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Hen welfare in different housing systems[1]

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ABSTRACT Egg production systems have become subject to heightened levels of scrutiny. Multiple factors such as disease, skeletal and foot health, pest and parasite load, behavior, stress, affective states, nutrition, and genetics influence the level of welfare hens experience. Although the need to evaluate the influence of these factors on welfare is recognized, research is still in the early stages. We compared conventional cages, furnished cages, noncage systems, and outdoor systems. Specific attributes of each system are shown to affect welfare, and systems that have similar attributes are affected similarly. For instance, environments in which hens are exposed to litter and soil, such as noncage and outdoor systems, provide a greater opportunity for disease and parasites. The more complex the environment, the more difficult it is to clean, and the larger the group size, the more easily disease and parasites are able to spread. Environments such as conventional cages, which limit movement, can lead to osteoporosis, but environments that have increased complexity, such as noncage systems, expose hens to an increased incidence of bone fractures. More space allows for hens to perform a greater repertoire of behaviors, although some deleterious behaviors such as cannibalism and piling, which results in smothering, can occur in large groups. Less is understood about the stress that each system imposes on the hen, but it appears that each system has its unique challenges. Selective breeding for desired traits such as improved bone strength and decreased feather pecking and cannibalism may help to improve welfare. It appears that no single housing system is ideal from a hen welfare perspective. Although environmental complexity increases behavioral opportunities, it also introduces difficulties in terms of disease and pest control. In addition, environmental complexity can create opportunities for the hens to express behaviors that may be detrimental to their welfare. As a result, any attempt to evaluate the sustainability of a switch to an alternative housing system requires careful consideration of the merits and shortcomings of each housing system.

Key words: poultry, housing, welfare, alternative, health

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INTRODUCTION

Much progress has been made over the past 20 yr in developing valid methods to assess hen health and welfare. However, assessing hen health and welfare is difficult and multifactorial. Freedom from disease, ability to perform specific behaviors, ability to cope with sometimes stressful environments, and protection from housing-specific challenges all need to be considered to assess hen welfare properly. A further question to

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consider is not only how to prevent hens from suffering as a result of negative environmental influences but also how to provide them with positive features in their environment to improve welfare. Comparing data across studies adds complexity because of potentially confounding differences in environment, genetics, nutrition, and management. It is also hard to replicate the size of commercial systems in a laboratory. Data collected on commercial farms also found that mortality differed significantly between noncage, outdoor, conventional cages, and furnished cages, with mortality in furnished cages being numerically lower than any other system (Sherwin et al., 2010). Small-scale studies may be applicable to the commercial situation, but this scenario cannot be universally assumed.

Here, we review the following factors related to poultry welfare: disease, skeletal and foot health, nutrition, pest and parasite load, behavior, stress, affective states, and genetics, all areas that provide specific challenges when managing flocks in the various housing systems. The following document compares systems based on discrete criteria that are used in assessing hen welfare and that are required to fully and comprehensively make judgments on hen welfare relative to housing systems.

Disease

Recently, *Escherichia coli* peritonitis, coccidiosis, necrotic enteritis, *Mycoplasma gallisepticum*, calcium depletion-tetany, infectious bronchitis, and cannibalism have been listed as diseases of concern in the United States (United States Animal Health Association, 2007). Caution must be exercised when interpreting this list because some of these diseases (*E. coli* peritonitis and necrotic enteritis) are considered to be regional, whereas cannibalism is reported in both caged and noncaged hens. Several surveys report cannibalism and feather pecking as the primary causes of mortality in commercial laying hens (refer to Behavior section for discussion on cannibalism; Savory, 1995; Abrahamsson and Tauson, 1997; Weitzenbürger et al., 2005). Mortality in a healthy, well-managed flock housed in conventional cages is generally less than 0.1% per week.

As early as 1986, there were reports of clinical problems such as decreased egg production, egg drop syndrome adenovirus (EDS 76) infection, and cannibalism in free-range flocks in the United Kingdom (Swarbrick, 1986). Mortality is generally greater in laying hens raised in litter-based housing compared with furnished cages (Michel and Huonnic, 2003; Rodenburg et al., 2008). A recent 4-yr Scandinavian study of laying hens, surveying birds raised commercially in litter-based, free-range, and conventional cage systems, reported the greatest mortality in the litter-based and free-range systems compared with conventional cages. The greatest number of laboratory submissions came from litter-based and free-range systems. Bacterial infections were the most common cause of mortality in birds raised on litter-based systems and included erysipelas, colibacillosis, and pasteurellosis (Fossum et al., 2009). Hens raised on litter and free-range also had greater mortality associated with viral disease (lymphoid leukosis, Marek's disease, and Newcastle disease), coccidiosis, and red mites (*Dermanyssus gallinae*) compared with hens raised in conventional cages. A study from Germany indicated that there is a higher risk of erysipelas in laying hens raised in litter-based housing systems compared with cages (Mazaheri et al., 2005). The greater incidence of bacterial infections and ectoparasitism in litter-based and free-range flocks is reflected in a survey of German layer flocks that reported increased use of antibiotics and acaricides in hens raised in litter-based systems (Kreienbrock et al., 2003).

Many of the infectious diseases of layers are a result of contact with soil, litter, and fomites (e.g., rodents, beetles, and equipment) known to carry the agents of those diseases. Histomoniasis is generally associated with soil contact and has been reported in free-range laying hens (Esquenet et al., 2003). *Erysipelothrix rhusiopathiae*, a soilborne microorganism, occurs more often in hens exposed to litter-based and free-range systems (Mazaheri et al., 2005; Fossum et al., 2009).

A higher percentage of hens with access to free-range (73%) excreted a greater number of coccidial oocysts in feces compared with hens (58%) without free-range access (Hane, 1999). Layers raised in free-range systems have a greater incidence of intestinal helminths compared with hens raised in cages (Hane, 1999; Permin et al., 1999). Approximately 80% of the cases of pasteurellosis in Danish poultry occurred in free-range flocks (Christensen et al., 1998). In addition, laying hens raised on free-range are at risk for predation and can contract diseases through contact with wild animals (Lervik et al., 2007). Diseases such as avian influenza, Newcastle disease, and ectoparasites, such as mites, have been detected in wild birds and can spread to domestic poultry.

Findings of increased incidence of infectious disease in litter-based flocks are contrasted with a recent Swiss survey of chick and laying hen mortality in commercial flocks. This study recorded viral, bacterial, parasitic, and noninfectious diseases in poultry presented to a veterinary diagnostic laboratory during the 12 yr after battery cages were banned. There was a consistent decrease in incidence of viral disease (mostly a result of decreased Marek's disease), parasitism (mostly coccidia and helminths), and noninfectious disease (cannibalism and feather pecking) during this period, whereas bacterial infections consistently increased (Kaufmann-Bart and Hoop, 2009). The decreased incidence of these diseases was attributed to greater emphasis on poultry management in litter-based and free-range systems. The same authors also reported an increase in fatty liver in cage-reared hens compared with those on litter-based-free-range systems, and a similar finding was reported in a survey of hens in various laying flocks in Germany (Weitzenbürger et al., 2005)

General management practices emphasize air quality as playing an important role in contributing to respiratory disease in poultry. Poor air quality, particularly related to accumulation of aerosolized dust and bacteria, can have a significantly negative effect on animal health (Pedersen et al., 2000). High dust concentrations have been linked with high mortality rates in laying hens (Guarino et al., 1999). Air quality has been shown to be poorer in litter-based systems (floor housing and aviary) compared with furnished cages (Rodenburg et al., 2008). Cage systems produced significantly lower aerosolized inhalable (particle size: 1 to 100 μm in diameter) and respirable (particle size: <8.5 μm) dust particles when compared with litter-based systems. Total numbers of aerosolized aerobic bacteria were also significantly higher in litter-based systems compared with furnished cages. In an additional study, dust levels were found to be higher in litter-based systems compared with conventional cages or wire floors (Michel and Huonnic, 2003; De Reu et al., 2005). These findings on air quality may explain, in part, why hens raised in litter-based systems generally have more bacterial diseases compared with hens in conventional cages.

Diseases affecting laying hens depend on the conditions to which they are exposed. Appropriate vaccines, effective disinfectants, and reduction of biosecurity risks can reduce the incidence of infectious diseases in litter-based housing systems. However, currently these strategies need to be optimized. Hens that have contact with solid flooring-litter, including those in furnished cages, all risk contracting the same diseases. Hens that are raised free-range are in direct contact with soil-borne microorganisms and parasites and are at greatest risk for predation and contracting infectious diseases from wild animals when compared with hens kept in enclosed systems.

Skeletal Health

Due to the varied components in the different types of housing, hens may suffer from a variety of skeletal problems including osteoporosis, cage layer fatigue, and keel bone deformities. Osteoporosis is a noninfectious disease caused by an age-related decrease in the amount of mineralized structural bone leading to skeletal fragility and susceptibility to fracture (Whitehead and Wilson, 1992; Hudson et al., 1993; Whitehead, 2004). Osteoporosis is widespread in today's commercial laying hens and contributes to approximately 20 to 35% of all mortalities during the egg production cycle of caged hens (McCoy et al., 1996; Anderson, 2002). In its most severe state, it is referred to as cage layer fatigue. First described by Couch (1955) when cage systems were being adopted by the egg industry, cage layer fatigue causes bone brittleness, paralysis, and death in hens. An S-shaped curvature of the keel bone is characteristic of hens with cage layer fatigue. As the name implies, this condition occurs with caged hens and is not common with other housing systems. Osteoporosis in today's egg-laying strains of chickens is not so severe as to lead to cage layer fatigue (Whitehead and Fleming, 2000) unless hens experience osteomalacia because of inadequate nutritional intake or absorption of calcium, phosphorus, or metabolites of vitamin D.

The major skeletal health issue of conventionally caged hens, as compared with loose housing systems, is the increased susceptibility to osteoporosis mainly due to lack of exercise (Rowland and Harms, 1970, 1972; Meyer and Sunde, 1974; Knowles and Broom, 1990; Nørgaard-Nielsen, 1990; Fleming et al., 1994; Tauson and Abrahamsson, 1994a; Van Niekerk and Reuvekamp, 1994; Tauson, 1998; Whitehead and Fleming, 2000; Jendral et al., 2008). Hens housed in a single-level noncage system with a floor of either deep litter or raised wire (manure pit below) had similar bone strength, whereas hens in conventional cages had lower bone strength, suggesting that skeletal quality was not influenced by the wire flooring but instead by hen activity (Rowland and Harms, 1970). Even brief exposures of hens to housing systems that allow for increased static and dynamic loading of bones improved skeletal quality (Meyer and Sunde, 1974; Newman and Leeson, 1998). In contrast, rearing pullets in deep litter and then switching them to conventional or furnished cages for egg laying had a negative effect on bone strength at end of lay as compared with chickens kept in cages their entire life cycle (Gregory et al., 1991; Gregory and Wilkins, 1992; Vits et al., 2005). Perhaps the floor-reared pullets when placed in cages reacted to the new environment by displaying less activity. Levels of activity may also explain the improved bone strength of hens housed in taller cages (Harner and Wilson, 1985) or in conventionally caged hens given more floor space (Tauson and Abrahamsson, 1994b).

Old Bone Fractures

Although bone strength of caged hens is poorer than that of hens in extensive housing, caged hens have a lower incidence of old fractures (McLean et al., 1986; Gregory et al., 1990; Abrahamsson and Tauson, 1995; Tauson et al., 1999; Fleming et al., 2004, 2006; Wilkins et al., 2004; DEFRA, 2006). Old breaks are of a great concern from a welfare point of view because of chronic pain. The incidence of old keel breaks of hens in noncage systems ranges from 52 to 73% (Freire et al., 2003; Nicol et al., 2006) and is likely due to the increased mobility and bumping of the keel bone when hens move from litter to raised slats or access the nest boxes (DEFRA, 2006).

Perches

The addition of perches to a housing system can have both positive and negative consequences. Installation of perches in cages improves bone strength (Hughes and Appleby, 1989; Duncan et al., 1992; Wilson et al., 1992; Hughes et al., 1993; Tauson and Abrahamsson, 1994b; Abrahamsson and Tauson, 1997; Barnett et al., 1997; Leyendecker, 2003; Jendral et al., 2008; Tactacan et al., 2009), but landing failures when jumping between perches in extensive systems may contribute to old breaks. Strategically arranging perches within a noncage system with multiple levels could potentially reduce hen injuries by improving the probability of successful landings (Scott et al., 1997). High use of perches can also lead to keel bone deviations (Tauson and Abrahamsson, 1994a; Abrahamsson et al., 1996; Tauson, 1998; Vits et al., 2005).

Depopulation

High rates of new fractures occur among conventionally caged hens during depopulation and transport (Gregory and Wilkins, 1989; Gregory et al., 1990) as compared with extensive systems or furnished cages with wider door openings (DEFRA, 2006). Cage front designs that allow for easier removal of spent hens reduce bone breakage (Walker et al., 1997; DEFRA, 2006). During depopulation, gently handling and grasping hens by 2 legs as opposed to 1 leg reduces bone breakage (Gregory and Wilkins, 1992; Gregory et al., 1992).

Foot Health

The most common foot problems in chickens are footpad dermatitis, bumblefoot, hyperkeratosis, and excessive claw growth.

Footpad dermatitis is inflammation of the s.c. tissue of the plantar region of the foot. In its earlier stages, the epidermis becomes discolored and the condition can later progress to necrosis and ulceration of the footpad. Wet litter conditions and high ammonia content of the litter can cause footpad dermatitis (Wang et al., 1998). If footpads become infected with bacteria such as *Staphylococcus aureus*, the condition can lead to bumblefoot (Gross, 1984). Bumblefoot is a localized bulbous lesion of the ball of the foot due to the penetration of a foreign body followed by invasion of *S. aureus*. Lameness is often the first sign of the condition and is the most costly problem for birds reared in deep litter. Poorly designed and maintained perches used in floor systems have been associated with bumblefoot because of accumulation of manure and litter on the surface of the perch, especially under wet litter conditions (Tauson and Abrahamsson, 1994b; Wang et al., 1998).

Hyperkeratosis (hypertrophy of the corneus layer of the skin) occurs on the toe- and footpads of caged hens (Duncan et al., 1992; Weitzenbürger et al., 2006). A lower incidence of toepad hyperkeratosis occurs in furnished as compared with conventional cages (Abrahamsson and Tauson, 1997). Hyperkeratosis is caused by increased compression load of the toe- or footpad on the wire floor of the cage as well as the perch (Weitzenbürger et al., 2006). The slope of the wired cage floor has also been implicated as causing a higher frequency of hyperkeratosis among caged hens as compared with noncage hens (Abrahamsson and Tauson, 1995). Hyperkeratosis is most likely less painful than bumblefoot (Tauson, 2002).

If claws grow too long, they can break off more easily, leading to open, bleeding wounds and greater susceptibility to infection. Excessive claw growth can occur if hens do not have access to abrasive materials for trimming nails. Noncage systems with deep litter allow for hen scratching, thus preventing excessive claw growth (Vits et al., 2005).

Skeletal integrity is rated as poor in all housing systems except furnished cages (Table 1; Newman and Leeson, 1997; Newberry et al., 1999; Tauson, 2002; Appleby et al., 2004; Webster, 2004; Rodenburg et al., 2005). Hens in conventional and furnished cages have overall better foot health than hens in other systems with access to litter or range (Table 1; Tauson et al., 1999, 2006). Claw health is poor in conventional cages (Taylor and Hurnik, 1996; Abrahamsson and Tauson, 1997).

Pests and Parasite Load

Arthropod pests of poultry (Axtell and Arends, 1990) include flies or beetles that develop in the accumulated manure or feed and several ectoparasites. Conventional cages, and possibly some furnished cages or floor operations, can encourage accumulations of manure and manure-feed mixtures. Especially when moist, they can allow flies such as the house fly, *Musca domestica*, or

Table 1. The effect of housing systems on skeletal quality and foot health of hens[1]

		Furnished cage			Noncage (barn)		
Indicator	Conventional cage	Small	Medium	Large	Single level	Multiple levels	Outdoor (free-range)
Skeletal quality	++[2]	+++[3]	+++	+++	++[4]	++[4]	++[4]
Footpad dermatitis/bumblefoot/hyperkeratosis	+++	+++	+++	+++	++	++	++
Claws	++	++++	++++	++++	++++	++++	++++

[1]This table was revised from a chart from LayWel (2006a,b) and the American Veterinary Medical Association (2009). Scale of how well welfare measures are met by housing systems: ++ = poor; +++ = medium; ++++ = good.

[2]Reduced bone strength, fractures when birds are caught.

[3]Bones stronger from perch use culminating in reduced incidence of old fractures but increased incidence of keel bone deformities.

[4]More fractures during lay despite stronger bones.

beetles such as the lesser mealworm, *Alphitobius diaperinus*, to thrive. The house fly is a human nuisance pest, and both flies and beetles may harbor pathogens important to poultry or possibly human health (McAllister et al., 1994; Kinde et al., 2005; Templeton et al., 2006; Ahmad et al., 2007; Chakrabarti et al., 2007). High-density open-style or deep pit conventional cage systems are the worst for fly problems due to accumulated manure (as opposed to cage systems with manure belts). Beetle problems occur via bird consumption of possibly pathogen-contaminated beetles or by beetle damage to insulation. Beetles can be serious in suspended cage systems as well as in floor operations (e.g., pullets or breeders). Beetles, with their long lifespan (months), conceivably may maintain pathogens within a poultry house environment (e.g., between flocks). In general, lower bird density yields better manure drying and lessens problems with flies and probably with beetles. Bird access to their manure (floor or outdoor) allows them to scatter it and eat fly larvae or beetles. Although there are very serious biosecurity concerns, loose birds probably will largely control flies and help control beetles by predation (Glofcheskie and Surgeoner, 1993). Roughly, the ranking (most to least risk) of primary housing types for fly and total beetle production is conventional cage systems, furnished cages, and noncage systems. However, risk of beetle consumption by birds, and the possible transmission related to it, is probably highest in noncage systems, which can produce very high numbers of beetles in litter near water and feed lines.

Ectoparasites fit into 1 of 2 categories: nest-dwelling or permanent. Blood-feeding mites, *Dermanyssus* and *Ornithonyssus*, can cause direct economic damage through irritation, blood loss, and forcing the hens to mount a metabolically costly immune response (Kilpinen et al., 2005; Mullens et al., 2009). The mites can also become nuisance or biting pests of people working on poultry operations (Höglund et al., 1995; Mullens et al., 2004). Mites may harbor or transmit several poultry pathogens as well (Chirico et al., 2003; Valiente Moro et al., 2007).

The nest dwellers live in the bird environment and travel to the birds (usually to blood-feed) for part of their life cycle. Examples include the red mite (*D. gallinae*), soft ticks such as *Argas*, bedbugs (*Cimex* spp.), and certain fleas such as the sticktight flea (*Echidnophaga*). Although studies with nest dwellers are mostly limited to the red mite, a more complex nest environment with lots of small hiding places (as exemplified in free-range or noncage systems) favors such arthropods relative to suspended wire cage systems (Maurer et al., 1993; Höglund et al., 1995; Drakley and Walker, 2002; Meyer-Kuhling et al., 2007). If the United States moves toward noncage and environmentally complex housing, we can predict greater problems with the nest-dwelling ectoparasites, but no recent surveys exist. Relatively sterile environments, such as suspended wire cages, have largely eliminated nest ectoparasites. The trade-off has been that high densities of hens in suspended wire cages allow rapid spread and reproduction by the permanent ectoparasites, notably the northern fowl mite (*Ornithonyssus sylviarum*) and the body louse (*Menacanthus stramineus*). Both complete their entire life cycle on the host, and populations of the northern fowl mite are regulated by host immunity (Owen et al., 2008). Recent work (B. A. Mullens, B. L. Chen, and J. P. Owen, University of California, Riverside, unpublished data) has shown that beak-trimmed hens used in such housing harbor at least 3 to 10 times as many of these ectoparasites as do beak-intact hens, no doubt due to impaired feather-grooming ability. For the industry, if docile genetic lines can be developed that can be held without beak trimming, an additional bonus should be lessening of problems with northern fowl mite and body louse.

The red mite currently is a negligible problem in US conventional cages but is of paramount concern in Europe due to a reversion to nest systems and simultaneous elimination of many or all pesticide options. A recent, comprehensive United Kingdom survey also showed that red mite numbers can be high in conventional cage systems as well (Sherwin et al., 2010). More use of furnished and noncage systems in the United States is likely to cause a resurgence of the red mite. Most other poultry ectoparasites almost never kill the host, but extreme infestations of red mites may directly kill hens in habitats with lots of mite harborage (Kirkwood, 1967; Kilpinen et al., 2005; Rodenburg et al., 2008). Although data are lacking, an intact beak (and better grooming ability) is probably less important for red mite control than it is for permanent ectoparasites because red mites do not actually live in the feathers and feed only for brief periods at night.

Roughly, the order of risk (most to least) for nest-dwelling ectoparasites would be noncage systems, furnished cages, and conventional cages. For permanent ectoparasites such as the northern fowl mite and body louse, too little is known of their performance in noncage systems to predict their effect. Certain aspects of pesticide or repellent applications will change with housing. For example, the high-pressure pesticide applications from beneath the hens, common in suspended cage systems for thorough host treatment and control of the northern fowl mite or the body louse, will be either much more difficult or impossible in furnished housing or noncage hens. Other means of control must be devised.

The complexity of the environment in which hens are housed lends itself to different challenges when working to control parasites in the flock. Relatively simple environments such as conventional cages allow for ease of parasite control through the use of pesticides and the inherent lack of hiding environment in which some parasites can live. However, these environments also allow for parasites that are associated with accumulated

Table 2. Predicted levels of behavioral expression in different housing systems for commercial egg production (depending on space and resource provision)[1]

Behavioral opportunity	Conventional cage	Furnished cage		Noncage (barn)[2]		Outdoor (free-range)[3]
		Small	Large	Slats/litter	Aviaries	
Flying	+	+	+	++++	++++	++++
Running	+	+	++	++++	++++	++++
Walking	++	++	+++	++++	++++	++++
Wing flapping[4]	+	++	++	++++	++++	++++
Stretching	++	+++	+++	++++	++++	++++
Preening	+++	++++	++++	++++	++++	++++
Standing	++++	++++	++++	++++	++++	++++
Sitting	+++	++++	++++	++++	++++	++++
Feeding	+++	+++	++++	++++	++++	++++
Drinking	+++	+++	++++	++++	++++	++++
Foraging	+	++	++	+++	+++	+++
Dust bathing	+	++	++	++++	++++	++++
Nesting	+	+++	+++	++++	++++	++++
Brooding[5]	+	+	+	+	+	+
Perching	+	++	++	+++	+++	+++
Mating[6]	+	+	+	+	+	+
Stereotyped and sham behaviors	++++	++	++	++	++	++
Cannibalism and feather pecking	++	++	+++	++++	++++	++++
Social aggession[7]	++	+++	+++	++	++	++
Smothering[8]	++	++	+++	++++	++++	+++

[1]+ = none or incomplete, ++ = relatively low, +++ = moderate, ++++ = full or relatively high. Results heavily influenced by other factors, including strain, rearing conditions, management, and precise details of the housing, within general housing type. An increased opportunity to perform a behavior does not necessarily translate into increased performance of the behavior. Comparative data supporting the above predictions across all behaviors in all housing types are limited or lacking.

[2]Predictions assume that hens have access to litter and perches. In the United States, there is no legal requirement to provide litter or perches. Barn systems may have all slatted or wire floors, resulting in outcomes similar to conventional cages for foraging, dust bathing, perching, and stereotyped and sham behaviors.

[3]Predictions assume that hens have access to litter and perches indoors and daily access to an outdoor range primarily covered with vegetation. In the United States, there is no legal requirement for daily time spent outdoors or provision of litter, perches, or vegetation. Hens may be confined indoors for extended periods on fully slatted or wire floors, resulting in outcomes similar to conventional cages for foraging, dust bathing, perching, and stereotyped and sham behaviors.

[4]If sufficient cage height.

[5]Broodiness toward eggs occasionally seen in noncage and free-range systems.

[6]Depends on presence of roosters (roosters are housed with hens rarely in noncage systems and occasionally in free-range systems).

[7]Depends on strain, group size (groups of around 30 hens show the most aggression), density (peaks at around 600 cm^2/hen), and accessibility of resources (limited, defendable resources increase aggression).

[8]Depends on strain (risk higher in flighty strains), group size (larger groups increase risk), and presence of perches and other enrichments (reduce risk).

manure to thrive, and the close proximity of large flocks allows rapid spread and reproduction by some permanent ectoparasites. In contrast, complex environments provide an advantage to nest-dwelling ectoparasites, but they also allow hens to act as predators on some pests such as flies and beetles, particularly in noncage systems.

Behavior

The normal or natural behavioral repertoire of modern domestic hens comprises ancestral behavior patterns exhibited when hens are provided with adequate space and access to diverse resources. The extent to which these behavior patterns are expressed by adult hens depends not only on their housing but also on genetics, previous experience in the rearing environment, environmental conditions during embryonic development, and epigenetic effects (Janczak et al., 2007; Lindqvist et al., 2007). Welfare concerns arise if hens are motivated to perform certain behaviors but are unable to express them due to housing constraints, resulting in emotional distress or emergence of harmful variants of those behaviors such as feather pecking and hysteria, or both. Table 2 summarizes the predicted level of behavioral expression possible in the different housing systems.

Conventional Cages

Performance of locomotory, body maintenance, and thermoregulatory behaviors is greatly curtailed in conventional cages (Nicol, 1987a; Dawkins and Hardie, 1989) to an extent determined by cage size and stocking density. Hens in a small cage will work to expand their cage size but only some of the time (Lagadic and Faure, 1987) because they prefer more space to perform certain behaviors (Cooper and Albentosa, 2003). Rebound levels of wing flapping, tail wagging, and stretching occur when hens are moved to a large space after several weeks of confinement in a small area, with the intensity of rebound of some behaviors being correlated with the duration of confinement, indicating that hens do not fully acclimatize to prolonged, severe spatial restriction (Nicol, 1987b). At high densities, rubbing against cage walls and other hens when moving across the cage can cause plumage damage and reduce thermoregulatory capacity (Hughes and Black, 1976). High density can also make it more difficult to gain access to food and water because other hens block the path, especially in deep cages with food at the front and water at the back (Hughes, 1983).

Increased group size in cages can elevate the risk of feather pecking, cannibalism, and smothering (Hansen, 1976; Newberry, 2004), risks countered by beak trimming and group selection (Craig and Muir, 1996). In some strains, dominant individuals aggressively defend the feeder, resulting in low-ranking hens obtaining less food (Hughes, 1983). In contrast, hens of at least one modern, group-selected strain share limited feeder space without aggression or stress (Thogerson et al., 2009a,b).

Conventional cages lack foraging materials that stimulate ground pecking and scratching and thus claw and beak wear (Fickenwirth et al., 1985; Glatz, 2002). Depending on cage design, overgrown claws increase the risk of hens becoming trapped in cage fixtures (Tauson, 1998). Sham dust bathing occurs in some strains (Lindberg and Nicol, 1997), whereby hens repeatedly perform wing movements on the wire floor (that would normally result in scooping dust into the plumage) without completing the dust-bathing sequence (shaking off lipid-saturated dust). This behavior is thought to indicate reduced welfare (Van Liere, 1991) or absence of pleasurable feedback (Widowski and Duncan, 2000). Certainly, sham dust bathing does not appear to return dust-bathing motivation to baseline levels (Olsson and Keeling, 2005). When dust bathing is not performed to completion, plumage is likely to be dirtier, less waterproof, and less insulative.

Hens of some strains pace repetitively in cages before oviposition, interpreted as a sign of frustration (Yue and Duncan, 2003). This behavior arises when hens fail to find an enclosed location in which to lay their eggs (Struelens et al., 2008b). Caged hens lack substrates for nest building, which may reduce welfare given that hens prefer to deposit eggs in a molded nest rather than on a sloping wire floor (Hughes et al., 1989) and nesting behavior is a behavioral priority (Weeks and Nicol, 2006). Caged hens do not exhibit broodiness, in part because of genetic selection against this behavior and in part because eggs roll out of the cage immediately after they are laid, removing access to eggs that stimulate this behavior.

Furnished Cages

Although initial models of furnished cages were not much larger than conventional cages, some current designs house 40 to 80 hens. Furnished cages thus provide varying amounts of horizontal space for locomotion and comfort behaviors and allow for some foraging, dust bathing, nesting, and perching but continue to limit behaviors in the vertical plane such as wing flapping and flying (Appleby et al., 2002).

Litter provided in small quantities inside furnished cages is rapidly depleted by foraging and dust-bathing activity. Hens are strongly motivated to forage even though feed is available ad libitum in the feed trough (Bubier, 1996; Lindqvist et al., 2002). Motivation to access litter for dust bathing is more variable and, despite the provision of litter, some hens sham dust bathe on the wire floor (Olsson and Keeling, 2005). Restricted access to litter in both time and space could be stressful, especially when subordinate hens are excluded from the litter area by dominant hens (Shimmura et al., 2008a). Some furnished cages deliver small amounts of feed as litter material onto an Astroturf mat (AstroTurf LLC, Dalton, GA) in the main area of the cage, increasing its accessibility for synchronized foraging and dust bathing. Foraging activity keeps the mat relatively clean and minimizes its use for oviposition.

Most hens are strongly motivated to lay eggs in the enclosed nest area of a furnished cage rather than in the main cage area (Abrahamsson and Tauson, 1997; Appleby et al., 2002; Cooper and Appleby, 2003). Some hens prefer to lay eggs in more open locations (Zupan et al., 2008), but this habit may incite cloacal cannibalism if other hens are able to see the cloaca during oviposition (Newberry, 2004).

Similarly, most hens are motivated to use perches (Olsson and Keeling, 2002), although perch use differs between individuals and strains (Faure and Jones, 1982). If sufficient perch space is provided, about one-quarter to one-half of the hens can be found perching at any one time during the daytime, and almost all can be found perching at night (Appleby et al., 2002). Perches in furnished cages have been associated with an increased risk of cloacal cannibalism (Moinard et al., 1998), possibly because some hens lay eggs while crouched on the perch, exposing the cloaca to hens on the floor. Perches may reduce the risk of piling and smothering in large cages (Hansen, 1976), but empirical data are lacking.

Noncage Systems

In these systems, there is sufficient space for performance of a full repertoire of locomotory and body-maintenance behaviors, and the large enclosures and flock sizes (>1,000 hens) enhance opportunities for exploratory behavior. Locomotion is increased because resources are more spread out horizontally and, sometimes, vertically, although high densities impair movement (Leone and Estevez, 2008). More learning and memory must be devoted to finding and utilizing resources, and hens adapt best to these systems as adults if they gain experience in a similar housing system during rearing. The incidence of cannibalism and feather pecking can be high if the hens have intact beaks, probably due to large flock sizes and spread of the behavior through social learning (Cloutier et al., 2002; Newberry, 2004).

Noncage systems may have 100% slatted floors, 100% litter floors, or various proportions of slats and litter. When boxes containing litter are placed on slatted floors, the litter is rapidly depleted. The opportunity to forage in litter for much of the day, both during rearing and in the laying house, may lower the risk of feather pecking and cannibalism if the litter materials stimulate and diversify foraging behavior (Huber-eicher and Weschler, 1997; Aerni et al., 2000; Nicol et al., 2001). Litter accessibility, litter quality, and experience of litter during rearing thus appear to be critical factors affecting behavior in noncage systems.

Although most hens use the nest boxes, some (floor) eggs are laid outside of the nests. Access to floor eggs occasionally triggers broodiness. Lights may be provided in nests to attract hens to use the nests, but this practice has been correlated with an increased risk of cannibalism (Zimmerman et al., 2006). Rearing chicks with access to perches reduces floor eggs (Appleby et al., 1988; Gunnarsson et al., 1999). To discourage oviposition in the litter, producers may place electric wire along the edges of the litter area and deny access to litter when pullets are first moved to the laying house. The welfare consequences of these practices have not been evaluated, although there is some evidence that restricting early access to litter increases the risk of feather pecking.

Rearing chicks with access to perches by 4 wk of age has been associated with increased use of perches, and reduced cannibalism, in adulthood (Gunnarsson et al., 1999). Other benefits of perches include lower aggression (Cordiner and Savory, 2001) and, anecdotally, calmer hens that may be less likely to pile and smother (e.g., during catching). Hens tend to prefer higher rather than lower perches (Newberry et al., 2001). However, falls from perches may contribute to keel and furculum fractures (Wilkins et al., 2004). Noncage systems in the United States generally do not provide sufficient perch space for all hens to perch at night, and some provide no perches. The extent to which raised slatted areas can substitute for perches is unclear.

The effects of stocking density can be unpredictable in noncage systems. At lower densities, hens cluster around key resources, creating localized areas of high density (Nicol et al., 1999; Channing et al., 2001). Declining numbers around a particular resource may trigger aggressive defense by the remaining hens (Estevez et al., 2002). Furthermore, some feather-pecked hens are attacked by other hens if they venture onto the litter, effectively confining them to the slats (Freire et al., 2003). At higher densities, hens are more evenly distributed across all areas of the house, including the litter, which may explain their lower levels of aggression and feather pecking (DEFRA, 2007).

Outdoor (Free-Range) Systems

Access to the outdoors allows hens to spread out to preferred distances when foraging, typically greater than 5,000 cm^2/hen (Savory et al., 2006), and greatly expands behavioral options, especially if the range offers a variety of plant types. Hens may spend much of their active day engaged in foraging behavior, searching for, investigating, selecting, extracting, and ingesting preferred food items (e.g., grass seeds, earthworms, and flying insects). They also ingest grit and engage in sun bathing and dust bathing outdoors.

Cannibalism and feather pecking can be problematic in free-range flocks (Swarbrick, 1986), especially in large flocks if only a small proportion of hens go outside because the outdoor area is devoid of vegetation, there is insufficient pophole space, or the weather is hot, windy, or rainy (Hegelund et al., 2005). Increasing use of range by rearing pullets with access to the outdoors, keeping roosters with the hens, and limiting flock sizes to $\leq$1,000 hens can lower the incidence of severe feather pecking (Bestman and Wagenaar, 2003). Range use is also enhanced by trees, bushes, and artificial cover structures (Nicol et al., 2003; Zeltner and Hirt, 2008) that provide shade and some protection from aerial predators. Crop impaction with grass, predation, and drowning in water troughs are potential risks when hens go outdoors.

Inclusion of roosters in the flock is rare except in free-range organic production systems. The presence of roosters has been reported to reduce aggression among hens (Odén et al., 2005), and allows for mating behavior. Roosters sometimes injure hens and can be a target for feather pecking by hens.

The concern regarding conventional cages is that behavioral restriction is inherent to the system and hens are prevented from expressing highly motivated behaviors for their entire laying lifespan. Furnished cages allow for some expression of the most highly motivated behaviors prevented in conventional cages but retain a degree of restriction due to limited space. Noncage systems enable the expression of a more diverse array of ancestral behavior patterns, with the greatest behavioral diversity occurring in free-range systems. However, increased behavioral freedom can also be accompanied by welfare problems such as cannibalism and predation. Behavioral problems in noncage systems generally affect a proportion of hens rather than all hens and are potentially solvable but have not proved easy to solve.

Nutrition

The move from conventional cages to pasture-based systems or even furnished cages can affect the nutrition of the laying hen. Access to pasture provides a substantial opportunity for laying hens to ingest forage material affecting their nutrition. Hens have the capacity to obtain a large amount of their diet from forage after a period of about 6 to 7 wk of behavioral adaptation and adaptation of their digestive system (Horsted and

Hermansen, 2007). Although hens on pasture are usually provided supplemental feed, pasturing allows for savings on feed costs but presents the opportunity for diets to become unbalanced.

In furnished cages and noncage systems, the hen's nutrition may be influenced by the provision of litter. Hetland and Svihus (2007) compared the feed consumption and egg production of hens housed in furnished cages in which litter consisted of wood shavings, coarsely cut hard paper, or no material. The 35-wk-old hens with access to paper material consumed more than twice the amount of paper material compared with wood shavings as evidenced by the gizzard contents. As a result, the amount of feed consumed by the hens was highest with paper material and lowest with wood shavings. The softer paper material does not facilitate the gizzard's retention of feed. This allows feed to move more quickly through the gizzard and thus larger particles pass into the small intestine. These larger particles result in a decrease in digestibility and absorption. As a result, the hens consume more feed to meet the required nutrients. Hetland and Svihus (2007) evaluated the gizzard weight when empty, finding it was 70% greater in hens with access to wood shavings compared with the control. The increased weight is a result of the gizzard retaining feed components and wood shavings to grind them to a smaller particle size before passage through the small intestine. Therefore, the wood shavings increased the nutrient digestibility, whereas the paper material reduced digestibility, influencing the overall nutrition of the hens.

Environments that provide the hen access to both nutrient and nonnutrient substrates will affect the balance of her diet and her ability process feed. Thus as alternative housing systems are created and used, it becomes imperative to understand all factors in the systems, which may affect the overall nutrition of the laying hen.

Stress

The stress response is largely characterized by activation of 2 systems, the hypothalamic-pituitary-adrenal axis and the sympathoadrenal axis. The common measures of stress that result from the activation of these systems are glucocorticoids, predominantly corticosterone in poultry, and the hormones epinephrine and norepinephrine. Researchers can measure changes in these hormones when assessing the animal's response to potential stressors and gain information about how the individual perceives the stressor. Typically, low concentrations indicate mild or limited stress, whereas high concentrations indicate severe stress. The administration of adrenocorticotropic hormone to hens will cause the hen to produce corticosterone. If the adrenal gland is larger, it is more capable of producing glucocorticoids and indicates the animal is experiencing chronic stress. Another measure of stress resides in the immune response. Activation of the stress response can alter the immune system; for instance, an increase in glucocorticoids increases circulating heterophils and thus the ratio of heterophils to lymphocytes is considered a reliable indicator of stress in poultry (Maxwell, 1993).

Table 3 summarizes the responses of hens from studies reporting stress hormone levels and other responses indicative of stress. It is important to note that, unlike some measures of welfare that clearly indicate positive or negative states, the measures represented in this table are indicative only of relative states of stress when compared with the treatments in the same study. What is evident is that, in addition to housing system, other factors are influencing the level of stress to which the hens are exposed.

Although Table 3 summarizes many studies indicating that housing environment can influence the amount of stress experienced by hens, several other studies have shown no differences in the stress levels of hens due to housing. For instance, Mench et al. (1986) found no differences in measures of stress (corticosterone, heterophil:lymphocyte ratio, antibody titers) when comparing hens in conventional cages to hens in noncage systems. Similarly, Guesdon et al. (2004), Moe et al. (2004), and Guémené et al. (2004) found few differences when comparing conventional cages with furnished cages. Different outcomes depend upon the precise conditions being compared in each study.

Welfare Concerns During Depopulation of Specific Housing Systems

Researchers (DEFRA, 2006) have found that hens from extensive environments (noncage and outdoor) were more stressed by depopulation (had greater corticosterone) compared with hens from furnished cages, with hens from conventional cages not being different from either treatment. They also found that the larger the door size of the cage, the less corticosterone in the hens' blood. Thus, the greater concentrations of corticosterone in hens from extensive environments and cages with smaller openings were most likely related to the amount of time and difficulty involved in catching the birds. Improved handling methods, whether in extensive or cage systems, decreased hen corticosterone.

Based on the very few published, peer-reviewed studies that have conducted controlled comparisons among different housing systems, there is not a clear distinction between housing systems based on the stress response of the hen. Few studies have compared all 4 systems, or used a wide range of physiological measures. Additionally, potential housing treatment effects are often confounded by differences in breed, climate, or other management variables.

Affective States

Affective states are emotions that humans label with terms such as happiness, sadness, fear, and anxiety.

Understanding these states in animals is critical to a better understanding of animal welfare. Humans experience complex subjective feelings alongside these emotional states, but we cannot be sure that animals do. Nevertheless, basic emotions are clearly accompanied by behavioral, physiological, and cognitive changes in birds. Despite growing interest in markers of affective state in farmed animals, work on cognitive or behavioral markers of emotional states in chickens has been somewhat limited. Most published work has focused on frustration, pain, and fear. Research on frustration has been referred to earlier in this paper in the context of the effects of preventing the performance of various behaviors such as nesting, dust bathing, and perching

Table 3. Relative levels of stress in different housing systems[1,2]

	Conventional cage		Furnished cage		Noncage (barn)[3]		
Item	6/cage	1 or 4/ cage	Small	Large	Slats/ litter	Aviaries	Outdoor (free-range)[4]
Craig et al. (1986)							
Corticosterone	+++	++				+++	
Shini (2003)							
Heterophil:lymphocyte	++++		+++				++
Ability to make antibodies (λ)	++		++				+++
Koelkebeck and Cain (1984)[5]							
Corticosterone	++					+++	++
Koelkebeck et al. (1986)							
Corticosterone	+++					++++	
Koelkebeck et al. (1987)[6]							
Corticosterone	++					+++	
Adrenocorticotropic hormone challenge	++					+++	
Ability to make antibodies (λ)	+++					++	
Viability	++					+++	
Guémené et al. (2004)[7]							
Corticosterone	+++		++				
Adrenocorticotropic hormone challenge	++		+++				
Colson et al. (2005)[8]							
Adrenocorticotropic hormone challenge	+++					++	
Basal corticosterone	+++					++	
Buil et al. (2006)[9]							
Experiment 1							
Corticosterone	+++		++				
Experiment 2							
Corticosterone	++					+++	
Campo et al. (2008)[10]							
Heterophil:lymphocyte						+++	++
Pohle and Cheng (2009)[11]							
Catecholamines	+		+				
Corticosterone	+++		++				
Serotonin (λ)	++		+++				
IgG	++		++				
Nicol et al. (2009)							
Corticosterone	++		+			+++	++
Black and Christensen (2009)							
Corticosterone	++						++

[1]+ = none or incomplete; ++ = low; +++ = moderate; ++++ = full or high. The scale used in this table is relative to treatments. Thus, although a treatment may have 4 +'s, this only shows a greater response relative to the other treatments, not that it was a maximal response indicative of poor welfare. λ = indicates that this measure is indicative of less stress, so a greater number of +'s indicates less stress.

[2]Results heavily influenced by other factors, including strain, rearing conditions, management, and precise details of the housing, within general housing type. Comparative data supporting the above predictions across all housing types are limited or lacking.

[3]Predictions assume that hens have access to litter and perches. In the United States, there is no legal requirement to provide litter or perches. Barn systems may have all slatted or wire floors.

[4]Predictions assume that hens have access to litter and perches indoors and daily access to an outdoor range primarily covered with vegetation. In the United States, there is no legal requirement for daily time spent outdoors or provision of litter, perches, or vegetation. Hens may be confined indoors for extended periods on fully slatted or wire floors.

[5]Authors used multiple cage treatments and aviary treatments; data are grouped relative to main treatment type.

[6]Ability to make antibody is a sign of less stress.

[7]Authors did not find clear distinctions between cage types but did for interactions of cage and group size.

[8]Authors found an interaction with rearing environment as well, noting that moving hens to an environment in which they were not raised was stressful regardless of the environment into which they were moved.

[9]The authors also report a significant breed × cage interaction × stage of lay interaction.

[10]Authors found a significant breed effect with no differences between treatments for 3 of the 5 breeds; data above are relevant to the 2 breeds that showed differences.

[11]Less serotonin is interpreted as more stressed; thus, conventional hens were more stressed.

on welfare. This section will therefore focus on fear and pain.

Pain. Pain is an aversive sensory experience, and reduction or elimination of pain is considered to be an essential component of ensuring good animal welfare. The pain system in birds is still not completely understood, particularly with respect to how birds process and conceptualize pain stimuli (Gentle and Wilson, 2004). Potential sources of pain in laying hen production systems include injuries due to predators, other birds, health problems such as bone breakage or bumblefoot, human handling, disease, and beak trimming. Only the last source has been studied to any extent. Beak trimming is performed to minimize injury due to feather pecking and cannibalism in the flock and is routinely practiced in US flocks. However, beak trimming has been banned in some countries (e.g., Sweden), and bans are under consideration in some other countries (United Kingdom) due to the pain associated with the procedure. Research has shown that hens trimmed at later ages can experience both acute and chronic pain, the latter resulting from the formation of neuromas in the highly enervated beak stump. If trimming is conducted when the birds are younger (less than 10 d of age), chronic pain may be avoided, but there is still acute pain (Hester and Shea-Moore, 2003). Thus, there is a trade-off to housing systems that are associated with higher risks for cannibalism and feather pecking like noncage systems because it is difficult to discontinue beak trimming in these systems at present.

Fear. Fear is an adaptive response, but it can also be undesirable if it results in extreme distress or injury or if it is chronic (Jones, 1996). Several studies have been conducted to compare levels of fear in different housing systems as an indicator of hen welfare in those systems (Hansen et al., 1993; Colson et al., 2005; Campo et al., 2008; Graml et al., 2008). However, such studies are very difficult to interpret and extrapolate to commercial housing conditions. A measure of fear that has validity in one system may be invalid or confounded in another. A common test of fearfulness, for example, is the tonic immobility test, in which hens are caught and restrained until an immobile state is induced. This test is likely to generate more fear in noncage hens than in caged hens because of the difficulty and thus potential stress involved in catching the hens in noncage systems. In addition, there are strong genetic effects on levels of fearfulness (Tauson et al., 1999). Because commercial producers use different genetic stocks in different systems, it is impossible to determine whether differences found in published studies are due to genetic predispositions, housing system, or an interaction between the two. The development of fear tests that are valid under different housing conditions, and carefully controlled studies of the relationships between genetics, environment, and fear responses, will be needed to better assess the relationships between housing systems and fearfulness.

Genetics

Breeding companies routinely evaluate hundreds of thousands of individual birds across a range of populations selected as egg-laying strains in multiple environments each selection cycle. Breeders have continued to adapt birds to different environments as production environments have evolved over the past 70 decades (Craig, 1982) and a recent shift to more extensive housing systems requires breeders to once again adapt (Flock and Norman, 2008). Breeders are evaluating as many as 30 traits, in the areas of egg production, egg quality, efficiency, well-being, and reproductive traits. In addition to routine evaluations in multiple environments, a relationship matrix and genotype data form part of the selection process (Abasht et al., 2009). Both individual and group data are combined for animal well-being traits (Craig and Adams, 1984). As statistical methodologies and marker data continue to advance, rates of genetic change should increase, but new traits continue to enter the selection matrix as traits such as nesting behavior (Settar et al., 2006) become necessary from an animal well-being perspective in extensive housing systems.

Breeders continue to select for intact feather cover and bird livability in multibird groups, leading to reductions in feather pecking and cannibalism. Considerable additive genetic variation is known to exist for these traits (Hocking et al., 2004), with estimates of heritability ranging from 0.22 to 0.54. Based on direct observation (Kjaer and Sørensen, 1997), heritability values ranged from 0.00 to 0.38. Lines were developed by selection for high or low feather pecking, confirming a genetic basis for variation in this trait (Kjaer et al., 2001). No estimates of heritability of cannibalism have been developed. A trait that combines feather pecking and cannibalism leading to severe injury or death was used in a study of group selection (Craig and Muir, 1993, 1996; Muir, 1996). Heritability was high in these beak-intact birds at 0.65. Less work at the molecular level has been completed. Major genes for feather pecking have been found along with the polygenes (Laboriau et al., 2009). Buitenhuis et al. (2003) reported markers for severe feather pecking on chromosomes 1, 2, and 10. Jensen et al. (2005) also suggested a feather-pecking marker on chromosome 3. Bird color has been associated with increased risk of being a victim of feather pecking (Keeling et al., 2004). Recent work on dopamine D1 antagonists (Kjaer et al., 2004) and D4 receptor genes (Flisikowski et al., 2009) suggests one mechanism to explain genetic variation in feather pecking in the lines developed by Kjaer et al. (2001). Testing of family groups with all individuals having intact beaks in commercial environments is now routine for evaluation of feathering pecking and cannibalism. However, beak-intact birds are more fearful than beak-trimmed birds (Vestergaard et al., 1993). It has not been determined if selection against fearfulness is most effective when fear is expressed at high, moderate, or low levels (Jones et al., 1995).

Genetic variation in skeletal health due to poor bone quality, bone fractures, paralysis, and leading to death has been studied in Leghorns (Bishop et al., 2000). A bone strength heritability of 0.40 was reported. Markers have also been found for bone strength (Schreiweis et al., 2005). Perches affect welfare of birds on many levels, reducing fear, improving motor activity, and providing preferred resting locations. Recent studies have concentrated on perch orientation (Struelens et al., 2008b), perch height (Struelens et al., 2008a), and access to an outdoor area (Shimmura et al., 2008b). Genetic differences in susceptibility to fear in a given social environment affect perch usage and thus the social environment.

Nesting behavior and range use are vital characteristics needed by hens adapted to extensive housing systems. Range use differed between breeds (Kjaer and Isaksen, 1998). Heritabilities for number of passages from the house and out onto a covered range area varied from 0.21 to 0.32 and genetic correlations to laying performance were negative (Icken et al., 2008). Nesting behavior is a characteristic sequence of behaviors associated with site selection, nest building, and oviposition. Incubation starts when all eggs of a clutch have been laid, but incubation has almost completely disappeared in modern laying hens due to selection against broodiness and, indirectly, due to selection for egg-laying ability, resulting in increased clutch length and shortened interclutch pauses. Nest selection and use of nests for laying varies with strain (Appleby et al. 1984). Perching ability affects nest use, but other factors also play a role. Selection against floor laying was found to respond at one experimental site but not at another (McGibbon, 1976). Sørensen (1992) described a selection program on egg number in which only eggs laid in trap nests were recorded. He concluded that there was genetic variation for nest-laying use. More recently, Settar et al. (2006) reported heritabilities for nest laying of 0.37 to 0.44, and Icken et al. (2009) were able to record individual nesting behavior in larger groups of hens in a barn systems using radio-frequency identification transponders and single nests with antennas (Weihenstephan funnel nest boxes).

Breeders need to be able to use tools that can be tested on very large populations. A typical hybrid layer is a 4-line cross with more than 10,000 pure-line hens evaluated individually per line plus another 15,000 group-housed hens, evaluated in family groups, housed under commercial environments for cross-line performance testing. New breeding tools must be practical at such large-scale levels of phenotyping. Although automation of genotype collection may be done with ease, in the near future, the collection of phenotype data needed each generation will continue to be the largest cost in genetic selection programs.

GENERAL CONCLUSIONS

It is evident that very little literature exists that compares all factors in different housing systems. However, some generalities are certain. Mortality is generally lower in furnished cages when compared with conventional cages, and mortality can reach unacceptably high levels in noncage systems. The degree of complexity of the environment certainly has an effect. Complex environments allow for parasites and diseases to persist, whereas simpler environments are easily cleaned and these problems are more easily eliminated. Although complex environments, and particularly noncage systems, provide an advantage to some nest-dwelling parasites, they also allow hens to act as predators on some pests such as flies and beetles. Furnished cages, which offer an intermediate level of complexity, may reduce the risk of bone breakage compared with either conventional cages or more extensive systems. Hens in conventional cages and furnished cages have less footpad dermatitis and bumblefoot than more extensively housed hens, but claw health is worse in conventional cages than in all other systems. Complex environments allow hens to have more control and to make more choices, for instance expressing thermal and social preferences; an animal's ability to make choices and have control is well known to positively affect welfare. Environments that are more restrictive in space and complexity prevent hens from performing specific behaviors. This is no trivial matter because prevention of the performance of behaviors is known to have a negative effect on welfare. However, increased behavioral freedom can also be accompanied by welfare problems such as cannibalism and predation. The nutritional effect of allowing the hen access to substrate or forage is poorly understood. Hens can experience stress in all housing types and no single housing system ranks high on all welfare parameters. Likewise, no single breed of laying hen is perfectly adapted to all types of housing systems. Management of each system has a profound effect on the welfare of the birds in that system; thus, even a housing system that is considered to be superior relative to hen welfare can have a negative effect on welfare if poorly managed. The right combination of housing design, breed, rearing conditions, and management is essential to optimize hen welfare and productivity.

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