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MODELLING ANIMAL SYSTEMS PAPER

Application of the law of diminishing returns to estimate maintenance requirement for amino acids and their efficiency of utilization for accretion in young chicks

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SUMMARY

Suitability of the monomolecular equation, specifically re-parameterized for analysing energy balance data, has recently been investigated in broilers and turkeys. In the current study, this equation was applied to literature data from growing chicks fed crystalline amino acid (AA) diets, in order to provide estimates for AA requirements for maintenance, body-weight gain and protein accretion. Non-linear regression was used with the data to estimate parameters and combine them to determine other biological indicators. The predictive ability of the model was evaluated with reference to model behaviour when fitting the data, biologically meaningful parameter estimates and statistical performance. The model estimated the maintenance requirements for valine, threonine and lysine to be in the range 80–111, 96–109 and 52–209 mg/kg of liveweight/day, respectively, depending on the response criterion. Requirements for maintenance were in good agreement with values reported previously. Average efficiency of recovering AAs in whole body protein, between maintenance and four × maintenance, was in the reported range of 0·80–1·0 and greatest at low intakes and decreasing as intakes increase.

INTRODUCTION

Essential amino acid (AA) requirements for broiler chickens are well documented, but for practical prediction of performance, difficulty remains in deciding the most advantageous dietary AA patterns to use. This difficulty is partly due to non-linearity of the growth response to change in dietary AA concentrations (Gous & Morris 1985; Oviedo-Rondón & Waldroup 2002). To develop accurate models of AA requirements, estimates of maintenance requirements and efficiencies of utilizing indispensable AAs for whole body protein accretion are essential (Edwards & Baker 1999). There are models for predicting the AA requirements of poultry. Curnow (1973) introduced a smooth population curve to describe egg production based on a broken-stick assumption and information about the standard deviations of body weight (BW) and egg output. The model was used by Fisher *et al.* (1973) for laying hens and Boorman & Burgess (1986) for growing chickens to estimate AA requirements. Researchers at Edinburgh (e.g. Emmans 1981) proposed a programme that utilizes projected Gompertz growth curves to partition energy and protein intake of broilers between daily maintenance requirement, protein and feather growth. Hurwitz *et al.* (1978) constructed a model to estimate protein and AA requirements of broilers for maintenance and growth. The model was later modified to take into account effects of environmental temperature and differences in composition of weight gain

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(proportion of lipid) on energy needs in both chickens and turkeys (Hurwitz *et al.* 1983). National Research Council (NRC) (1994*a*) accepted this model as a good estimator of requirements for some AAs for which no experimental results were available. However, the model of Hurwitz *et al.* (1978) is founded on the premise that growth rate determines requirements based on some fixed rate of nutrient utilization, which does not represent adequately the biological phenomena involved (Pesti & Miller 1997). There are numerous studies suggesting that a limiting AA is utilized with constant efficiency over the range of intakes from maintenance to that required for maximal protein accretion (e.g. Hurwitz *et al.* 1978, 1983; Baker 1991; Baker *et al.* 1996; Edwards *et al.* 1997, 1999; Edwards & Baker 1999). In contrast, Heger & Frydrych (1985), Gahl *et al.* (1994), Vazquez & Pesti (1997), Baker *et al.* (2002) and Fatufe *et al.* (2004, 2005), demonstrated that efficiency of utilization of AAs declined as their intake approached optimum.

Non-linear models have been used to estimate AA requirements. For example, Samadi & Liebert (2007*a, b*) used an exponential function relating N intake to N retention and calculated lysine and threonine requirements in growing chicks. The potential and validity of a specially re-parameterized monomolecular model (Darmani Kuhi *et al.* 2001) to partition AA intakes between requirements for maintenance and growth have been demonstrated recently in relation to broilers using results from two types of study, namely bioassay and nitrogen balance experiments (Kebreab *et al.* 2008). The present study aims to apply this model to provide estimates of AA requirement for maintenance and efficiency of utilization of dietary AA for live weight gain (LWG), protein and AA accretion using the results of four studies (Baker *et al.* 1996; Edwards *et al.* 1997, 1999).

MATERIALS AND METHODS

Experimental data

Results of four bioassays, conducted to determine maintenance requirement and efficiency of utilization of dietary AA in young chicks, taken from the literature for slow and fast growing broiler strains, were used in the current study (Baker *et al.* 1996; Edwards *et al.* 1997, 1999). In each assay, chicks were given free access to crystalline AA diets containing graded levels of AA to meet ideal levels of indispensable AA requirements (Table 1).

The model

The suitability of the monomolecular equation (Eqn 1), specifically re-parameterized for analysing energy balance data, in relation to broilers and turkeys has been investigated recently (Darmani Kuhi *et al.* 2001, 2003, 2004; Kebreab *et al.* 2008). In the current study, this equation was used to provide estimates of AA requirements for maintenance, gain and protein (or AA) accretion in fast and slow growing broilers:

$$y = y_{\max}[1 - e^{-K(x - x_m)}] \quad x \geqslant 0 \qquad (1)$$

where y is BW gain (BWG) or protein (or AA) accretion [g of BWG or g of protein (or mg of AA) accretion/g of BW/d], $y_{\max}$ is the theoretical maximum attainable value for y, K is a fractional rate parameter [mg of AA intake/g of BW/d]$^{-1}$, x is AA intake [mg of AA/g of BW/d] and x_m is AA intake at maintenance. The model was fitted to the data and the parameters and AA requirements for maintenance estimated. The average efficiency of utilization between $\Delta_1 \times$ maintenance and $\Delta_2 \times$ maintenance ($\Delta_2 \geqslant \Delta_1 \geqslant 1$) is determined by

$$\bar{k}_g(\Delta_1, \Delta_2) = \frac{y(\Delta_2 x_m) - y(\Delta_1 x_m)}{(\Delta_2 - \Delta_1)x_m}$$

Statistical procedures

Due to the absence of a single robust criterion for model evaluation, three criteria were used to evaluate model adequacy: (1) model behaviour when fitting the curves using non-linear regression, (2) statistical performance and (3) comparison of biologically meaningful indicators obtained using the model. All statistical analyses were performed using the non-linear function of SigmaPlot (SPSS 1998). The proportion of variation accounted for (R^2), the amount of total variation about the mean value of y explained by the fitted curves, was used as a measure of adequacy of the model.

RESULTS

Figure 1 shows the fit of the model to the data on BWG (or protein (or AA) accretion) *v.* AA intake. The resultant curves (Fig. 1) and general goodness of fit, based on variation accounted for (R^2) and standard error (S.E.) estimated for the growth parameters, indicated that fits of the model to the data sets were acceptable (Table 2). The curves shown in Fig. 1 were extrapolated to the y-axis, so that x at y zero (which represents the AA requirement for maintenance) can be computed. Estimates of maintenance AA requirements for zero BWG, zero protein accretion and zero AA accretion were then calculated (Table 2). The maintenance requirements estimated by the model were in the range of 80–111, 96–109 and 52–209 mg/kg of live weight (LW)/day for valine, threonine and lysine, respectively, depending on the response criterion. The results giving higher maintenance requirements of AA using zero AA accretion are in agreement with the results of Baker *et al.* (1996) and

Table 1. *Accretion of body-weight* (ΔW)*, protein, and AA in chicks fed graded levels of valine, threonine and lysine*

Baker *et al.* (1996), Avian × Avian males*

Dietary valine		Intake		Accretion		
Level (g/kg of diet)	Proportion of ideal	Diet (g/d)	Valine (mg/d)	ΔW (g/d)	Protein (g/d)	Valine (mg/d)
0·35	0·05	19·2	6·7	−1·2	−0·10	−8·7
0·69	0·10	22·4	15·5	0·4	0·02	−2·4
2·77	0·40	32·8	90·9	8·2	1·30	53·1
3·81	0·55	42·2	160·8	14·3	2·13	100
4·85	0·70	41·8	202·6	18·4	3·14	139·6
0·658	0·95	42	276·2	22·8	4·02	190·1

Edwards *et al.* (1997), Avian × Avian males†

Dietary Threonine		Intake		Accretion		
Level (g/kg of diet)	Proportion of ideal	Diet (g/d)	Threonine (mg/d)	ΔW (g/d)	Protein (g/d)	Threonine (mg/d)
3·00	0·05	15·4	4·6	−1·20	−0·23	−11·9
6·00	0·10	16·5	9·9	−0·83	−0·11	−6·4
9·00	0·15	16·7	15·1	−0·38	0·00	−2·3
24·1	0·40	25·8	62·3	5·88	0·97	40·0
33·2	0·55	34·7	115·2	11·70	1·94	83·2
42·2	0·70	36·7	154·7	15·25	2·67	116·9
57·3	0·95	37·3	213·6	20·92	3·62	158·37

Edwards *et al.* (1999), assay 1, New Hampshire × Columbian males‡

Dietary lysine		Intake		Accretion		
Level (g/kg of diet)	Proportion of ideal	Diet (g/d)	Lysine (mg/d)	ΔW (g/d)	Protein (g/d)	Lysine (mg/d)
0·45	0·05	15·3	6·9	0·0	0·0	−20·9
3·60	0·40	15·0	54·2	3·0	0·3	15·1
4·95	0·55	19·6	96·9	6·2	1·1	50·5
6·30	0·70	22·7	143·1	10·1	1·8	100·9
8·55	0·95	30·4	260·0	14·6	2·9	167·2

Edwards *et al.* (1999), assay 2, Avian × Avian males‡

Dietary lysine		Intake		Accretion		
Level (g/kg of diet)	Proportion of ideal	Diet (g/d)	Lysine (mg/d)	ΔW (g/d)	Protein (g/d)	Lysine (mg/d)
0·45	0·05	18·2	8·2	−0·12	0·01	−20
0·90	0·10	22·1	19·9	1·07	0·17	−8·4
3·60	0·40	33·2	119·4	9·35	1·46	74·7
4·95	0·55	37·4	185·3	14·27	2·19	118·5
6·35	0·70	43·0	270·9	17·35	3·01	181·7
8·55	0·95	39·6	338·2	20·45	3·88	247·1

* Data are means of four pens of four chicks during a 10-d assay (10–20 post-hatching). Average initial weight was 158 g.

† Data are means of four pens of four chicks during a 10-d assay (10–20 post-hatching). Average initial weight was 157 g.

‡ Data are means of three (assay 1) and four (assay 2) pens of four chicks during a 10-d assay (10–20 post-hatching). Average initial weight of chicks was 103 and 157 for assay 1 and 2, respectively.

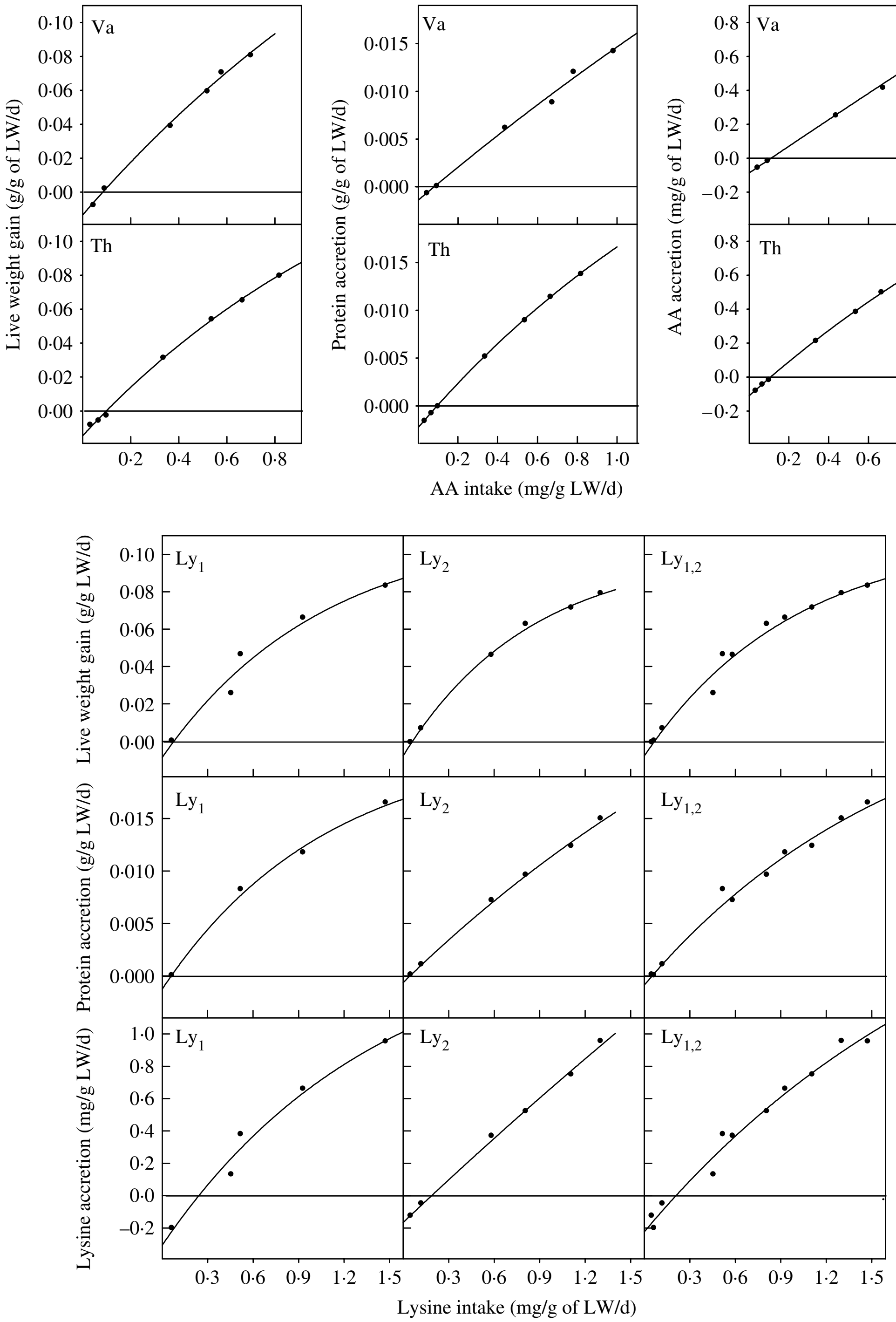

Fig. 1. Plots of LWG, protein and AA accretion against AA intake, showing fit of monomolecular equation to data. The AA were valine (Va), threonine (Th) and lysine (Ly). The data for Va were from Baker *et al.* (1996), Th from Edwards *et al.* (1997) and Ly from Edwards *et al.* (1999). For Ly, the numbers indicate fit of equation to data from assays 1 and 2, and pooled data (assays 1 and 2).

Table 2. *The maintenance requirements* (x_m) *for individual AAs* (*mg/kg of BW/day*) *obtained using the model together with reported values of maintenance requirements.* S.E. *are given in brackets*

AA	Data source*	R^2	x_m	(Reference)† values Maintenance mg/kg of BW/d
Valine	(B), BWG$_{\text{zero}}$	99·76	84·0 (9·63)	(F) 73, (M) 73, (W) 82
	(B), PA$_{\text{zero}}$	99·33	79·6 (25·12)	
	(B), Val. A$_{\text{zero}}$	99·84	111 (11·9)	
Threonine	(E1), BWG$_{\text{zero}}$	99·86	98·6 (6·14)	(F) 40, (M) 32, (W) 86
	(E1), PA$_{\text{zero}}$	99·99	95·9 (1·44)	
	(E1), Thr. A$_{\text{zero}}$	99·98	109 (2·58)	
Lysine	(E2), BWG$_{\text{zero}}$ (assay 1).	96·66	77·6 (73·62)	(F) 60, (M) 76, (W) 70
	(E2), BWG$_{\text{zero}}$ (assay 2).	99·82	62·5 (11·57)	
	(E2), BWG$_{\text{zero}}$ (pooled data).	98·32	67·8 (24·23)	
	(E2), PA$_{\text{zero}}$ (assay 1).	99·55	61·2 (39·45)	
	(E2), PA$_{\text{zero}}$ (assay 2).	99·84	45·3 (17·80)	
	(E2), PA$_{\text{zero}}$ (pooled data).	98·96	52·2 (26·21)	
	(E2), Lys. A$_{\text{zero}}$ (assay 1).	97·67	242 (51·68)	
	(E2), Lys. A$_{\text{zero}}$ (assay 2).	99·75	187 (18·39)	
	(E2), Lys. A$_{\text{zero}}$ (pooled data).	98·13	209 (26·63)	

* (B) Baker *et al.* (1996), (E1) Edwards *et al.* (1997), (E2) Edwards *et al.* (1999), BWG$_{\text{zero}}$ = based on zero BWG, PA $_{\text{zero}}$ = based on zero protein accretion, Val. A$_{\text{zero}}$ = based on zero valine accretion, Thr. A$_{\text{zero}}$ = based on zero threonine accretion and Lys. A$_{\text{zero}}$ = based on zero lysine accretion.

† References: (F) Fisher (1998), (M) McDonald & Morris (1985) and (W) Wiseman (1994).

Table 3. *Parameter estimates obtained and growth indicators calculated from the monomolecular equation together with their reported values*

Parameter estimates

Data source	$y_{\max}$	K	$x_{\max}$	R^2	–	–	–
Lysine	2·34 (1·06)	0·437 (0·243)	209 (26·6)	98·13	–	–	–
Threonine	2·24 (0·36)	0·449 (0·082)	109 (2·6)	99·98	–	–	–
Valine	17·4 (62·8)	0·045 (0·184)	111 (11·9)	99·84	–	–	–

Growth indicators

	$K\,y_{\max}$*	$\bar{k}_g$ (1, 2)†	$\bar{k}_g$ (2, 3)†	$\bar{k}_g$ (2, 4)†	λ_g‡	$[0{\cdot}1*(1/\lambda_g)]^{\S}$ Model	References|| (values) g/100 g protein
Lysine	1·0	0·96	0·88	0·84	0·016	6·3	E2 (6), F (7·5), W (6·2)
Threonine	1·0	0·98	0·93	0·91	0·022	4·6	E1 (4·35), F (4·2), W (4·2)
Valine	0·79	0·79	0·79	0·78	0·019	5·26	B (4·72), F (4·2), W (4·99)

* The product $K\,y_{\max}$ is the maximum efficiency (mg of lysine, threonine or valine accretion/mg of lysine, threonine or valine intake) and occurs when y equals zero (i.e. at maintenance).

† Average efficiency of AA utilization for AA accretion (mg of AA accreted/mg of AA ingested) between 1–2, 2–3 and 2–4 × maintenance.

‡ Average efficiency of AA utilization for protein accretion between 1–4 × maintenance (g of protein accretion/mg of AA).

§ Average AA requirement for protein accretion between 1–4 × maintenance (g of AA/100 g of protein accretion).

|| Reported values of AA composition of the whole carcass of young chicken. (B) Baker *et al.* (1996), (E1) Edwards *et al.* (1997), (E2) Edwards *et al.* (1999), (F) Fisher (1998) and (W) Wiseman (1994).

Edwards *et al.* (1997, 1999) who stated that the maintenance requirement for a given AA depends on the response criterion being measured.

Indicators calculated from the monomolecular equation together with reported values of growth indicators are shown in Table 3. From values of $\bar{k}_g$ at different multiples of maintenance, it can be seen that efficiency of utilization of threonine and lysine is greatest at low intake levels and decreases as intake is increased.

DISCUSSION

Development of a more dynamic approach to determining AA requirements requires knowledge of digestibility of dietary protein, pattern of AA deposition, partial efficiency with which absorbed AAs (protein) are used for maintenance and deposition, and how metabolic modifiers alter rate of protein accretion and maintenance requirement (NRC 1994*b*). AA requirements of broilers have been determined using different methodologies, such as growth variables, carcass analysis, radioactive isotope studies, plasma AA analysis and rates of AA oxidation. However, the most common procedures are the evaluation of broiler performance as a function of graded levels of AA intake (the graded supplementation technique, D'Mello 1982), where a basal diet deficient in the test AA is progressively supplemented with increasing doses of the synthetic form of the test AA, and the summit dilution technique (Fisher & Morris 1970), in which a summit diet with excessive amounts of all AAs but with the test AA first limiting is progressively diluted with either a non-protein diluent or a dilution feed with the balance of AAs reflecting that in the summit diet (Gous & Morris 1985; Gous 2007). The concentration of an AA in the diet producing maximal BW, highest feed conversion efficiency, etc. is determined as being requirement for the AA and is normally expressed as a fixed concentration of diet. These fixed values of AAs are compiled in tables of requirements and utilized for feed-cost formulation. With fixed requirements, it is impossible to predict the effect on rate of growth, feed intake, or carcass composition by manipulation of concentration and balance of dietary AAs. Furthermore, single fixed numbers for requirements are not useful for applying to an accurate cost-benefit analysis. Since responses of birds to dietary energy, protein and AAs are diminishing returns phenomena, they should be evaluated as such to estimate optimum economic levels, rather than as biological maxima (Clark *et al.* 1982; Gous & Morris 1985). A linear or 'broken stick' method was used by Gous & Morris (1985) to determine lysine requirement. Samadi & Liebert (2008) applied the principles of the diet dilution technique using an exponential function for the modelling of lysine and threonine requirements in a stochastic manner. In the current study, a nonlinear deterministic model was used and an alternative simple method to estimate AA requirements in poultry was offered.

Darmani Kuhi *et al.* (2001, 2003, 2004) and Kebreab *et al.* (2008) developed a monomolecular equation to estimate energy and crude protein needed by growing broilers and turkeys for maintenance and gain. In the study presented here, the aim was to assess applicability of this model in estimating AA requirements for maintenance, gain and protein (or AA) accretion in fast- and slow-growing broiler strains fed crystalline AA diets with a wide range of dosing levels. With regard to the estimates of AA requirements for maintenance (Table 2) and average AA requirement for protein accretion between 1× and 4× maintenance (Table 3), it can be seen that these estimates lie in the range reported by different researchers. The estimated maintenance requirements for lysine are higher based on lysine accretion than on either BW gain or protein accretion, which are in agreement with the results of Edwards *et al.* (1999) who pointed out that the maintenance requirement estimates from zero lysine accretion were much higher than those obtained from zero protein accretion. According to Edwards *et al.* (1999) this reflects a shift in type of protein in the body, with more collagen protein and less contractile protein being present in chicks fed lysine levels near maintenance. They conclude that the lysine requirement for maintenance of broiler chicks is not low but instead is high. The maintenance requirements for AAs can be influenced by a multitude of factors such as different concentrations of dietary AA, response criteria (protein or AA accretion), environmental conditions and genetics. According to Leclercq (1998) and Vazquez & Pesti (1997) the particular mathematical model being used to calculate AA requirement can also influence AA requirement profiles. With the current estimates of the maintenance requirements for lysine (67·5, 52·2 and 209 mg/kg of LW/d for zero BW, protein and lysine accretion, respectively) together with the estimates of the total lysine requirements when growth rate, protein and lysine accretion reach their maximum values, the maintenance requirements for lysine represent 0·45, 0·35 and 0·13 of the total requirements which are in the range reported previously by researchers. A higher maintenance requirement for lysine as a percentage of total lysine requirements is in agreement with the result of Emmert & Baker (1997), who pointed out that the use of lysine accretion as a criterion led to much larger estimates of maintenance requirement as a percentage of the total requirements. Additionally, an estimate of 6·3 g lysine for 100 g protein accretion and an efficiency of lysine utilization of 1·0–0·85, which are both biologically meaningful, can be considered as further evidence of the predictive ability of the model.

Average efficiency of recovering AA in whole body protein, between maintenance and 4 × maintenance, estimated by the model was 1·0–0·91 for threonine, 1·0–85 for lysine and 0·79–0·78 for valine (Table 3), which is in agreement with values of 0·95–1·00 reported by Harper *et al.* (1970) and Morris (1972) for efficiency of utilization of limiting AAs. These results are also in agreement with reported values of 0·85–1·0 and 0·80–0·94 achieved in growing pigs given semi-purified diets and fed to optimum rates of growth (Whittemore 1983; NRC 1994*b*). Considering the values of $\bar{k}_g$ at different multiples of maintenance, the efficiency of utilization of threonine and lysine is greatest at low intake levels and decreases as intake is increased. These results are supported by conventional wisdom, namely that a gradual decrease in utilization of nutrients for producing gain occurs as intake increases. This is partly due to a slight fall in digestive efficiency of the animal with increased feeding level and partly to the fact that anabolic processes are less efficient than catabolic ones. Protein turnover is higher as protein intake is increased, as any excess in AA supply causes a rise in AA degradation rates (Riis 1983*a*, *b*). Therefore, successive increments of daily intake of nutrients result in progressively smaller increments in daily gain (Blaxter & Boyne 1978).

In conclusion, results presented here and those previously reported for broilers and turkeys (Darmani Kuhi *et al.* 2001, 2003) and Kebreab *et al.* (2008) can be considered as a basis for accepting the general validity of the monomolecular equation to predict the magnitude and direction of responses of growing broilers and turkeys to dietary energy and protein (or AA) intake without making any initial assumptions.

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