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Reevaluation of the practice of forced molting informed by natural molting and brooding processes

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KEYWORDS

Brooding, egg production, natural molting, physiological health remodeling, poultry

HIGHLIGHTS

- Physiological health remodeling (PHR) can prolong the egg-laying cycle in poultry.
- PHR is a cost-saving and efficiency-enhancing feeding management technique.
- PHR holds the potential to restore the function of damaged tissues and organs.
- PHR can offer guidance for extending human lifespan.

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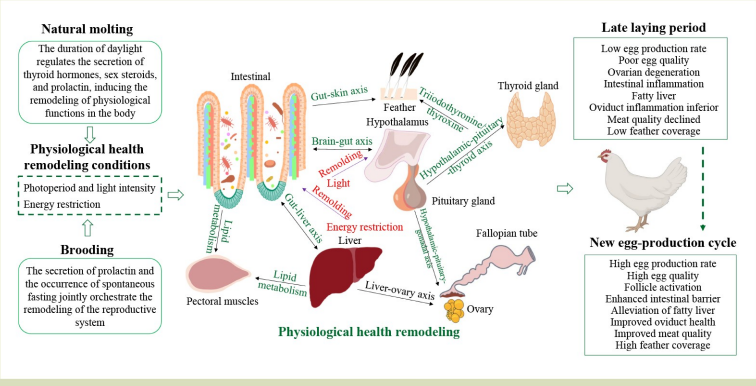
GRAPHICAL ABSTRACT



ABSTRACT

Physiological health remodeling (PHR) refers to coordinated adjustment of photoperiod and energy intake to simultaneously drive feather renewal and remodel degraded reproductive, endocrine and metabolic systems, thereby facilitating a rapid transition into a new laying cycle. During brooding, poultry reduce feed intake, prolactin rises and sex steroid levels decline, causing atrophy of the oviduct and ovaries, and cessation of egg production. Following brooding, after a chick-rearing period, molting is initiated and completed before winter to adapt to seasonal environmental changes. With the advent of spring, physiological function gradually recovers, enabling the onset of a new reproductive cycle. In production, the rapidly initiated egg-laying cycle, combining broodiness and natural molting, is commonly known as forced or induced molting. However, these terms emphasize feather renewal and do not

adequately reflect the coordinated physiological changes across multiple organs. Therefore, this process was designated as PHR. This paper outlines the physiological changes in birds during brooding and natural molting, and their implications for PHR in poultry. It discusses the recovery of tissues and organs after remodeling, feed efficiency improvements and potential issues, with the aim of informing prolongation strategies for laying and breeding hens, and offering insights for human health and biomedical research.

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1 Introduction

Eggs are a nutrient-dense, affordable animal-source food that constitutes a major component of national diets and provides high-quality protein along with essential vitamins and minerals[1]. They are important for safeguarding public health and promoting nutritional balance[2]. Eggs occupy an important position in food processing, feed production and export trade, positively contributing to rural economic development and farmer income. China faces several challenges in egg production, notably in sourcing laying hens and in production costs. Driven by rising consumption, China's demand for eggs has increased annually, with some regions experiencing relative supply shortages that challenge market stability[3]. Rising feed costs and tighter environmental regulations have markedly increased the overall cost of laying-hen production, compressing farmer profit and challenging small-scale operations, thereby aggravating market imbalances. Against the backdrop of cost containment and efficiency improvements, and the international target of achieving high production with 700 days of laying and over 500 eggs per hen[4], extending the laying period has attracted increasing industry attention.

In commercial poultry production, rearing environments are controlled and optimized to suppress external cues of broodiness and molting. Selective breeding attenuates responsiveness to environmental signals, reducing or eliminating endogenous signals driving broodiness and seasonal molting, thereby extending the laying cycle[5]. After a prolonged period of high egg production, hens experience a cascade of physiological challenges, including metabolic disturbances, compromised immune performance and disease resistance, degeneration of physiological functions and a subsequent decline in production performance, ultimately transitioning into the late laying phase[6–8]. In the late laying period, the absorption, metabolism and immune functions of laying hens decline[9,10], causing endocrine and hormonal imbalances and ultimately triggering a resting phase. During this rest period, restoration of physiological functions requires not only feather renewal but also the remodeling of the reproductive, endocrine, and metabolic systems. Under natural conditions, the rest period from late laying to resumption of lay typically lasts three to four months or longer, with start and end timing highly variable, posing significant challenges for intensive production and high-efficiency management[11]. Consequently, for commercial egg producers, the flock in the late laying period ceases to hold economic value[5]. In wild conditions, the energy expenditure during broodiness and brooding periods, together with the effects of spontaneous fasting, markedly alters the physiological state of birds[12]. As brood care ends and autumn day length shortens, birds rapidly start to molt, completing it before winter to adapt to the changing environment[5]. In production, light exposure and feed intake are adjusted to rapidly induce molting, enabling hens to quickly resume laying and enter the next production cycle. This approach is commonly referred to as forced or induced molting.

Based on extensive literature and research conducted by our team, we argue that the established term, forced or induced molting, merely reflects the superficial phenomenon of artificial intervention in the process of feather replacement in poultry. It does not capture the essential underlying changes in the physiological functions of the birds, which undergo a series of physiological health remodeling (PHR). These changes enable the birds to more effectively enter a new laying cycle and maintain better production performance. Therefore, this paper proposes that the essence of forced molting is PHR of poultry and suggests renaming forced molting to PHR.

This paper examines the physiological changes in broodiness

and natural molting in poultry and their implications for PHR. It provides a comprehensive analysis of how PHR affects tissues and organs, economic returns and practical challenges. The study aims to inform strategies to extend the laying cycle and optimize PHR to achieve the target of 500 eggs within a 700-day laying period. Also, the findings offer valuable lessons for extending reproductive cycles in other productive and endangered species and may inform human reproductive health research.

2 Natural molting in poultry

2.1 Survival strategy of natural molting in poultry

In the natural environment, the survival and reproduction of birds typically require adaptation to seasonal and environmental changes. Birds maintain their body temperature and adapt to flight through the renewal of feathers, with high-quality feathers being crucial for their survival[13]. Reproduction and molting are two stages in the avian physiological process that are extremely energy-intensive. Both processes have particularly high demands for nutrition and energy, and the nutritional supply within birds cannot meet the needs of both molting and reproduction simultaneously. Therefore, birds alternate reproduction and molting at different seasons of the year[14]. During the spring and summer seasons, when food is abundant and the climate is favorable, birds reproduce to ensure the continuation of their offspring. In autumn, as day length shortens, birds cease reproduction and initiate molting, thereby adapting to the cold winter environment. This alternating survival process enhances bird survival capabilities and reproductive success in environments with limited resources.

2.2 Impact of environment and hormones on avian molting and reproduction

During the spring and summer seasons, as day length increases and temperatures rise, the hypothalamic-pituitary-ovarian axis in birds is activated[13]. This activation stimulates elevated secretion of sex hormones and prolactin (PRL). The high levels of these hormones support reproductive behaviors and the development of reproductive organs, indicating the onset of the reproductive period in birds. During this time, elevated levels of PRL or gonadotropins (sex hormones) inhibit molting, ensuring that birds maintain optimal physiological conditions during reproduction and can achieve reproductive activities. As autumn arrives, the diminishing day length and falling temperatures trigger the activation of the hypothalamic-pituitary-thyroid axis (HPT) axis. This, in turn, stimulates the synthesis and secretion of thyroid hormones, predominantly triiodothyronine and thyroxine[13]. The rise in thyroid hormone levels not only promotes the growth and development of new feathers[15]. This process is essential for birds to maintain stable body temperatures during the cold season and also enhances the texture, color and protective properties of the feathers. Concurrently, the reduction in day length and temperature exerts an inhibitory effect on the hypothalamic-pituitary-gonadal (HPG) axis, leading to a decline in the synthesis and secretion of sex hormones. Currently, in the wild state, the balance among thyroid hormones, sex steroids and PRL is key to birds alternating between reproduction and molting. Although interactions among these hormones are partially understood, their specific regulatory mechanisms require further investigation.

2.3 Physiological changes during natural molt in poultry

Thyroid hormones, sex steroids and PRL exert multifaceted influences on the body, encompassing energy, protein and fat metabolism, as well as the repair, remodeling and adaptation of tissues and organs[15], These effects include: (1) during molting, the avian immune system is suppressed, with a significant increase in the levels of heterophils and lymphocytes[16]; (2) the elevated thyroid hormone levels during molting significantly boost the metabolic rate of the body; (3) the rate of protein synthesis in the liver, muscles and throughout the body of birds increases during molting[17–19]; (4) the loss of calcium ions during molting can lead to osteoporosis in the legs of birds; (5) birds experience a decrease in body fat and reduced abdominal fat deposition during molting; (6) the circulatory system undergoes adaptive adjustments during molting to provide sufficient oxygen and nutrients for feather growth and the repair of other tissues in birds; and (7) tissues and organs such as feathers, liver, intestines, oviduct and ovaries are rapidly repaired during molting. Clearly, the molting induces widespread physiological changes across the organism, with important implications for poultry health management-particularly for boosting lay performance, refining feeding strategies, and enhancing disease resistance.

3 Physiological adaptations of poultry during brooding

3.1 Physiological adaptations between brooding and foraging in poultry

Brooding, also known as nesting behavior, is a unique reproductive activity of birds under natural conditions, characterized by ovarian atrophy, reduced food and water intake, follicle regression and atresia, and cessation of egg-laying. The female bird undertakes all the incubation work, and the male bird does not provide food or protection for the female during brooding, resulting in the female being unable to forage to maintain its body weight during this period[20]. Hens rarely leave the nest during brooding, and even if they do, it is generally for no more than 10 min. During brooding, the food intake of hens is about 20% of that before brooding, and their body weight has decreased by about 20% when brooding ends[20]. Studies on the red junglefowl have found that the decrease in food intake during brooding does not stimulate the appetite of the hens. Even when water and food are placed near the nest, the red junglefowl consumes very little food and water[20]. Hens exhibit voluntary food intake reduction during brooding, which is referred to as spontaneous fasting. This type of fasting can be distinguished from that of sick animals from the outset because it occurs regularly at a specific stage in the life cycle. It is a reproductive strategy of poultry in an environment where brooding and foraging are incompatible, and spontaneous fasting during brooding is beneficial for avian reproduction. In natural conditions, after brooding concludes, birds undergo a defined nestling-rearing period before transitioning to molt. During molting, the female reallocates energy and nutrients to maintain its own physiological needs to cope with the complex winter environment.

3.2 Hormonal regulation during brooding in poultry

The brooding behavior in birds is controlled by a complex interplay of hormones. Prior to oviposition, the ovaries release substantial amounts of estrogen (E_2), which in turn stimulates the pituitary gland to secrete luteinizing hormone (LH) and follicle-stimulating hormone (FSH). These hormones facilitate follicle maturation and ovulation. LH prompts mature follicles to produce progesterone, and the synergistic actions of E_2 and progesterone induce the female bird to lay eggs within the nest. Concurrently, PRL secretion gradually increases. The rise in PRL concentration inhibits LH secretion, thereby terminating egg-laying behavior. This increase in PRL also enhances the frequency of nest entry, ultimately culminating in brooding behavior. Extensive research has demonstrated that PRL is the most direct and primary factor in inducing and maintaining brooding behavior in birds. Elevated PRL levels lead to ovarian dysfunction, follicle atresia and the cessation of egg-laying, which are critical for successful incubation[21]. PRL secretion is regulated by both photoperiod and brooding behavior[22]. During the molting period, when day length gradually decreases, PRL secretion levels are relatively low. In contrast, during the breeding season, as day length increases, PRL secretion levels rise accordingly. The presence of a nest or eggs can stimulate PRL secretion and PRL concentrations peak in birds during the incubation period. Therefore, after the onset of laying, PRL concentrations in the blood gradually increase with the rise in egg production[23]. During egg-laying, the concentrations of sex steroid hormones in birds continue to rise. This hormonal surge activates the activity of dopaminergic and serotonergic neurons in the hypothalamus and promotes the secretion of vasoactive intestinal peptide[5,21,24]. This is a physiological PRL-releasing factor that stimulates and regulates PRL release, further promoting brooding behavior in hens. The fixed brooding behavior, in turn, promotes or enhances the secretion of endogenous PRL, which maintains brooding behavior. During brooding, high levels of PRL inhibit the release of gonadotropin-releasing hormone (GnRH) from the hypothalamus and the release of FSH and LH from the pituitary gland. This hormonal inhibition leads to the regression of the ovaries and oviducts and the cessation of egg-laying[25,26]. When brooding concludes, during the recovery period, PRL concentrations gradually decrease, while the concentrations of FSH and LH and other sex hormones gradually increase. This hormonal shift promotes follicle maturation and ovulation, thereby restarting the follicle development process. While it is well established that PRL is a crucial regulator of brooding behavior of birds, the precise mechanisms by which environmental factors (e.g., day length, nests and eggs) stimulate PRL secretion during the breeding season in birds remain a subject of ongoing research.

3.3 Impact of brooding on production performance in birds

After brooding, the secretion of sex steroid hormones in birds gradually decline. This hormonal shift precipitates the regression and atrophy of the oviduct and ovaries, culminating

in the cessation of egg production. During brooding, the ovaries of birds undergo a significant reduction in both volume and weight. The cytoplasmic cavities within the follicles expand, and the degree of inward concavity intensifies, leading to follicular atresia[27]. Throughout brooding, birds experience pronounced oxidative stress, which is accompanied by an elevation in apoptotic levels. The development of small white follicles is markedly impeded, preventing their transition into small and large yellow follicles. Concurrently, small yellow follicles undergo direct atresia[28]. As brooding finishes, the gradual increase in sex steroid hormone secretion facilitates the recovery of oviduct structure and function. This recovery is essential for supporting the formation of eggs. During brooding, a substantial portion of the weight loss of hens, about half, can be attributed to the regression of the reproductive organs. For example, in the ring-necked pheasant (*Phasianus colchicus*), by the eighth day of brooding, the resorption of the ovaries and oviducts accounts for 23.7% of the total weight loss[20]. This phenomenon underscores that during spontaneous fasting, the ovaries and oviduct tissues provide essential energy for the body through autodigestion and absorption. The autolysis and reabsorption of the ovaries and oviducts also contribute to the comprehensive remodeling of the reproductive system in female birds following brooding. This remodeling enables the poultry to reach a new peak in egg-laying. The duration of post-brooding recovery period of hens varies due to individual differences, production seasons, breeds and environmental factors, typically ranging from 2 to 4 weeks. In the wild, when brooding finishes, red junglefowl enter a relatively complex nestling-rearing phase and upon its completion they typically advance to molt to finish plumage renewal before winter, thereby enhancing insulation and flight capability. In modern poultry production, broodiness is a significant factor contributing to the decline in poultry production performance. However, this natural behavior is a crucial regulator in the breeding process of birds. In commercial poultry breeding and production, eliminating broodiness in birds is a means of enhancing production efficiency. However, effectively leveraging the PHR characteristics during brooding can also yield substantial benefits. Especially under the background of ecological protection and food-saving and efficiency-enhancing, the understanding and utilization of resting behavior hold significant importance for the preservation of breeds and healthy poultry production.

4 Forced molting is PHR of poultry

4.1 Challenges faced by laying hens in the late laying period

In commercial layer production, farmers often implement environmental and nutritional management practices to maximize the laying performance of the hens, thereby aiming to achieve maximum economic returns. During the peak egg-laying period, energy allocation is primarily directed towards egg production. This process may lead to injury, wear and tear, or oxidative stress in key tissues and organs such as feathers, liver, intestines, oviduct and ovaries due to the continuous physiological load. Consequently, these tissues and organs may not receive sufficient resources for effective self-repair. This continuous physiological stress can weaken the immune function of poultry, thereby affecting overall health and egg-laying performance. Accordingly, in a commercial laying-hen production cycle, the egg-laying peak usually lasts for a period of time then gradually declines. The decline in intestinal absorption capacity for nutrients, such as calcium and trace elements, coupled with a reduced metabolic capability for these nutrients within the body, contributes to an increased incidence of diseases related to lipid metabolism, such as fatty liver syndrome. Concurrently, the disruption of the gut microbiota structure, with a rise in pathogenic bacteria, has weakened immune function and diminished disease resistance. Additionally, skeletal deformities and osteoporosis have emerged, and the functions of the ovaries and oviducts have deteriorated. These multifaceted physiological changes ultimately result in decreased egg production, culminating in the cessation of egg-laying and the onset of the non-laying period[5,29,30]. After resting, poultry need to undergo PHR to enter a new laying cycle. However, under natural conditions, the PHR cycle is lengthy; the timing of molting is inconsistent and the duration of the molting period varies. Consequently, the recovery of egg-laying is uneven, making it difficult for the entire flock to reach an ideal egg-laying peak. This poses significant challenges for intensive rearing and management[11]. Typically, commercial laying hens are culled before entering the late laying period, resulting in a short usage cycle, low utilization efficiency and unsecured economic benefits[5]. Therefore, exploring an economically viable and efficient method to induce a synchronized resting period followed by prompt physiological adjustments and re-entry into the laying cycle is paramount for extending the efficiency

of layer production, reducing the costs associated with rearing and development and enhancing food-saving and efficiency-enhancing practices.

4.2 Brooding and molting provide insights into the PHR in poultry

In the wild, during the incubation period, PRL secretion and nest-guarding behavior under spontaneous fasting suppress hen physiology, particularly the reproductive axis, leading to reduced reproductive function and cessation of lay[5,23,31]. During the nestling-rearing phase, maternal nutrient allocation shifts toward offspring, and maternal metabolism and recovery may be comparatively slow[32]. When breeding ends and with shortening autumn photoperiods, plumage renewal accelerates to cope with cold and maintain insulation; conversely, recovery of the reproductive axis is inhibited, requiring extended energy accumulation and improved environmental conditions. In the following spring, when day length and forage resources increase, the avian reproductive system often attains higher activity, initiating a new breeding cycle[33]. Forced molting exploits the natural lull in reproduction during brooding and molt (Fig. 1), by inducing lay cessation it redirects resources toward survival and rest, enabling physiological restoration and improved production performance[34,35].

4.3 Main methods for PHR in hens

Currently, four primary methods are commonly used for forced molting: fasting, hormonal, chemical and integrated approaches. The fasting method, encompassing complete starvation and staged weight control, primarily involves a period of food and water deprivation or reduced feed intake. Combined with changes in lighting regimes, this stimulates the

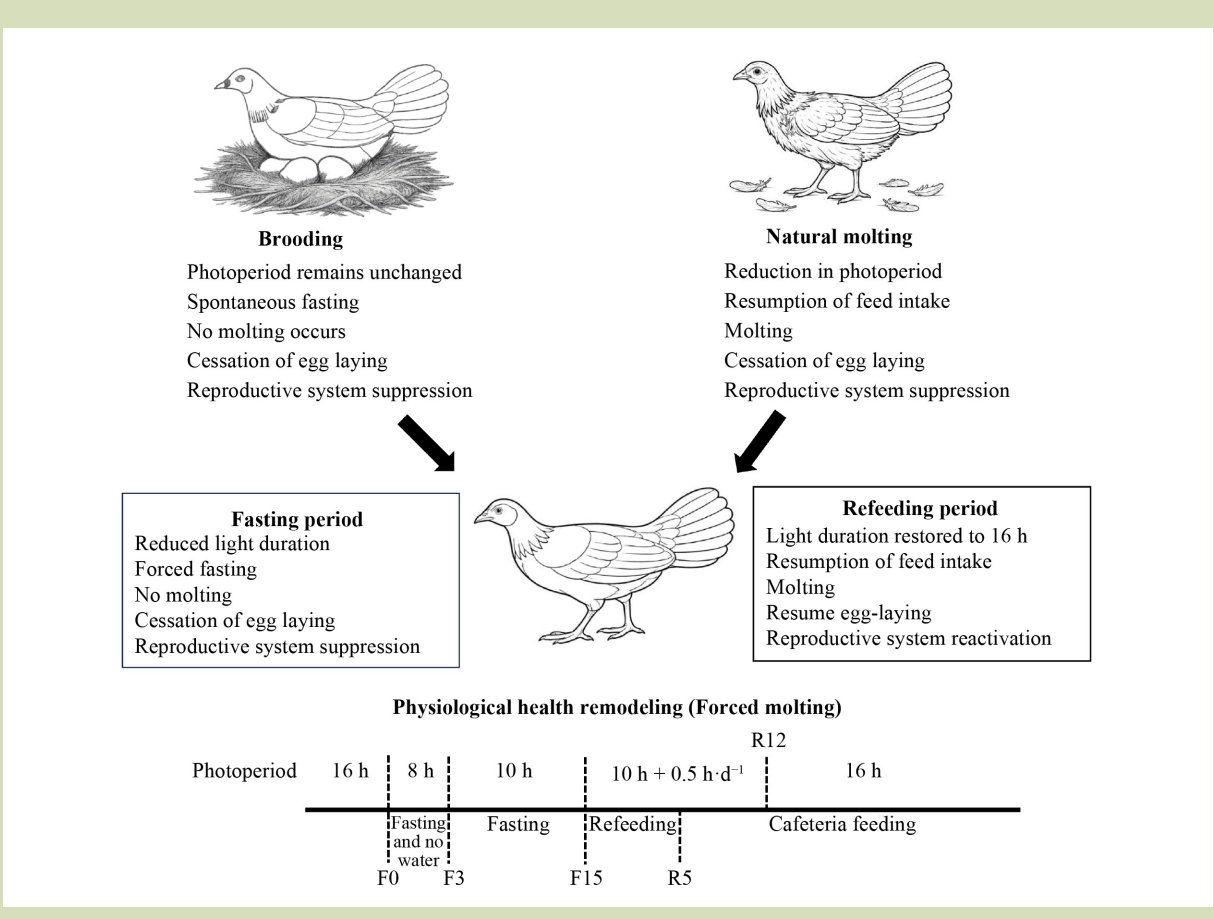

Fig. 1 Brooding and molting provide insights into the PHR. The chicken models were created with the assistance of ChatGPT5.2.

flock, leading to rapid weight loss, increased secretion of thyroid hormones, and decreased secretion of sex steroid hormones and PRL. This achieves a cessation of laying and molting. After resuming feeding, the molted hens quickly enter a new laying period[34,36]. The hormonal method involves intramuscular injections of hormones, such as adrenalin, thyroid hormones and progesterone, to the flock[5,37]. This induces a hormonal imbalance within the body, causing laying hens to stop producing eggs and undergo PHR. However, the cessation and remodeling require the synergistic action of multiple hormones. Without energy restriction, the reproductive system cannot be fully remodeled. Consequently, the recovery period after normal feeding is prolonged or the flock may fail to enter an ideal new peak laying period. This method is rarely used in commercial production. The chemical method involves adding or reducing certain amounts of chemical agents in the diet to induce changes in steroid hormones within the molting hens, thereby achieving cessation of egg production and molting[38,39]. For example, feeding low-sodium, sodium-free diets, low-sodium combined with low-zinc diets, low-calcium diets, high-zinc diets and high-iodine diets can all lead to cessation of egg production and molting in the flock. Compared to light regulation, chemical agents have a more limited impact on sex steroid hormones. Also, without the coordination of fasting regulation, the effect of this method on PHR is not thorough. The integrated method combines fasting with chemical or hormonal approaches. Studies have shown that regulating steroid hormone secretion through light duration is safer, more economical, and more efficient than hormonal or chemical methods. Staged fasting induces rapid degeneration of the reproductive system, laying the foundation for subsequent reproductive system remodeling following refeeding. This process is pivotal to the PHR in poultry. Therefore, compared with other molting methods, fasting has several advantages: a short cycle, low mortality rate, longer duration of egg production and peak laying period, and lower breeding costs. It is the most commonly used method in egg production or breeding of laying hens[40]. During the forced molt in laying hens, in addition to plumage renewal, the reproductive, endocrine and metabolic systems undergo degeneration and remodeling. Although the terms, forced or induced molt, are commonly used, they fail to adequately reflect the physiological changes across multiple tissues and organs. Consequently, we term this process a PHR.

5 Impact of PHR on the in hens

5.1 HPG axis and hormonal regulation

The HPG axis is a sophisticated endocrine regulatory system that is crucial under various physiological and environmental stresses. Under the intervention of fasting and photoperiod control, the hypothalamus is essential for regulating the secretion of thyroid hormones and sex hormones through the HPT and HPG axes. It is also crucial in regulating lipid metabolism in the liver and maintaining blood glucose stability. Zhang et al.[41] determined that during PHR, the neuroactive ligand-receptor interaction signaling pathway in the hypothalamus is activated. This pathway can regulate the synthesis and release of thyroid hormones and sex steroid hormones, suggesting that PHR may modulate the synthesis of these hormones through neuroactive ligand-receptor interactions. However, the precise regulatory mechanisms remain unclear. Similar to natural molting, during PHR, a decrease in photoperiod leads to a gradual decline in the concentrations of reproductive hormones, such as FSH and LH, whereas an increase in photoperiod results in a gradual elevation of these hormone levels[34,36]. This is related to light exposure stimulating the secretion of GnRH in the hypothalamus. In addition, the stress response triggered by fasting stimulates the hypothalamus to release thyrotropin-releasing hormone (TRH), which in turn prompts the pituitary gland to secrete thyroid-stimulating hormone, ultimately leading to an increase in thyroid hormone secretion. This stress response can counteract the inhibitory effect of shortened photoperiod on thyroid hormone secretion and ensure the smooth progression of the molting process in poultry. Through the regulation of the HPG and HPT axes, fasting and photoperiod influence the secretion of GnRH and TRH, thereby controlling the synthesis and release of sex hormones and thyroid hormones. This ultimately regulates feather renewal and the restoration of ovarian physiological function during the PHR in poultry.

5.2 PHR alleviates liver damage

During the late laying period, laying hens experience a decrease in nutritional requirements and a decline in their capacity to synthesize and transport fat. Excess nutrients consumed can exacerbate hepatic fat deposition, thereby increasing the risk of fatty liver syndrome and other lipid metabolism-related diseases[42,43]. Egg formation in birds is closely linked to liver

function. Fat in poultry is primarily synthesized in the liver and transported to the oocyte in the form of very low-density lipoprotein to form the precursor substances of the yolk, providing the necessary nutritional basis for egg formation[44]. Metabolic diseases, such as fatty liver syndrome, in laying hens can impair liver function, disrupt normal fat metabolism and lead to a gradual decline in egg production[45]. This can shorten the peak laying period and, in severe cases, cause death, resulting in significant economic losses. PHR can effectively guide the reallocation of nutrients and energy within the avian body, thereby mitigating the occurrence of fatty liver, and the associated hepatic injury, in hens[29]. PHR can regulate the expression of inflammation-related genes and endogenous retrovirus in the liver of chickens and geese[46], thereby influencing immune function. Our team's previous research has shown that staged fasting induces oxidative stress in laying hens, leading to the consumption of liver fat. After resuming feeding, the antioxidant capacity of the liver in laying hens is enhanced, and hepatic lipid accumulation is alleviated. Also, during fasting, three autophagy-related genes (including phosphoinositide 3-kinase (*PI3K*)) and an apoptosis inhibitory gene are upregulated, while the expression of a key autophagy inhibitory gene and three apoptosis-related genes is significantly downregulated. The body activates autophagy and inhibits apoptosis to avoid liver damage caused by fasting. PHR not only provides a theoretical basis for grain-saving and efficiency enhancement in egg-laying chicken production but also offers new insights into the prevention and treatment of diseases related to fatty liver.

5.3 PHR improves intestinal function

Poultry metabolism is subjected to a high burden due to the intense production demands, which can cause intestinal dysfunction, immune system imbalance and disruption of gut microbiota. These factors are the primary reasons for the decline in production performance and egg quality during the late laying period[47]. During PHR, the microbial community in the gut of laying hens undergoes changes, and the intestinal mucosa experiences a physiological process of injury and remodeling to adapt to the nutritional and metabolic demands of a new laying cycle[40]. During fasting, the regenerative capacity of intestinal stem cells is enhanced. After resuming feeding, these stem cells differentiate into secretory lineages to repair epithelial damage[48]. Studies in fruit flies have shown that dietary restriction can stimulate the intestinal stem cells of female fruit flies, improve age-related intestinal damage and ultimately extend their lifespan[49]. After PHR of hens, the ability of the gut to adapt to the nutritional and metabolic demands of a new laying cycle is a key factor affecting the production performance of molted laying hens. Our team's previous research found that staged fasting-induced intestinal damage is accompanied by increased expression of genes, such as cyclin B1/G2/mitotic-specific cyclin-B1 (*CCNB1*), cyclin-dependent kinase 1 (*CDK1*), transforming growth factor beta 3 (*TGFβ3*) and leucine-rich repeat-containing G protein-coupled receptor 5 (*LGR5*), and the activation of signaling pathways, such as wingless-related integration site (Wnt), hedgehog (HH), and mitogen-activated protein kinase (MAPK). Intestinal stem cells enter an activated state, thereby laying the foundation for the repair and remodeling of the damaged intestinal mucosa after resuming feeding. After PHR of hens, activating the AMPK-lipid metabolism pathway in the gut can effectively enhance the digestive and absorptive capacity of the gut in molted laying hens. Additionally, the concentration of Ca^{2+}-binding proteins in the gut of molted laying hens increases, improving their Ca^{2+} absorption capacity[5,50,51]。

The gut microbiota have potential for mitigating the common issue of declining egg quality in the later stages of egg production[52]. In the early laying period, the phylum Firmicutes dominates, with Bacteroidetes being the second most abundant phylum. During the peak production, Bacteroidetes (47.5%–62.0%), Firmicutes (30.8%–60.4%), Proteobacteria (2.0%–10.0%) and Fusobacteria (2.0%–5.0%) account for the majority of the microbial community. The relative abundance of Firmicutes gradually decreases in the mid-laying period, while that of Bacteroidetes increases. In the late laying period, Bacteroidetes surpasses Firmicutes in relative abundance, becoming the dominant phylum, while the abundance of Proteobacteria and Fusobacteria declines[53]. During PHR, the microbial community in the gut of laying hens undergoes significant changes, and the intestinal mucosa experiences a physiological process of injury and subsequent remodeling. The functionality of the gut is adjusted during this process to meet the nutritional and metabolic demands of a new laying cycle. PHR not only induces shifts in the gut microbiota but also influences the production of metabolites in the gut contents. Sequencing of the cecal microbiota of Zhejiang White Geese during the laying and brooding periods revealed that *Bacteroides fragilis* increases serotonin levels in the serum, stimulating the pituitary gland to secrete PRL and thereby promoting brooding behavior[54]. When the host and gut bacteria engage in the co-metabolism of food or exogenous

substances, a large number of small-molecule metabolites are produced. Of these, there are key factors involved in information transfer between host cells and gut bacteria. Therefore, gut microbiota and metabolites can be harnessed as exogenous additives to enhance the health and recovery capabilities of the body during PHR.

5.4 PHR activates the functions of the ovaries and oviducts

During the late laying period, laying hens undergo a reduction in the number of follicles at various developmental stages within the ovaries, an increase in follicular atresia and a decline in both egg production rate and egg quality. PHR can enhance ovarian function and restore the egg production rate of aging laying hens to peak levels. In studies on PHR in laying hens, fasting leads to a decrease in serum concentrations of reproductive hormones, such as FSH, LH, E_2 and progesterone. Meanwhile, the v-kit hardy-zuckerman 4 feline sarcoma viral oncogene homolog (KIT)-PI3K-phosphatase and tensin homolog (PTEN)-protein kinase B (AKT) signaling pathway in the ovaries is activated, promoting the activation of primordial follicles. After resuming feeding, the secretion of gonadotropins gradually increases, facilitating follicle development and ovulation [34]. The decline in sex steroid hormones results in the atresia and absorption of growing follicles, while primordial follicles are activated, and the numbers of primary and secondary follicles increase. After egg production resumes, there is a significant increase in the number of large white follicles, ensuring the egg production rate in the new laying cycle[34]. Through ovarian transcriptome sequencing, genes, such as vitronectin (*VTN*), prostaglandin d2 synthase (*PTGDS*), cytochrome P450 family 3 subfamily a member 5 (*CYP3A5*), hydroxysteroid 11-beta dehydrogenase 2 (*HSD11B2*) and UDP glucuronosyltransferase family 1 member a1 (*UGT1A1*), have been identified as candidate genes related to reproductive traits that influence ovarian function remodeling in the new laying cycle after PHR[55]. Additionally, epigenetic modifications are crucial regulators in follicle development during PHR. Zhang et al.[56] found that differentially methylated genes in ovarian and hypothalamic tissues during PHR epigenetically modify differential genes, leading to the rapid shutdown and restart of reproductive functions, promoting follicle development and enhancing egg production. During fasting, after the loss of ovarian steroid hormone support function, the oviduct begins to regress[57]. The mucosal epithelial surfaces of the infundibulum, magnum, isthmus, uterus and vagina of the oviduct are all thinned, with the capillaries of the tubular glands being particularly visible and an increase in the aggregation of white blood cells; the sub-basement membrane layer of the magnum, isthmus and uterus shows significant regression[58]. Fat deposition in the shell gland portion of the oviduct is the main cause of impaired Ca^{2+} transport and deposition in eggshell formation during the late laying period[5]. When the weight loss rate exceeds 25%, lipids in the oviduct are completely broken down, and the ability of the shell gland to transport and deposit Ca^{2+} is optimal. After resuming feeding and the resumption of sex steroid production in ovaries, the oviduct begins to remodel. After PHR, there is a significant improvement in eggshell quality and egg production rate. This also explains why PHR in laying hens requires a weight loss rate of over 25%.

5.5 PHR enhances the value of cull laying hens

China holds a globally leading position in terms of annual egg production and the number of laying hens in stock. Annually, about one billion laying hens are culled, which constitutes a substantial proportion of the total. During their egg-laying period, the majority of nutrients in laying hens are allocated to egg production. As a result, when these hens are culled and brought to market, they have a low meat yield, low muscle moisture content, poor water-holding capacity, high shear force and tough meat texture. Overall, the carcass quality is relatively poor[59]. Consequently, the market price for culled laying hens is generally low. Compared to other types of meat chickens available in the market, they do not have an advantage in terms of market price or market share. Therefore, improving the appearance, carcass traits and meat quality of laying hens before they are culled and brought to market could potentially enhance their market competitiveness. Our research team has found that PHR can significantly improve the quality of culled laying hens. Specifically, PHR can reduce the abdominal fat rate, subcutaneous fat thickness and intramuscular fat band width. It can also enhance their slaughter traits and increase intramuscular fat deposition. Transcriptomic and lipidomic analyses of the breast muscle revealed that PHR significantly upregulates the acyl-CoA synthetase long-chain family member 4 (*ACSL4*) gene. This upregulation leads to an increase in the number of acyl groups, more acyl-CoA linked to phosphatidylcholine, and a significant upregulation of lysophosphatidylcholine acyltransferase (*LPCAT*). Enhanced reacylation promotes the generation of new phospholipid molecules, altering the lipid composition of the breast muscle

and thereby improving meat quality[60]. Therefore, PHR can significantly enhance the slaughter traits and meat quality of culled laying hens, effectively increasing their economic value. This approach not only improves the market competitiveness of culled laying hens but also creates a new opportunity for added value for poultry farmers.

5.6 PHR induces feather renewal

The most evident manifestation of PHR is the transformation of feathers. As derivatives of the skin that provide protective functions in poultry, extensive wear and loss of feathers not only affect the health, behavior and overall appearance of birds, but also reduce production performance and increase feed costs, thereby affecting economic efficiency[61,62]. Before reaching 40 weeks old, laying hens may lose 10% to 15% of their feathers. Compared with hens with intact feathers, those with severe feather wear and tear tend to be more active and engage in more frequent feather-pecking behavior, which further exacerbates the damage. Improved feather quality in laying hens is associated with better egg quality and reduced average daily feed intake, which enhances the economic efficiency of poultry production. Conversely, feather damage reduces feather coverage. To maintain normal body temperature, hens with severe feather damage will significantly increase their feed intake, leading to higher feed consumption. Poor feather coverage also reduces hatchability and affects production performance. With the shift in chicken consumption from live poultry markets to chilled markets, the breeding focus of broiler chickens has also shifted from appearance traits to carcass traits. Pore size and density are key indicators of carcass aesthetics. Previous research by our team has shown that PHR not only ensures complete feather coverage and improves the live appearance of chickens but also increases pore density and reduces pore diameter. This enhances the carcass appearance of chilled chickens and improves their market economic benefits[36]. In the PHR of Houdan chickens, the period from 5 to 25 days after resuming feeding is identified as critical for the shedding and regeneration of primary wing feathers. Feather shedding begins 13 days into fasting and ceases 25 days after resuming feeding. By 32 days after resuming feeding, the shedding of old feathers stops and the new feathers have fully grown and matured. Similar to the mechanism of natural molting, thyroid hormones are important for feather and follicle growth and development[36]. Understanding the patterns and mechanisms of feather and follicle remodeling in culled laying hens can provide a theoretical basis for improving the carcass and carcass appearance of these birds.

5.7 PHR of testicular function in roosters

Rooster semen quality is a pivotal factor in poultry production[63]. From a genetic perspective, both roosters and hens contribute equally (50% each) to the genetic makeup of their offspring. Consequently, the semen quality of roosters is crucial for determining the quality and production performance of the chicks. Sperm motility stands out as a key indicator for assessing the reproductive traits of roosters, directly influencing the quality and quantity of offspring, as well as the economic benefits of poultry farms. Extensive research has demonstrated that a decline in sperm density and motility in roosters correlates with reduced fertilization rates and fertility[64]. As roosters age, their semen quality and fertilization rates tend to deteriorate, which can negatively impact the economic benefits of poultry farms if these roosters are culled prematurely. To optimize economic benefits, it is highly desirable for roosters to maintain high levels of sperm quality, including sperm density and motility, for an extended period[65]. Regrettably, research on extending the productive lifespan of aged breeding roosters remains limited. However, our research team has made significant strides in this area. Our previous studies have revealed that PHR not only significantly enhances the semen quality of aged breeding roosters but also boosts fertilization and hatching rates[66,67]. Also, this process can stimulate infertile aged roosters to resume semen production[68]. Importantly, the damage to reproductive performance caused by fasting induction is reversible. During PHR, the regulation of the actin cytoskeleton is closely associated with spermatogenesis. In this pathway, we have identified that the non-receptor protein kinase SRC is negatively correlated with spermatogenesis. Additionally, the aging-related gene Rho-associated coiled-coil-containing protein kinase 2 (*ROCK2*) is highly expressed during fasting, which may trigger testicular atrophy. After resuming feeding, *ROCK2* expression declines, allowing the testes to develop anew and resume semen production. Thus, PHR not only conserves feed but also improves semen quality and extends the service life of breeding roosters, which is of great significance for breeding and conservation.

6 Economic benefits of PHR

In recent years, the demand for PHR in poultry in China has

been on the rise, driven by several key factors. Firstly, improving egg production and quality can reduce costs and increase efficiency. PHR can extend the productive lifespan of laying hens from about 80 weeks to 110–140 weeks, extending feed utilization, and reducing feed and rearing costs for pullets. Secondly, China's reliance on imports for its white-feathered broiler breeders (great-grandparent and grandparent generations) means that the quantity and price of imported breeding stock are controlled by foreign companies. Extending the usage period of broiler breeders through PHR is an effective measure to reduce import costs and alleviate the shortage of parent-generation breeders at present. Thirdly, it enables flexibility in responding to market conditions and recovering losses. By controlling the resting and laying periods through PHR, the supply of eggs to the market can be regulated, effectively easing the problems of overproduction and seasonal unsold products. This can reduce rearing costs and increase profits. Also, implementing PHR in flocks affected by epidemics can effectively control disease spread. It also helps restore egg production and recover economic losses. Fourthly, it improves carcass traits and meat quality of culled laying hens. After PHR, culled laying hens exhibit improved slaughter and meat quality indicators, achieving meat production performance comparable to local specialty free-range chickens. Therefore, there is a huge market potential for culled laying hens after PHR, which can bring more benefits to poultry farms. Lastly, it reduces the cost of raising chicks and growing pullets, increase efficiency and safeguard national food security, PHR can extend the laying cycle of aged laying hens, saving the rearing costs during the period of raising new chicks. For example, in 2024, China had about one billion birds, including breeding chickens for egg and meat production and spent laying hens. If 50% of these birds underwent PHR, the feed ingredients saved would be equivalent to the output of about 690 million ha of grain production.

7 Issues and prospects

PHR, as a cost-effective and efficient husbandry management technique, offers significant economic benefits to enterprises while also presenting potential issues and challenges. Firstly, during fasting, the enterohepatic circulation of bile acids is disrupted, leading to their accumulation in the gut. This causes cytotoxicity, gut microbiota imbalance and damage to the intestinal barrier, thereby triggering inflammation[40,45]. This increases the risk of invasion by pathogens such as *Salmonella*[69]. How to improve PHR techniques and develop scientific gut health strategies to mitigate the negative impacts of fasting is an issue that requires continuous attention. Secondly, there is a lack of comprehensive studies on the nutritional needs of laying hens at different stages of PHR. When laying hens resume production before full recovery, egg output in the new cycle drops and the peak laying period shortens. This also reduces breeding egg quality, hatchability and the proportion of healthy chicks. How to enhance the health indicators of offspring, such as survival rate, body weight and immunity, and ensure the health and production performance of the next generation poses higher demands and challenges for PHR in breeding poultry. Thirdly, research on secondary or more repeated PHR in modern laying hens may further extend the production cycle of egg-laying hens, achieving grain-saving, increased efficiency and green sustainable production. Due to border closures caused by pandemics or other political factors, the application of this technology can help alleviate the problem of interruptions breeding chicken supply. Lastly, there are questions and challenges from the perspective of animal welfare. The welfare issues during the PHR process, including the breeding environment, mental behavior, and health indicators, need to be properly monitored and evaluated. In response to the welfare problems and potential risks that fasting may cause to laying hens, the development of non-fasting methods to induce PHR is a demand for future technological reserves. With a long-term perspective, research on avian PHR should be committed to achieving a balance between green and sustainable poultry production and animal welfare. This direction not only promotes the scientific development of poultry production sector but also has far-reaching implications for global food security and environmental protection. Additionally, systematically extending the experience of avian PHR to livestock can significantly improve livestock health and extend their productive lifespan. This approach also provides important scientific support for humans pursuing healthier and longer lifestyles.

8 Conclusions

This study systematically examines the physiological changes in poultry during brooding and natural molting and the implications for the so-called practice of forced molting, while adopting the term PHR to better reflect the multisystem

coordination involved in the molting process. Future work should optimize PHR by reducing fasting-induced stress and injuries in laying hens and by assessing generality and reproducibility across breeds and rearing conditions. Extending these concepts to human health management requires interdisciplinary research to verify safety, efficacy and ethical compliance, and to evaluate long-term impacts and cost-effectiveness.

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Compliance with ethics guidelines

Ruirui Jiang, Hao Zhang, and Xiangtao Kang declare that they have no conflicts of interest or financial conflicts to disclose. This article does not contain any studies with human or animal subjects performed by any of the authors.

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