CLIMATE-NUTRITION INTERACTIONS IN POULTRY

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SUMMARY
In poultry, nutrition interacts with thermal environment throughout the temperature range. In terms of food intake and production, there may be an economically optimum temperature but there is no true “thermoneutral zone”. Two ambient temperature zones are discernible, a lower one in which the main effect on nutrition and production is by changing intake and a higher one in which the direct physiological effects of heat stress become critical and it becomes difficult to improve production by nutritional means. High temperature influences intake, digestion, absorption and metabolism of energy and nutrients. The most direct effects of climate are on transfer of energy between the bird and the environment - at high temperatures, the bird has difficulty in getting rid of metabolic heat to the environment. This determines both intake and the optimal composition of the feed. Protein (and specific amino acid) utilisation strongly interacts with energy metabolism under these conditions. This paper will deal with direct and indirect effects of high ambient temperature on energy and protein metabolism and utilisation. Energy is required at all stages of amino acid utilisation: intake, digestion, absorption, transport, conversion, protein synthesis and nitrogen excretion. Amino acids can also act as a source of energy, especially when they are provided in excess. Because food intake is strongly controlled in terms of energy intake, it is essential to maintain the correct ratio between individual amino acids and dietary energy concentration. This has the corollary that, if a bird is allowed to eat to satisfy its energy requirement and amino acid:energy ratios are kept constant, decreased energy intake (e.g. at high temperature) will always be associated with decreased amino acid intake.
Heat stress is largely a problem in birds selected for high rates of growth or egg production under temperate conditions. A high rate of production usually carries the penalty of higher metabolic heat production and the necessity to dissipate this heat to a warm or hot environment. “Indigenous” poultry in hotter countries are closer in body shape and production rate to the ancestral Jungle Fowl. Their lower rate of production also fits them for a foraging lifestyle in which they do not compete with humans for high value, high protein and high-energy foods. Where socio-economic conditions have encouraged intensive poultry farming in hot climates, environmental modification or control is usually the first recommendation. When this is not possible—or adequate—some nutritional strategies have been employed, often involving time of feeding or temporary feed withdrawal.

**INTRODUCTION**

**Nutrition and heat stress**
Heat stress is largely a problem in birds selected for high rates of growth or egg production under temperate conditions. A high rate of production usually carries the penalty of higher metabolic heat production and the necessity to dissipate this heat to a warm or hot environment. “Indigenous” poultry in tropical countries are closer in body shape and production rate to the ancestral Jungle Fowl. Their lower rate of production also fits them for a foraging lifestyle in which they do not compete with humans for high value, high protein and high-energy foods. Where socio-economic conditions have encouraged intensive poultry farming in hot climates, environmental modification or control is usually the first recommendation. When this is not possible—or adequate—some nutritional strategies have been employed, often involving time of feeding or temporary feed withdrawal (MacLeod and Jewitt, 1984; Francis et al., 1991).

**Interaction between energy and protein requirement**
Energy is required at all stages of amino acid utilisation: intake, digestion, absorption, transport, conversion, protein synthesis and nitrogen excretion. Amino acids can also act as a source of energy, especially when they are provided in excess. Because food intake is strongly controlled in terms of energy intake, it is essential to maintain the correct ratio between individual amino acids and dietary energy concentration. This has the corollary that, if a bird is allowed to eat to satisfy its energy requirement and amino acid:energy ratios are kept constant, decreased energy intake (e.g. at high temperature) will always be associated with decreased amino acid intake. If a bird is
selected for increased growth rate and its food intake increases proportionally, it is therefore possible that the absolute intake of an amino acid may be sustained at a level that supports maximum growth without the nutritionist having to increase the concentration of that amino acid in the diet. This may explain why scientists do not always find an increase in amino acid requirement (expressed as concentration in the diet) when birds are selected for more rapid growth (e.g. Han and Baker, 1991). However, theory would dictate that amino acid requirements must change as growth rate and body composition change, since the amounts of amino acids being used for "maintenance", muscle protein synthesis and feather protein synthesis must be changing. Such changes can be predicted by a modelling approach but may sometimes be difficult to detect in experiments. Matching the amino acid composition of the diet as closely as possible to the bird's requirements is essential for maximising performance. Current broiler diets are kept at the same composition for two or three weeks. This may be purely for operational reasons and we should eventually aim for more exact matching between requirements and provision (e.g. Pope and Emmert, 2002).

**FOOD INTAKE**
As temperature increases, food intake initially decreases because less energy is required to maintain body temperature. In broilers, the reduction is typically 1.5 to 2.5% per oC increase in temperature above 20 oC (Howlider and Rose, 1987). However, if temperature increases to the point where physiological means of controlling body temperature by reducing heat production or by increasing heat loss heat approach saturation then feed intake begins to decrease even more steeply. This is because reducing feed intake reduces the heat increment of feeding, giving a further mechanism for reducing heat stress. It has often been hypothesised that reducing protein content or increasing the fat content of diets would be beneficial at high temperatures because protein gives a high and fat a low heat increment. However, this has not been borne out under practical conditions. In fact, if production is to be maximised, the intake of essential amino acids must be sustained whatever the temperature.
There may be benefits in maintaining intakes of essential amino acids and at the same time reducing total protein intake by greater use of supplementary amino acids. Reduction in feed intake at high temperature explains only about 50% of the reduction in growth rate (Geraert et al., 1996a,b). There must also be direct effects of heat stress on growth. Even when taking into account the reduction in feed intake, nitrogen retention decreases by up to 30% (Temim et al., 1999).

DIGESTION AND ABSORPTION

When growing broilers were kept at 35 °C for 2 weeks, in vivo jejunal uptakes of galactose and methionine increased by 36% and 50% respectively per unit of intestinal dry weight (Mitchell and Carlisle, 1992). The absorptive area was probably reduced by heat stress, since villus height decreased by 19% and wet and dry weights per unit length of jejunum decreased by about 30%. The authors suggested that there may have been adaptation to optimise nutrient absorption in the face of reduced food intake and reduced absorptive area. On the other hand, Brake et al. (1998) found that in vitro arginine uptake, in the presence of an equimolar concentration of lysine, was reduced in heat-stressed birds (32 °C). Measurements at a more practical level have usually suggested that amino acid digestibility and absorption is reduced by high temperature. Zuprizal et al. (1993) found decreases in the digestibility of amino acids and protein from rapeseed meal and soya bean meal at 32 °C as compared with 21 °C. There was a 12% reduction in true protein digestibility from rapeseed and a 5% reduction from soya. Balnave and Oliva (1991) found that in vivo digestibility of arginine was reduced at high ambient temperatures, which ties in with the in vitro measurements of Brake et al. (1998).

METABOLISM

Energy

Most of the energy provided by a poultry diet is in the form of carbohydrate and fat. Any amino acids which are surplus to requirements may also function as energy substrates, but this is economically undesirable and may also be physiologically troublesome, especially at high temperatures. The argument to be considered here is, therefore, whether the relative merits of carbohydrate and fat alter with ambient temperature. Fat has a net availability of metabolisable energy (ME; Figure 1) of about 95%, compared with 80% for carbohydrate. This means that for every 1 kJ of net energy (NE) obtained from carbohydrate, about 0.25 kJ is liberated as heat while for every 1 kJ from fat only 0.05 kJ is lost in this form. For that reason alone,
scientists have hypothesised that replacement of carbohydrate by fat should be particularly beneficial at high temperatures. Diets containing fat have also been shown to have a higher-than-calculated ME value, possibly because of an associative effect on the metabolisability of other ingredients (Mateos and Sell, 1980). Further expected advantages of fat, especially at high temperatures where energy intake should be boosted are increased energy density, increased palatability and improved feed handling qualities. Despite the widespread acceptance of the notion of adding fat to poultry diets at high temperatures, expectations have not often been borne out in practice or, indeed, in experiment. There seems to be little published evidence of beneficial effects which do not occur equally at lower temperatures (i.e. higher energy intake and higher efficiency of energy deposition; the latter is often due to increased fat content and is therefore not detected as an improvement in weight conversion efficiency). In preference experiments, growing broilers demonstrated a preference for high-fat diets at temperatures from 10 to 32.5 oC even when physical texture was equalised by pelleting (Dale and Fuller, 1978; 1979). Ain Baziz et al. (1990) used a range of fat contents from 50 to 150 g/kg of diet and found no advantage of high-fat diets at high temperatures; the main effects were large changes in fat deposition. Furthermore, altering protein content over a wide range does not always result in an increase in heat production, either at high (Ain Baziz et al., 1990) or moderate temperatures (MacLeod, 1997). In the latter paper, it was found that metabolic rate was related more to concentration of the first-limiting amino acid and hence growth rate than to total dietary protein content. The effects of a high fat diet on tolerance of acute heat stress (e.g. 41 oC) appear to be small (Kubena et al., 1972, 1973; Francis et al., 1991). If fat encourages a greater ME intake, it follows that the bird’s total metabolism may be no less than on a carbohydrate diet and there may, therefore, be no reason to expect greater tolerance of a sudden increase in ambient temperature. Indeed, if the bird uses an immediate reduction in feed intake to reduce heat production when stressed, it may have to reduce the intake of a high-fat diet by more than that of a carbohydrate diet to produce the same effect on heat production.

Protein

Heat stress and protein turnover. The rate of protein accretion is always a balance between breakdown and synthesis. The reduction in protein accretion under conditions of chronic heat stress is because the rate of protein synthesis is more greatly affected than the rate of protein breakdown (Temin et al., 1999; 2000a;
2000b). Protein synthesis was reduced more in the breast muscle (-35%) than in the leg muscles (-20%); this may be related to the more glycolytic metabolism of the breast muscle and the more oxidative metabolism of the leg muscles. (Temin et al., 1999). Increasing dietary protein content from 20 to 25% at 32 °C did not affect rate of protein synthesis but did increase muscle protein deposition, probably by reducing protein breakdown (Temim et al., 2000b). It has been suggested that energy for protein synthesis at the molecular level may be limited at high temperatures; glucose supplementation has been shown to improve growth rate at high ambient temperatures (Hayashi et al., 2001).

**Amino acids**

Amino acid requirements in relation to ambient temperature must primarily be considered in terms of absolute intakes (e.g. g/bird/day) and not as concentrations in the diet or amino acid:ME ratios. It is the actual quantity of an amino acid consumed that determines performance, not its concentration in the feed. In general, there is no evidence that the absolute requirements of amino acids either for growth or egg production are significantly affected by thermal environment (Bray and Gessell, 1961). We know, however, that total food intake decreases with temperature; daily intakes of amino acids can, therefore, be sustained at the required level only by boosting their concentrations in the diet as food intake declines. These well-known principles are subject to modification, especially at the high temperature end of the scale. Studies with both broilers (e.g. Cowan and Michie, 1978) and laying hens (e.g. Reid and Weber, 1973) suggest that, at temperatures of about 30 °C upwards, increased amino acid concentrations can not compensate adequately for reduced food intake – factors other than amino acid intake are becoming limiting. Energy intake, for instance, is decreasing more rapidly than maintenance energy requirement; maintenance requirement may even begin to increase as the birds begin to work (pant) to lose heat by evaporative means. There are also direct performance-depressing effects of high temperature, possibly acting through the thyroid-growth hormone axis. Under such circumstances, what may be needed is some generalised method of reducing heat stress rather than increases in nutrient concentrations. Hurwitz et al. (1980) argued that amino acid concentrations (expressed as a ratio of ME) in the diet of 6-7-week broilers should increase only up to 27 °C and should then decrease because of decreasing requirements for growth. Amino acid balance and temperature. Padilha (1995; P.A. Geraert, unpublished) found that increasing total protein content of a finisher diet from 15 to 25% increased growth rate at 32 °C, although there was
no further response beyond 20% at low temperature. It is not clear whether the effect of high protein diets is due to increased requirement for specific amino acids. Indeed, supplementation with methionine, lysine or threonine does not always produce an improvement. Balnave and Oliva (1991) found a lower methionine requirement at high temperatures. Most research indicates that there is no increase in absolute amino acid requirements at high temperature (Austic, 1985), although it must be re-emphasised that it may be necessary to increase the concentration of amino acids relative to energy and total food mass as food and energy intake decrease. Alleman and Leclercq (1997) found that a low protein diet supplemented with lysine, methionine, arginine, threonine and valine to meet requirements produced the same growth rate as the control (high protein) diet at 22 oC but not at 32 oC (Table 1). This suggests that some other amino acids may have limited growth rate at the higher temperature.

There are specific antagonistic effects, such as those between lysine and arginine and among leucine, isoleucine and valine (Harper et al., 1970). Such antagonisms are summarised specifically for poultry by d’Mello (1994). They usually involve interactions between structurally similar amino acids. Lysine specifically antagonises the utilisation of arginine and this has received recent attention in relation to high ambient temperature. Leucine impairs the utilisation of isoleucine and valine; all three of these compounds are branched-chain amino acids. In practice, the antagonisms can be alleviated by supplementation of the diet with arginine, isoleucine or valine.

Because their main excretory product is uric acid, poultry are not able to synthesise arginine. This makes them particularly sensitive to lysine antagonism. There is increased activity of kidney arginase in chicks receiving excess lysine, leading to increased arginine breakdown (d’Mello, 1994).

Brake et al. (1998) found that increasing the arginine:lysine ratio for broilers kept at high temperature gave improved conversion efficiency. The effect of increased arginine was greatest in lower-sodium diets and decreased with sodium chloride or sodium bicarbonate supplementation. Balnave and Brake (2002) suggested that sodium ions may reduce lysine resorption by the kidney and therefore give a higher “effective” arginine:lysine ratio. There are also interactions between arginine:lysine ratio and the form (DL-methionine or 2-hydroxy-4-(methylthio)-butanoic acid) in which methionine activity is supplied (Chen et al., 2003).
M G MacLeod, 2004

Veldkamp et al. (2000) found, in turkeys, that increasing the arginine:lysine ratio from 1.00 to 1.25 did not alleviate the effect of high temperature on performance except when dietary lysine concentration was marginal in relation to requirement. The higher arginine:lysine ratio increased feed intake significantly until 56 d of age (200.6 vs. 197.6) and also resulted in significantly greater weight gain until 98 d of age (10.03 vs. 9.84 kg). Arginine:lysine ratio did not affect feed:gain throughout the experiment. Processing yields were affected significantly by temperature, but not by arginine:lysine ratio.

Arginine has functions which are probably related to its role as a source of nitric oxide (NO). Nitric oxide is known to be required for phagocytosis. During heat stress, the phagocytic functions of monocytes and macrophages are affected by the arginine:lysine ratio (Qureshi et al., 2000).

Rose and Salah Uddin (1997) demonstrated that growing broilers were less sensitive to the ratio of lysine to crude protein when kept at 30°C than at temperatures between 15 and 25°C.

BODY COMPOSITION, PART YIELD AND MEAT QUALITY

Body composition. Despite their lower feed intake, broilers kept at higher temperature tend to have a higher body fat content. The abdominal, subcutaneous and intramuscular fat deposits were respectively 15, 21 and 22% higher at 32°C than at 22°C. The differences were even larger between birds at 32°C and pair-fed controls kept at 22°C (58, 64 and 33%) (Aïn Baziz et al., 1996). High ambient temperature has also been shown to decrease the ratio of unsaturated to saturated fatty acids in abdominal and subcutaneous fat (Sonaiya, 1988). Palmitic acid (C16:0) showed the largest increase, at the expense of oleic and linoleic acid. Under more practical (imperfectly controlled) conditions in Turkey, Yalçin et al. (1999) showed that the fat content of the breast increased and protein content decreased in summer. The increased fat content of birds grown under hot conditions is associated with reduced oxidation of fatty acids rather than increased fat synthesis or peripheral uptake. Malic and isocitric dehydrogenase enzyme concentrations, as well as that of lipoprotein lipase, are reduced under hot conditions. However, indicators of lipolysis, such as β-hydroxyacyl-dehydrogenase and plasma D-3-hydroxybutyrate are also reduced (Aïn Baziz et al., 1996). There have been some reports that high temperature improves flavour, an effect which may be related to the higher fat content (Sonaiya et al., 1990).
Looking into composition in greater detail, Tawfik et al. (1992) found that the breast muscle of broilers exposed to high temperature had lower glycine and proline contents.

**Part yield** Ambient temperature also can affect proportional growth (Temim et al., 1999). High-temperature-related growth reduction was associated with decreased nitrogen retention (-30 to -35 %), which could not be explained by lower feed intake alone. Tissue samples from 5- to 6-week-old chicks showed varying effects of heat according to the muscles studied: at 32 C, the proportion of pectoralis major muscle appeared slightly reduced (by less than 10%), whereas the proportion of two leg muscles were increased (by 10-15 % for the sartorius muscle and 5 % for the gastrocnemius muscle). At 32 oC, providing a high protein diet significantly increased weight gain and feed efficiency and slightly improved whole body protein deposition. Mendes et al. (1997) found that environmental temperature significantly influenced many characteristics. High, cycling, temperatures reduced feed intake, weight gain, breast meat yield and feed conversion efficiency and increased dressing percentage, leg quarter yield and abdominal fat content. Lysine concentration affected leg quarter yield and abdominal fat content over all environments but increased breast meat yield only under cool conditions.

**Meat quality in relation to heat stress.** Exposure of broilers to acute heat stress just before slaughter has effects on meat quality. Northcutt et al. (1994) noted that heat stress immediately prior to slaughter caused pale, soft exudative meat (PSE) in broilers. The effects included lower muscle pH (related to increased glycolytic metabolism), increased water loss and greater incidence of breast muscle haemorrhages (Sandercock et al., 2001). Pre-slaughter exposure to high temperature should be prevented to avoid the development of undesirable meat characteristics.

**Feeding Management At High Temperature.** Feeding management can include such tactics as (1) altering times of feeding or lighting, (2) feed restriction, (3) short-term feed withdrawal and (4) choice feeding. Feed form (e.g. pellets or mash) can also be considered under this heading. Some of the suggestions in this area are based on small-scale experiments and require field-scale validation. Conversely, other practices are already in use but need more detailed scientific evaluation.
Feeding And Lighting Manipulation. The first three tactics mentioned above are based on knowledge of the diurnal rhythm in heat production and the effect of feeding on heat production (Lundy et al., 1978). In layers and broiler breeders, heat production is about 35% higher during the day than at night, which means that the bird is producing most heat at a time when it has most difficulty in getting rid of it. Feeding the bird last thing in the day means that the heat increment of metabolising the food is dissipated mainly at night, allowing lower heat production during the day (MacLeod and Jewitt, 1984; Figure 2). Some types of lighting manipulation are only operable in light-proof accommodation; the extreme example would be lighting at night when it is relatively cool and keeping the birds in darkness during the day. Even in open-sided houses, lighting can be extended into the dark period so as to allow night-time feeding by layers. Intermittent lighting during the “day” in enclosed housing may reduce overall heat production and therefore heat stress.

Feed restriction in breeding stock, as well as having the advantages for which it is primarily used, is likely to improve heat tolerance; the birds will be lighter, will have a lower heat increment and may even have a lower heat production per unit of weight (MacLeod et al., 1978). There is also some evidence that feed restriction early in life may reduce the negative effects of heat stress on immunocompetence (Khajavi et al., 2003) and on heat shock protein 70 expression (Zulkipli et al., 2003).

Withdrawal of feed immediately (0-2 h) before the onset of stressful temperature conditions had an immediate beneficial effect on the body temperature responses of 4-6-week broilers under experimental conditions (Francis et al., 1991; Figure 3). Switching lights off during the hot period had a quantitatively similar effect. Methods such as these may be useful as emergency measures and should be tested on a larger scale (e.g. Ertas and Sahin, 2002). The beneficial effects may include increases in antioxidant and vitamin activities and a decrease in lipid peroxidation (Naziroglu et al., 2000).

Feed Form. Laying hen diets are usually fed in mash form. This may have the advantage of reducing feather-pecking and other “vices” (Aerni et al., 2000). The most likely explanation is that feeding on mash is more time-consuming for the bird than eating pellets and also gives more opportunity for oral behaviour patterns. The negative side of this is that more energy is expended on mash feeding and there may also be more spillage, so the birds may show a slightly lower conversion efficiency (Jensen et al., 1962; Savory, 1974). The process of pelleting usually involves a temperature increase, which may have beneficial effects; in experiments comparing
pellets and mash it is therefore a good tactic to use re-ground pellets for the “mash” treatments. Broilers are usually fed on pellets, which should have the advantage of reducing heat production during feeding. To maximise this advantage, the pellets should be of good quality (high integrity) so that “fines” (small particles, dust) are kept to a minimum.

CHOICE FEEDING. MacLeod and Dabutha (1997) used quail as a model to test the hypothesis that ambient temperature would affect selection between energy-rich and protein-rich diets through its effects on thermoregulatory energy requirements. As with other poultry, there are several possible outcomes: (1) that quail do not select successfully or consistently between a high-protein and a high-energy food; (2) that quail select the same proportions of a high-protein and a high-energy food at all temperatures; (3) that quail increase the proportional consumption of the high-protein food as energy intake decreases with increasing temperature, allowing a sustained rate protein accretion in spite of a reduced energy intake; (4) that quail decrease the proportional consumption of the high-protein food as temperature increases; this would minimise the heat increment of feeding, which would have the effect of reducing heat stress. With broiler chickens, results have been found which conform with alternatives (2), (3) and (4) above ((2) - Cowan and Michie, 1977; (3) - Mastika and Cumming, 1987; Hruby et al., 1995; (4) - Sinurat and Balnave, 1986). There is clearly scope for different choice strategies even within the same species. There is also the possibility that the bird apparently fails to “choose wisely” for some reason unidentified by the experimenter (Forbes and Kyriazakis, 1995).

In our experiment, increasing ambient temperature had no significant effect on food intake by weight, but the proportion of the high-energy choice decreased and, conversely, the proportion of the lower-energy but higher-protein choice increased (Table 2). Energy intake was therefore negatively correlated with ambient temperature, but protein intake per unit of energy intake increased, allowing the birds to gain weight at about the same rate at all temperatures. Heat production decreased as ambient temperature increased. Respiratory quotient decreased with increasing temperature, which would indicate a reduced utilisation of carbohydrate as an energy source. Water intake increased with temperature but there were no overt signs of heat stress and no significant change in body temperature. Japanese quail selected a dietary mixture which maintained similar growth rates over a wide range of ambient
temperature, by sustaining protein intake but altering energy intake in line with thermoregulatory energy demands.

In relation to previous results with the domestic fowl, it could be suggested that factors determining the bird’s selection of diet may be given different priorities by the bird and by the producer. The immediate priority for the bird may be to avoid the increased risk of heat stress associated with a higher metabolic rate. This may over-ride the drive towards attaining the bird’s genetic potential for protein synthesis. The quail in this experiment may have had the option of maintaining growth rate at higher temperatures because their more favourable surface:volume ratio and lower intensity of selection for rate of protein synthesis allowed them more scope for the loss of metabolic heat. It was also clear that the choice of protein:ME ratio was lower than that of the previously fed compound diet at all temperatures below 35°C. This is again an indication that the birds’ preference does not necessarily correspond with the recommendations derived for maximum growth rate.

However, factors other than an exact fit to metabolic and nutritional requirements are involved in diet selection and this may mean that choice feeding does not always give optimal production. These other factors include palatability, previous experience, social factors and even trough position (Hughes, 1984).

An alternative to having two or more feeds available at all times is to use a sequential feeding programme. De Basilio et al. (2001) offered a high protein diet overnight (1600 – 0900) and an energy rich diet 0900-1600 and found reduced mortality during heat stress although growth rate and breast muscle yield were slightly reduced.

**Vitamins and minerals.** Dietary bicarbonate may be beneficial during heat stress, since panting increases the loss of carbon dioxide. Teeter et al. (1985) found that adding either sodium bicarbonate or ammonium chloride to the diet resulted in enhanced growth rate. Supplementing drinking water with either sodium or potassium caused an increase in water intake, which was associated with a reduction in body temperature and an increase in body weight gain (Smith and Teeter, 1989). Gous (2004) suggests that producers should encourage birds to drink more water by adding mineral salts to the drinking water (2 g sodium bicarbonate per litre) and using sodium bicarbonate (up to 16 g/kg) in the feed as a sodium source, rather than sodium chloride. This has the advantages that bicarbonate intake is increased and sodium intake is reduced.

Supplementation of the diet with vitamin E has been shown to alleviate the depression in egg production caused by high ambient temperature (Bollengier-Lee et al., 1998).
There is also evidence that increased supplementation with vitamin A has beneficial effects on the immune system and egg production at high temperature (Lin et al., 2002). Vitamin C is not an essential nutrient for poultry under most conditions but does appear to alleviate heat stress (Pardue et al., 1985; Kutlu and Forbes, 1993).

REFERENCES


protein 70 expression and body temperature of heat-stressed broiler chickens. 

Table 1. An experiment (Alleman and Leclercq, 1997) in which amino acid balance ideal at low temperature did not give good performance at high temperature.

<table>
<thead>
<tr>
<th>Dietary protein (g/kg)</th>
<th>Ambient temperature</th>
<th>22 °C</th>
<th>32 °C</th>
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<tr>
<td></td>
<td>160 (ideal)</td>
<td>200 (high)</td>
<td>160</td>
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<tr>
<td>Weight gain (g)</td>
<td>1783&lt;sup&gt;c&lt;/sup&gt;</td>
<td>1779&lt;sup&gt;c&lt;/sup&gt;</td>
<td>939&lt;sup&gt;a&lt;/sup&gt;</td>
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<tr>
<td>Feed intake (g)</td>
<td>3256&lt;sup&gt;c&lt;/sup&gt;</td>
<td>3108&lt;sup&gt;b&lt;/sup&gt;</td>
<td>2279&lt;sup&gt;a&lt;/sup&gt;</td>
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<tr>
<td>Feed:gain ratio</td>
<td>1.81&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.77&lt;sup&gt;a&lt;/sup&gt;</td>
<td>2.41&lt;sup&gt;d&lt;/sup&gt;</td>
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<td>Abdominal fat (g/kg)</td>
<td>2.78&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>2.20&lt;sup&gt;a&lt;/sup&gt;</td>
<td>3.77&lt;sup&gt;c&lt;/sup&gt;</td>
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<td>Breast meat yield (g/kg)</td>
<td>14.7&lt;sup&gt;c&lt;/sup&gt;</td>
<td>15.4&lt;sup&gt;c&lt;/sup&gt;</td>
<td>12.1&lt;sup&gt;a&lt;/sup&gt;</td>
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**Table 2.** Metabolic, thermoregulatory, food and water intake and weight gain responses of Japanese quail to ambient temperature. Values in the same row not sharing a common superscript are significantly different at the P<0.05 level.

<table>
<thead>
<tr>
<th></th>
<th>20°C</th>
<th>25°C</th>
<th>30°C</th>
<th>35°C</th>
<th>SEM</th>
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<tr>
<td>Heat production (kJ/kg W$^{0.75}$ d)</td>
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<td></td>
<td>1123$^a$</td>
<td>870$^b$</td>
<td>801$^c$</td>
<td>741$^c$</td>
<td>6.0</td>
<td>&lt;0.01</td>
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<td>Respiratory quotient</td>
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<td></td>
<td>1.10$^a$</td>
<td>0.96$^b$</td>
<td>0.90$^{bc}$</td>
<td>0.85$^c$</td>
<td>0.01</td>
<td>&lt;0.01</td>
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<td>Rectal temperature (°C)</td>
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<td></td>
<td>41.4</td>
<td>41.4</td>
<td>41.4</td>
<td>41.4</td>
<td>0.03</td>
<td>NS</td>
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<td>Intake of low CP:ME diet (g/d)</td>
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<td></td>
<td>8$^a$</td>
<td>6$^{bc}$</td>
<td>6$^d$</td>
<td>4$^d$</td>
<td>0.3</td>
<td>&lt;0.05</td>
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<td>Intake of high CP:ME diet (g/d)</td>
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<td></td>
<td>5$^a$</td>
<td>6$^a$</td>
<td>7$^b$</td>
<td>7$^b$</td>
<td>0.3</td>
<td>&lt;0.05</td>
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<td>Total food intake (g/d)</td>
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<td>0.64$^a$</td>
<td>0.55$^b$</td>
<td>0.44$^c$</td>
<td>0.38$^c$</td>
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<td>&lt;0.01</td>
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<tr>
<td>Proportion of intake as “soya”</td>
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<tr>
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<td>0.36$^a$</td>
<td>0.45$^b$</td>
<td>0.56$^c$</td>
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<td>0.01</td>
<td>&lt;0.01</td>
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<tr>
<td>Crude protein (CP) intake (g/d)</td>
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<td>3.7</td>
<td>3.7</td>
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<tr>
<td>Energy (TME) intake (MJ/d)</td>
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<td>NS</td>
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<tr>
<td>CP intake:TME intake (g/MJ)</td>
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<tr>
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<td>17$^a$</td>
<td>19$^b$</td>
<td>23$^c$</td>
<td>25$^d$</td>
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<td>Body weight gain (g/d)</td>
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<td>Water intake (ml/d)</td>
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<td>25$^a$</td>
<td>31$^a$</td>
<td>29$^b$</td>
<td>43$^b$</td>
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