having a closed aviary system, partly opened, or a floor-based system with levels) on minimal distance to a human observer at week 5 or 10 of age when birds were all housed in an open system. The use of different areas within rearing systems could enable chicks to be able to choose their own strategy when dealing with novel or fearful items, which may reduce fearfulness in opposition to being unable to hide.

Overall, reduction in excessive fear during rearing is important for optimal well-being and production of hens. However, more research on the benefits of rearing treatment throughout the production cycle is needed, where rearing treatments may need to be combined with further interventions during laying (Brantsæter et al., 2017). Excessive fear can be reduced through multiple avenues where mechanisms may be desensitization, increased exploration leading to improved adaptation to novel situations, development of appropriate reactions to stimuli or greater cognitive capacity to navigate complex environments. Specific timelines for reducing fear within the rearing phase are currently unclear—whether stimuli need to occur within an early sensitive period only, throughout rearing or intermittently. Aviary rearing systems with different levels of

height help to reduce fear by giving birds increased environmental complexity, and opportunities to hide and explore, as well having additional benefits on physical and behavioral capabilities (see section on *Skeletal development*). These aviary systems may provide an ideal enrichment but only when this type of rearing system also fits with the laying system (Brantsæter et al., 2016b). More research may also enable determination of simple, effective enrichments that could be added to floor-rearing systems to maximize bird development in these settings. Exposing birds to various novel colors or objects in their housing could be a simple option for producers to acclimate birds to changes in management practice and/or surroundings. Producers on commercial farms within Australia have communicated (personal communication to DLMC, 2017) the negative behavioral responses by pullets to simple changes in daily routine such as a change in house-walk direction, or wearing a different item of clothing. If simple novel objects were added to rearing pens regularly throughout rear, birds may become better adapted to change and show appropriate behavioral responses to new stimuli. Making the environment more controllable and predictable may also help reduce fear and stress (Wiepkema and Koolhaas, 1993). Knocking on the door before entering, implementing gradual dawn and dusk, and playing a sound before the feed belt runs can help birds predict any management changes intentionally made to the bird's surroundings resulting in greater perception of control.

Behavioral Development—Pecking

Adult jungle fowl in semi-natural environments are observed to spend 60% of their active time ground-pecking and 34% of observed time ground-scratching (Dawkins, 1989). Domesticated adult hens spend less than 10% of their time foraging in commercial indoor litter systems (Carmichael et al., 1999; Channing et al., 2001; Campbell et al., 2017a). This may be due to domestic hens investing less time in energetically expensive behaviors compared to jungle fowl (Schütz and Jensen, 2001). The foraging opportunities indoors are also less favorable than what is available in the natural habitat, or available in free-range systems (Campbell et al., 2017b). Nevertheless, foraging is a highly valued behavioral need in domesticated hens (Weeks and Nicol, 2006). In a foraging-thwarted environment, abnormal feather pecking will develop as likely re-directed foraging behavior (Blokhuys, 1986; Huber-Eicher and Wechsler, 1997, 1998). Feather pecking can manifest in several different forms (see definitions in Savory, 1995), and when aimed at conspecifics with force (cf. gentle feather pecking), this severe feather pecking can result in feather loss, injury, and lead to cannibalism.

Stimulating foraging by having litter to forage in during the early rearing environments is important for preventing feather pecking during rearing (van de Weerd

and Elson, 2006; Rodenburg et al., 2013; de Haas et al., 2014a,b; Janczak and Riber, 2015). Chicks start gently pecking conspecifics and foraging in the first week of life as they explore their environment with their beak (Huber-Eicher and Wechsler, 1998; Roden and Wechsler, 1998; Riedstra and Groothuis, 2002). Lack of litter substrate in the first 4 wk of life increases plumage damage and feather pecking (Johnsen et al., 1998; Bestman et al., 2009; Tahamtani et al., 2016b), although the subsequent housing conditions during lay do play a large role in feather pecking and plumage damage in adult birds (de Jong et al., 2013a,b; de Haas et al., 2014a,b; Nicol et al., 2001; Tahamtani et al., 2016b). A foraging substrate where ground pecking and scratching is possible is preferred by birds over other pecking devices (Dixon et al., 2010). However, pecking devices for birds reared on slats or in cages (or in addition to litter) may still suit as a pecking enrichment option that minimizes the development of feather pecking behavior. Several farm certification schemes do require pecking enrichments to be on-farm during rearing (e.g., Australian RSPCA Approved Farming Scheme Standards for pullets 2015 and UK RSPCA welfare standards for pullets 2016) and practically, multiple types of enrichments may be used such as hay bales, hanging CD's, strings, toy balls, or aerated pecking blocks (Tahamtani et al., 2016b). However, there are limited published data on the bird use and effectiveness of these varying pecking devices on commercial rearing farms (Zepp et al., 2018). The ability for birds to exhibit foraging behavior during rear has significant impact on reducing incidence of feather pecking at rear and at lay (Bestman et al., 2009; Gilani et al., 2013; Rodenburg et al., 2013).

For pecking devices to effectively stimulate pecking, birds need to be attracted to them and not fearful to minimize stress responses to them and/or avoidance due to novelty (Jones, 2001). Thereby it is critical (and often challenging) to select enrichment devices that are valued by the birds. Pecking strings are shown to work positively as a pecking enrichment for young birds (Jones and Carmichael, 1999b), but should be applied with caution to ensure young birds cannot swallow the strings. Experimentally, chicks housed in wooden boxes with wire mesh floors showed more pecking at strings when presented these items from 2 d of age compared to birds presented these items at 10 d of age (Jones and Carmichael, 1999b) and white strings were most attractive (Jones et al., 2000). For floor-housed chicks with access to litter, McAdie et al., (2005) showed that pecking string provision caused a clear reduction in gentle and severe feather pecking behavior at 8 wk of age for chicks with access to the strings from day 1 of age in comparison to chicks that never received strings. Pecks to the string were still observed 8 wk following provision (McAdie et al., 2005). Adult hens in cages with access to string devices had better plumage condition at 35 wk than those birds with no string devices, with no differences between birds having had strings continuously from day 1 of age, 1 d at monthly intervals, or

continuously from 16 wk of age (McAdie et al., 2005). However, provision of pecking strings at 12 d of age, scattering whole grain oats, and having a deep litter at rear in floor-housed hens did not impact on plumage damage at 43 wk of age (Hartcher et al., 2015b). Thus, pecking strings show potential, but longer-term studies show discrepancies. Recent evidence from commercial rearing farms shows clear reductions in several types of feather pecking with provision of pecking stone devices and hay throughout the rearing period (Zepp et al., 2018). Different types of forages supplementary to the normal diet (e.g., cabbage leaves, seeds, hay) may decrease feather pecking behavior (Dixon et al., 2010) and the use of live insect feeding in the litter could also be a way to stimulate foraging pecking (Ruis et al., 2017). However, the health and safety implications of these and other perishable feeds may in some cases limit the practicality of this on-farm. Assessment of the nutritional impacts of consuming alternative forages would also confirm their suitability during rear (Steenfeldt et al., 2007).

Overall, devices that stimulate pecking appear useful in reducing redirected foraging but as stated within the UK RSPCA pullet rearing guidelines (2016) “It should be demonstrated that the items provided are valued by the birds. Effective environmental enrichment will be used well by the birds and any items which are not well used should be replaced with alternatives. This may vary from flock to flock”. On commercial farms the success of pecking enrichments does vary between layer flocks (Pettersson et al., 2017c). As a result, producers may get discouraged over an unpredictable cost/benefit ratio and choose to not provide enrichments at all (personal communication to DLMC, 2017). The ability for birds to exhibit foraging behavior during rear has significant impact on reducing incidence of feather pecking at rear and at lay (Bestman et al., 2009; Gilani et al., 2013; Rodenburg et al., 2013). Producers play a critical role in being attentive to how their birds respond to different types of pecking enrichments including ensuring the devices are not negatively impacting the birds through inadvertently increasing alarm and feather pecking (Lindberg and Nicol, 1997). The first few days following placement may require a behavior-analytic methodology as suggested for zoo enrichment studies (Allgood et al., 2017) where it is the specific response of the current flock that is important rather than what may have worked for other flocks (either on the same or different farms). Approach, avoidance, or panic responses are critical to observe. Dramatic reduction in interest and use across weeks following placement may indicate a need for enrichment change and replacement may be necessary for highly used enrichments. Although this likely requires an increase in labor on-farm, use of technologies for individual monitoring (Siegford et al., 2016) may become valuable in helping determine pecking enrichment use, impacts on daily time budgets (Bubier, 1996), whether birds compete for

access to enrichments, and appropriate numbers of enrichments to place.

Pecking devices have to be effective in stimulating foraging and reducing feather pecking, and be economically feasible. Simple, readily available devices on farm such as suspended nets with egg cartons, white string bunches, and manipulative feeding sources may suit for this purpose but flexibility is required to cater to preferences of particular flocks. If the birds are observed to peck at provided devices, then it is likely to be successfully redirecting their pecking behavior away from conspecifics. However, more commercial validation of the impacts of pecking devices through rear and the implications throughout lay are warranted. Litter during rearing is also critical for appropriate development of pecking behavior. Adult birds will likely still require pecking devices at the layer facility if this is to be their main pecking/foraging opportunity (e.g., furnished cages) as current environments have great impact on current behavior (Nicol et al., 2001). Transitioning from an enriched rearing environment to a layer environment with restricted foraging opportunities could then result in development of feather pecking despite the demonstration of appropriate foraging behavior during rear (Klein et al., 2000). Similarly, continual access to pecking devices throughout rearing (i.e., ensure device replacement as necessary) may also be important for preventing frustration and subsequent development of abnormal pecking behavior in birds that have become accustomed to device access.

Free-Range Hens: Indoor-Rearing for Outdoor Access

Free-range systems provide outdoor access for birds. However, pullets are often reared indoors (e.g., common practice in Australia and the UK), with wide variation in age of first outdoor access following transfer to the laying house. Reasons for indoor rearing may include current rearing house facilities (enclosed barns in close proximity to each other), availability of land for a range, greater climate control indoors, and risks to bird health when unvaccinated birds venture outdoors and are exposed to pathogens. In Australia and in the UK, for example, diverse systems are used for indoor rearing of free-range pullets including floor-based systems with or without perches, litter with slats, and single-tier or multi-tier aviaries. Typically birds are transferred to the free-range layer house at 16 wk of age. After arrival, farmers often use an indoor adjustment period for the birds. During this period, hens learn to use the nest box, and get habituated to the indoor spatial environment. After the adaptation period of several weeks (varies greatly between farms), pop holes that allow access to the range are opened. In contrast, in Switzerland for example, birds can be given access to a covered outdoor area (veranda) at 6 wk of age, with access to

the uncovered range provided at 24 wk of age on the same farm (Gebhardt-Henrich et al., 2014). Similarly, in Germany most free-range pullets have access to a covered outdoor concrete and straw-laid veranda (Keppler et al., 2012).

With birds having access to a range, they have a choice between indoor and outdoor areas which makes their environment more variable compared to only having indoor housing. The behavioral and physiological demands of the birds in a free-range system may also be higher than those experienced within enclosed indoor systems due to the large areas to navigate and variable environmental conditions. Birds may only use certain areas of the range, use varies throughout the flock cycle (Pettersson et al., 2016), and fearful birds may be hesitant to venture outside at all (Hartcher et al., 2016; Campbell et al., 2016b). Access to the range can also be inconsistent when birds are kept indoors during inclement weather which can cause stress in the birds (Campbell et al., 2018b) and increase feather pecking (Bestman et al., 2017). Conversely, daily access to the range and a high proportion of birds using the range during lay reduces the occurrence of feather pecking on a flock level (Bestman et al., 2017; Jung and Knierim, 2018). The rearing period can thus be critical for best preparing birds for successful outdoor access and adaptation to environmental variation. Enrichments may be particularly beneficial where outdoor access during rearing is not possible but research in this area is currently limited. In one study on indoor enrichment for free-range birds, exposure to novel and unpredictable structural, visual, auditory, and light stimuli during the first 3 wk of rearing resulted in greater behavioral adaptation to later environmental stress coupled with lower physiological stress indicators in adult free-range hens (Campbell et al., 2018b). However, there is scope for much further research. Particularly in relation to the impacts and potential benefits of early exposure to environmental variation on discriminatory abilities of adult birds for accurate response to predators (Bestman and Ouwejan, 2016), including alternating attention between foraging and vigilance (Dukas and Kamil, 2000). The impacts of enrichments on brain lateralization (see *Neurobehavioral development*) and on visuospatial selective attention abilities in chickens is unknown (Sridharan et al., 2014; also see the section *Visual development*) but the capacity for efficient decision-making is critical for optimal adaptation to a complex environment.

CONCLUSIONS

Early rearing environments for commercially housed laying hens are critical for development of species-appropriate behavior and optimal physical growth. Enriching the rearing environments with physical, sensory, and stimulatory additions can help to maximize the bird's developmental potential. This is becoming increasingly important for pullets being reared for hous-

ing systems alternative to the conventional cage but commercial-scale research is limited. This review has summarized the available literature regarding enrichments provided during rearing and the subsequent impact they have on different aspects of behavioral and physiological development, including identifying the ways enrichments could have biological impact. Enrichments are of value for improving the health, behavior, and welfare of layer pullets. However, numerous areas where future research is needed have been identified. The following provides a summary of the main findings and need for further study.

- Vision is a critical sense for chickens and appropriate visual development depends on lighting environments. Chicks will attend to multiple visual parameters such as color and patterns, and prefer moving over static images. However, static patterns and colors could be a simple way of providing visual stimulation where moving images are not feasible. Different structural-shaped areas may stimulate neural development but the precise visual enrichments for optimal brain growth still require further research. Robotic birds which provide both visual and potentially auditory stimulation are an avenue for future study.
- Chickens have high cognitive capabilities with lateralized brain development. There are defined critical periods of brain development within the first 2 wk of life. Enrichment strategies that target specific hemispheres/behavioral traits could prepare birds to be more suited to different types of adult housing environments (caged, indoor, outdoor). Birds that are more competent in spatial navigation will likely be more confident within complex housing systems (e.g., tiered aviaries). The role of light during incubation, subsequent brain lateralization, and impacts on bird behavior needs to be studied further.
- Chicks hatch with full auditory capabilities but are limited in species-specific development by the absence of the mother hen and loud surrounding noises of rearing facilities. Sound playbacks such as via radio may have positive impacts but the mechanisms by which auditory enrichment operates (masking other noises, habituating birds to noise, neurological development) require clarification and the impacts of maternal vocalizations need further study.
- Structural enrichments such as perches or elevated tiers are necessary for optimal skeletal development, but provision of such physical enrichments needs to be made in a way to avoid bird injury (e.g., soft perch material, ramps). Different types of exercise (e.g., running, jumping, flying) can impact bones in different ways, but more research across the developmental period is needed to identify potential critical periods of bone growth. The type of structural enrichments provided will depend on the layer housing system birds are destined for.

Aviary housing generally permits flight; thus, birds will need opportunities to develop their wing bones during the rearing period.

- Enriched housing environments can have positive impacts on immunocompetence but the precise mechanisms behind these impacts are currently poorly understood due to limited research in this area. Further investigation into the potential for enhancing immune responses through application of mild stressors such as novel objects is warranted. Overall, catering to the birds behavioral needs (dust bathing, perching, foraging) will improve well-being and will likely result in a bird that is able to respond better to infection.
- Reduction in fear through habituation to novelty/environmental change will have positive impacts on bird behavior and adaptation to the layer facility. Complex rearing systems may also act to reduce fear but additional commercial studies are warranted.
- The environment in the first 2 to 4 wk of development can have long-lasting impacts; thus, provision of pecking enrichments either in addition to litter or particularly where litter is not a practical option is recommended. Provision of pecking stimulation will reduce the development of gentle and severe feather pecking behavior. Producers may need to adapt to different flock preferences to provide enrichments that will be used by each current rearing group. Consideration of the layer housing environment needs to be made to ensure birds that are provided pecking enrichment during rearing are also supplied pecking enrichments during lay to avoid frustration and feather pecking onset.
- Pullets destined for free-range systems may require different/greater enrichment effort given the disparity between their rearing and layer housing environments. More research is needed to identify the best practice methods where outdoor access during rearing is not feasible.
- The current adult housing environment is still critical for optimal flock behavior, health, and welfare, and attention needs to be paid to enrichments during the layer phase too.

Overall, there is a need to identify practical cost-effective enrichments that producers would use on-farm and to have commercial validation of positive impacts on aspects of behavior and biology. The type of enrichments used will likely depend on both the rearing environment and the layer system the birds are destined for. Rearing systems without litter would need to focus on providing pecking enrichments, and birds destined for aviaries would need enrichments that allow for musculoskeletal and cognitive spatial development. Enrichments may be relatively easy to provide for young chicks, with caution to ensure objects do not harm the chicks (e.g., crushing, getting stuck), but enrichments for birds of larger weight become more

difficult. Enrichment items provided for pullets have to be sturdy to avoid getting destroyed by pecking, and also be able to support bird weight as growing birds are motivated to perch wherever possible (even with provision of perches). Chicken rearing sheds are also large and hold thousands of birds; thus, enrichments have to be provided in large quantities to ensure they are having maximal impact. This can be costly in terms of both set-up costs and labor for installation and maintenance. Enrichments will need to be either replaced between flocks or be able to be cleaned to maintain high biosecurity on-farm. However, items readily found around farms may provide some stimulation to birds such as brooms and buckets, or recyclable items such as milk jugs could be used. Validation data of rearing enrichments may be available within individual farms/enterprises that are constantly seeking to improve their own practices, but are currently poorly available within the literature for general access. Laying hens are increasingly being housed in more complex alternative systems but they still exhibit a multitude of behavioral and physical issues. Thus, enrichments are a method of targeting multiple aspects of behavioral and physiological development to rear pullets that are better adapted for layer production environments.

ACKNOWLEDGMENTS

Financial support was provided by PoultryHub. Thank you to Andrew Bean, Ian Colditz, Peter Hunt, and Peta Taylor for valued discussions and feedback. Thank you to Australian Eggs for financial support to DLMC for visiting commercial rearing and layer farms.

REFERENCES

- Allgood, C. A., N. R. Dorey, L. R. Mehrkam, and K. A. Leighty. 2017. Applying behavior-analytic methodology to the science and practice of environmental enrichment in zoos and aquariums. *Zoo Biol.* 36:175–185.
- Anderson, K. E., and A. W. Adams. 1994. Effects of floor versus cage rearing and feeder space on growth, long bone development, and duration of tonic immobility in single comb white leghorn pullets. *Poult. Sci.* 73:958–964.
- Andrew, R. J. 1988. The development of visual lateralization in the domestic chick. *Behav. Brain Res.* 29:201–209.
- Andrew, R. J., and A. Brennan. 1983. The lateralization of fear behaviour in the male domestic chick: a developmental study. *Anim. Behav.* 31:1166–1176.
- Archer, G. S., and J. A. Mench. 2017. Exposing avian embryos to light affects post-hatch anti-predator fear responses. *Appl. Anim. Behav. Sci.* 186:80–84.
- Archer, G. S., H. L. Shivaprasad, and J. A. Mench. 2009. Effect of providing light during incubation on the health, productivity, and behavior of broiler chickens. *Poult. Sci.* 88: 29–37.
- Barak, Y. 2006. The immune system and happiness. *Autoimmun. Rev.* 5:523–527.
- Barnett, J. L., P. C. Glatz, E. A. Newman, and G. M. Cronin. 1997. Effects of modifying layer cages with perches on stress physiology, plumage, pecking and bone strength of hens. *Aust. J. Exp. Agric.* 37:523–529.
- Bestman, M., P. Koene, and J. P. Wagenaar. 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. *Appl. Anim. Behav. Sci.* 121:120–125.
- Bestman, M. W. P., J., and Ouwejan. 2016. Predation of Free-Range Laying Hens. Page 283 in Proc. 50th Congr. Intl. Soc. Appl. Ethol. 12–15 July, Edinburgh, UK.
- Bestman, M., C. Verwe, C. Brenninkmeyer, A. Willett, L. K. Hinrichsen, F. Smajlhodzic, J. L. T. Heerkens, S. Gunnarsson, and V. Ferrantez. 2017. Feather-pecking and injurious pecking in organic laying hens in 107 flocks from eight European countries. *Anim. Welf.* 26:355–363.
- Blatchford, R. A., R. M. Fulton, and J. A. Mench. 2016. The utilization of the Welfare Quality® assessment for determining laying hen condition across three housing systems. *Poult. Sci.* 95:154–163.
- Blokhuys, H. J. 1986. Feather-pecking in poultry: its relation with ground-pecking. *Appl. Anim. Behav. Sci.* 16:63–67.
- Brantsæter, M., J. Nordgreen, T. B. Rodenburg, F. M. Tahamtani, A. Popova, and A. M. Janczak. 2016a. Exposure to increased environmental complexity during rearing reduces fearfulness and increases use of three-dimensional space in laying hens (*Gallus gallus domesticus*). *Front. Vet. Sci.* 3:14.
- Brantsæter, M., F. M. Tahamtani, R. O. Moe, T. B. Hansen, R. Orritt, C. Nicol, and A. M. Janczak. 2016b. Rearing laying hens in aviaries reduces fearfulness following transfer to furnished cages. *Front. Vet. Sci.* 3:13.
- Brantsæter, M., F. M. Tahamtani, J. Nordgreen, E. Sandberg, T. B. Hansen, T. B. Rodenburg, R. Oppermann Moe, and A. M. Janczak. 2017. Access to litter during rearing and environmental enrichment during production reduce fearfulness in adult laying hens. *Appl. Anim. Behav. Sci.* 189:49–56.
- Bright, A. 2008. Vocalisations and acoustic parameters of flock noise from feather pecking and non-feather pecking laying flocks. *Br. Poult. Sci.* 49:241–249.
- Broom, D. 1969. Effects of visual complexity during rearing on chicks' reactions to environmental change. *Anim. Behav.* 1969:773–780.
- Brydges, N. M., L. Hall, R. Nicolson, M. C. Holmes, and J. Hall. 2012. The effects of juvenile stress on anxiety, cognitive bias and decision making in adulthood: a rat model. *PLoS One* 7:e48143.
- Brydges, N. M., M. Leach, K. Nicol, R. Wright, and M. Bateson. 2011. Environmental enrichment induces optimistic cognitive bias in rats. *Anim. Behav.* 81:169–175.
- Bubier, N. E. 1996. The behavioural priorities of laying hens: the effects of two methods of environment enrichment on time budgets. *Behav. Processes.* 37:239–249.
- Campbell, D. L. M., A. B. A. Ali, D. M. Karcher, and J. M. Siegford. 2017a. Laying hens in aviaries with different litter substrates: behavior across the flock cycle and feather lipid content. *Poult. Sci.* 96:3824–3835.
- Campbell, D. L. M., G. N. Hinch, J. A. Downing, and C. Lee. 2017b. Outdoor stocking density in free-range laying hens: effects on behaviour and welfare. *Animal* 11:1036–1045.
- Campbell, D. L. M., S. L. Goodwin, M. M. Makagon, J. C. Swanson, and J. M. Siegford. 2016a. Failed landings after laying hen flight in a commercial aviary over two flock cycles. *Poult. Sci.* 95:188–197.
- Campbell, D. L. M., G. N. Hinch, J. A. Downing, and C. Lee. 2016b. Fear and coping styles of outdoor-preferring, moderate-outdoor and indoor-preferring free-range laying hens. *Appl. Anim. Behav. Sci.* 185:73–77.
- Campbell, D. L. M., A. C. Talk, Z. A. Loh, T. R. Dyal, and C. Lee. 2018a. Spatial cognition and range use in free-range laying hens. *Animals* 8:26.
- Campbell, D. L. M., G. N. Hinch, J. A. Downing, and C. Lee. 2018b. Early enrichment in free-range laying hens: effects on ranging behaviour, welfare and response to stressors. *Animal* 12:575–584.
- Campo, J. L., M. G. Gil, and S. G. Dávila. 2005. Effects of specific noise and music stimuli on stress and fear levels of laying hens of several breeds. *Appl. Anim. Behav. Sci.* 91:75–84.
- Campo, J. L., S. G. Dávila, and M. G. Gil. 2014. Comparison of the tonic immobility duration, heterophil to lymphocyte ratio, and fluctuating asymmetry of chicks reared with or without a broody hen, and of broody and non-broody hens. *Appl. Anim. Behav. Sci.* 151:61–66.
- Carmichael, N. L., A. W. Walker, and B. O. Hughes. 1999. Laying hens in large flocks in a perchery system: Influence of stocking density on location, use of resources and behaviour. *Br. Poult. Sci.* 40:165–176.
- Casey-Trott, T. M., M. T. Guerin, V. Sandilands, S. Torrey, and T. M. Widowski. 2017a. Rearing system affects prevalence of keel-bone damage in laying hens: a longitudinal study of four consecutive flocks. *Poult. Sci.* 96:2029–2039.
- Casey-Trott, T. M., D. R. Korver, M. T. Guerin, V. Sandilands, S. Torrey, and T. M. Widowski. 2017b. Opportunities for exercise during pullet rearing, Part I: Effect on the musculoskeletal characteristics of pullets. *Poult. Sci.* 96:2509–2517.
- Casey-Trott, T. M., D. R. Korver, M. T. Guerin, V. Sandilands, S. Torrey, and T. M. Widowski. 2017c. Opportunities for exercise during pullet rearing, Part II: Long-term effects on bone characteristics of adult laying hens at the end-of-lay. *Poult. Sci.* 96:2518–2527.
- Casey-Trott, T. M., and T. M. Widowski. 2016. Behavioral differences of laying hens with fractured keel bones within furnished cages. *Front. Vet. Sci.* 3:42.
- Channing, C. E., B. O. Hughes, and A. W. Walker. 2001. Spatial distribution and behaviour of laying hens housed in an alternative system. *Appl. Anim. Behav. Sci.* 72:335–345.
- Chaudhury, S., T. C. Nag, S. Jain, and S. Wadhwa. 2013. Role of sound stimulation in reprogramming brain connectivity. *J. Biosci.* 38:605–614.
- Chiandetti, C., B. S. Lemaire, E. Versace, and G. Vallortigara. 2017. Early- and later-light embryonic stimulation modulates similarly chicks' ability to filter out distractors. *Symmetry* 9:84.
- Chiandetti, C., and G. Vallortigara. 2011. Chicks like consonant music. *Psychol. Sci.* 22:1270–1273.
- Clara, E., L. Regolin, G. Vallortigara, and L. J. Rogers. 2009. Chicks prefer to peck at insect-like elongated stimuli moving in a direction orthogonal to their longer axis. *Anim. Cogn.* 12:755–765.
- Clarke, C.H., and R. B. Jones. 2001. Domestic chicks' runway responses to video images of conspecifics. *Appl. Anim. Behav. Sci.* 70:285–295.
- Cohen, Y., M. Belkin, O. Yehezkel, I. Avni., and U. Polat. 2008. Light intensity modulates corneal power and refraction in the chick eye exposed to continuous light. *Vision Res.* 48:2329–2335.
- Cohen, Y., M. Belkin, O. Yehezkel, A. S. Solomon, and U. Polat. 2011. Dependency between light intensity and refractive development under light-dark cycles. *Exp. Eye Res.* 92:40–46.
- Collias, N. E., and E. C. Collias. 1967. A field study of the red jungle fowl in North-Central India. *Condor* 69:360–386.
- Collias, N. E., E. C. Collias, D. Hunsaker, and L. Minning. 1966. Locality fixation, mobility and social organization within an unconfined population of red jungle fowl. *Anim. Behav.* 14:550–559.
- Collias, N. E., and M. Joos. 1953. The spectrographic analysis of sound signals of the domestic fowl. *Behaviour* 5:175–188.
- Colson, S., C. Arnould, and V. Michel. 2008. Influence of rearing conditions of pullets on space use and performance of hens placed in aviaries at the beginning of the laying period. *Appl. Anim. Behav. Sci.* 111:286–300.
- Cotter, P. F. 2015. An examination of the utility of heterophil-lymphocyte ratios in assessing stress of caged hens. *Poult. Sci.* 94:512–517.
- Daisley, J. N., E. Mascalzoni, O. Rosa-Salva, R. Rugani, and L. Regolin. 2009. Lateralization of social cognition in the domestic chicken (*Gallus gallus*). *Philos. Trans. Roy. Soc. B: Biol. Sci.* 364:965–981.
- Dawkins, M. S. 1989. Time budgets in Red Junglefowl as a baseline for the assessment of welfare in domestic fowl. *Appl. Anim. Behav. Sci.* 24:77–80.
- Dawkins, M. S. 1995. How do hens view other hens? The use of lateral and binocular visual fields in social recognition. *Behaviour* 132:591–606.
- Dawkins, M. S. 1996. Distance and social recognition in hens: implications for the use of photographs as social stimuli. *Behaviour* 133:663–680.
- Dawkins, M. S., and A. Woodington. 1997. Distance and the presentation of visual stimuli to birds. *Anim. Behav.* 54:1019–1025.

- Dávila, S. G., J. L. Campo, M. G. Gil, M. T. Prieto, and O. Torres. 2011. Effects of auditory and physical enrichment on 3 measurements of fear and stress (tonic immobility duration, heterophil to lymphocyte ratio, and fluctuating asymmetry) in several breeds of layer chicks. *Poult. Sci.* 90:2459–2466.
- de Haas, E. N., J. E. Bolhuis, B. Kemp, T. G. G. Groothuis, and T. B. Rodenburg. 2014a. Parents and early life environment affect behavioral development of laying hen chickens. *PLoS One* 9:e90577.
- de Haas, E. N., J. E. Bolhuis, I. C. de Jong, B. Kemp, A. M. Janczak, and T. B. Rodenburg. 2014b. Predicting feather damage in laying hens during the laying period. Is it the past or is it the present? *Appl. Anim. Behav. Sci.* 160:75–85.
- de Jong, I. C., H. Gunnink, J. M. Rommers, and M. B. M. Bracke. 2013a. Effect of substrate during early rearing on floor- and feather pecking behaviour in young and adult laying hens. *Arch. Geflügelkd.* 77:15–22.
- de Jong, I. C., B. F. J. Reivekamp, and H. Gunnink. 2013b. Can substrate in early rearing prevent feather pecking in adult laying hens? *Anim. Welfare* 22:305–314.
- Della Chiesa, A., M. Speranza, L. Tommasi, and G. Vallortigara. 2006a. Spatial cognition based on geometry and landmarks in the domestic chick (*Gallus gallus*). *Behav. Brain Res.* 175:119–127.
- Della Chiesa, A., T. Pecchia, L. Tommasi, and G. Vallortigara. 2006b. Multiple landmarks, the encoding of environmental geometry and the spatial logics of a dual brain. *Anim. Cogn.* 9:281–293.
- Dhabhar, F. S. 2009. A hassle a day may keep the pathogens away: the fight-or-flight stress response and the augmentation of immune function. *Integr. Comp. Biol.* 49:215–236.
- Dharmaretnam, M., V. Vijitha, K. Priyadharshini, T. Jashini, and K. Vathany. 2002. Ground scratching and preferred leg use in domestic chicks: changes in motor control in the first two weeks post-hatching. *Laterality* 7:371–380.
- Dharmaretnam, M., and L. J. Rogers. 2005. Hemispheric specialization and dual processing in strongly versus weakly lateralized chicks. *Behav. Brain Res.* 162:62–70.
- Dixon, L. M., I. J. H. Duncan, and G. J. Mason. 2010. The effects of four types of enrichment on feather-pecking behaviour in laying hens housed in barren environments. *Anim. Welf.* 19:429–435.
- Douglas, C., M. Bateson, C. Walsh, A. Bédoué, and S. A. Edwards. 2012. Environmental enrichment induces optimistic cognitive biases in pigs. *Appl. Anim. Behav. Sci.* 139:65–73.
- Drake, K. A., C. A. Donnelly, and M. Stamp Dawkins. 2010. Influence of rearing and lay risk factors on propensity for feather damage in laying hens. *Br. Poult. Sci.* 51:725–733.
- Dukas, R., and A. C. Kamil. 2000. The cost of limited attention in blue jays. *Behav. Ecol.* 11:502–506.
- Edgar, J., S. Held, C. Jones, and C. Troisi. 2016. Influences of maternal care on chicken welfare. *Animals* 6:2.
- Edgar, J., I. Kelland, S. Held, E. Paul, and C. Nicol. 2015. Effects of maternal vocalisations on the domestic chick stress response. *Appl. Anim. Behav. Sci.* 171:121–127.
- EFSA AHAW Panel (European Food Safety Authority Panel on Animal Health and Animal Welfare). 2015. Scientific Opinion on welfare aspects of the use of perches for laying hens. *EFSA J.* 2015;13:4131, 70 pp.
- El-Lethey, H., B. Huber-Eicher, and T. W. Jungi. 2003. Exploration of stress-induced immunosuppression in chickens reveals both stress-resistant and stress-susceptible antigen responses. *Vet. Immunol. Immunopathol.* 96:91–101.
- Enneking, S. A., H. W. Cheng, K. Y. Jefferson-Moore, M. E. Einstein, D. A. Rubin, and P. Y. Hester. 2012. Early access to perches in caged White Leghorn pullets. *Poult. Sci.* 91:2114–2120.
- Ericsson, M., R. Henriksen, J. Béltéky, A. S. Sundman, K. Shionoya, and P. Jensen. 2016. Long-term and transgenerational effects of stress experienced during different life phases in chickens (*Gallus gallus*). *PLoS One* 11:e0153879.
- Field, S. E., N. S. Rickard, S. R. Toukhsati, and M. E. Gibbs. 2007. Maternal hen calls modulate memory formation in the day-old chick: the role of noradrenaline. *Neurobiol. Learn. Mem.* 88:321–330.
- Fiszer de Plazas, S., D. Conterjnic, and V. Flores. 1991. Effect of a simple visual pattern on the early postnatal development of GABA receptor sites in the chick optic lobe. *Int. J. Dev. Neurosci.* 9:195–201.
- Fleming, R. H., C. C. Whitehead, D. Alvey, N. G. Gregory, and L. J. Wilkins. 1994. Bone structure and breaking strength in laying hens housed in different husbandry systems. *Br. Poult. Sci.* 35:651–662.
- Forkman, B., A. Boissy, M. C. Meunier-Salaün, E. Canali, and R. B. Jones. 2007. A critical review of fear tests used on cattle, pigs, sheep, poultry and horses. *Physiol. Behav.* 92:340–374.
- Fossum, O., D. S. Jansson, P. E. Etterlin, and I. Vågsholm. 2009. Causes of mortality in laying hens in different housing systems in 2001 to 2004. *Acta Vet. Scand.* 51:3.
- Fraise, F., and J. F. Cockrem. 2006. Corticosterone and fear behaviour in white and brown caged laying hens. *Br. Poult. Sci.* 47:110–119.
- Freire, R., H. W. Cheng, and C. J. Nicol. 2004. Development of spatial memory in occlusion-experienced domestic chicks. *Anim. Behav.* 67:141–150.
- Freire, R., and H. W. Cheng. 2004. Experience-dependent changes in the hippocampus of domestic chicks: a model for spatial memory. *Eur. J. Neurosci.* 20:1065–1068.
- Freire, R., and L. J. Rogers. 2007. Experience during a period of right hemispheric dominance alters attention to spatial information in the domestic chick. *Anim. Behav.* 74:413–418.
- Gao, H., and Y. Lu. 2008. Early development of intrinsic and synaptic properties of chicken nucleus laminaris neurons. *Neuroscience.* 153:131–143.
- Garnham, L., and H. Løvlie. 2018. Sophisticated fowl: the complex behaviour and cognitive skills of chickens and red junglefowl. *Behav. Sci.* 8:13.
- Genhardt-Henrich, S. G., A. Pflug, E. K. F. Fröhlich, S. Käppeli, D. Guggisberg, A. Liesegang, and M. H. Stoffel. 2017. Limited associations between keel bone damage and bone properties measured with computer tomography, three-point bending test, and analysis of minerals in Swiss laying hens. *Front. Vet. Sci.* 4: 128.
- Gebhardt-Henrich, S. G., M. J. Toscano, and E. K. F. Fröhlich. 2014. Use of outdoor ranges by laying hens in different sized flocks. *Appl. Anim. Behav. Sci.* 155:74–81.
- Gilani, A. M., T. G. Knowles, and C. J. Nicol. 2012. The effect of dark brooders on feather pecking on commercial farms. *Appl. Anim. Behav. Sci.* 142:42–50.
- Gilani, A. M., T. G. Knowles, and C. J. Nicol. 2013. The effect of rearing environment on feather pecking in young and adult laying hens. *Appl. Anim. Behav. Sci.* 148:54–63.
- Gregory, N. G., L. J. Wilkins, S. C. Kestin, C. G. Belyavin, and D. M. Alvey. 1991. Effect of husbandry system on broken bones and bone strength in hens. *Vet. Rec.* 128:397–399.
- Grindstaff, J. L. 2016. Developmental immune activation programs adult behavior: Insight from research on birds. *Curr. Opin. Behav. Sci.* 1:21–27.
- Gunnarsson, S., J. Yngvesson, L. J. Keeling, and B. Forkman. 2000. Rearing without early access to perches impairs the spatial skills of laying hens. *Appl. Anim. Behav. Sci.* 67:217–228.
- Häne, M., B. Huber-Eicher, and E. Fröhlich. 2000. Survey of laying hen husbandry in Switzerland. *Worlds Poult. Sci. J.* 56:21–31.
- Hartcher, K. M., K. A. Hickey, P. H. Hemsworth, G. M. Cronin, S. J. Wilkinson, and M. Singh. 2016. Relationships between range access as monitored by radio frequency identification technology, fearfulness, and plumage damage in free-range laying hens. *Animal* 10:847–853.
- Hartcher, K. M., M. K. T. N. Train, S. J. Wilkinson, P. H. Hemsworth, P. C. Thomson, and G. M. Cronin. 2015a. Plumage damage in free-range laying hens: behavioural characteristics in the rearing period and the effects of environmental enrichment and beak-trimming. *Appl. Anim. Behav. Sci.* 164:64–72.
- Hartcher, K. M., K. T. N. Train, S. J. Wilkinson, P. H. Hemsworth, P. C. Thomson, and G. M. Cronin. 2015b. The effects of environmental enrichment and beak-trimming during the rearing period on subsequent feather damage due to feather-pecking in laying hens. *Poult. Sci.* 94:852–859.

- Heerkens, J. L. T., E. Delezie, B. Ampe, T. B. Rodenburg, and F. A. M. Tuytens. 2016. Ramps and hybrid effects on keel bone and foot pad disorders in modified aviaries for laying hens. *Poult. Sci.* 95:2479–2488.
- Heikkilä, M., A. Wichman, S. Gunnarsson, and A. Valros. 2006. Development of perching behaviour in chicks reared in enriched environment. *Appl. Anim. Behav. Sci.* 99:145–156.
- Hemsworth, P. H. 2003. Human-animal interactions in livestock production. *Appl. Anim. Behav. Sci.* 81:185–198.
- Hester, P. Y. 2014. The effect of perches installed in cages on laying hens. *Worlds Poult. Sci. J.* 70:247–264.
- Hester, P. Y., S. A. Enneking, B. K. Haley, H. W. Cheng, M. E. Einstein, and D. A. Rubin. 2013. The effect of perch availability during pullet rearing and egg laying on musculoskeletal health of caged White Leghorn hens. *Poult. Sci.* 92:1972–1980.
- Hill, E. M., G. Koay, R. S. Heffner, and H. E. Heffner. 2014. Audiogram of the chicken (*Gallus gallus domesticus*) from 2 Hz to 9 kHz. *J. Comp. Physiol. A* 200:863–870.
- Hoerr, F. J. 2010. Clinical aspects of immunosuppression in poultry. *Avian Dis.* 54:2–15.
- Huber-Eicher, B., and B. Wechsler. 1997. Feather pecking in domestic chicks: its relation to dustbathing and foraging. *Anim. Behav.* 54:757–768.
- Huber-Eicher, B., and B. Wechsler. 1998. The effect of quality and availability of foraging materials on feather pecking in laying hen chicks. *Anim. Behav.* 55:861–873.
- Hughes, B. O., and S. Wilson. 1993. Comparison of bone volume and strength as measures of skeletal integrity in caged laying hens with access to perches. *Res. Vet. Sci.* 54:202–206.
- Huth, J. C., and G. S. Archer. 2015. Effects of LED lighting during incubation on layer and broiler hatchability, chick quality, stress susceptibility and post-hatch growth. *Poult. Sci.* 94:3052–3058.
- Janczak, A. M., and A. B. Riber. 2015. Review of rearing-related factors affecting the welfare of laying hens. *Poult. Sci.* 94:1454–1469.
- Jendral, M. J., D. R. Korver, J. S. Church, and J. J. R. Feddes. 2008. Bone mineral density and breaking strength of white leghorns housed in conventional, modified, and commercially available colony battery cages. *Poult. Sci.* 87:828–837.
- Jenkins, B. N., J. F. Hunter, M. P. Cross, A. M. Acevedo, and S. D. Pressman. 2018. When is affect variability bad for health? The association between affect variability and immune response to the influenza vaccination. *J. Psychosom. Res.* 104:41–47.
- Johnsen, P. F., K. S. Vestergaard, and G. Nørgaard-Nielsen. 1998. Influence of early rearing conditions on the development of feather pecking and cannibalism in domestic fowl. *Appl. Anim. Behav. Sci.* 60:25–41.
- Jones, R. B. 1982. Effects of early environmental enrichment upon open-field behavior and timidity in the domestic chick. *Dev. Psychobiol.* 15:105–111.
- Jones, R. B. 1993. Reduction of the domestic chick's fear of human beings by regular handling and related treatments. *Anim. Behav.* 46:991–998.
- Jones, R. B. 1994. Regular handling and the domestic chick's fear of human beings: generalisation of response. *Appl. Anim. Behav. Sci.* 42:129–143.
- Jones, R. B. 1995. Ontogeny of response to humans in handled and non-handled female domestic chicks. *Appl. Anim. Behav. Sci.* 42:261–269.
- Jones, R. B. 2001. Does occasional movement make pecking devices more attractive to domestic chicks? *Br. Poult. Sci.* 42:43–50.
- Jones, R. B. 2004. Environmental enrichment: the need for practical strategies to improve poultry welfare. Pages 215–225 in: *Welfare of the Laying Hen*. G. C. Perry, ed. CABI Publishing, Oxfordshire, UK.
- Jones, R. B., G. Beuving, and H. J. Blokhuis. 1988. Tonic immobility and heterophil/lymphocyte responses of the domestic fowl to corticosterone infusion. *Physiol. Behav.* 42:249–253.
- Jones, R. B., and N. L. Carmichael. 1999a. Can 'environmental enrichment' affect domestic chickens' preferences for one half of an otherwise symmetrical home cage? *Anim. Welf.* 8:159–164.
- Jones, R. B., and N. L. Carmichael. 1999b. Responses of domestic chicks to selected pecking devices presented for varying durations. *Appl. Anim. Behav. Sci.* 64:125–140.
- Jones, R. B., N. L. Carmichael, and E. Rayner. 2000. Pecking preferences and pre-dispositions in domestic chicks: implications for the development of environmental enrichment devices. *Appl. Anim. Behav. Sci.* 69:291–312.
- Jones, R. B., C. Larkins, and B. O. Hughes. 1996. Approach/avoidance responses of domestic chicks to familiar and unfamiliar video images of biologically neutral stimuli. *Appl. Anim. Behav. Sci.* 48:81–98.
- Jones, R. B., and D. Waddington. 1992. Modification of fear in domestic chicks, *Gallus gallus domesticus*, via regular handling and early environmental enrichment. *Anim. Behav.* 43:1021–1033.
- Jones, R. B., and D. Waddington. 1993. Attenuation of the domestic chick's fear of human beings via regular handling: in search of a sensitive period. *Appl. Anim. Behav. Sci.* 36:185–195.
- Jung, L., and U. Knierim. 2018. Are practice recommendations for the prevention of feather pecking in laying hens in non-cage systems in line with the results of experimental and epidemiological studies? *Appl. Anim. Behav. Sci.* 200:1–12.
- Kaiser, P., Z. Wu, L. Rothwell, M. Fife, M. Gibson, T. Y. Poh, A. Shini, W. Bryden, and S. Shini. 2009. Prospects for understanding immune-endocrine interactions in the chicken. *Gen. Comp. Endocrinol.* 163:83–91.
- Keeling, L. J., and J. F. Hurnik. 1993. Chickens show socially facilitated feeding behaviour in response to a video image of a conspecific. *Appl. Anim. Behav. Sci.* 36:223–231.
- Keppler, C., W. Bauman, F. Smajlhodzic, K. Niebuhr, N. F. Johansen, M. Staack, and U. Knierim. 2012. Free range for organic pullets? In G. Rahmann, and D. Godinho (Eds.) *Tackling the Future Challenges of Organic Animal Husbandry*. Proc. 2nd OAH, Hamburg/Trenthorst, Germany, Sep 12–14, 2012.
- Klein, T., E. Zeltner, and B. Huber-Eicher. 2000. Are genetic differences in foraging behaviour of laying hen chicks paralleled by hybrid-specific differences in feather pecking? *Appl. Anim. Behav. Sci.* 70:143–155.
- Knierim, U., S. Van Dongen, B. Forkman, F. A. M. Tuytens, M. Špinková, J. L. Campo, and G. E. Weissengruber. 2007. Fluctuating asymmetry as an animal welfare indicator – A review of methodology and validity. *Physiol. Behav.* 92:398–421.
- Knowles, T. G., and D. M. Broom. 1990. Limb bone strength and movement in laying hens from different housing systems. *Vet. Rec.* 126:354–356.
- Koshiba, M., S. Nakamura, C. Deng, and L. J. Rogers. 2003. Light-dependent development of asymmetry in the ipsilateral and contralateral thalamofugal visual projections of the chick. *Neurosci. Lett.* 336:81–84.
- Kozak, M., B. Tobalske, C. Martins, S. Bowley, H. Wuerbel, and A. Harlander-Mataushek. 2016. Use of space by domestic chicks housed in complex aviaries. *Appl. Anim. Behav. Sci.* 181:115–121.
- Kruijt, J. P. 1964. Ontogeny of social behaviour in Burmese red junglefowl (*Gallus gallus spadiceus*) Bonnaterrre. *Behaviour S* 12:1–201.
- Lambton, S. L., C. J. Nicol, M. Friel, D. C. J. Main, J. L. McKinstry, C. M. Sherwin, J. Walton, and C. A. Weeks. 2013. A bespoke management package can reduce levels of injurious pecking in loose-housed laying hen flocks. *Vet. Rec.* 172:423–423.
- Lay, D. C., Jr., R. M. Fulton, P. Y. Hester, D. M. Karcher, J. B. Kjaer, J. A. Mench, B. A. Mullens, R. C. Newberry, C. J. Nicol, N. P. O'Sullivan, and R. E. Porter. 2011. Hen welfare in different housing systems. *Poult. Sci.* 90:278–294.
- Lazic, M., S. M. Schneider, and R. Lickliter. 2007. Enriched rearing facilitates spatial exploration in northern bobwhite (*Colinus virginianus*) neonates. *Dev. Psychobiol.* 49:548–551.
- LeBlanc, C., B. Tobalske, S. Bowley, and A. Harlander-Mataushek. 2018. Development of locomotion over inclined surfaces in laying hens. *Animal* 12:585–596.
- LeBlanc, S., B. Tobalske, M. Quinton, D. Springthorpe, B. Szkotnicki, H. Wuerbel, and A. Harlander-Mataushek. 2016. Physical health problems and environmental challenges influence balancing behaviour in laying hens. *PLoS One* 11:e0153477.
- Leenstra, F., V. Maurer, F. Galea, M. Bestman, Z. Amsler-Kepalaite, J. Visscher, I. Vermeij, and M. van Krimpen. 2014. Laying hen performance in different production systems; why do they differ and how to close the gap? Results of discussion with groups

- of farmers in The Netherlands, Switzerland and France, benchmarking and model calculations. *Arch. Geflügelkd.* 78, DOI: 10.1399/eps.2014.53.
- Lewis, P.D., and R. M. Gous. 2009. Photoperiodic responses of broilers. II. Ocular development. *Br. Poult. Sci.* 50:667–672.
- Leyendecker, M., H. Hamann, J. Hartung, J. Kamphues, U. Neumann, C. Sürrie, and O. Distl. 2005. Keeping laying hens in furnished cages and an aviary housing system enhances their bone stability. *Br. Poult. Sci.* 46:536–544.
- Lindberg, A. C., and C. J. Nicol. 1994. An evaluation of the effect of operant feeders on welfare of hens maintained on litter. *Appl. Anim. Behav. Sci.* 41:211–227.
- Lorenzi, E., U. Mayer, O. Rosa-Salva, and G. Vallortigara. 2017. Dynamic features of animate motion activate septal and preoptic areas in visually naïve chicks (*Gallus gallus*). *Neuroscience* 354:54–68.
- Marino, L. 2017. Thinking chickens: a review of cognition, emotion, and behavior in the domestic chicken. *Anim. Cogn.* 20:127–147.
- Matur, E., I. Akyazi, E. Eraslan, E. Ergul Ekiz, H. Eseceli, M. Keten, K. Metiner, and D. Aktaran Bala. 2016. The effects of environmental enrichment and transport stress on the weights of lymphoid organs, cell-mediated immune response, heterophil functions and antibody production in laying hens. *Anim. Sci. J.* 87:284–292.
- Matur, E., E. Eraslan, I. Akyazi, E. Ergul Ekiz, H. Eseceli, M. Keten, K. Metiner, and D. Aktaran Bala. 2015. The effect of furnished cages on the immune response of laying hens under social stress. *Poult. Sci.* 94:2853–2862.
- Mayer, U., R. Bhushan, G. Vallortigara, and S. Ah Lee. 2018. Representation of environmental shape in the hippocampus of domestic chicks (*Gallus gallus*). *Brain Struct. Funct.* 223:941–953.
- McArdie, T. M., L. J. Keeling, H. J. Blokhuis, and R. B. Jones. 2005. Reduction in feather pecking and improvement of feather condition with the presentation of a string device to chickens. *Appl. Anim. Behav. Sci.* 93:67–80.
- McKenzie, P., R. J. Andrew, and R. B. Jones. 1998. Lateralization in chicks and hens: New evidence for control of response by the right eye system. *Neuropsychologia* 36:51–58.
- Michel, V., and D. Huonnic. 2003. A comparison of welfare, health and production performance of laying hens reared in cages or in aviaries. In *Abstracts from the Spring Meeting of the WPSA French Branch*, pp 775–776, Br. Poult. Sci. 44:769–831.
- Moe, R. O., D. Guémené, M. Bakken, H. J. S. Larsen, S. Shini, S. Lervik, E. Skjerve, V. Michel, and R. Tauson. 2010. Effects of housing conditions during the rearing and laying period on adrenal reactivity, immune response and heterophil to lymphocyte (H/L) ratios in laying hens. *Animal* 4:1709–1715.
- Moinard, C., J. P. Morisse, and J. M. Faure. 1998. Effect of cage area, cage height and perches on feather condition, bone breakage and mortality of laying hens. *Br. Poult. Sci.* 39:198–202.
- Moinard, C., P. Statham, and P. R. Green. 2004. Control of landing flight by laying hens: Implications for the design of extensive housing systems. *Br. Poult. Sci.* 45:578–584.
- Nasr, M. A. F., J. Murrell, and C. J. Nicol. 2013. The effect of keel fractures on egg production, feed and water consumption in individual laying hens. *Br. Poult. Sci.* 54:165–170.
- Nasr, M. A., C. J. Nicol, and J. C. Murrell. 2012. Do laying hens with keel bone fractures experience pain? *PLoS One* 7:e42420.
- Newberry, R. C. 1995. Environmental enrichment: Increasing the biological relevance of captive environments. *Appl. Anim. Behav. Sci.* 44:229–243.
- Newberry, R. C. 1999. Exploratory behaviour of young domestic fowl. *Appl. Anim. Behav. Sci.* 63:311–321.
- Nicol, C. J., A. C. Lindberg, A. J. Phillips, S. J. Pope, L. J. Wilkins, and L. E. Green. 2001. Influence of prior exposure to wood shavings on feather pecking, dustbathing and foraging in adult laying hens. *Appl. Anim. Behav. Sci.* 73:141–155.
- Nicol, C. J. 2015. *Sensory biology*, Pages 15–34 in *The Behavioural Biology of Chickens*. CABI Publishing, Oxfordshire, UK.
- Nordquist, R. E., E. C. Zeinstra, T. B. Rodenburg, and F. J. van der Staay. 2013. Effects of maternal care and selection for low mortality on tyrosine hydroxylase concentrations and cell soma size in hippocampus and nidopallium caudolaterale in adult laying hen. *J. Anim. Sci.* 91:137–146.
- Olsson, P., O. Lind, and A. Kelber. 2015. Bird colour vision: Behavioural thresholds reveal receptor noise. *J. Exp. Biol.* 218:184–193.
- Ortega, C. P. 2012. Chapter 2: Effects of noise pollution on birds: A brief review of our knowledge. *Ornithol. Monogr.* 74:6–22.
- Parmentier, H. K., T. B. Rodenburg, G. De Vries Reilingh, B. Beerda, and B. Kemp. 2009. Does enhancement of specific immune responses predispose laying hens for feather pecking? *Poult. Sci.* 88:536–542.
- Patzke, N., S. Ocklenburg, F. J. van der Staay, O. Güntürkün, and M. Manns. 2009. Consequences of different housing conditions on brain morphology in laying hens. *J. Chem. Neuroanat.* 37:141–148.
- Petterson, I. C., R. Freire, and C. J. Nicol. 2016. Factors affecting ranging behaviour in commercial free-range hens. *Worlds Poult. Sci. J.* 72:137–150.
- Petterson, I. C., C. A. Weeks, K. I. Norman, T. G. Knowles, and C. J. Nicol. 2017a. Internal roosting location is associated with differential use of the outdoor range by free-range laying hens. *Br. Poult. Sci.* 59:135–140.
- Petterson, I. C., C. A. Weeks, K. I. Norman, and C. J. Nicol. 2017b. The ability of laying pullets to negotiate two ramp designs as measured by bird preference and behaviour. *Peer J.* 5:e4069.
- Petterson, I. C., C. A. Weeks, and C. J. Nicol. 2017c. Provision of a resource package reduces feather pecking and improves ranging distribution on free-range layer farms. *Appl. Anim. Behav. Sci.* 195:60–66.
- Pickel, T., L. Schrader, and B. Scholz. 2011. Pressure load on keel bone and foot pads in perching laying hens in relation to perch design. *Poult. Sci.* 90:715–724.
- Prescott, N. B., J. R. Jarvis, and C. M. Wathes. 2004. *Vision in the laying hen*. Pages 155–164 in *Welfare of the Laying Hen*. G. C. Perry, ed. CABI Publishing, Oxfordshire, UK.
- Reed, H. J., L. J. Wilkins, S. D. Austin, and N. G. Gregory. 1993. The effect of environmental enrichment during rearing on fear reactions and depopulation trauma in adult caged hens. *Appl. Anim. Behav. Sci.* 36:39–46.
- Regmi, P., T. S. Deland, J. P. Steibel, C. I. Robison, R. C. Haut, M. W. Orth, and D. M. Karcher. 2015. Effect of rearing environment on bone growth of pullets. *Poult. Sci.* 94:502–511.
- Regmi, P., N. Smith, N. Nelson, R. C. Haut, M. W. Orth, and D. M. Karcher. 2016. Housing conditions alter properties of the tibia and humerus during the laying phase in Lohmann white Leghorn hens. *Poult. Sci.* 95:198–206.
- Regolin, L., L. Tommasi, and G. Vallortigara. 2000. Visual perception of biological motion in newly hatched chicks as revealed by an imprinting procedure. *Anim. Cogn.* 3:53–60.
- Regolin, L., and G. Vallortigara. 1996. Lateral asymmetries during responses to novel-coloured objects in the domestic chick: A developmental study. *Behav. Processes* 37:67–74.
- Riber, A. B., and D. A. Guzman. 2016. Effects of dark brooders on behavior and fearfulness in layers. *Animals* 6:3.
- Riber, A. B., and D. A. Guzman. 2017. Effects of different types of dark brooders on injurious pecking damage and production-related traits at rear and lay in layers. *Poult. Sci.* 96:3529–3538.
- Riedstra, B., and T. G. G. Groothuis. 2002. Early feather pecking as a form of social exploration: the effect of group stability on feather pecking and tonic immobility in domestic chicks. *Appl. Anim. Behav. Sci.* 30:127–138.
- Roden, C., and B. Wechsler. 1998. A comparison of the behaviour of domestic chicks reared with or without a hen in enriched pens. *Appl. Anim. Behav. Sci.* 55:317–326.
- Rodenburg, T. B., N. J. T. Scholten, and E. N. de Haas. 2017. Light during incubation and noise around hatching affect cognitive bias in laying hens (Abstr). *Proc. 51st. Congr. Intl. Soc. Appl. Ethol.* 7–10 Aug, Aarhus, Denmark, Pg 165.
- Rodenburg, T. B., M. M. van Krimpen, I. C. de Jong, E. N. de Haas, M. S. Kops, B. J. Riedstra, R. E. Nordquist, J. P. Wagenaar, M. Bestman, and C. J. Nicol. 2013. The prevention and control of feather pecking in laying hens: Identifying the underlying principles. *Worlds Poult. Sci. J.* 69:361–374.
- Rogers, L. J. 1990. Light input and the reversal of functional lateralization in the chicken brain. *Behav. Brain Res.* 38:211–221.

- Rogers, L. J. 1993. The molecular neurobiology of early learning, development, and sensitive periods, with emphasis on the avian brain. *Mol. Neurobiol.* 7:161–187.
- Rogers, L. J. 1995. *The Development of Brain and Behaviour in the Chicken*. CAB International, Wallingford, UK.
- Rogers, L. J. 1997. Early experiential effects on laterality: research on chicks has relevance to other species. *Laterality* 2:199–219.
- Rogers, L. J. 2008. Development and function of lateralization in the avian brain. *Brain Res. Bull.* 76:235–244.
- Rogers, L. J. 2010. Relevance of brain and behavioural lateralization to animal welfare. *Appl. Anim. Behav. Sci.* 127:1–11.
- Rogers, L. J. 2012. The two hemispheres of the avian brain: their differing roles in perceptual processing and the expression of behavior. *J. Ornithol.* 153:61–74.
- Rogers, L. J. 2014. Asymmetry of brain and behavior in animals: its development, function, and human relevance. *Genesis* 52:555–571.
- Rogers, L. J., P. Zucca, and G. Vallortigara. 2004. Advantages of having a lateralized brain. *Proc. Roy. Soc. B: Biol. Sci.* 271:S420–S422.
- RSPCA Australia. 2015. RSPCA Approved Farming Scheme Standards for Pullets (Layer Hens). Deakin West, ACT, Australia. Accessed Oct 24, 2017. https://rspcaapproved.org.au/wp-content/uploads/2017/02/RSPCA_Pullet_Standards_September2015.Web.pdf.
- RSPCA UK. 2016. RSPCA Welfare Standards for Pullets (Laying Hens). Accessed Oct 24, 2017 <https://science.rspca.org.uk/sciencegroup/farmanimals/standards/pullets>.
- Ruis, M. A. W., A. Mens, R. Zanders, and J. Katoele. 2017. Feeding live black soldier fly larvae and effects on health, welfare and production of laying hens. WAFL, Sept 5–8 2017, Ede-Wageningen (Abstr.).
- Salamano, G., E. Mellia, M. Tarantola, M. S. Gennero, L. Doglione, and A. Schiavone. 2010. Acute phase proteins and heterophil:lymphocyte ratio in laying hens in different housing systems. *Vet. Rec.* 167:749–751.
- Sandilands, V., C. Moinard, and N. H. C. Sparks. 2009. Providing laying hens with perches: fulfilling behavioural needs but causing injury? *Br. Poult. Sci.* 50:395–406.
- Saunders, J. C., R. B. Coles, and G. R. Gates. 1973. The development of auditory evoked responses in the cochlea and cochlear nuclei of the chick. *Brain Res.* 63:59–74.
- Savory, C. J. 1995. Feather pecking and cannibalism. *Worlds Poult. Sci. J.* 51:215–219.
- Schütz, K. E., and P. Jensen. 2001. Effects of resource allocation on behavioural strategies: a comparison of Red Junglefowl (*Gallus gallus*) and two domesticated breeds of poultry. *Ethology.* 107:753–765.
- Shini, S., G. R. Huff, A. Shini, and P. Kaiser. 2010. Understanding stress-induced immunosuppression: exploration of cytokine and chemokine gene profiles in chicken peripheral leukocytes. *Poult. Sci.* 89:841–851.
- Shini, S., P. Kaiser, A. Shini, and W. L. Bryden. 2008. Biological response of chickens (*Gallus gallus domesticus*) induced by corticosterone and a bacterial endotoxin. *Comp. Biochem. Physiol. B Biochem. Mol. Biol.* 149:324–333.
- Shini, S., A. Shini, and G. R. Huff. 2009. Effects of chronic and repeated corticosterone administration in rearing chickens on physiology, the onset of lay and egg production of hens. *Physiol. Behav.* 98:73–77.
- Siegford, J. M., J. Berezowski, S. K. Biswas, C. L. Daigle, S. G. Gebhardt-Henrich, C. E. Hernandez, S. Thurner, and M. J. Toscano. 2016. Assessing activity and location of individual laying hens in large groups using modern technology. *Animals* 6:10.
- Singh, M., I. Ruhnke, C. de Koning, K. Drake, A. G. Skerman, G. N. Hinch, and P. C. Glatz. 2017. Demographics and practices of semi-intensive free-range farming in Australia with an outdoor stocking density of ≤ 1500 hens/hectare. *PLoS One* 12:e0187057. <https://doi.org/10.1371/journal.pone.0187057>.
- Sridharan, D., D. L. Ramamurthy, J. S. Schwarz, and E. I. Knudsen. 2014. Visuospatial selective attention in chickens. *Proc. Natl Acad. Sci. USA* 111:E2056–E2065.
- Staack, M., B. Gruber, C. Keppler, K. Zaludik, K. Niebuhr, and U. Knierim. 2007. Importance of the rearing period for laying hens in alternative systems (Abstract in English). *Dtsch. Tierärztl. Wochenschr.* 114:86–90.
- Steenfeldt, S., J. B. Kjaer, and R. M. Engberg. 2007. Effect of feeding silages or carrots as supplements to laying hens on production performance, nutrient digestibility, gut structure, gut microflora and feather pecking behaviour. *Br. Poult. Sci.* 48:454–468.
- Stratmann, A., E. K. F. Fröhlich, A. Harlander-Matauschek, L. Schrader, M. J. Toscano, H. Würbel, and S. G. Gebhardt-Henrich. 2015. Soft perches in an aviary system reduce incidence of keel bone damage in laying hens. *PLoS One* 10:e0122568.
- Tahamtani, F. M., J. Nordgreen, M. Brantsæter, G. C. Østby, R. E. Nordquist, and A. M. Janczak. 2016a. Does early environmental complexity influence tyrosine hydroxylase in the chicken hippocampus and ‘prefrontal’ caudolateral nidopallium? *Front. Vet. Sci.* 3:8.
- Tahamtani, F. M., M. Brantsæter, J. Nordgreen, E. Sandberg, T. B. Hansen, A. Nødtvedt, T. B. Rodenburg, R. O. Moe, and A. M. Janczak. 2016b. Effects of litter provision during early rearing and environmental enrichment during the production phase on feather pecking and feather damage in laying hens. *Poult. Sci.* 95:2747–2756.
- Tahamtani, F. M., J. Nordgreen, R. E. Nordquist, and A. M. Janczak. 2015. Early life in a barren environment adversely affects spatial cognition in laying hens (*Gallus gallus domesticus*). *Front. Vet. Sci.* 2:3.
- Tommasi, L., and G. Vallortigara. 2001. Encoding of geometric and landmark information in the left and right hemispheres of the avian brain. *Behav. Neurosci.* 115:602–613.
- Tommasi, L., and G. Vallortigara. 2004. Hemispheric processing of landmark and geometric information in male and female domestic chicks (*Gallus gallus*). *Behav. Brain Res.* 155:85–96.
- Vallortigara, G. 2005. The cognitive chicken: Visual and spatial cognition in a non-mammalian brain. In *Comparative Cognition: Experimental Explorations of Animal Intelligence*. E. A. Wasserman, and T. R. Zentall, eds. Oxford University Press, Oxford, UK.
- Vallortigara, G., and R. J. Andrew. 1994. Differential involvement of right and left hemisphere in individual recognition in the domestic chick. *Behav. Processes* 33:41–57.
- Vallortigara, G., R. J. Andrew, L. Sertori, and L. Regolin. 1997. Sharply timed behavioral changes during the first 5 weeks of life in the domestic chick (*Gallus gallus*). *Bird Behav.* 12:29–40.
- Vallortigara, G., and L. Regolin. 2006. Gravity bias in the interpretation of biological motion by inexperienced chicks. *Curr. Biol.* 16:R279–R280.
- Vallortigara, G., L. Regolin, G. Bortolomol, and L. Tommasi. 1996. Lateral asymmetries due to preferences in eye use during visual discrimination learning in chicks. *Behav. Brain Res.* 74:135–143.
- van Praag, H., G. Kempermann, and F. H. Gage. 2000. Neural consequences of environmental enrichment. *Nat. Rev. Neurosci.* 1:191–198.
- van de Weerd, H. A., and J. Day. 2009. A review of environmental enrichment for pigs housed in intensive housing systems. *Appl. Anim. Behav. Sci.* 116:1–20.
- van de Weerd, H. A., and A. Elson. 2006. Rearing factors that influence the propensity for injurious feather pecking in laying hens. *Worlds Poult. Sci. J.* 62:654–664.
- Vits, A., D. Weitzenbürger, H. Hamann, and O. Distl. 2005. Production, egg quality, bone strength, claw length, and keel bone deformities of laying hens housed in furnished cages with different group sizes. *Poult. Sci.* 84:1511–1519.
- Walsh, N. P., M. Gleeson, R. J. Shephard, M. Gleeson, J. A. Woods, N. C. Bishop, M. Fleshner, C. Green, B. K. Pedersen, L. Hoffman-Goetz, C. J. Rogers, H. Northoff, A. Abbasi, and P. Simon. 2011. Position statement, Part one: immune function and exercise. *Exerc. Immunol. Rev.* 17:6–63.
- Walstra, I., J. ten Napel, B. Kemp, H. Schipper, and H. van den Brand. 2010. Early life experiences affect the adaptive capacity of rearing hens during infectious challenges. *Animal* 4:1688–1696.
- Webster, A. B. 2004. Welfare implications of avian osteoporosis. *Poult. Sci.* 83:184–192.
- Weeks, C. A., S. L. Lambton, and A. G. Williams. 2016. Implications for welfare, productivity and sustainability of the variation in reported levels of mortality for laying hen flocks kept in

- different housing systems: A meta-analysis of ten studies. *PLoS One* 11:e0146394.
- Weeks, C. A., and C. J. Nicol. 2006. Behavioural needs, priorities and preferences of laying hens. *Worlds Poult. Sci. J.* 62:296-307.
- Wells, D. L. 2009. Sensory stimulation as environmental enrichment for captive animals: a review. *Appl. Anim. Behav. Sci.* 118:1-11.
- Whitehead, C. C. 2004. Overview of bone biology in the egg-laying hen. *Poult. Sci.* 83:193-199.
- Whitehead, C. C., and R. H. Fleming. 2000. Osteoporosis in cage layers. *Poult. Sci.* 79:1033-1041.
- Whiteside, M. A., R. Sage, and J. R. Madden. 2016. Multiple behavioural, morphological and cognitive developmental changes arise from a single alteration to early life spatial environment, resulting in fitness consequences for released pheasants. *R. Soc. Open Sci.* 3:160008.
- Wiepkema, P. R., and J. M. Koolhaas. 1993. Stress and animal welfare. *Anim. Welf.* 2:195-218.
- Wilkins, L. J., J. L. McKinstry, N. C. Avery, T. G. Knowles, S. N. Brown, J. Tarlton, and C. J. Nicol. 2011. Influence of housing system and design on bone strength and keel bone fractures in laying hens. *Vet. Rec.* 169:414.
- Wilkins, L. J., S. Pope, C. Leeb, E. Glen, A. Phillips, P. Zimmerman, C. J. Nicol, and S. N. Brown. 2005. Fracture rate in laying-strain hens at the end of the rearing period and the end of the laying period. *Anim. Sci. Pap. Rep.* 23:189-194.
- Workman, L., and R. J. Andrew. 1989. Simultaneous changes in behaviour and in lateralization during the development of male and female domestic chicks. *Anim. Behav.* 38:596-605.
- Woodcock, M. B., E. A. Pajor, and M. A. Latour. 2004. The effects of hen vocalizations on chick feeding behavior. *Poult. Sci.* 83:1940-1943.
- Yan, F. F., P. Y. Hester, and H. W. Cheng. 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. *Poult. Sci.* 93:1318-1326.
- Zepp, M., H. Louton, M. Erhard, P. Schmidt, F. Helmer, and A. Schwarzer. 2018. The influence of stocking density and enrichment on the occurrence of feather pecking and aggressive pecking behavior in laying hen chicks. *J. Vet. Behav.* 24: 9-18.
- Zimmerman, P. H., S. A. F. Buijs, J. E. Bolhuis, and L. J. Keeling. 2011. Behaviour of domestic fowl in anticipation of positive and negative stimuli. *Anim. Behav.* 81:569-577.
- Zulkifli, I., and P. B. Siegel. 1995. Is there a positive side to stress? *Worlds Poult. Sci. J.* 51:63-76.