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Interactions of diet and circadian rhythm to achieve precision nutrition of poultry

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ABSTRACT

Precision nutrition regimes currently rely on the assumption that broilers will grow in a steady and predictable way on a daily basis, with the continuous deposition of nutrients into muscle or, in the case of laying hens, into an egg. However, it has been observed that this is not the case for egg production, with Ca requirements being aligned with eggshell formation. Recent research has suggested that muscle is also deposited at differing rates over a 24-h cycle. The circadian rhythm synchronises various biological processes to oscillate within a 24-h cycle. Thus, the cyclic nature of body systems should be explored, to determine whether consideration of the circadian rhythm is required for precision nutrition programs, achieving peak efficiency of performance and accurate nutrient requirement recommendations. Recent advances in nutrition have demonstrated the powerful effect of the circadian rhythm on human health and animal growth and production. Therefore, this review discusses recent circadian-rhythm research with relevance to poultry. Specific focus is given to the interaction of the circadian rhythm with diet and dietary nutrients, for the precision nutrition of poultry and optimising production.

Keywords: broiler, circadian rhythm, clock genes, digestion, laying hen, metabolism, nutrition, poultry.

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Introduction

Precision nutrition is the practice of adjusting and feeding diets to ensure dietary nutrient supply equals the nutrient requirement of an animal at any given time (Pomar *et al.* 2009). Modern broiler chickens grow rapidly, and as such, their nutrient requirements change daily throughout their production (Ross 308 Performance Objectives 2019). However, broilers are fed between three and five diets or phases in commercial practice, meaning that nutrients are often under- and over-supplied throughout production (Moss *et al.* 2021). This under- and over-supply leads to reduced efficiency. For example, excess energy may be stored as fat, and amino acids may be deaminated (Bedford and Summers 1985), which is an energy-expensive process and leads to ammonia formation, with the majority of ammonia being excreted as uric acid (Salter and Fulford 1974). Microbes within the hind gut of poultry may also utilise any excess amino acids to synthesise microbial proteins (Ravindran *et al.* 1999), ammonia and amines (Qaisrani *et al.* 2015) and use the excess protein as an energy source (Reid and Hillman 1999), which may reduce birds' production performance and gut health and worsen environmental outcomes (Gilbert *et al.* 2018). Production of ammonia, the predominant metabolites of caecal undigested protein fermentation (He *et al.* 2015), has been shown to increase birds' intestinal pH and facilitate the proliferation of *Clostridium perfringens*, the causative agent for necrotic enteritis (Paiva and McElroy 2014; Qaisrani *et al.* 2015). It is estimated that necrotic enteritis causes a loss of US$6 billion to the global broiler industry annually (Wade and Keyburn 2015). Additionally, it is known that ammonia negatively influences the ecosystem and environment, and has been considered one of the greatest environmental pollution sources from poultry production (Naseem and King 2018). Within laying hen production, precision nutrition programs may also be implemented, with the gradual blend between peak-, mid- and late-lay hens to ensure that nutrients are met for egg production.

Thus, the implementation of a precision nutrition program involves blending two or more diets on a daily basis to precisely meet the daily nutrient requirement of poultry, with the goal to avoid excess or deficiency of dietary nutrient. Due to logistical and equipment constraints on poultry farms such as extra investment on feed silos and automatic feeding system, medication management, etc., this concept is currently limited to the flock level, which limits the potential benefits. However, this may be possible at an individual level with the introduction of precision feeding equipment for poultry, similar to that currently used in pigs, such as in the work by Zuidhof *et al.* (2017) and Zuidhof (2018).

Precision nutrition regimes currently rely on the assumption that birds will grow in a steady and predictable way on a daily basis, with the continuous deposition of nutrients into muscle, or that laying hens form eggs with a constant ratio of nutrients (Moss *et al.* 2021). However, at least for egg production, we know this is not the case as the nutrients required throughout the day fluctuate on approximately a 24-h cycle as per the requirements of yolk, albumin and eggshell formation (Bootwalla *et al.* 1983; Leeson and Summers 2009). Thus, the cyclic nature of body systems should be explored, to determine whether it is an important consideration for precision nutrition programs, so as to achieve peak efficiency of performance and accurate nutrient requirement recommendations.

Recent advances in nutrition have demonstrated the powerful effect on animal growth and production of the circadian rhythm, which regulates the cyclic nature of metabolism. Therefore, this review discusses recent circadian-rhythm research with relevance to poultry. Specific focus is given to the interaction of the circadian rhythm with diet and dietary nutrients, for the precision nutrition of poultry and optimising production.

The circadian rhythm

The term circadian rhythm refers to endogenous biological fluctuations occurring about the cycle of a day (Halberg *et al.* 1959). Today, we know that the circadian rhythm manipulates the expressions of genes in many tissues and synchronises various biological processes to oscillate within a 24-h cycle (Jastrebski *et al.* 2017; Song *et al.* 2021). Within intensively farmed livestock systems, this knowledge is particularly powerful, as there is opportunity to manipulate biological processes with common animal husbandry treatments, such as artificial lighting regimes. Light is often described to be the most potent regulator for many bodily systems within the circadian rhythm, and poultry are no exception (Bessei 2006). An early study in laying hens demonstrated the power of this effect; after reversal of light and dark periods, only 4 days were required to change the time of lay (Warren and Scott 1936). To compensate for the reduced feed intake caused by heat stress during the day, artificial lighting at night is usually used to stimulate nocturnal feeding during warm periods (Daghir 2009). However, the internal circadian clock of the birds, which is set to day-active and night-inactive, may prevent birds from consuming feed in the night-time, thus limiting the benefits of this practice. Hence, it has been suggested that applying darkness during the day and providing light during the night may be advantageous to manipulate the birds to a night-active endogenous rhythm when nocturnal feeding is required (Vandana *et al.* 2021). Other environmental regulators can also have influence on regulating the time of lay via the circadian rhythm, such as visual, auditory and thermal stimulus (Cain and Wilson 1974). Recent research has also drawn attention to the impact of diet on the circadian rhythm (Lin *et al.* 2018). It has been shown that the circadian clock may be reset by acute heat stress (Buhr *et al.* 2010; Tamaru *et al.* 2011). Resetting the circadian rhythm may synchronise clock genes to the heat stress cycle, leading to the circadian rhythm response as a way of adaptation to cope with cyclic heat stress in birds (Jastrebski *et al.* 2017). In commercial poultry sheds where birds are raised under temperature-controlled conditions, the effect of housing temperature on the circadian rhythm is well controlled. However, as poultry industry is moving towards free-range production, it may be worthwhile to explore further possible effects and/or applications of thermal stimuli on circadian rhythm in birds. Visual stimuli, in the form of light and dark periods, are among the most studied factor and the most well known for laying hens in particular, with breeder recommendations in order to optimise egg production in the transition from rearing to lay, and throughout the laying period. However, the impact of other factors on lay are less well understood, and, in particular, the impact of diet, and the changing nutrient requirements relating to the phases of lay, require elucidation. Furthermore, there is a lack of research exploring the possibilities of manipulating the performance and behaviour of broiler chickens via the circadian rhythm, and possible impacts of manipulations for biological processes. Within the field of nutrition, attention must be brought to the potential impact of diet, feeding behaviour and the gut biome on the circadian rhythm and implications for nutritional requirements and feeding programs.

Interaction of diet and the circadian rhythm

The circadian rhythm often uses light to regulate the body's systems, and the effect of time of day on appetite is no exception. In humans, despite overnight fasting, people are often paradoxically not hungry in the morning and breakfast is the smallest meal of the day. Scheer *et al.* (2013) explored this phenomenon and found that the endogenous circadian rhythm in humans peaks in the evening, and is naturally reduced overnight, independent of food and caloric intake over the day. The authors warned of the implication for shift workers, spending the majority of their time awake during the evening when the circadian rhythm was at its peak, and thereby having proportionally more time available for consumption of food, and thereby increasing their risk of obesity. Poultry have also been observed to have higher feed intakes during the evening (Wang *et al.* 2021), and so this observation is not restricted to humans alone. While this is detrimental for humans in modern society, determining the greatest times of motivation for food consumption in animals in relation to differing lighting regimes may be of interest to promote performance.

Thus, dusk feeding, or the practice of feeding at night, may be performed to reduce nutrient insufficiencies during the night period. This is a particularly important consideration for laying hens, who lay down the shell portion of the egg in the evening, and insufficient calcium supply during this period has been shown to result in poor eggshell quality (Keshavarz 1998). Taking advantage of an increased appetite in the evening, Liu *et al.* (2023) demonstrated that offering hens feed in the afternoon increased eggshell thickness. Alternatively, the ability to feed during times of least appetite and manipulating lighting regimes to reduce feed intake may be helpful to reduce the weight gain and aggression during feeding of broiler breeders, for example. However, to the best of the author's knowledge, this has yet to be explored.

Not only can daylight affect appetite via its stimulus to the circadian rhythm, but peripheral clock systems located in the stomach may also be regulated by diet composition and feeding behaviour (Mattson *et al.* 2014). Within the gut, the circadian rhythm regulates gastrointestinal health and dysfunction, including cell proliferation, motility, digestion and absorption (Voigt *et al.* 2019). The microbiome also plays a critical role in maintaining the host circadian rhythms and metabolic homeostasis, and the microbiome undergoes temporal fluctuations following diurnal rhythmicity (Song *et al.* 2021). The majority (60%) of the microbiome in mice fluctuate in this fashion and consist of Clostridiales, Lactobacillales, and Bacteroidales, where species may increase or decrease depending on the time of day (Thaiss *et al.* 2014). Furthermore, the absence of a microbiome in germ-free mice showed significantly impaired central circadian clock gene expression (Leone *et al.* 2015), demonstrating the strong link between brain and gut via the microbiome and circadian rhythm. To the best of the author's knowledge, the study of the fluctuation of microbiome throughout the day in poultry has not yet been completed, and thus it is undetermined how much of the chicken microbiome fluctuates on a daily cycle, and what impact this may have on nutrition and performance. This may also have important consequences for the methodology of microbiome studies, possibly explaining some of the great variance in results among studies and should therefore be investigated as a matter of priority.

Due to the strong link among the microbiome, the circadian rhythm and metabolism, supplementation of diets with a pre- or probiotic may provide beneficial effects for poultry metabolism via pathways not yet considered. While an ongoing research area in poultry, probiotics have been demonstrated to regulate circadian rhythms in mice and humans (including the fluctuations in microflora) and thereby improve gut health and reduce metabolic disease (Thaiss *et al.* 2014; Asher and Sassone-Corsi 2015). In this way, the circadian rhythm has been described as a critical interface between nutrition and homeostasis, in which microbiota has a critical role (Asher and Sassone-Corsi 2015).

Despite the need for more research in this area for poultry, some studies have been conducted focusing on feeding practices in laying hens, which are thus inextricably linked to the circadian rhythm. Additionally, studies in other species exploring the effects of diet and the circadian rhythm may also hold direct implications for poultry.

Circadian rhythm and lay

The importance of circadian rhythm is very evident in the laying hen via the daily cycle of egg laying. The circadian rhythm and day–night cycle are closely linked with egg production and the time of oviposition. In fact, the number of eggs in a clutch and the 'lag' when day skipped between clutches of eggs may be determined and thus manipulated by the light:dark ratio (Koops and Grossman 1992). So as to maximise the nutrients available for deposition into the egg, and in particular, minimise the impact of calcium (Ca) drawn from bone, several feeding practices focus on meeting Ca requirements throughout the daily lay cycle. One such feeding practice that follows the circadian rhythm in hens is AM–PM or split feeding, which involves the feeding of two diets daily to achieve more precise nutrition and integrate what we know about the nutrient requirements of the hen with their underlying biology.

In Australian laying hen production, it is common to feed three diet phases across the laying period, with a peak lay diet from the point of lay to 28 weeks, a second diet from 28 to 60 weeks, and the third diet from 60 weeks onward. These separate dietary phases attempt to meet the nutrient requirements of the hens as they change throughout production. However, due to the hen's cyclic reproductive physiology, high dietary protein and energy levels are required for the yolk and albumin formation in the early morning and high dietary Ca concentrations are required for the membrane and shell formation in the afternoon/evening. Therefore, feeding one diet across the day may be problematic, as there is excess Ca in the morning and excess protein/amino acids and energy in the evening. These excess nutrients may be wasted and excess energy may be deposited as fat, which could increase the incidence of overweight hens and promote fatty liver syndrome, which are common problems in commercial laying hen production (Trott *et al.* 2014; Shini *et al.* 2019). Excess amino acids may also be deaminated, which increases nitrogen excretion and is an energy-expensive process (Bedford and Summers 1985). Additionally, excess Ca significantly reduces nutrient digestibility and feed efficiency in poultry (Lagos *et al.* 2019). Thus, the very high Ca within laying hen diets when it is not required may be needlessly hindering protein digestibility. To minimise excess nutrients, AM–PM feeding may be used where a high energy and protein diet with a lower Ca concentration is provided in the morning (AM), roughly from 0700 hours to 1500 hours, and a lower energy and protein diet with a higher Ca concentration is fed in the afternoon/evening (PM), roughly from 1500 hours to 0700 hours (de los Mozos *et al.* 2012). The AM–PM feeding has been illustrated to improve feed efficiency, eggshell quality, and reduce environmental pollution in laying hens (de los Mozos *et al.* 2012; van Krimpen *et al.* 2018) and improve egg production and behaviours in broiler breeders (van Emous and Mens 2021). In a study that is ongoing at the University of New England (N. Akter, T. H. Dao, D. J. Cadogan, A. F. Moss, unpubl. data), AM–PM diets were offered to hens in a cage setting via a box behnken response surface design to determine the optimal ratios of Ca, energy and protein in AM–PM diets. Then, the optimised diet was used in a 20-week free-range trial to determine the effect of AM–PM feeding on various performance, nutrition, health, behaviour and welfare parameters. The work is ongoing, but preliminary results from the box behnken cage experiment demonstrated the complexity of feed selection in the laying hens, where the amount of nutrient present in the AM and PM diets influenced the amount of each AM and PM feed consumed. However, in comparison to a control diet, the majority of AM–PM treatments (with differing nutrient concentrations in the AM–PM diets) achieved a more efficient performance. Within the free-range study, the preliminary results also indicated an improvement in efficiency and egg mass with AM–PM feeding in comparison to hens fed a commercial control diet.

Despite our current knowledge and recent findings of the advantages of meeting the daily fluctuations of nutrient requirements, this aspect is not considered in nutrient recommendations. Limitations are likely to include the practical logistics of offering two diets.

Circadian rhythm and muscle deposition

While reproductive function in laying hens is critical for profitability, the most economically important metabolic function of broiler chickens is muscle deposition. While it is quite obvious that the circadian rhythm is at play for the egg-laying cycle, it is less well understood whether there are any links between the circadian rhythm and muscle deposition. Despite the importance of muscle growth in meat chickens, the significance and implications of circadian rhythms for muscle growth in chickens has not been investigated, nor what this means for the nutrient requirements and optimal feeding behaviour of the meat chicken. However, increasing evidence in other species has demonstrated that the circadian rhythm is a key regulatory mechanism for multiple important aspects of muscle physiology, including muscle structural organisation, growth and maintenance, energy production, and glucose metabolism (Chatterjee and Ma 2016). The circadian clock system comprises a hierarchal organisation where the central clock resides in the hypothalamus, transmitting timing signals through light–dark cycles to control peripheral tissue clocks (Reppert and Weaver 2002; Dibner *et al.* 2010). Almost all the tissue and cell types in the animal body have cell-autonomous clock circuits controlled by central clock signals; however, they can be entirely uncoupled via manipulations of diet timing such as restricted feeding (Damiola *et al.* 2000; Schibler and Sassone-Corsi 2002). Studies in mice have shown that a considerable number of genes (17%) display circadian-like oscillations in skeletal muscle (Miller *et al.* 2007). In humans, muscle reaction time, strength, and flexibilities significantly depend on the time of the day (Drust *et al.* 2005; Reilly and Waterhouse 2009). Specifically, skeletal muscle strength, torque, and power are higher in the late afternoon from 1600 hours to 1800 hours than in the morning (Nicolas *et al.* 2005; Pearson and Onambele 2006; Sedliak *et al.* 2008). Similarly, it has been reported that maximal isometric strength in male athletes occurs during mid- to late afternoon from 1600 hours to 2000 hours, reflecting the diurnal pattern of knee extensor muscles (Sedliak *et al.* 2007). Others have indicated that circadian rhythms play a key role in the expression of androgens, as shown by delayed peak androgen production in night-shift workers compared with day-shift workers (Papantoniou *et al.* 2015). Besides reproductive functions, androgens stimulate muscle deposition (Crowley and Matt 1996) and are involved in the process of muscular tissue maintenance by enhancing protein synthesis and reducing protein degradation (Rozenboim *et al.* 2004). Studies in broilers have shown that blue light increases plasma androgen concentrations and stimulates muscle growth in older birds (Rozenboim *et al.* 1999, 2004). Also, broiler chickens raised under blue or green light have significantly higher body weights than do those raised under white or red light (Rozenboim *et al.* 2004). These findings suggest possible links among light spectra, muscle growth, androgen production, and circadian rhythm in broilers. Additionally, Ye *et al.* (2014) indicated that intramuscular fat deposition in birds is partially regulated by circadian rhythms-related genes. In mice, a strong link has been established between the molecular clock circuit and maintenance of skeletal muscle development, growth and hypertrophy, and it is possible that disruptions in environmental lighting cycle, for example, may influence muscle growth and remodelling process (Chatterjee and Ma 2016). Recent research in zebra fish demonstrated that circadian rhythms control muscle development, and that it is cyclic throughout the day/night and not continuous (Kelu *et al.* 2020). Kelu *et al.* (2020) demonstrated that active muscle anabolises more in the day and grows faster, while overall growth is lower at night because the circadian clock enhances proteolysis, catabolising more muscle at night and slowing growth. Thus, if the muscle in poultry is controlled under the same mechanisms, lighting regimes, diet and feeding programs may need to be optimised for enhanced muscle growth. Further research is needed to confirm whether circadian rhythms regulate muscle development in poultry, and whether muscle development is also cyclic.

Of particular importance in the context of the effect of the circadian rhythm and diet may be skip-a-day feeding programs offered to broiler feeders. Unlike laying hen or broiler production where birds typically have given free access to the feed throughout production cycles to maximise production performance and genetic potential, the primary objective of skip-a-day feeding in broiler breeders is to increase reproductive efficiency by reducing bodyweight and delaying sexual maturity (Wilson *et al.* 1983). It is well known that the bodyweight uniformity of the broiler breeder flock is crucial as it affects feed allocation, incubation conditions, and egg-size uniformity (Sweeney *et al.* 2022). Feed restriction may not only help mitigate excessive bodyweight gain and over-fleshing but also prevent health and reproductive dysfunction causing decreased liability, lameness, ruptured tendons, decreased fertility and laying performance once broiler breeders enter the laying period (de Beer and Coon 2006; De Jong and Guémené 2011). Different feed-restriction methods can be used to control bodyweight in broiler breeders; however, skip-a-day is the most common method due to its good results, ample feed distribution, and ease of application (Hudson *et al.* 1999). However, as discussed previously, the circadian rhythm, appetite, diet and microbiome are linked. As the circadian rhythm is critical for metabolic regulation, the implementation of a non-24-h cyclic feeding schedule may not be the optimal feeding program for broiler breeders. In humans, the effect of fasting on health has been studied. It is observed that during fasting, circadian cortisol rhythm is disrupted, which may alter the gut microbiome (Daas and de Roos 2021) and may also cause evening hypercortisolism, and increase cardiometabolic risk (Ajabnoor *et al.* 2014). It is concluded that central clock signals may be entirely uncoupled through diet timing manipulations, such as during restricted feeding (Chatterjee and Ma 2016). Skip-a-day feeding of broiler breeders is less feed efficient as the deposition and re-utilisation of nutrients is costly (van Emous 2022); it may also have greater health and welfare repercussions by simply not following a 24-h cyclic schedule, and warrants further exploration. Previous studies have shown that skip-a-day feeding may cause chronic hunger, feeding anxiety, and general welfare issues such as disruption of the natural tendency to forage daily in broiler breeders (Aranibar *et al.* 2020; Sweeney *et al.* 2022). Recently, Sweeney *et al.* (2022) reported that feeding low-density high-fibre diets daily during the pullet rearing period increased flock uniformity, egg weight, eggshell quality, and intestinal development in broiler breeders during laying periods compared with pullets offered skip-a-day feeding. This suggests the great potential of low-density high-fibre diets in improving reproductive performance, while minimising health and welfare issues in broiler breeders.

Conclusions

The circadian rhythm controls many metabolic functions and recent research suggests that it may hold an important role in the regulation of egg production and muscle deposition in poultry. Additionally, the circadian rhythm may be closely linked with nutrition, gut microbiome and lighting regimes of poultry. These factors are all readily manipulable in commercial practice, and so it is of great importance that we understand the effects that these interactions have for production. Nevertheless, there is little research in poultry, with much of the current work being conducted in humans and mice. Thus, further research in poultry is required, and warranted, on the basis of the broad and substantial influence of the circadian rhythm on the body. Possible future research may include exploring the effects of lighting programs and spectra, heat stress, diet composition and nutrient density, and feeding programs on production performance, gut microbiota, behaviours, circadian rhythm related-hormones, and clock genes in birds over the production cycle.

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