The response of laying hens to dietary amino acids

A.A. AL-SAFFAR[1,2] and S.P. ROSE[1]*

[1]National Institute of Poultry Husbandry, Harper Adams University College, Newport, Shropshire, TF10 8NB, United Kingdom, and [2]Kuwait Institute for Scientific Research, Safat, 13109, Kuwait

The level of a single essential amino acid that is either deficient or in excess of requirement may result in a diet that does not optimise the economic efficiency of a laying hen production system. The objectives of this study were, first, to quantitatively describe the effect of increasing the dietary levels of a single limiting amino acid on the egg production characteristics of laying hens by a statistical analysis and assessment of the published literature. Second, to compare three methods of describing the dietary amino acid concentration; as a proportion of the diet (g/kg of feed), as a proportion of the crude protein (g/kg crude protein) or as a proportion of the ideal crude protein (g/kg ideal crude protein). Sufficient published experiments were available to give statistically valid comparisons of lysine (42 experiments), methionine (77 experiments), methionine *plus* cystine (77 experiments) and tryptophan (21 experiments). Amino acid concentration was described by three different methods; concentration in diet (g/kg of feed), concentration in the crude protein (g/kg crude protein) or concentration in the ideal crude protein (g/kg ideal crude protein). An exponential curve gave the best fit to these data sets for almost all variables. The exceptions were egg weights with tryptophan (no relationship (p>0.05)) and egg weights and egg mass output with methionine *plus* cystine (linear relationship only). Expressing the egg production responses as a proportion of the crude protein, as compared to a proportion of the diet, gave a reduction in the residual standard deviation and increased the proportion of explained variation for all variables examined. The results indicated that expressing amino acid supply as a proportion of crude protein is preferable in laying hen nutrition.

Keywords: Lysine, tryptophan, methionine, cystine, amino acid, laying hens, egg production

Introduction

Amino acid levels in laying hen diets and the supply of an optimum dietary concentration are economically important to an egg laying enterprise. The level of a single essential amino acid that is either deficient or in excess of requirement may result in a diet that does not optimise the economic efficiency of an egg production system. There is a need to quantitatively describe the egg laying performance of hens to varying dietary levels of limiting amino acids.

*Corresponding author: e-mail: sprose@harper-adams.ac.uk

Supplementation of a very deficient diet with the limiting amino acid will give a marked increase in egg mass output of the flock. Further supplementation of the diet with this limiting amino acid will give egg mass output responses that decrease in magnitude as the amino acid requirement for individual birds with the flock is reached (Morris, 1983). Limiting amino acids have the highest per unit weight economic value of all the major nutrients supplied in a poultry feed. The poultry feedstuff industry thus needs the information that allows them to calculate the economic level of addition of the major limiting amino acids. A precise description of the response curves that describe the increasing egg mass output, egg numbers and egg weights to increasing amino acid supply is essential information for this economic evaluation.

Standard texts of nutrient requirements for laying hens (e.g. NRC 1994) express requirement as a concentration of the diet for each essential amino acid (*Table 1*). However, Morris *et al.* (1999) have recently suggested that the best method of describing amino acid requirement of growing chicken is to express as a proportion of the crude protein supply. There is a need to empirically assess which method of describing amino acid requirement gives the better explanation of reported experimental data in laying hens.

A potential problem of describing a limiting amino acid response to the proportion of dietary crude protein is that the protein supply may also be limiting in another one or more amino acids. Therefore, a proportion of this supplied crude protein may not be utilizable by the hen for protein deposition because of the deficiency in the second limiting amino acid. ARC (1980) suggested describing the protein supply as the amount of ideally balanced protein. This is the amount of protein that has an ideal balance of amino acids relative to the requirements of the animal. It is possible that describing the amino acid response of laying hens as a proportion of the ideal crude protein may be a further refinement in describing their amino acid requirements.

The objectives of this study were, first, to quantitatively describe the relationship between increasing dietary levels of single limiting amino acids and the egg production characteristics of laying hens by a statistical analysis and assessment of the published literature. Second, to compare three methods of describing the dietary amino acid concentration; as a proportion of the diet (g/kg of feed), as a proportion of the crude protein (g/kg crude protein) or as a proportion of the ideal crude protein (g/kg ideal crude protein).

Methods of selection and analysis data

A detailed literature search was conducted for all published laying hen experiments in which a single basal diet was supplemented with different levels of a single, first-limiting amino acid.

The selected experiments had to meet four main criteria:

1. The experiment must have examined the change of only a single dietary essential amino acid within an otherwise constant diet formulation.
2. The range of amino acid concentrations examined must have included the ideal balance for this limiting amino acid within the crude protein (as specified in *Table 1*).
3. One treatment group must have been at or within ± 20% of this ideal balance for the limiting amino acid.
4. The crude protein and composition of all limiting amino acids must have been given in the published paper or, if not, the ingredient composition of the diet must have been given so that the amino acid concentrations could be calculated using feed composition data from NRC (1994).

Sufficient published experiments were available to give statistically valid comparisons of lysine (42 experiments), methionine (77 experiments), methionine *plus* cystine (77 experiments) and tryptophan (21 experiments) (*Table 2*). The selected experiments spanned 50 years and included a large number of production methods and different strains of laying hens kept under varied management conditions. There were, therefore, large variations between experiments in the egg production characteristics of the laying hens, so the amino acid treatment differences were described as a proportion of the treatment group within that experiment that were given a dietary treatment with the ideal balance of that amino acid. All the variables were expressed as a proportion (%) of the egg laying performance obtained in the experiment from the treatment group fed this ideal amino acid treatment. Linear and non-linear regression analyses were conducted on these data for each of the different single amino acids using their concentrations as the explanatory variable and with egg numbers, egg weights and egg mass outputs as the dependent variables.

Amino acid concentration was described by three different methods:

1. Concentration in diet (g/kg of feed).
2. Concentration in crude protein (g/kg Crude Protein).
3. Concentration in ideal crude protein (g/kg Ideal Crude Protein). Ideal crude protein was calculated by examining the total essential amino acid composition of the basal diet. The concentration of each of the amino acids was examined. If any amino acid, apart from the single amino acid that was being tested, was deficient then the ideal crude protein concentration was changed to become less than the crude protein concentration. The percentage deficiency of this amino acid was determined and the crude protein concentration of the diet was multiplied by this factor to derive the ideal crude protein concentration. An example of this calculation is as follows: An experiment that examined different levels of tryptophan had a basal diet that contained 150 g/kg Crude Protein. Examination of the amino acid composition of the diet indicated (apart from tryptophan) that lysine (5.8 g/kg) was the next limiting amino acid in the protein. The diet supplied 5.8 g/kg of lysine (equivalent to (5.8x1000÷150= 38.7g/kg of the Crude Protein)). The ideal balance of lysine within protein is 46 (*Table 1*), therefore the deficiency of lysine was (38.7÷46=0.826). Therefore, the amount of ideal crude protein supplied was (0.826x150=123.9 g/kg).

Results

The relationships between dietary amino acid concentration expressed by the three methods, with three variables of egg laying performance are shown in *Figures 1 to 12*. The results show that increases in dietary amino acid concentration gave small increases in egg numbers, egg weights and egg mass output of the laying hens until a critical concentration was reached. A curvilinear exponential model (equation 1) gave the best fit to these data sets for all variables except egg weights with tryptophan (no significant relationship ($p>0.05$)). Positive linear responses gave the best fit to the data sets for egg weights and egg mass output with methionine *plus* cystine.

Equation 1: $$y = a + b\,(r^{x})$$

Where y = egg laying response (expressed as a percent of the laying response of birds given a diet with an ideal balance of that amino acid), x = proportion of crude limiting amino acid concentration and b and r are constants. The ideal balances used for the individual amino acids are given in *Table 1.*

Discussion

The balance of amino acids in laying hen diets is an important nutritional variable that affects the economic efficiency of an egg laying enterprise. Lysine, methionine, methionine *plus* cystine and tryptophan are the major amino acids that can be limiting in practical laying hen feeds. Knowledge of the exact shape of the response curves to changes of each of these amino acids is important in formulating practical diets that optimise the economic efficiency of a laying hen production system, especially in countries that need to import large quantities of protein concentrations.

The statistical analysis used in this study indicated that a curvilinear exponential model gave the best fit to almost all egg production variables with all four sets of limiting amino acid data (egg weight and egg mass output responses with methionine *plus* cystine were exceptions). There was no evidence of a reduction in productive output with an increase in the limiting amino acid concentration above an optimum. This contrasts with the response of broiler chickens to dietary amino acids in which there is a reduction of growth performance above an optimum and the response curve is best described by a quadratic equation (Abebe and Morris, 1990a). Broiler chickens given a very high dietary concentration of a single amino reduce their voluntary feed intakes consequently reducing growth and feed conversion efficiency, whereas laying hen do not appear to reduce feed intakes with an excess of a single dietary amino acid.

Morris (1983) compared the mathematical models that can be used to describe the response of laying hens to dietary amino acid supply. He concluded that there were deficiencies in all of these models but that an asymptotic curve gave a good fit to experiment data. Morris (1983) also suggested that the Reading Model gave an equally as good fit. *Figure 13* shows that applying the Reading Model to the present data set also gave a good fit to the data for tryptophan, lysine, methionine and methionine plus cystine. This indicated that this factorial method of estimating the responses of layers to increasing amounts of a limiting dietary amino acid gave a good representation of the published experimental data. The coefficients that gave the best fit to the data for each of the limiting amino acids that were studied are given in *Figure 13*. However, this approach of describing the data was not pursued further in this evaluation because it would not allow for a comparison of the different methods of expressing dietary amino acid concentrations.

Work from the 1960s onward has demonstrated that the limiting amino acid requirements of growing chickens are directly related to the concentration of the total dietary protein. Bornstein (1970) observed a constant lysine: crude protein requirement in chickens and Boomgaardt and Baker (1971) observed a similar response with dietary tryptophan. Nelson *et al.* (1960) observed that the maximum growth rates of chickens were obtained at a constant sulphur amino acid: total crude protein rates although this has not been supported in some other studies (Boomgaardt and Baker, 1973). The constant amino acid: crude protein relationship with growing chicken has also been confirmed in recent studies (Abebe and Morris, 1990a, b; Morris *et al.*, 1992). Morris *et al.* (1987) concluded that expressing dietary limiting amino acid supply as a proportion of the crude protein was the best practical method of describing the requirements of flocks of growing broiler chicks. Morris *et al.* (1999) re-examined these experiments with growing chicks and concluded that practical diet formulation programmes should be modified to maintain an optimum proportion of essential amino acids to the total crude protein supply.

Laying hens are expected to respond in a similar manner to growing chickens (Almquist, 1952). However, there is a lack of experimental evidence that directly examines whether expressing amino acid supply as a proportion of crude protein supply is preferable for laying hens. A major objective of the present study was to compare this method of description of amino acid supply in layers. This comparison has shown that, in all cases, expressing the dietary amino acids as a proportion of the crude protein gave a reduction in the residual standard deviation and increased the r^2 value. The present statistical analysis has thus clearly demonstrated that describing amino acid supply as a proportion of the diet protein supply (lysine, methionine, methionine *plus* cystine and tryptophan) was the preferable method of describing their dietary concentrations.

Cole (1979) and ARC (1981) proposed that, to quantify the amount of dietary protein that was available to an animal, the amount of ideal protein should be described in a feed. The ideal protein consisted of the amount of protein in which there was an ideal balance of all essential amino acids and an ideal balance of essential to non-essential amino acids. ARC (1981) discussed and proposed an ideal amino acid balance for pigs but not for poultry. No expert committee has specifically considered the ideal amino acid balance for poultry, so we used the crude protein and amino acid specifications of NRC (1994) for laying hens to derive an ideal balance.

All the experiments considered in this study examined a single basal diet formulation that was deficient in the test amino acid, and supplemented it with different levels of the test amino acid. However, the basal feed protein could also have been deficient in one or more other essential amino acids. Supplementation of the test amino acid in this type of basal feed would not be expected to give the same egg production response compared to supplementation of a basal diet that otherwise had an ideal balance of all other amino acids.

However, the statistical comparisons in this present study indicated that there was no ($p>0.05$) improvement in precision by describing the limiting amino acid supply as a proportion of the ideal crude protein concentration. It is possible that laying hen responses to an amino acid supply do not depend upon the balance of other amino acids. Alternatively, in the majority of the data sets used, the total essential amino acid balance was not determined, and so was predicted from published values (NRC 1994) for each of the feed ingredients in the basal feed. It may be that this calculation method was not precise enough to give any measurable improvement in the precision in describing the experimental data.

In conclusion, this study has shown that the egg laying responses of hens to a limiting dietary amino acid are curvilinear. The Reading Model can be used to give a good fit to these data but an asymptotic equation also gave a good fit and allowed for statistical comparisons of the methods of describing amino acid concentrations. Expressing dietary amino acid concentrations as a proportion of the crude protein supply reduced the unexplained variation in the data compared to expressing as a proportion of the diet. The study therefore supports the proposal by Morris *et al.* (1999) that in practical feed formulation, amino acid concentration is best described as a proportion of the crude protein and also gives evidence that this approach is valuable not only for growing chicken but also for laying hen diets. No improvement in precision could be demonstrated by describing the amino acid concentration as a proportion of the ideal crude protein.

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Table 1 Amino acid requirements of laying hens. Adapted from NRC (1994).

Amino Acid	Methods of expressing requirement		
	Proportion of diet	Ideal balance as proportion of lysine supply	Ideal balance as proportion of crude protein supply*
Lysine	0.69	—	46.0
Arginine	0.70	1.01	46.7
Histidine	0.17	0.25	11.3
Isoleucine	0.65	0.94	43.3
Leucine	0.82	1.19	54.7
Methionine	0.30	0.43	20.0
Methionine + Cystine	0.58	0.84	39.0
Phenylalanine	0.47	0.68	31.3
Phenylalanine + Tyrosine	0.83	1.20	55.3
Threonine	0.47	0.68	31.3
Tryptophan	0.16	0.23	10.5
Valine	0.70	1.01	46.7

* Assuming a 150 g/kg Crude Protein diet (Specified by NRC (1994))

Table 2 Sources of data used to compare the egg production, egg weight and egg mass output of laying hens fed different amino acid levels.

Reference[1]	Experimental Basal diet	Crude Protein (g/kg)	Calculated Ideal crude Protein (g/kg)	Amino Acid levels (g/kg CP) used within experiment
Lysine				
Bray (1969)#5	Maize + Soyabean meal	119.7	119.7	26.23, 27.07, 28.74, 31.24, 34.59, 38.76, 43.78, 49.62, 56.31
Chi *et al.* (1976)	Sesame meal + Maize starch	140.5	140.5	25, 32.14, 39.29, 46.43, 53.57, 60.71
Fontaine and Reyntens (1968)	Maize + Barley	132.5	132.5	45.28, 48.3, 51.32
Fontaine (1974)	Maize + Milo	119.4	115.0	37.69, 45.23, 52.76, 60.3
Gardiner and Dubetz (1978)#1a	Wheat + Soyabean meal	160.0	160.0	39.38, 58.13
Gardiner and Dubetz (1978)#1b	Wheat + Soyabean meal	160.0	160.0	27.5, 46.25
Gardiner and Dubetz (1978)#1c	Wheat + Soyabean meal	17.4	17.4	30.46, 47.7
Gruhn (1969)	Not specified	125.0	110	28, 32, 36, 40
Harms *et al.* (1995)§ #2	Maize + Soyabean meal	109.5	109.5	47.03, 49.77
Harms *et al.* (1995)§ #3	Maize + Soyabean meal	104.38	104.38	45.88, 52.2
Harms *et al.* (1995)§ #4	Maize + Soyabean meal	99.24	98.0	44.96, 54.94
Harms *et al.* (1995)§ #5	Maize + Soyabean meal	94.10	90.0	43.89, 57.92
Harms *et al.* (1995)§ #6	Maize + Soyabean meal	89.0	84.0	42.7, 61.24
Hijikuro and Horiguchi (1974)	Maize + Maize gluten meal	160.0	95.0	21.25, 36.25
Ingram *et al.* (1951)#2a	Maize + Maize gluten meal	190.0	190.0	21.05, 35.95, 65.26
Ingram *et al.* (1951)#2b	Maize + Maize gluten meal	190.0	190.0	21.05, 31.58, 38.95, 47.37, 65.26
Jensen *et al.* (1974a)	Wheat + Soyabean meal	160.6	143.0	35.62, 43.71, 48.07
Jensen *et al.* (1974b)	Maize + Soyabean meal	155.1	133.0	32.24, 38.68, 45.13, 51.58
Karunajeewa (1974) §	Wheat + Barley + Peanut meal	158.0	95.0	32.28, 34.81, 50.63
Karunajeewa and Tham (1987)#2a	Wheat + Barley	137.5	137.5	48.23, 51.24, 54.26
Karunajeewa and Tham (1987)#2b	Oats groats + Barley	132.7	132.7	46.51, 49.42, 52.33
Koelkebeck et al. (1991)	Maize + Soyabean meal	160.0	130.0	49.38, 55.63
Latshaw (1976)#1a	Maize + Maize gluten meal	140.0	140.0	32.14, 36.43, 40, 43.57
Latshaw (1976)#1b	Maize + Maize gluten meal	140.0	140.0	40.71, 44.29, 47.86, 51.43
Latshaw (1976)#2a	Maize + Maize gluten meal	140.0	140.0	32.14, 35, 37.86, 40.71
Latshaw (1976)#2b	Maize + Maize gluten meal	140.0	140.0	35, 37.86, 40.71, 43.57
McDonald (1979)#1	Wheat + Sorghum	166.0	115.0	32.53, 37.35
Nathanael *et al.* (1980)#1	Maize + Maize gluten meal	152.0	125.0	30.07, 36.64, 43.22, 49.8
Nathanael *et al.* (1980)#2	Maize + Maize gluten meal	133.0	133.0	42.86, 45.11, 47.37, 49.62, 51.88, 54.14, 56.39, 58.65

[1]Number and letter represent the experiment number within the published paper (number) and the diet series within a specific experiment (letter).

*Brown feathered-laying hens. § Broiler Breeders. NA= Sufficient data not available to calculate ideal CP.

Table 2 Continued

Reference[1]	Experimental Basal diet	Crude Protein (g/kg)	Calculated Ideal crude Protein (g/kg)	Amino Acid levels (g/kg CP) used within experiment
Pepper *et al.* (1962)#1a	Maize + Wheat + Soyabean meal	158.0	158.0	56.96, 60.13
Pepper *et al.* (1962)#1b	Maize + Wheat + Soyabean meal	142.0	142.0	51.41, 60.21
Pepper *et al.* (1962)#1c	Maize + Wheat + Soyabean meal	124.0	124.0	45.16, 65.32
Prochaska *et al.* (1996)#1	Milo + Soyabean meal	136.0	136.0	51.47, 83.09, 116.18
Prochaska *et al.* (1996)#2	Milo + Soyabean meal	151.3	151.3	47.59, 58.82, 76.01, 90.55
Schutte and Smink (1998)	Maize + Soyabean meal	164.0	143.0	39.63, 42.07, 44.51, 46.95, 49.39, 51.83, 54.27, 56.71
Summers *et al.* (1991)	Maize + Soyabean meal	100.0	85.0	38, 64
Uzu and Larbier (1985)* 1a	Maize + Soyabean meal	130.0	130.0	44.62, 50.0, 57.69
Uzu and Larbier (1985)* 1b	Maize + Soyabean meal	145.0	145.0	44.83, 51.72
Uzu and Larbier (1985)* 2a	Maize + Soyabean meal	130.0	130.0	44.62, 49.23, 52.31
Uzu and Larbier (1985)* 2b	Maize + Soyabean meal	145.0	145.0	44.83, 47.24, 49.66
Uzu and Larbier (1985)* 2c	Maize + Soyabean meal	160	160	44.38, 46.88
Van Weerden and Schutte (1980)	Maize + Soyabean meal	135.0	135.0	47.41, 51.11, 54.81, 62.22
Methionine				
Bertram *et al.*(1995a)#1	Maize + Tapioca + Soyabean meal	148.0	131.0	16.89, 20.27, 23.65, 27.03, 30.41
Bertram *et al.*(1995a)#2	Maize + Tapioca + Soyabean meal	151.0	128.0	16.56, 19.87, 23.18, 26.49, 29.80
Bertram *et al.*(1995b)*	Maize + Tapioca + Soyabean meal	156.0	126.0	14.74, 17.31, 19.87, 22.44, 25.0, 27.56
Bray (1965)#1a	Maize Starch + Soyabean meal	70.0	70.0	11, 16, 21, 26, 31, 36
Bray (1965)#1b	Maize Starch + Soyabean meal	100.0	100.0	11, 16, 21, 26, 31, 36
Bray (1965)#3	Maize Starch + Soyabean meal	120.0	120.0	11.83, 14.75, 17.67, 20.58, 23.5, 26.42, 29.33
Bray (1965)#4	Maize Starch + Soyabean meal	120.0	120.0	13.08, 13.92, 14.75, 15.58, 17.25, 19.75, 23.08, 27.25
Calderon and Jensen (1990)#1a	Maize + Soyabean meal	130.0	130.0	19.62, 20.0, 20.38, 20.77
Calderon and Jensen (1990)#1b	Maize + Soyabean meal	160.0	145.0	15.94, 16.25, 16.56, 16.88
Calderon and Jensen (1990)#2a	Maize + Soyabean meal	130.0	130.0	19.62, 21.54, 23.46, 25.38, 27.31, 29.23
Calderon and Jensen (1990)#2b	Maize + Soyabean meal	160.0	149.0	15.94, 17.50, 19.06, 20.63, 22.19, 23.75
Calderon and Jensen (1990)#2c	Maize + Soyabean meal	190.0	167.0	13.42, 14.74, 16.05, 17.37, 18.68, 20.0
Campbell *et al.*(1980)#1a	Barley + Fababean + Soyabean meal	160.0	118.0	17.05, 20.0, 22.5
Campbell *et al.*(1980)#1b	Barley + Fababean + Soyabean meal	160.0	118.0	19.38, 30.0, 36.25
Cave and De Grote (1990)#1a	Maize + Soyabean meal	135.0	135.0	18.44, 20.67, 22.89, 25.11, 27.33, 29.56
Cave and De Grote (1990)#1b	Maize + Soyabean meal	155.0	155.0	16.06, 18.0, 19.94, 21.87, 23.81, 25.74
Daenner and Bessei (2000)	Maize + Barley + Soyabean meal	150.0	126.0	14.67, 17.33, 20.67, 24.0
Daghir *et al.*(1964)§	Maize + Soyabean meal	155.4	136.0	18.02, 21.24, 24.45, 27.67
Elwinger and Wahlstrom (2000)	Maize + Barley + Soyabean meal	159.0	159.0	19.50, 27.04
Fontaine (1974)	Maize + Milo	119.4	98.0	20.94, 25.13, 29.31, 33.5
Harms *et al.* (1998)#1a	Maize + Soyabean meal	127.0	127.0	19.69, 21.65, 23.62
Harms *et al.* (1998)#1b	Maize + Soyabean meal	150.0	133.0	16.67, 18.33, 20.0
Harms *et al.* (1999)	Maize + Soyabean meal	170.0	154.0	17, 18.59, 20.18, 21.76, 23.29, 24.82
Heywang (1956)#1	Maize + Soyabean meal	169.0	169.0	15.98, 18.32, 21.01
Heywang (1956)#2a	Maize + Soyabean meal	155.0	155.0	17.42, 20.65, 22.26
Heywang (1956)#2b	Maize + Soyabean meal + Fish meal	155.0	155.0	18.71, 20.32, 21.94

Table 2 Continued

Reference[1]	Experimental Basal diet	Crude Protein (g/kg)	Calculated Ideal crude Protein (g/kg)	Amino Acid levels (g/kg CP) used within experiment
Hsu *et al.* (1998)	Maize + Soyabean meal	140.3	135.0	16.89, 26.73
Jackson *et al.* (1987)	Maize + Soyabean meal	122.0	122.0	19.10, 21.56, 24.02, 26.48, 28.93, 31.39
Jensen *et al.* (1974b)#1a	Maize + Soyabean meal	160.0	160.0	17.5, 20.0, 22.5, 25.0
Jensen *et al.* (1974b)#1b	Maize + Peas	160.0	129.0	15.5, 18.0, 20.5, 23.0, 25.5, 28.0
Jensen *et al.* (1974b)#2	Maize + Soyabean meal	140.0	140.0	17.79, 20.64
Karunajeewa (1974) §	Wheat + Barley + Peanut meal	158.0	100.0	12.03, 15.19, 24.05
Kim and McGinnis (1972)	Maize + Wheat + Soyabean meal	135.0	90.0	12.59, 16.30, 20.0, 23.7, 27.41
Koelkebeck *et al.* (1991)	Maize + Soyabean meal	160.0	141.0	16.25, 22.5
Latshaw (1974)	Maize + Soyabean meal	148.0	131.0	16.89, 30.41
Leong and McGinnis (1952)	Maize + Peas	152.0	136.0	11.84, 14.47, 15.79, 18.42
McDonald (1979)#1	Wheat + Sorghum	166.0	117.0	13.86, 19.88
Mueller (1967)	Maize + Soyabean meal	164.0	144.0	17.68, 35.98
Muller and Balloun (1974)#1a	Maize + Soyabean meal	120.0	95.0	17.50, 25.83
Muller and Balloun (1974)#1b	Maize + Soyabean meal	140.0	110.0	16.43, 20.0
Muller and Balloun (1974)#1c	Maize + Soyabean meal	160.0	123.0	16.25, 19.38
Muller and Balloun (1974)#2	Maize + Soyabean meal	160.0	123.0	16.25, 19.38
Muller and Balloun (1974)#3a	Maize + Soyabean meal	120.0	77.0	16.67, 20.83, 25.0
Muller and Balloun (1974)#3b	Maize + Soyabean meal	160.0	108.0	15.63, 18.75, 21.88
Muller and Balloun (1974)#4a	Maize + Soyabean meal	135.0	92.0	14.81, 18.52, 22.22
Muller and Balloun (1974)#4b	Maize + Soyabean meal	155.0	100.0	14.84, 18.06, 21.29
Parsons and Leeper (1984)#1a	Maize + Soyabean meal	140.0	140.0	18.57, 25.71
Parsons and Leeper (1984)#1b	Maize + Soyabean meal	160.0	136.0	16.25, 22.50
Pepper *et al.* (1962)#1a	Maize + Wheat + Soyabean meal	158.0	158.0	22.78, 25.95
Pepper *et al.* (1962)#1b	Maize + Wheat + Soyabean meal	142.0	142.0	22.54, 24.65
Pepper *et al.* (1962)#1c	Maize + Wheat + Soyabean meal	124.0	124.0	22.58, 27.42
Petersen *et al.* (1983)	Maize + Milo + Soyabean meal	170.0	170.0	15.0, 15.88, 16.76, 17.65
Pourreza and Smith (1988)*†	Wheat + Soyabean meal	165.0	138.0	15.76, 17.58, 19.39, 21.21, 23.03
Reid and Weber (1974)#1a	Milo + Soyabean meal	140.0	116.0	14.29, 17.86, 19.29, 21.43
Reid and Weber (1974)#1b	Milo + Soyabean meal	162.0	128.0	14.81, 18.52
Roberson and Trujillo (1975)	Maize + Milo + Soyabean meal	160.0	126.0	15.63, 20.0
Salman and McGinnis (1968)	Maize + Soyabean meal	170.0	126.0	14.12, 20.0, 25.88, 31.18, 37.65, 43.53
Schutte and Van Weerden (1978)#1	Maize + Soyabean meal	135.0	128.0	16.67, 20.45, 24.24, 28.03
Schutte *et al.* (1983)#1a	Maize + Soyabean meal	141.0	141.0	23.4, 26.95, 39.72
Schutte *et al.* (1983)#1b	Maize + Soyabean meal	142.0	128.0	19.72, 23.24, 24.65
Schutte *et al.* (1984)	Maize + Soyabean meal	138.0	128.0	16.67, 20.29, 23.91, 27.54, 31.16
Schutte *et al.* (1994)#1	Maize + Soyabean meal	145.0	123.0	15.86, 19.31, 20.69, 22.41, 24.48, 27.24
Schutte *et al.* (1994)#2	Maize + Soyabean meal	154.0	131.0	22.08, 25.32, 28.57, 31.82
Scott *et al.*(1975)	Milo + Soyabean meal	120.0	103.0	16.67, 23.33
Shafer *et al.*(1996)#1	Maize + Soyabean meal	147.5	138.0	18.98, 29.15
Shafer *et al.*(1996)#2	Maize + Soyabean meal	147.0	147.0	21.09, 23.13, 24.49, 26.53
Shafer *et al.*(1998)	Maize + Soyabean meal	165.0	144.0	23.03, 27.88, 32.12
Slinger *et al.*(1972)#1a	Wheat + Soyabean meal	122.0	97.0	15.57, 20.74
Slinger *et al.*(1972)#1b	Wheat + Soyabean meal	138.0	108.0	15.22, 19.78
Slinger *et al.*(1972)#1c	Wheat + Soyabean meal	153.0	118.0	15.03, 19.15
Slinger *et al.*(1972)#1d	Wheat + Soyabean meal	168.0	128.0	14.88, 18.63
Slinger *et al.*(1972)#1e	Wheat + Maize + Soyabean meal	135.0	108.0	17.04, 21.70
Slinger *et al.*(1972)#1f	Wheat + Blood meal	135.0	105.0	14.81, 24.07
Speers and Chi (1974)	Maize + Soyabean meal	130.0	NA	17.69, 21.54, 25.38
Summers *et al.*(1991)	Maize + Soyabean meal	100.0	83.0	20.0, 52.0
Waldroup and Hellwing (1995)	Maize + Soyabean meal	122.0	110.0	19.1, 21.56, 24.02, 26.48, 28.93, 31.39
Yamazaki and Takemasa (1998)	Maize + Milo	155.0	155.0	19.35, 25.81

Table 2 Continued

Reference[1]	Experimental Basal diet	Crude Protein (g/kg)	Calculated Ideal crude Protein (g/kg)	Amino Acid levels (g/kg CP) used within experiment
Methionine + Cystine				
Bertram *et al.*(1995a)#1	Maize + Tapioca + Soyabean meal	156.0	115.0	32.05, 34.62, 37.18, 39.74, 42.31
Bertram *et al.*(1995a)#2	Maize + Tapioca + Soyabean meal	148.0	125.0	33.78, 37.16, 40.54, 37.16, 40.54, 43.92
Bertram *et al.*(1995b)*	Maize + Wheat + Soyabean meal	151.0	125.0	33.11, 36.42, 39.74, 43.05, 46.36
Bray (1965)#1a	Maize Starch + Soyabean meal	70.0	70.0	19.0, 26.14, 33.14, 35.43, 41.5
Bray (1965)#1b	Maize Starch + Soyabean meal	100.0	100.0	18.5, 28.7, 34.3, 41.6, 46.4, 51.8
Bray (1965)#3	Maize Starch + Soyabean meal	120.0	120.0	25.0, 33.5, 36.17, 38.42, 41.58, 46.33, 47.17
Bray (1965)#4	Maize Starch + Soyabean meal	120.0	120.0	23.5, 25.0, 26.08, 26.83, 30.33, 34.17, 37.58, 43.0
Calderon and Jensen (1990)#1a	Maize + Soyabean meal	130.0	130.0	39.23, 43.08, 46.92, 50.77
Calderon and Jensen (1990)#1b	Maize + Soyabean meal	160.0	145.0	31.88, 35.0, 38.13, 41.25, 41.25
Calderon and Jensen (1990)#2a	Maize + Soyabean meal	190.0	163.0	26.84, 29.47, 32.11, 34.47
Calderon and Jensen (1990)#2b	Maize + Soyabean meal	130.0	130.0	39.23, 41.15, 43.08, 45.0 46.92, 48.85
Calderon and Jensen (1990)#2c	Maize + Soyabean meal	160.0	145.0	31.88, 33.44, 35.0, 36.56, 38.13, 39.69
Calderon and Jensen (1990)#2c	Maize + Soyabean meal	190.0	163.0	26.84, 28.16, 29.47, 30.79, 32.11, 33.42
Campbell *et al.*(1980)#1a	Barley + Fababean + Soyabean meal	160.0	140.0	28.75, 31.25, 33.75
Campbell *et al.*(1980)#1b	Barley + Fababean + Soyabean meal	160.0	140.0	28.75, 39.38, 45.63
Cave and De Grote (1990)#1a	Maize + Soyabean meal	135.0	125.0	37.78, 40.0, 42.22, 44.44, 46.67, 48.89
Cave and De Grote (1990)#1b	Maize + Soyabean meal	155.0	125.0	32.90, 34.84, 36.77, 38.71, 40.65, 42.58
Daenner and Bessei (2000)	Maize + Barley + Soybean meal	150.0	126.0	32.67, 35.33, 38.67, 42.0
Daghir *et al.*(1964)§	Maize + Soyabean meal	155.4	140.0	34.11, 37.42, 40.54, 43.76
Elwinger and Wahlstrom (2000)	Wheat + Barley + Soyabean meal	159.0	159.0	37.74, 45.9
Fontaine (1974)	Maize + Milo	119.4	98.0	37.69, 41.88, 46.06, 50.25
Harms *et al.* (1998)#1a	Maize + Soyabean meal	127.0	127.0	39.37, 41.34, 43.31
Harms *et al.* (1998)#1b	Maize + Soyabean meal	150.0	150.0	33.33, 35.0, 36.67
Harms *et al.* (1999)	Maize + Soyabean meal	170.0	170.0	34.71, 36.29, 39.47, 41.06, 42.65
Heywang (1956)#1	Maize + Soyabean meal	169.0	169.0	33.14, 35.5, 38.17
Hsu *et al.* (1998)	Maize + Soyabean meal	140.3	135.0	34.14, 43.98
Jackson *et al.*(1987)	Maize + Soyabean meal	122.0	122.0	35.49, 37.95, 40.41, 42.87, 45.33, 47.79
Jensen *et al.* (1974b)#1a	Maize + Soyabean meal	160.0	140.0	38.13, 40.63, 43.13, 45.63
Jensen *et al.* (1974b)#1b	Maize + Peas	160.0	124.0	31.38, 33.88, 36.38, 38.88, 40.13, 42.63
Jensen *et al.* (1974b)#2	Maize + Soyabean meal	140.0	123.0	37.64, 40.5
Karunajeewa (1974) §	Wheat + Barley + Peanut meal	158.0	95.0	24.68, 27.85, 36.71
Kim and McGinnis (1972)	Maize + Wheat + Soyabean meal	138.0	85.0	25.93, 29.63, 33.33, 37.04, 40.74
Koelkebeck *et al.* (1991)	Maize + Soyabean meal	160.0	130.0	34.38, 40.63
Latshaw (1974)	Maize + Soyabean meal	148.0	125.0	34.46, 47.97
Leong and McGinnis (1952)	Maize + Peas	152.0	140.0	34.87, 36.18, 37.5, 38.82
McDonald (1979)#1	Wheat + Sorghum	166.0	115.0	30.12, 36.14
Mueller (1967)	Maize + Soyabean meal	165.0	145.0	34.15, 58.54
Muller and Balloun (1974)#1a	Maize + Soyabean meal	120.0	105.0	30.83, 35.0
Muller and Balloun (1974)#1b	Maize + Soyabean meal	140.0	115.0	30.71, 34.29
Muller and Balloun (1974)#1c	Maize + Soyabean meal	160.0	130.0	30.0, 33.13
Muller and Balloun (1974)#3a	Maize + Soyabean meal	120.0	100.0	25.0, 29.17, 33.33
Muller and Balloun (1974)#3b	Maize + Soyabean meal	160.0	125.0	26.25, 29.38, 32.5
Muller and Balloun (1974)#4a	Maize + Soyabean meal	135.0	100.0	34.07, 37.78, 41.48
Muller and Balloun (1974)#4b	Maize + Soyabean meal	155.0	115.0	33.55, 36.77, 40.0
Parsons and Leeper (1984)#1a	Maize + Soyabean meal	140.0	130.0	37.86, 45.0
Parsons and Leeper (1984)#1b	Maize + Soyabean meal	160.0	130.0	33.13, 39.38

Table 2 Continued

Reference[1]	Experimental Basal diet	Crude Protein (g/kg)	Calculated Ideal crude Protein (g/kg)	Amino Acid levels (g/kg CP) used within experiment
Pepper *et al.* (1962)#1a	Maize + Wheat + Soyabean meal	158.0	158.0	39.24, 42.41
Pepper *et al.* (1962)#1b	Maize + Wheat + Soyabean meal	142.0	142.0	43.66, 47.18
Pepper *et al.* (1962)#1c	Maize + Wheat + Soyabean meal	124.0	124.0	52.7, 49.4
Petersen *et al.* (1983)	Maize + Milo + Soyabean meal	170.0	170.0	30.59, 31.47, 32.35, 33.24
Pourreza and Smith (1988)*	Wheat + Soyabean meal	165.0	123.0	33.33, 35.76, 37.58, 39.39, 41.21
Reid and Weber (1974)#1a	Milo + Soyabean meal	140.0	100.0	32.14, 35.71, 39.29, 42.86
Reid and Weber (1974)#1b	Milo + Soyabean meal	162.0	120.0	27.78, 30.86,
Roberson and Trujillo (1975)	Maize + Milo + Soyabean meal	160.0	125.0	32.14, 35.71, 39.29, 42.86
Salman and McGinnis (1968)	Maize + Soyabean meal	170.0	120.0	29.41, 35.29, 41.18, 47.06, 52.94, 58.82
Schutte and VanWeerden (1978)#1	Maize + Soyabean meal	165.0	135.0	36.36, 39.39
Schutte *et al.* (1983)#1a	Maize + Soyabean meal	141.0	115.0	35.46, 39.0, 51.77
Schutte *et al.* (1983)#1b	Maize + Soyabean meal	142.0	115.0	33.21, 38.73, 40.14
Schutte *et al.* (1984)	Maize + Soyabean meal	138.0	115.0	36.23, 39.86, 43.48, 47.1, 50.72
Schutte *et al.* (1994)#1	Maize + Soyabean meal	145.0	115.0	33.1, 36.55, 37.93, 39.66, 41.38, 68.97
Schutte *et al.* (1994)#2	Maize + Soyabean meal	154.0	120.0	32.9, 36.13, 39.35, 42.58
Scott *et al.*(1975)	Milo + Soyabean meal	120.0	100.0	33.33, 40.0
Shafer *et al.*(1996)#1	Maize + Soyabean meal	147.5	147.5	36.61, 46.78
Shafer *et al.*(1996)#2	Maize + Soyabean meal	147.0	147.0	40.82, 42.86
Shafer *et al.*(1998)	Maize + Soyabean meal	165.0	135.0	43.52, 49.39, 51.45
Slinger *et al.*(1972)#1a	Wheat + Soyabean meal	122.0	95.0	31.15, 36.31
Slinger *et al.*(1972)#1b	Wheat + Soyabean meal	138.0	105.0	30.43, 35.0
Slinger *et al.*(1972)#1c	Wheat + Soyabean meal	153.0	115.0	30.07, 34.18
Slinger *et al.*(1972)#1d	Wheat + Soyabean meal	168.0	125.0	29.76, 33.51
Slinger *et al.*(1972)#1e	Wheat + Maize + Soyabean meal	135.0	115.0	31.11, 35.78
Slinger *et al.*(1972)#1f	Wheat + Blood meal	135.0	100.0	30.37, 39.63
Speers and Chi (1974)	Maize + Soyabean meal	130.0	NA	43.08, 46.92, 50.77
Summers *et al.*(1991)	Maize + Soyabean meal	100.0	83.0	33.0, 65.0
Vogt and Krieg (1983)	Maize + Soyabean meal	145.0	145.0	41.38, 44.14, 46.9, 49.66, 52.41, 55.17, 47.93
Waldroup and Hellwing (1995)	Maize + Soyabean meal	122.0	115.0	35.25, 37.7, 40.16, 42.62, 45.08
Yamazaki and Takemasa (1998)	Maize + Milo	155.0	155.0	38.71, 45.16
Tryptophan				
Al-saffar and Rose (2000)*	Maize + Maize gluten meal	170.0	161.0	6.3, 6.3, 10.5, 15, 20.0
Bray (1969)#6	Maize + Soyabean meal	119.7	119.7	6.27, 6.52, 7.02, 7.94, 9.27, 11.1 11.2, 13.7, 16.96, 20.97, 25.7
Ingram *et al.* (1951)#2a	Maize + Maize gluten meal	190.0	190.0	6.32, 14.74, 22.11, 30
Ingram *et al.* (1951)#2b	Maize + Maize gluten meal	190.0	190.0	6.32, 8.95, 11.58, 16.84, 22.11
Ishibashi (1985)#1	Maize + Fish meal	151.0	151.0	6.16, 8.28, 11.13, 16.16, 21.19
Ishibashi (1985)#2	Maize + Fish meal	154.0	154.0	7.27, 8.18, 9.16, 10.13, 11.10
Ishibashi (1985)#3	Maize + Fish meal	154.0	154.0	5.66, 6.58, 7.5, 8.42, 10.26
Ishibashi (1985)#4	Maize + Fish meal	152.0	152.0	7.37, 9.28, 11.25, 13.16, 15.13
Jensen *et al.* (1990)#1	Maize + Soyabean meal	145.0	145.0	9.31, 11.03, 12.76, 14.48
Jensen *et al.* (1990)#3a	Maize + Soyabean meal	140.0	140.0	9.29, 10.71, 12.14, 13.57, 15
Jensen *et al.* (1990)#3b	Maize + Soyabean meal	160.0	160.0	10, 11.25, 12.5, 13.75, 15
Jensen *et al.* (1990)#3c	Maize + Soyabean meal	180.0	162.0	10.56, 11.67, 12.78, 13.89, 15
Jensen *et al.* (1990)#4a	Maize + Soyabean meal	140.0	140.0	7.86, 9.29, 10.71, 12.14, 13.57
Jensen *et al.* (1990)#4b	Maize + Soyabean meal	160.0	160.0	8.13, 9.38, 10.63, 11.88, 13.13
Jensen *et al.* (1990)#4c	Maize + Soyabean meal	180.0	180.0	8.33, 9.44, 10.56, 11.67, 12.78
Koelkebeck *et al.* (1991)#3	Maize + Soyabean meal	160.0	130.0	11.25, 17.5
Morris and Wethli (1978)	Maize + Maize gluten meal	279.0	241.0	8.4, 9.6, 10.8, 12, 14.4, 16.8
Ohtani *et al.* (1989)	Maize + Soyabean meal	152.4	139.0	9.84, 11.48, 13.12
Russell and Harms (1999)	Maize + Soyabean meal	131.9	131.9	8.34, 9.86, 11.37, 12.89, 14.4, 15.92, 17.44
Tasaki (1983)	Maize + Soyabean meal	160.0	128.0	4.13, 6.06, 8.0, 13.81, 45.06
Wethli and Morris (1978)	Maize + Maize gluten meal	155.0	NA	8.4, 10.2, 12, 13.8, 15.6, 17.4, 19.2

Figure 1 Relationship between dietary variation in tryptophan concentration and the numbers of eggs laid by hens. Eligible data for all published experiments are included and egg numbers are expressed as a percentage of the treatment group with the experiment that was given 10.5 g/kg of tryptophan within the crude or ideal crude protein. Three methods of describing the tryptophan supply are compared.

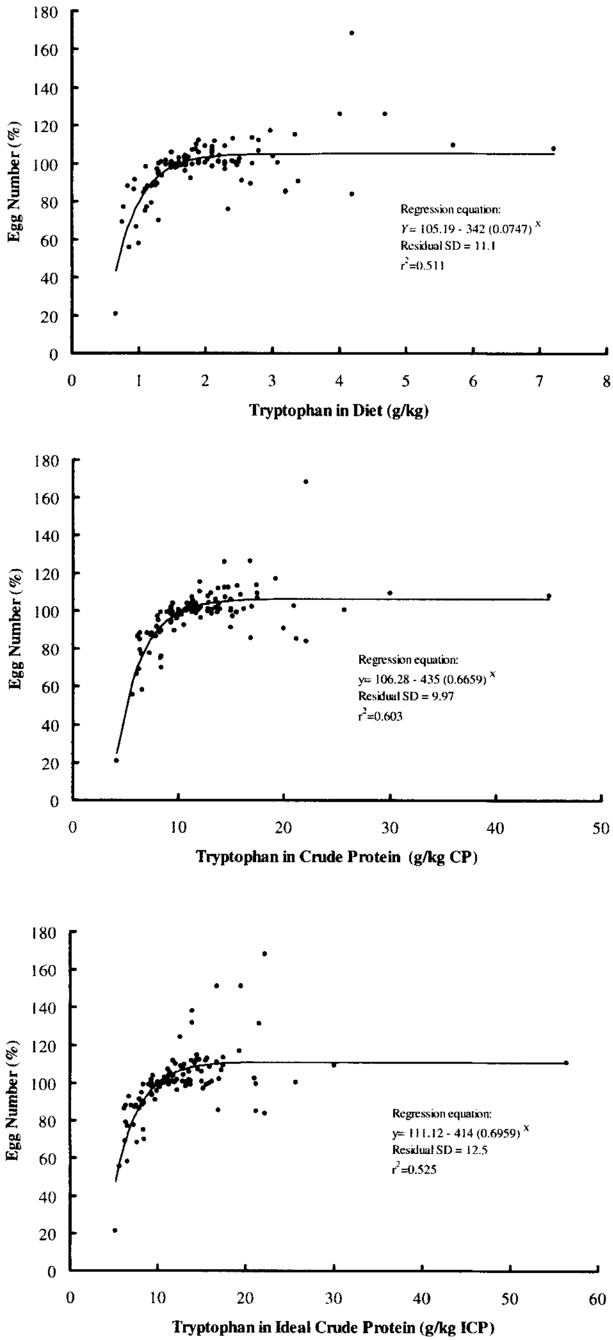

Figure 2 Relationship between dietary variation in tryptophan concentration and the mean weights of eggs laid by hens. Eligible data for all published experiments are included and mean egg weights are expressed as a percentage of the treatment group with the experiment that was given 10.5 g/kg of tryptophan within the crude or ideal crude protein. Three methods of describing the tryptophan supply are compared.

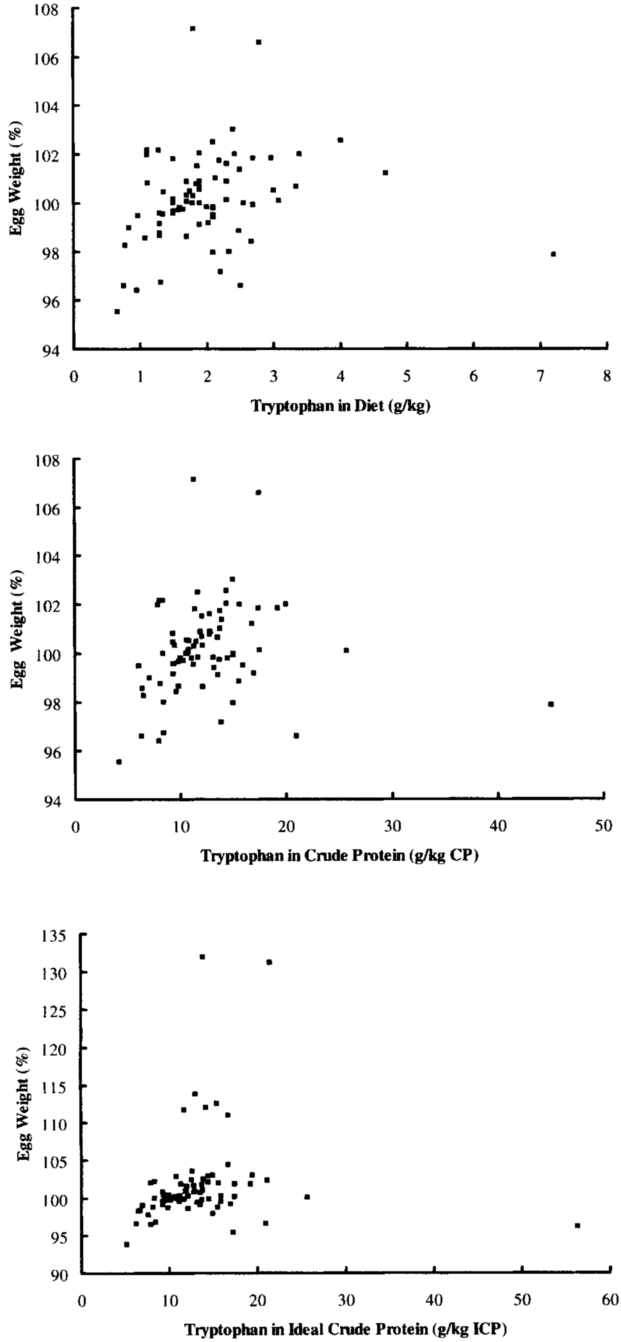

Figure 3 Relationship between dietary variation in tryptophan concentration and the mass outputs of eggs laid by hens. Eligible data for all published experiments are included and egg mass outputs are expressed as a percentage of the treatment group with the experiment that was given 10.5 g/kg of tryptophan within the crude or ideal crude protein. Three methods of describing the tryptophan supply are compared.

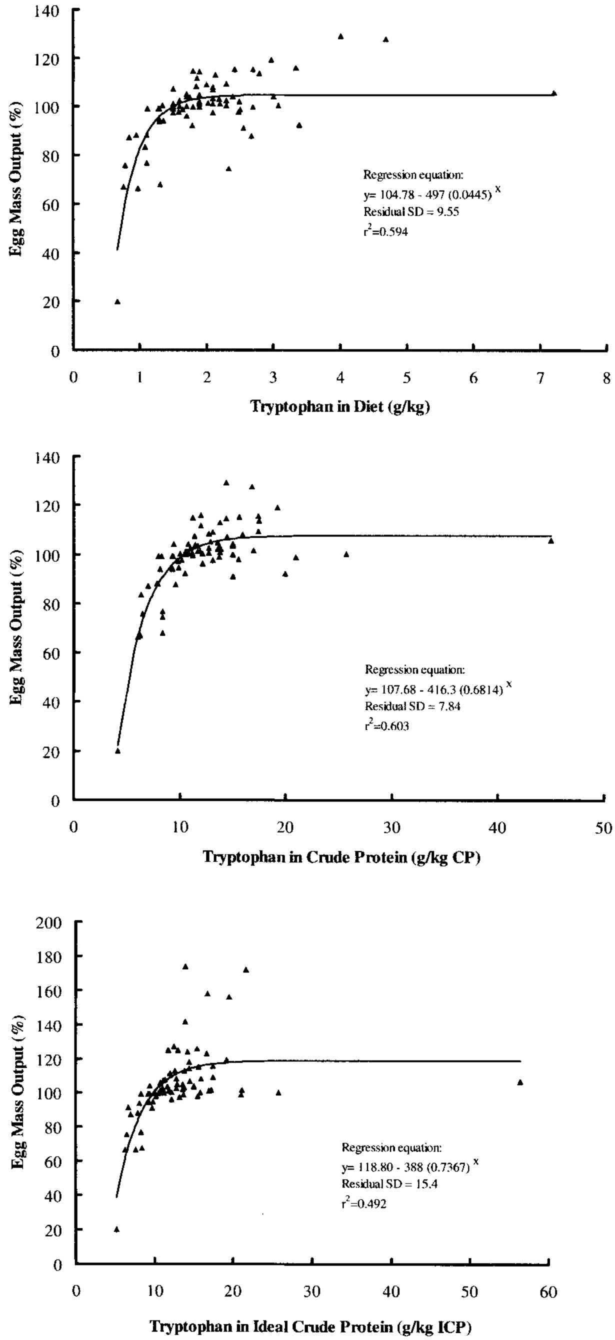

Figure 4 Relationship between dietary variation in lysine concentration and the numbers of eggs laid by hens. Eligible data for all published experiments are included and egg numbers are expressed as a percentage of the treatment group with the experiment that was given 46 g/kg of lysine within the crude or ideal crude protein. Three methods of describing the lysine supply are compared.

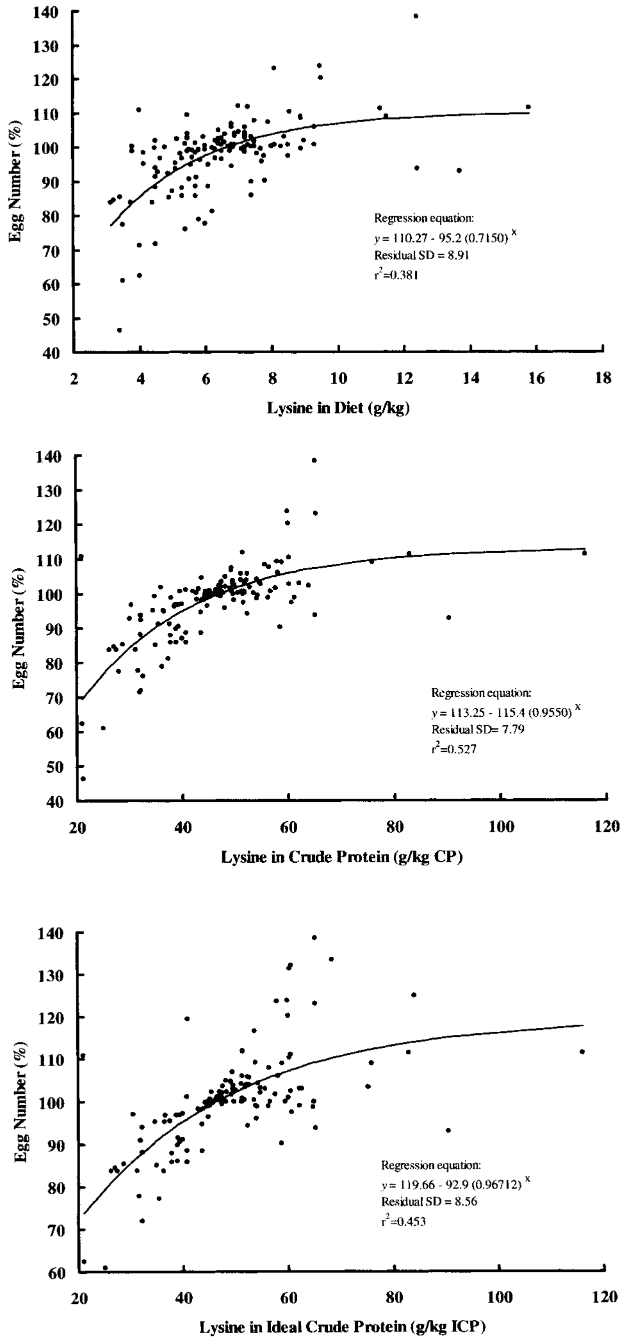

Figure 5 Relationship between dietary variation in lysine concentration and the mean weights of eggs laid by hens. Eligible data for all published experiments are included and mean egg weights are expressed as a percentage of the treatment group with the experiment that was given 46 g/kg of lysine within the crude or ideal crude protein. Three methods of describing the lysine supply are compared.

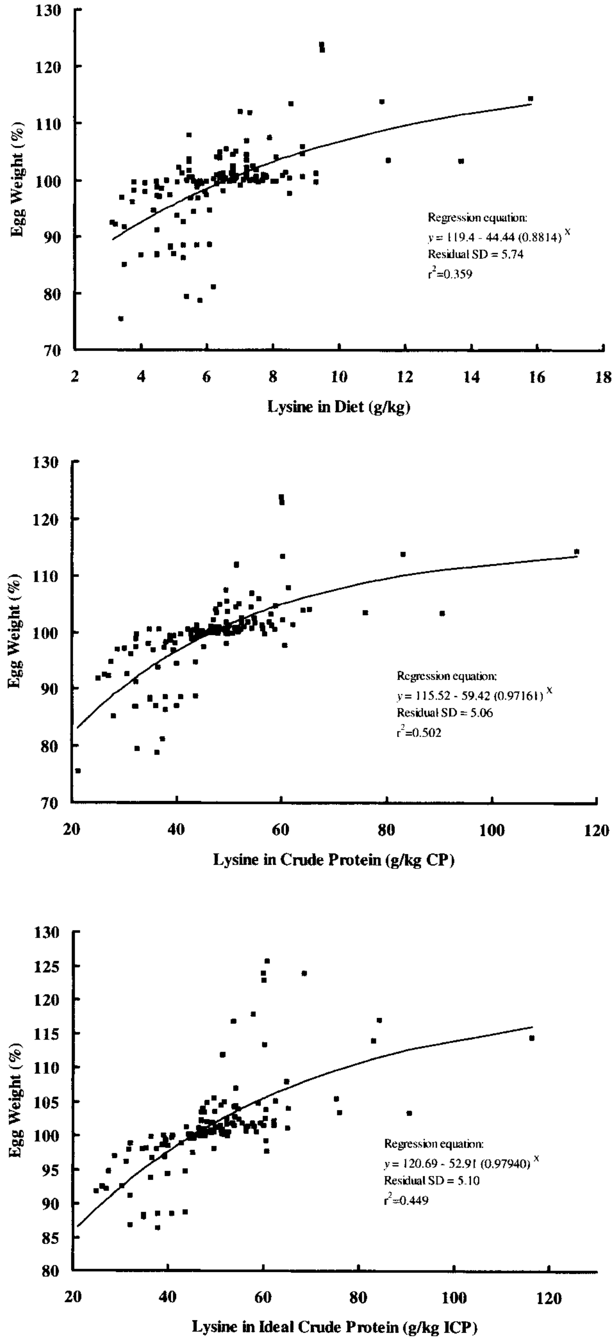

Figure 6 Relationship between dietary variation in lysine concentration and the mass outputs of eggs laid by hens. Eligible data for all published experiments are included and egg mass outputs are expressed as a percentage of the treatment group with the experiment that was given 46 g/kg of lysine within the crude or ideal crude protein. Three methods of describing the lysine supply are compared.

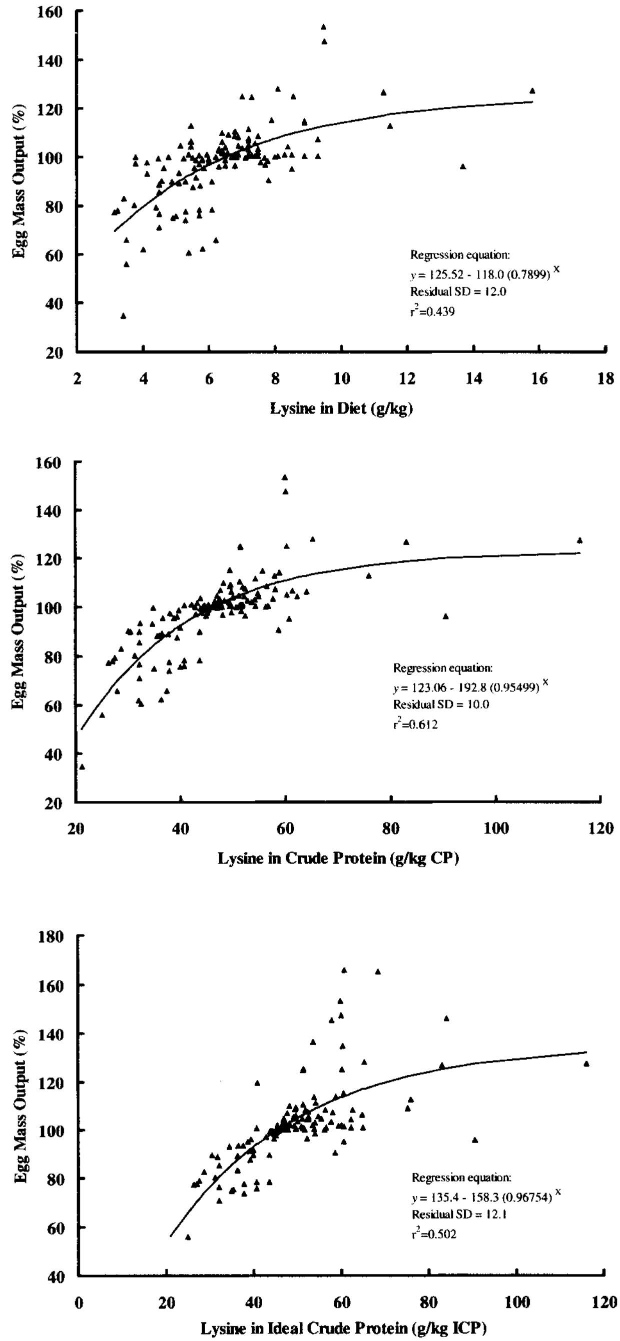

Figure 7 Relationship between dietary variation in methionine concentration and the numbers of eggs laid by hens. Eligible data for all published experiments are included and egg numbers are expressed as a percentage of the treatment group with the experiment that was given 20 g/kg of methionine within the crude or ideal crude protein. Three methods of describing the methionine supply are compared.

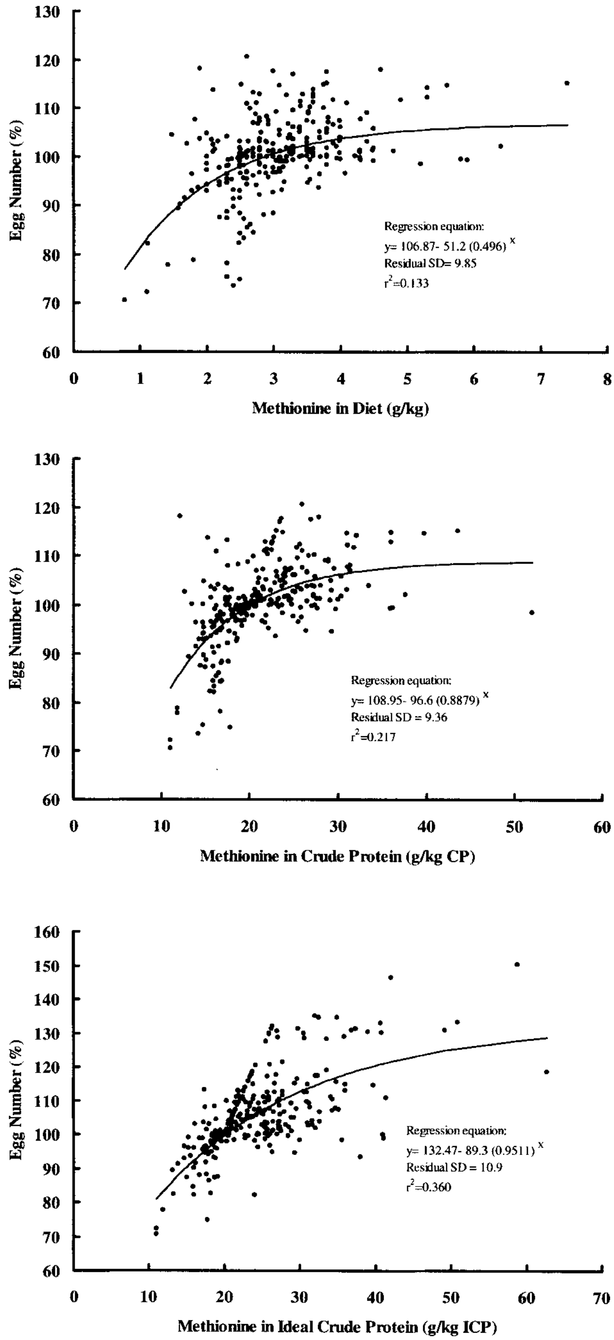

Figure 8 Relationship between dietary variation in methionine concentration and the mean weights of eggs laid by hens. Eligible data for all published experiments are included and mean egg weights are expressed as a percentage of the treatment group with the experiment that was given 20 g/kg of methionine within the crude or ideal crude protein. Three methods of describing the methionine supply are compared.

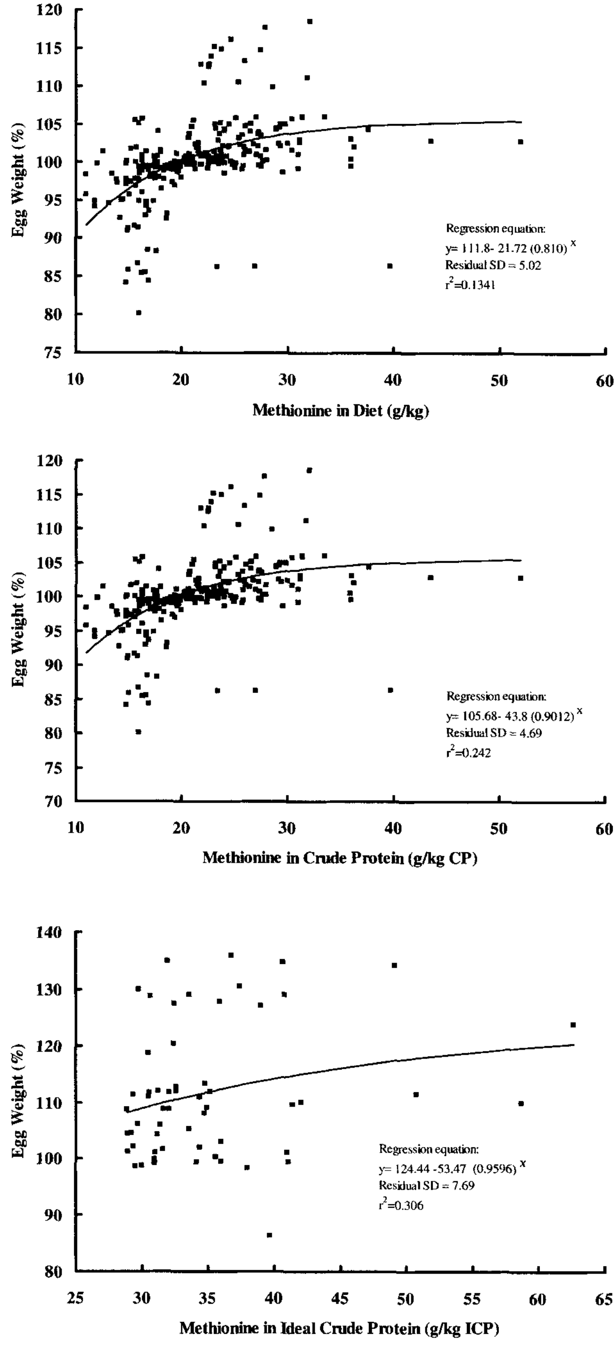

Figure 9 Relationship between dietary variation in methionine concentration and the mass outputs of eggs laid by hens. Eligible data for all published experiments are included and egg mass outputs are expressed as a percentage of the treatment group with the experiment that was given 20 g/kg of methionine within the crude or ideal crude protein. Three methods of describing the methionine supply are compared.

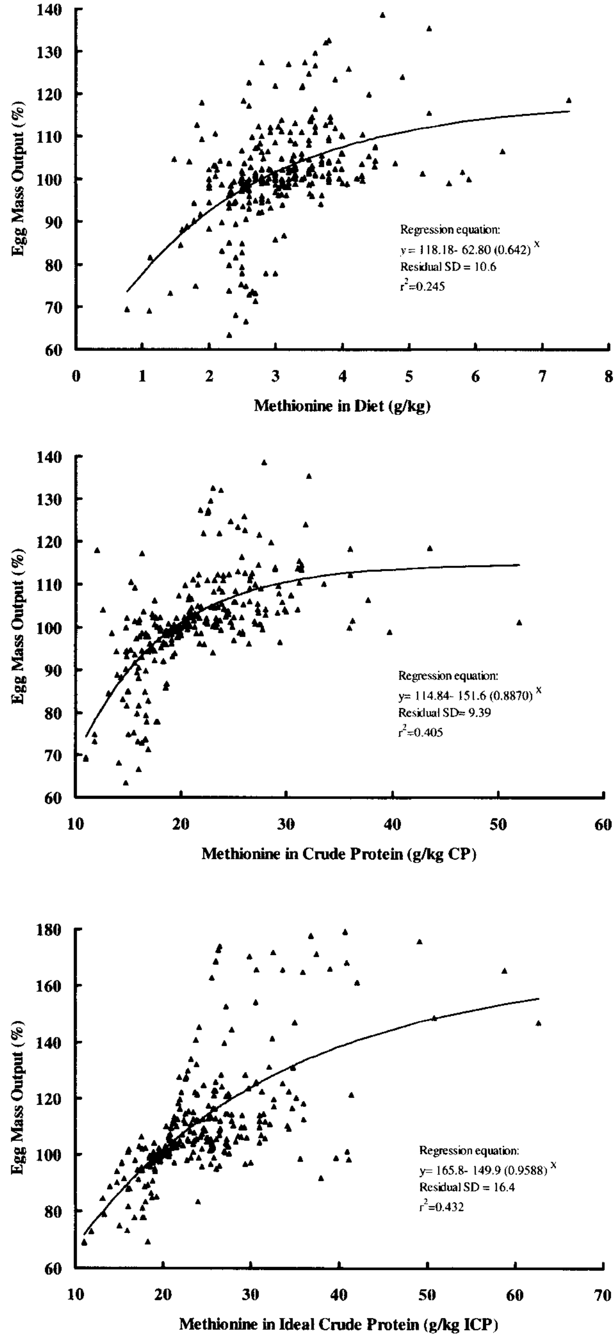

Figure 10 Relationship between dietary variation in methionine + cystine concentration and the numbers of eggs laid by hens. Eligible data for all published experiments are included and egg numbers are expressed as a percentage of the treatment group with the experiment that was given 39 g/kg of methionine + cystine within the crude or ideal crude protein. Three methods of describing the methionine + cystine supply are compared.

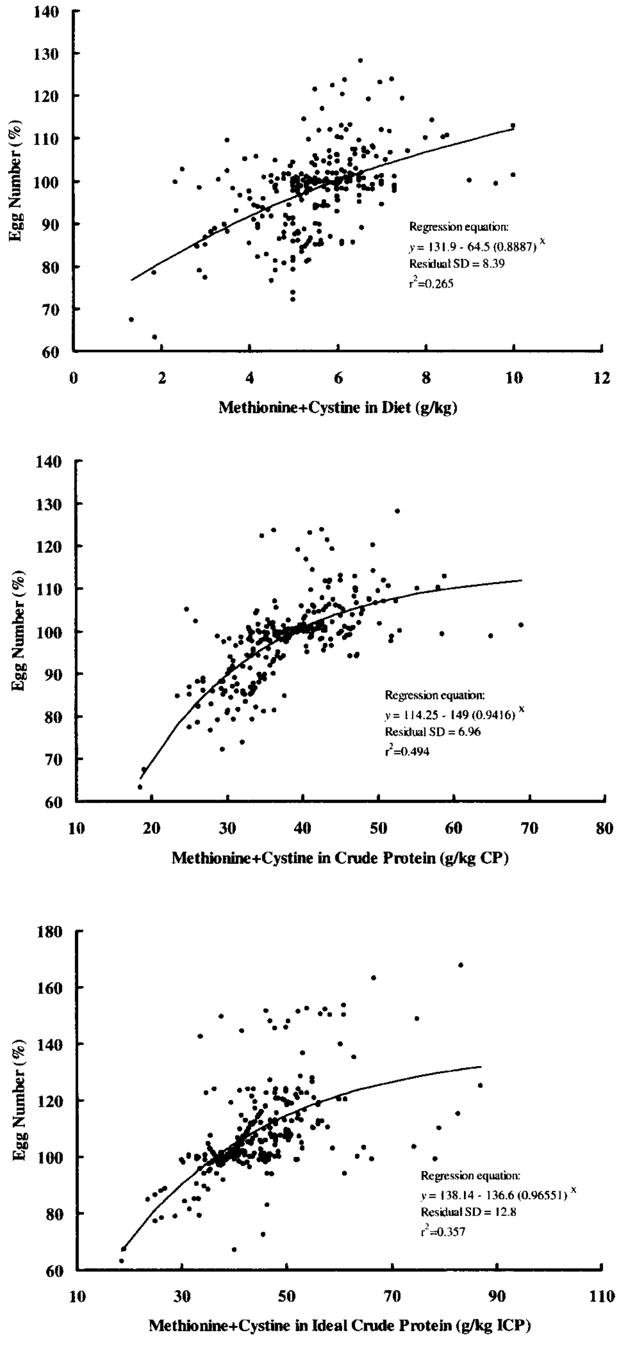

Figure 11 Relationship between dietary variation in methionine + cystine concentration and the ı weights of eggs laid by hens. Eligible data for all published experiments are included and meaı weights are expressed as a percentage of the treatment group with the experiment that was given 39 of methionine + cystine within the crude or ideal crude protein. Three methods of describiŋ methionine + cystine supply are compared.

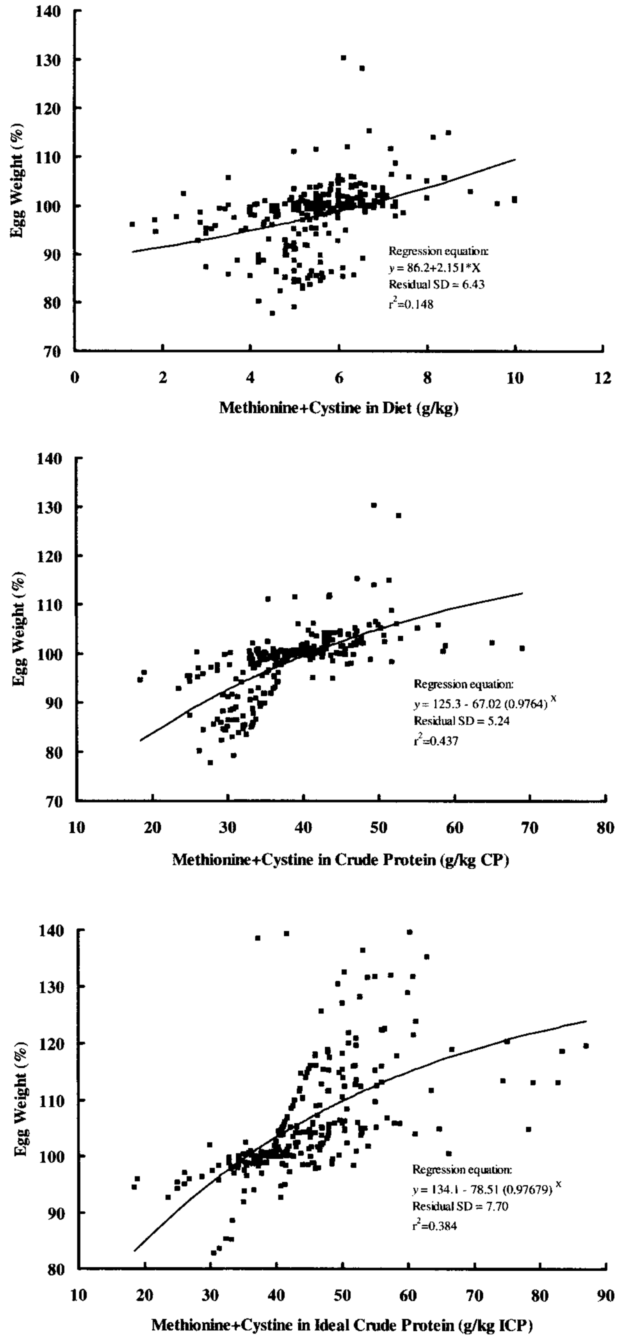

Figure 12 Relationship between dietary variation in methionine + cystine concentration and the mass outputs of eggs laid by hens. Eligible data for all published experiments are included and egg mass outputs are expressed as a percentage of the treatment group with the experiment that was given 39 g/kg of methionine + cystine within the crude or ideal crude protein. Three methods of describing the methionine + cystine supply are compared.

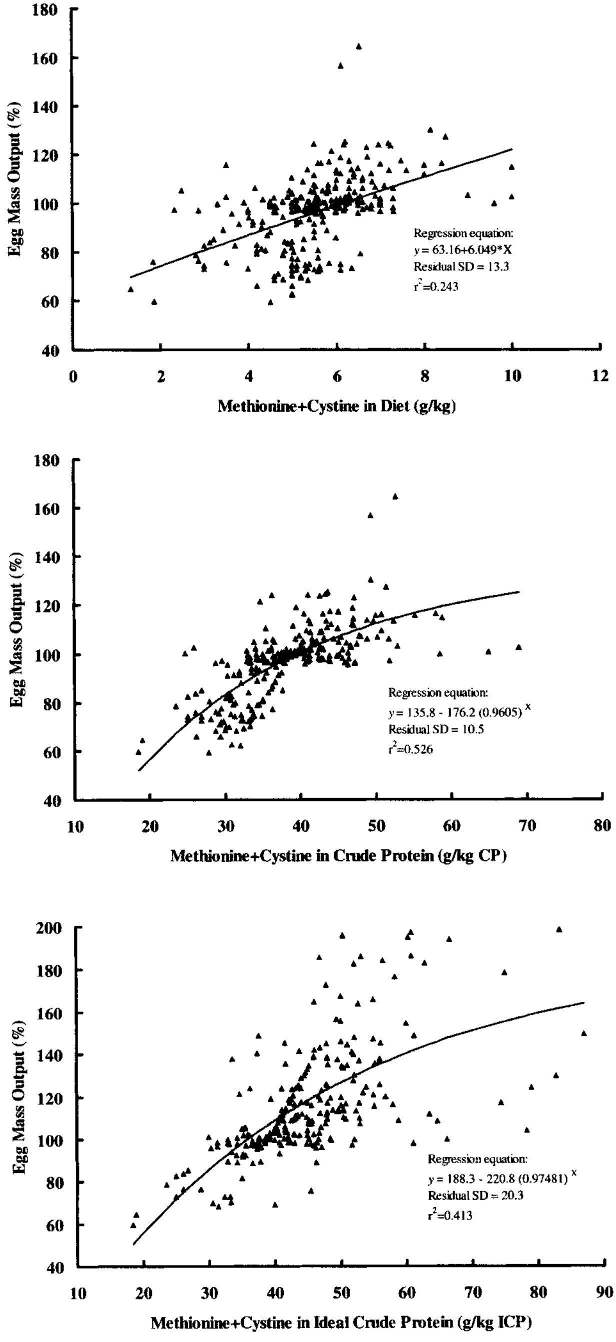

Figure 13 The response in egg mass output of laying hens to increasing intakes of dietary amino acids fitted using the Reading Model. The equation to predict egg mass output of individual birds within flock was:

Egg mass output = (amino acid intake – (b x W)) / a

Where W = body weight of birds (kg). A mean body weight of (1.727 kg) was used and a constant feed intake was assumed (112.79 g/bird d). A normal distribution of the maximum egg outputs of individual birds within a flock was assumed with a standard deviation of 10% of the mean of 56.98 bird d. *a* and *b* are coefficients that represent the requirement for production (mg/kg egg mass output) and maintenance (mg/kg body weight) respectively.