FEEDING PATTERNS IN CHICKENS:
EFFECTS ON ENDOCRINE AND METABOLIC STATUS

J. BUYSE and E. DECUYPERE

Summary

Domestic fowls are continuous feeders and the daily feed intake pattern is mainly determined by the imposed lighting regimen. Turning broiler chickens from having a nibbling feeding pattern into periodic or meal eaters can improve feed conversion, providing there are a sufficient number of meals per day of high quality feed. The use of intermittent lighting readily imposes a meal-feeding pattern on chickens that were previously continuous feeders. These lighting schedules assure an improved feed conversion, nitrogen retention efficiency and more uniform slaughter weight. The underlying causal physiological mechanism is the more concave growth trajectory. Feeding only a single meal per day or alternatively, skip-a-day feeding, have profound effects on endocrine status and intermediary metabolic processes. These changes can be explained in terms of maintaining metabolic homeostasis. Refeeding gradually restores these processes, and the time course of these changes in plasma metabolite levels precede those of hormones. Dietary macronutrients and especially protein also affect endocrine and metabolic functioning.

I. INTRODUCTION

Domestic fowls are photoperiodic nibblers by nature, meaning that they consume feed continuously throughout the entire daylight period. Commercial broiler chickens are reared under continuous lighting because it is believed that feed intake is then maximal and hence growth rate would also be maximal. In contrast, laying hens are kept under shorter photoperiods e.g. 14 or 16 h light per day because such lighting programs are necessary for the entrainment of the ovulatory cycle and hence egg production rate. When feed is provided *ad libitum*, feed intake behavior of continuously lit broiler chickens consists of short though very frequent and regular feeding bouts ("nibbling"), giving rise to a rather constant daily feed intake pattern. Laying hens show an increase in feed ingestion at the onset of lighting and an anticipatory increase towards the end of the photoperiod (Savory, 1980). Broiler chickens reared under a day: night lighting schedule also develop such an anticipatory feed intake behavior (Savory, 1980; Buyse et al., 1993). The changes in feeding pattern, whether compulsorily imposed (e.g. through meal feeding; fasting: refeeding cycles or skip-a-day feeding), or induced by the lighting program, have pronounced effects on the physiology of birds and hence on their performance.

The present paper focuses on the physiological consequences of alterations in feed intake pattern (quantitative factor) as well as diet composition (qualitative factor) for domestic fowl, mainly broiler chickens.

II. CHANGING THE FEEDING PATTERN

a) Shorter photoperiods (day: night schedules)

Broiler chickens have a voracious appetite and nibble feed throughout the photoperiod. By providing nearly continuous light (CL: 23 h light (L): 1 h darkness (D)), it is assumed that feed consumption is then maximal, a condition that is believed to be necessary for maximal body weight gain. Indeed, reducing the daily photoperiod from 23L to 18L or less has a negative effect on growth rate due to a lower feed consumption or lower feed efficiency (Robbins et al., 1984). If daylength is not too short (>12 – 14 h L), feed consumption during the scotoperiod is insignificant (Buyse et al., 1993). Broiler chickens however can learn to eat during darkness, and older work showed that light is not really essential for feeding to occur properly (Cherry and Barwick, 1962; Squibb and Collier, 1979). On the other hand, broiler chickens learn to develop strategies in order to try to overcome the long nocturnal period without feed intake. This includes increased anticipatory feed intake towards the end of the photoperiod, mechanical storage of ingesta in the gastrointestinal tract and its gradual release during the night (longer nocturnal feed transit time) (Buyse et al., 1993) and reduced gastric motility (Duke and Evan son, 1976). During the nocturnal fast, heat production declines by more than 40 % (Buyse et al., 1993) and heart rate and rectal temperature drop as well (Klandorf et al., 1978; Decuyper and Kühn, 1984). This reduction in metabolic rate is attributable to lower nocturnal levels of the metabolism stimulating thyroid hormone 3,3',5-triiodothyronine (T3) (Klandorf et al., 1978; Buyse et al., 1987). The anticipatory feed intake behavior towards the end of the photoperiod needs time to develop (Squibb and Collier, 1979) and this learning process can be speeded up by simulated dusk (Savory, 1976).

The practical relevance of such day: night lighting schedules for broiler chickens will necessarily receive renewed interest as in the framework of EU welfare legislation for broiler chickens, continuous lighting will be forbidden. It must be recognized that nearly continuous lighting has detrimental effects on sleep, eye conditions, physical activity and leg health, immune-competence, incidence of ascites and Sudden Death syndrome (for reviews, see Gordon, 1994; Buyse et al., 1996a,b).

b) Meal feeding schedules

The obligatory conversion of broiler chickens from being ‘nibblers’ to ‘periodic feeders’ may improve growth rate and feed efficiency, at least when a sufficient number of meals are provided on a daily basis and with a diet of a high energy content (Conard and Kuenzel, 1978). Furthermore, Reece et al.,(1986) concluded that certain meal feeding programs might improve feed conversion during periods of both hot and cold temperature stress but not if grow-out temperature is normal. Meal feeding also reduces the incidence of leg abnormalities, independently of changes in body weight (Su et al., 1999).

c) Intermittent lighting schedules

A behavioral pattern of meal feeding is easily achieved when intermittent lighting (IL) schedules consisting of repeated short L: D cycles such as 1L:2D or 1L:3D are used. The alternating short light: dark cycles drastically change the daily feed intake pattern. Feed intake is principally limited to the L period of each L: D cycle, though some feeding does
occur during the D period and more so as the D period increases in duration (Buyse and Decuypere, 1988). The plasma triglyceride (TG) concentrations clearly follow the feed intake pattern as increased levels are observed during the L period and beginning of the D period, and decrease towards the end of the D period. The increase is explained by the digestion of dietary lipids and their incorporation in portomicrons and Very Low Density Lipoproteins (VLDL) on the one hand, and the de novo lipogenesis and subsequent secretion of VLDL on the other hand. Plasma glucose levels remain unchanged across the L: D cycle, illustrating again the strict glucose homeostasis in chickens (Simon, 1989). This periodic feeding pattern is also associated with marked changes in energy expenditure rhythmicity (Buyse et al., 1994) compared to the more or less constant heat production of CL chickens throughout 24 h each day. When lights are turned on, heat production increases rapidly due to increased heat increment associated with feeding and physical activity. This may even lead to a higher heat production during this period of illumination compared to CL chickens (Ohtani and Leeson, 2000). When lights are turned off, heat production declines although at a slower rate (Buyse et al., 1994; Ohtani and Leeson, 2000). IL does not affect feed transit time (Buyse et al., 1994) but the crop alternatively is filled and emptied with the pattern of intermittent lighting (Hooppaw and Goodman, 1976).

There are many reports available comparing the impact of intermittent lighting programs introduced at young age on broiler performance compared to the widely used CL schedule 23L:1D (for reviews, see Buyse et al., 1996a,b). In summary, broiler chickens reared under IL attain similar or even higher commercial slaughter weights as compared to their CL counterparts, though endogenous (sex, genotype) as well as exogenous (diet composition, feeder space, etc) interact with the imposed lighting schedule on body weight. In contrast, feed conversion is consistently improved by using IL. The effect of IL on fat deposition is again variable as literature reports indicate reduced (in most cases), equivalent or even higher fat accretion with IL compared to CL. The major causal mechanism for the improved biological performance (and in this case also the financial returns) with IL is undoubtedly the changed growth trajectory. Imposing IL at young age (after a few days of CL) is associated with a temporary reduction in feed intake and hence growth rate. However, when the chicks are accustomed to the new lighting environment, compensatory growth is manifested. Due to this concave growth trajectory cumulative maintenance needs are reduced, which contributes to the improved feed conversion. IL schedules do not affect apparent metabolizability (Buyse et al., 1994; Ketelaars et al., 1986).

During the period of compensatory growth, endocrine changes occur as well. Indeed, IL chickens manifesting compensatory growth are characterized by significantly elevated plasma growth hormone (GH) levels, which is the mechanistic result of a higher GH mass secretion per burst, hence higher GH amplitude (Buyse et al., 1997). It is hypothesized that the enhanced GH secretion is a causative factor for the improved protein retention (Buyse and Decuypere, 1994) that occurs during catch-up growth (Buyse et al., 1996c). In addition, during the period of compensatory growth male broilers have significantly higher plasma testosterone levels (Kühn et al., 1996), suggesting a positive role of this androgen in catch-up growth and probably also in GH secretion.

d) Daily fasting and refeeding cycles

In intensive livestock production, it is important to provide the animals with sufficient feed of high quality in order to obtain the best performance. However, there is only one branch of animal husbandry that requires a rigorous feed restriction: broiler breeder
management. Indeed, if broiler breeder pullets are fed ad libitum, the hens become too heavy and obese, many animals have to be culled and above all, reproductive capacity is very low. Therefore, pullets have to be severely restricted in their daily feed allowance in order to reach an acceptable production of fertile eggs of sufficient quality. Such a single daily fasting and subsequent refeeding cycle has profound effects on metabolic and endocrine functioning.

We have recently investigated the effects of daily meal feeding (one daily meal of 40 to 45 g/chicken/day, consumed in about 0.5 h) as practiced during breeder rearing on the somatotrophic and thyrotrophic axes of 4-week-old broiler chickens (Buyse et al., 2000; Buyse et al., 2002). Compared to their ad libitum (AL) fed counterparts, feed-restricted (FR) chickens showed a much more pronounced pulsatile GH release as reflected in a higher amplitude and mass of GH secreted per burst and pulse frequency. Free and total hepatic GH receptor numbers of FR chickens were significantly lower than those of AL chickens, indicating that high circulating GH levels down regulate their own hepatic receptors. The reduced hepatic GH receptor capacity is also assumed to be the reason, at least in part, for the lower plasma Insulin-like growth factor-I (IGF-I) levels in FR chickens. This uncoupling of IGF-I from GH – which is also recognized in other animal species and in humans – represents a mechanism to reduce cell growth and proliferation in favor of substrate (catabolism) and energy (lipolysis) mobilization in order to maintain homeostasis. It was also demonstrated that feed restriction of broiler breeder pullets resulted in a progressive increase in plasma IGFBP-28kDa and IGFBP-34kDa but not in IGFBP-40kDa levels (Bruggeman et al., 1997). In this way, there is few free IGF-I available for its anabolic actions. During fasting conditions, energy expenditure decreases due to lower plasma T₃ levels as a means to preserve body homeostasis (Decuyper and Kühn, 1984). All studies have also clearly shown that plasma thyroxine (T₄) levels are increased with fasting (e.g. Buyse et al., 2000; Reyns et al., 2002). Simultaneously, hepatic T₃ and T₄ concentrations are decreased and increased, respectively (Reyns et al., 2002), illustrating that the T₄ availability in the liver is not diminished during fasting. All relevant studies reported a marked augmentation of the hepatic IRD-III activity during fasting whereas for ORD-I activity, a decrease or no changes were observed.

Feed deprivation is also associated with reduced plasma TG, uric acid, and lactate levels, whereas plasma free fatty acid (FFA) levels and ketone bodies are increased. It is evident that dietary sources of lipids are absent in feed-deprived animals and that the in vivo hepatic fatty acid synthesis activity is strongly impaired (Muiruri et al., 1975), which explains the low plasma TG levels in these animals. As fasting is associated with low circulating insulin (lipogenic activity) and elevated glucagon (lipolytic and antilipogenic activity) levels in chickens (Simon, 1989), this may be the endocrine basis of the reduced hepatic lipogenic activity in feed-deprived chickens. The elevated lipolytic activity in feed-deprived animals is very likely to be induced by glucagon, a very potent lipolytic hormone in avian species (Langslow and Hales, 1969) and possibly also by GH for which the lipolytic properties have been clearly demonstrated in vivo (Vasilatos-Younken et al., 1988) and in vitro (Buyse et al., 1992a). The high plasma FFA levels could also be directly responsible for the inhibition of the hepatic lipogenesis (Leveille et al., 1975). Plasma lactate levels are significantly depressed in feed-deprived chickens compared to the levels of their ad libitum fed counterparts. In view of the reduced metabolic rate of feed-deprived animals, there is no need for anaerobic energy production; hence lactate production from glucose is limited. The reduced plasma uric acid levels result from the absence of dietary protein degradation and low protein turnover. Wilson and Miles (1988) reported that plasma uric acid levels of meal-fed broiler breeder males were highest at 2 h and lowest at 24 h postfeeding. However,
prolonged fasting causes again an increase in plasma uric acid levels due to degradation of endogenous protein sources (Buyse et al., 1995). At first sight, the effects of fasting on plasma glucose levels of fowl seem to be inconsistent as some studies report a decline in plasma glucose concentrations whereas others found no differences in glycemia. However, the duration of feed deprivation is of utmost importance in this respect, as plasma glucose levels may initially decline but are then restored after prolonged fasting due to increased gluconeogenesis (Decuyper and Kühn, 1984; Dewil et al., 1999).

Refeeding gradually reverses the fasting-induced alterations in plasma hormone levels. Plasma GH and T₄ levels decrease whereas plasma T₃ and IGF-I levels increase after the introduction of feed (Buyse et al., 2000; Buyse et al., 2002). The activities of intermediary metabolic processes are restored as well; though typically show an initial ‘overshoot’ phenomenon (relative to control ad libitum fed counterparts) as demonstrated for plasma glucose (Buyse et al., 2002), and insulin (Rosebrough et al., 1984) levels, hepatic glycogen storage ((Rosebrough et al., 1984) and in vivo lipogenesis (Muiruri et al., 1975; Leveille et al., 1975).

It is important to stress that the time course of postprandial changes differs between metabolites, which clearly precede those of endocrine factors. The order in responsiveness after feed was reintroduced was glucose > uric acid > FFA > lactate > TG for the plasma metabolites and GH > T₃ > T₄ > IGF-I for hormones (Buyse et al., 2002). Based on these different postprandial time courses of changes, several functional relationships can be proposed. Glucose is believed to be the primary trigger for the normalization of the effects of fasting on these plasma parameters by restoring hepatic GH receptor capacity as well as decreasing IRD-III activity.

The magnitude of the postprandial hormone and metabolite responses is also dependent on the composition of the diet provided. Indeed, Collado and Tasaki (1981) clearly showed that the postprandial increase in plasma TG levels was more pronounced when the introduced diet contained a low % of protein (12 %) compared to a high protein diet (30 %). The sharp postprandial increase in plasma glucose levels is also more pronounced when carbohydrate is included in the provided meal, though without concurrent changes in plasma insulin concentrations (Aman Yaman et al., 2000). These authors also showed that dietary protein intake is more important for the stimulation of protein fractional synthesis rate in muscle and liver of previously fasted chickens compared to their carbohydrate or protein consumption. It was also demonstrated that the rapid increase (within 1 h) in liver and muscle protein synthesis in red fed chickens was not correlated with circulating plasma IGF-I concentrations, of which the postprandial increase lags considerably behind (Buyse et al., 2002).

e) Skip-a-day feeding

Feeding on alternate days or skip-a-day feeding programs exert even a more drastic effect on bird’s physiology. This management practice used to be applied in broiler breeder rearing as flock uniformity would be improved (Costa, 1981). However, such feeding programs lead to a higher feed conversion as reflected in the lower body weights of skip-a-day fed pullets compared to their daily fed counterparts receiving the same feed allotment (e.g. Bennett et al., 1990). Indeed, on the feeding day, all skip-a-day fed birds can consume enough feed, and the excess energy is stored mainly as fat. On the feed-off days, this energy is mobilized and the FFA are oxidized to yield metabolizable energy. The diurnal variations in heat production (HP) have been clearly demonstrated by Bennett et al. (1990). On the
feeding days, skip-a-day broiler breeder pullets had a much higher HP than their daily fed counterparts whereas the opposite was true on the feed-off days. On a daily basis, the total HP was significantly higher for the skip-a-day fed pullets, which were hence less efficient. These repeated cycles of energy storage and energy expenditure are energetically less efficient and are also reflected in the Respiratory Quotient, averaging 1.05 on the feeding days and decreasing to 0.67 on the feed-off days (daily fed hens had a RQ ranging from 0.8 to 0.9). These RQ values reflect carbohydrate oxidation (and fatty acid synthesis) and fatty acid oxidation, respectively. During the repletion days, the in vivo synthesis of proteins in various tissues was also much higher than during the fasting days, illustrating the anabolic status when feed is available (Pinchasov et al., 1988). Alternate-day feeding does however improve immunocompetence (Praharaj et al., 1996) and reduces the prevalence of leg deformities (Boa-Amponsem et al., 1991).

III. DIET COMPOSITION

Not only do the quantity of food consumed and the feeding frequency have marked effects on chicken performance and on endocrine and metabolic status, but also the diet quality, and in particular its macronutrient content affect performance (Buyse et al., 2001). The effects of dietary crude protein (CP) levels on these physiological processes are best documented. In summary, a reduction in dietary CP content results in increased plasma GH concentrations, as a consequence of the higher amplitude, baseline and pulse frequency values compared to broilers provided an isonenergetic diet with a normal protein (20 – 22 % CP) content (Buyse et al., 1992b). Again, it is believed that the enhanced pulsatile GH secretion is a causal mechanism for the improved protein conversion efficiency of moderately protein-restricted animals (Buyse and Decuypere, 1994). Chickens fed on a low CP diet also have reduced plasma uric acid levels, indicative of a low protein degradation rate, besides their low protein ingestion (Malheiro et al., unpublished results). Plasma IGF-I concentrations are lowered by feeding low CP diets whereas plasma IGF-II levels remain unchanged (Leili and Scanes, 1998). In addition, circulating IGFBP levels are also influenced by protein malnutrition, although dependent on their molecular mass and severity and duration of the protein restriction (Leili and Scanes, 1998). However, in contrast to feed-deprivation, there is no evidence that protein restriction is associated with a down regulation of hepatic GH receptors, but rather the contrary has been found. Protein-restricted chickens are characterized by reduced plasma T₄ and increased plasma T₃ levels (see Buyse et al., 2001). This is very likely to be a consequence of the high circulating GH levels, as this peptide is known to inhibit the IRD-III activity (Darras et al., 1995). The elevated plasma T₃ levels are thought to be the causal mechanism for the increased heat production of chickens fed a low CP diet, which is a way to deal with their ‘luxus’ energy consumption, besides a higher fat deposition (Buyse et al., 1992b). The higher fat deposition in protein-restricted chickens is also reflected in elevated in vitro and in vivo lipogenesis and hepatic lipogenic enzyme activities (e.g. Rosebrough and Steele, 1985).

We recently observed that an isocaloric substitution of fat by carbohydrate calories in isocaloric and isonitrogenous diets has no clear effects on plasma hormone and metabolite levels, except for a temporary elevation in plasma T₃ and FFA levels (Malheiro et al., in press and unpublished results). These results again démonstrate that the protein content per se has greater influence on these parameters and hence on chicken performance.

Although there is a wealth of information on the effects of dietary energy and macronutrient content on body weight gain and composition and on the amount of feed
consumed, there is little information on how these dietary variables affect the feed intake pattern or the voluntary regulation of feed intake in terms of meal size and frequency in the domestic fowl. Taher et al. (1985) reported that when SCWL roosters were abruptly changed to a diet with a higher energetic density, they decreased the amount of feed consumed by decreasing meal size and duration but increasing the number of meals. Roosters changed to a low energy diet ate more feed, increased their meal size and duration as well as number of meals. Other factors that affect feeding patterns are physical form of the diet (mash versus pellets: Nir et al., 1994; Aerni et al., 2000; protein concentrate versus ground, cracked or whole grain corn: Yo et al., 1997) and environmental temperature (Taher et al., 1985).

REFERENCES


