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Muscle protein degradation assessed by N^t-methylhistidine excretion in mature White Leghorn, dwarf broiler and normal broiler males maintained on either low- or high-protein diets

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Protein degradation rates were assessed by the excretion of N^t-methylhistidine (N^tMH) in four strains of mature chickens, two White Leghorns and two broilers (dwarf and normal), fed on diets containing two levels of dietary protein. Over 0·9 of labelled N^tMH was recovered within 7 d of injection from three White Leghorn, three dwarf and three normal broiler males. Protein degradation, measured by N^tMH output, was related to adult body-weight by the power 0·71 and strain intercepts were significantly different. Strain differences disappeared when the rate of output of N^tMH per unit lean was evaluated. The rate of output of N^tMH per unit muscle was higher in birds fed on a low-protein diet of 100 g crude protein (nitrogen × 6·25; CP)/kg compared with males fed on 150 g CP/kg. It was concluded that the lower rate of protein degradation in broiler compared with layer strains at young ages is related to increased adult body-weight in agreement with well-established biological principles.

Protein turnover: Body size: Poultry

Studies in embryos and in chicks up to 8 weeks of age have demonstrated that broiler stocks have a lower fractional muscle protein degradation rate than smaller, egg-laying genotypes of the same age (Orcutt & Young, 1982; Hayashi *et al.* 1985; Saunderson & Bryan, 1985; Klasing *et al.* 1987; Maramatsu *et al.* 1987). Saunderson & Leslie (1988) compared layers and broilers at different ages and showed that the differences became smaller as the birds approached 4–5 weeks of age. They also showed that the rate of muscle protein synthesis was higher in their broilers during the first 2 weeks post hatching. Similar results were reported by Maeda *et al.* (1984) and Klasing *et al.* (1987).

Broilers and layers vary greatly in the proportion of muscle in the body (Hocking *et al.* 1985; Bulfield *et al.* 1988; Saunderson & Leslie, 1988). Muscle growth and distribution changes rapidly during the first 4 weeks but has stabilized by 9 weeks of age (Wilson, 1954). It is possible that differences in fractional muscle protein degradation rates between broilers and layers would disappear as the birds approached maturity. Furthermore, the rate of many biological processes are directly related to mature body-weight raised to the power 0·73 (Taylor & Murray, 1987) and the lower degradation rate in broilers may be simply a consequence of increased mature size. It was, therefore, decided to examine fractional muscle protein degradation rates in mature birds where synthesis and degradation rates, in the absence of body-weight change, are similar, and where muscle distribution is relatively constant. The experiment was designed to test the hypothesis that fractional muscle protein turnover in mature chickens of widely different selection histories could be predicted entirely on the basis of their body-weight. Males were used to avoid complications associated with egg production in females. Two White Leghorn egg-laying strains and two broiler strains were used. The two broiler strains had a similar genetic background but one

Table 1. *Composition and analyses of diets*

	Low protein	High protein
Composition (g/kg)		
Barley	660	177
Maize	200	50
Wheat	100	177
Soya bean (410 g CP/kg)	—	77
Limestone	15	15
Dicalcium phosphate	17	17·2
Salt (NaCl)	1	0·8
Lysine hydrochloride	3	—
Vitamin–mineral premix*	5	5
Calculated analyses (g/kg)		
Metabolizable energy (MJ/kg)	11·1	11·1
CP	100	150
Diethyl ether-extractives	20	17
Calcium	10	10
Phosphorus	4	4

CP, crude protein (nitrogen × 6·25).
* Supplied (mg/kg diet): copper 3·6, iodine 0·4, iron 80, magnesium 300, manganese 100, zinc 50, retinol 600 μg, cholecalciferol 15 μg, α-tocopherol 17, menadione 1·3, riboflavin 4, nicotinic acid 28, pantothenic acid 10, biotin 50 μg.

carried the sex-linked dwarfing gene *dw*. The dwarf broiler was included because of claims that protein turnover was greater in birds carrying this gene compared with normal (*DW*) broilers (Guillaume, 1976).

In growing birds, diets with low protein or amino acid contents increase the total and fractional rates of muscle protein degradation (Maruyama *et al.* 1978; Saunderson & Leslie, 1989). It is not known whether the same would be true at maturity given that body-weight was stable. We, therefore, fed half of the birds on a low-protein diet for comparison with the remaining animals which were fed on a conventional diet.

Saunderson & Leslie (1983) reported the successful use of N^{t}methylhistidine (N^{t}MH) excretion in domestic fowl to measure muscle protein degradation, and several workers have used the method to study the control of protein deposition in poultry (Maeda *et al.* 1984; Hayashi *et al.* 1985; Tomas *et al.* 1988). Harris *et al.* (1987) reported that broilers did not excrete labelled N^{t}MH quantitatively after 6 weeks of age. Since we wished to use N^{t}MH excretion as a measure of muscle protein turnover in mature birds, an experiment was first performed to confirm the quantitative recovery of N^{t}MH in our birds.

MATERIALS AND METHODS

Animals and husbandry

Male chicks were obtained at 1 d old. The lightweight White Leghorn egg-laying strains were the Ross White (Ross Breeders Ltd, Newbridge, Midlothian) and a random-bred stock (S-line) maintained at Roslin which was based on a commercial hybrid. The heavyweight broiler strains were the Ross 1 and the Ross PM3 which is similar to the Ross 1 but carries the sex-linked dwarfing gene *dw*.

S-line chicks were reared in cages throughout. The Ross birds were reared in floor pens littered with wood shavings until they were caged at 30 weeks of age. Cages for adult birds measured 307 × 457 mm and could be fitted with a tray for collecting faeces. All birds received a photoperiod of 14 h light/24 h.

The S-line and half of the Ross chicks were fed *ad lib.* a conventional starter ration to

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6 weeks of age followed by a grower diet containing 150 g crude protein (nitrogen × 6·25; CP)/kg (Table 1). The remaining Ross birds were fed on the same starter diet *ad lib.* to 10 d of age and were subsequently fed on a low-protein diet containing 100 g CP/kg (Table 1). Neither of the experimental diets contained animal protein. Half of the S-line males were transferred to the low-protein diet at 50 weeks of age. The birds were weighed regularly and the observations were made when body-weight had stabilized. This occurred at 45 weeks in the Ross strains and a 70 weeks of age in the S-line.

Experimental observations

Expt 1. Three birds from each of the Ross 1, Ross PM3 and Ross White strains fed on the conventional diet (150 g CP/kg) were rehoused and allowed to adapt to the new cages for 3 d. Each bird was injected intraperitoneally with approximately 1·4 μCi $N^t[^{14}CH_3]$ histidine/kg body-weight. Excreta were collected daily for 4 d with a final collection after the seventh day. The radioactivity in acid extracts was measured as described by Saunderson & Leslie (1983).

Expt 2. Faeces were collected from each of eight birds per strain over four consecutive days and N^tMH was determined by ion-exchange chromatography as described by Saunderson & Leslie (1988). At the end of the experiment the birds were killed by cervical dislocation and the entire breast and leg muscles from one side were excised and weighed. The total weight of muscle was estimated as twice the sum of the breast and leg muscles.

Statistical analyses.

Analyses of variance for unbalanced data were used to evaluate the significance of strain and diet effects for body-weight, weight of muscle, and output of N^tMH. The derived variables, breast as a proportion of total muscle, muscle:bone ratio in the leg and N^tMH/muscle were also analysed. The relationships of N^tMH output and the rate of N^tMH output (N^tMH/muscle) with body-weight were evaluated by covariance analyses of the natural logarithms of the variables. The hypothesis that N^tMH (or N^tMH/muscle) was proportional to a power of body-weight was converted (by taking natural logarithms) to the linear form:

$$\log_e N^t\text{MH (or } \log_e N^t\text{MH/lean)} = a + b \log_e \text{body-weight},$$

in which tests for different powers (slopes, *b*) and adjusted means of the treatment variables could be made. Differences in slopes for treatments were tested by assessing the significance of interactions between them.

RESULTS

The proportion of labelled N^tMH excreted over time in Expt 1 by the three Ross strains is presented in Fig. 1. The total radioactivity collected after 7 d was 0·92, 0·95 and 0·97 of the injected dose in Ross 1, Ross PM3 and Ross White respectively. The results suggest that there was no significant retention of $N^t[^{14}CH_3]$ histidine by these birds.

Means of variables and summary analyses of variance for Expt 2 are presented in Table 2. There was some mortality, particularly among the Ross White on the low-protein diet. Four of these birds died from dehydration after a relatively hot spell although they had apparently been drinking normally beforehand. Values from a few males were not used because abnormal faeces indicated a disturbance of the gut.

Birds on the low-protein diet were lighter in body-weight and weight of muscle, and had a higher rate of output of N^tMH per unit muscle. Bodies of the two broiler genotypes contained more muscle, had a higher muscle:bone ratio in the leg and a greater proportion of breast muscle than the egg-laying strains. N^tMH/muscle was lower in the broilers on the high-protein diet, although the strain × diet interaction was not significant.

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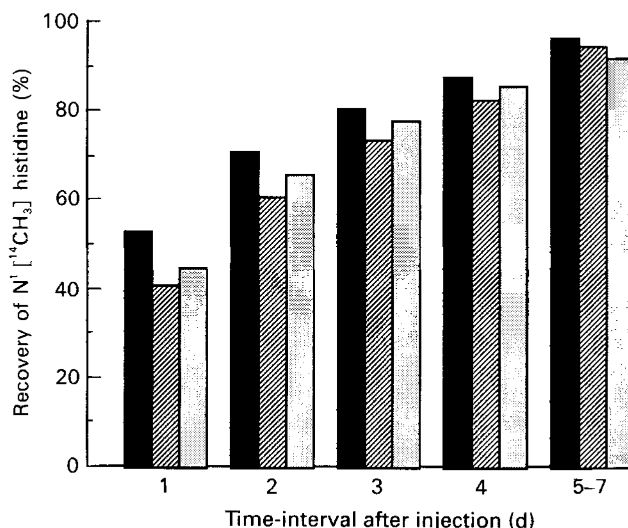

Fig. 1. Expt 1. Recovery of $N^{\tau}[^{14}CH_3]$ histidine in mature males of three strains (White Leghorn egg-laying (■) and normal (▨) and dwarf (▨) broilers) over 7 d. For details of birds and procedures, see pp. 392–393.

Table 2. *Body-weight, body composition and N^{τ}-methylhistidine ($N^{\tau}MH$) excretion in four strains of chickens fed on two diets differing in protein content*†

Strain	Dietary crude protein‡ (g/kg)	*n*	Body-wt (kg)	Total lean‖ (kg)	Breast lean/total lean (g/kg)	Leg lean/leg bone (g/g)	$N^{\tau}MH$ (μmol/d)	$N^{\tau}MH$/lean (μmol/d per g) (× 10^4)
Egg layer	100	3	1·60	0·49	390	4·24	15·6	313
(Ross)	150	6	2·01	0·62	367	4·93	17·9	287
Egg layer	100	6	2·02	0·57	373	4·29	15·1	269
(S-line)	150	7	2·19	0·65	386	4·71	16·3	254
Dwarf broiler	100	7	3·46	1·10	455	5·74	30·0	276
	150	6	3·91	1·36	422	6·56	28·3	206
Normal broiler	100	6	5·18	2·08	406	6·83	54·4	267
	150	7	5·27	2·23	421	6·49	47·0	215
Approximate SE§			0·18	0·09	11	0·31	2·0	21
Statistical significance of effects of:								
Strain			***	***	***	***	***	*
Diet			*	*	NS	NS	NS	**
Strain × diet			NS	NS	NS	NS	NS	NS

NS, not significant.
* $P < 0·05$, ** $P < 0·01$, *** $P < 0·001$.
† For details of birds and procedures, see pp. 392–393.
‡ Nitrogen × 6·25.
§ Standard error of mean of six observations.
‖ Twice the sum of breast and leg lean dissected from one side.

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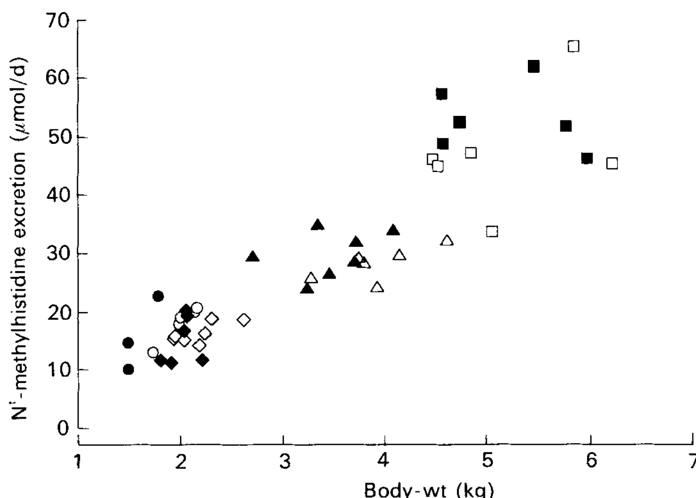

Fig. 2. Expt 2. Output of N^{τ}-methylhistidine in four strains of adult male chickens fed on two diets of differing protein content. (○, □, ◇, △) 150 g crude protein (nitrogen × 6·25; CP)/kg; (●, ■, ◆, ▲) 100 g CP/kg; (○), egg layer (Ross); (◇), egg layer (S-line); (△), dwarf broiler; (□), normal broiler. For details of birds and procedures, see pp. 392–393.

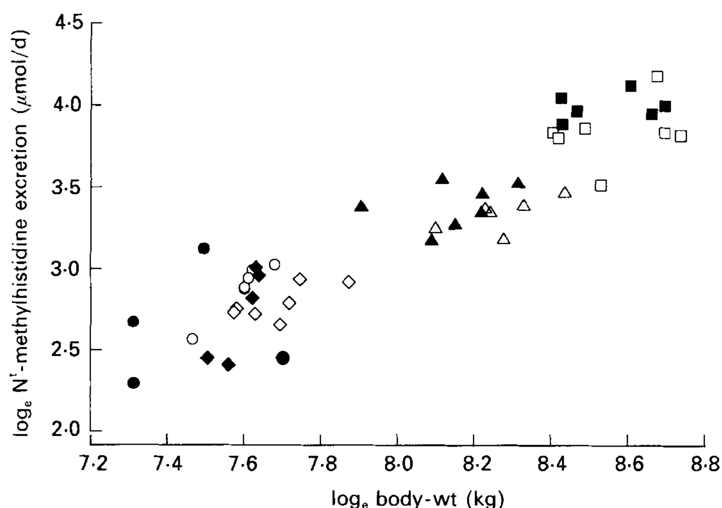

Fig. 3. Expt 2. Log-log plot of N^{τ}-methylhistidine output *v.* body-weight in four strains of adult male chickens fed on two diets of differing protein content. (○, □, ◇, △), 150 g crude protein (nitrogen × 6·25; CP)/kg; (●, ■, ◆, ▲), 100 g CP/kg; (○), egg layer (Ross); (◇), egg layer (S-line); (△), dwarf broiler; (□), normal broiler. For details of birds and procedures, see pp. 392–393.

The plot of N^{τ}MH output *v.* body-weight (Fig. 2) shows increasing variation in N^{τ}MH as body-weight increases. Plots of $\log_e$ N^{τ}MH and $\log_e$ (N^{τ}MH/muscle) *v.* $\log_e$ body-weight are presented in Figs. 3 and 4 and show no such effect. Covariance analyses showed no evidence for strain or diet differences in slopes of $\log_e$ N^{τ}MH or $\log_e$ (N^{τ}MH/muscle) against $\log_e$ body-weight, and the strain × diet interaction was not significant. The pooled regression coefficients are given in Table 3 with the treatment means adjusted to the overall mean body-weight.

There was a significant ($P < 0·001$) relationship between $\log_e$ N^{τ}MH output and $\log_e$ body-weight of 0·71, but the relationship between fractional output ($\log_e$ N^{τ}MH/lean) and

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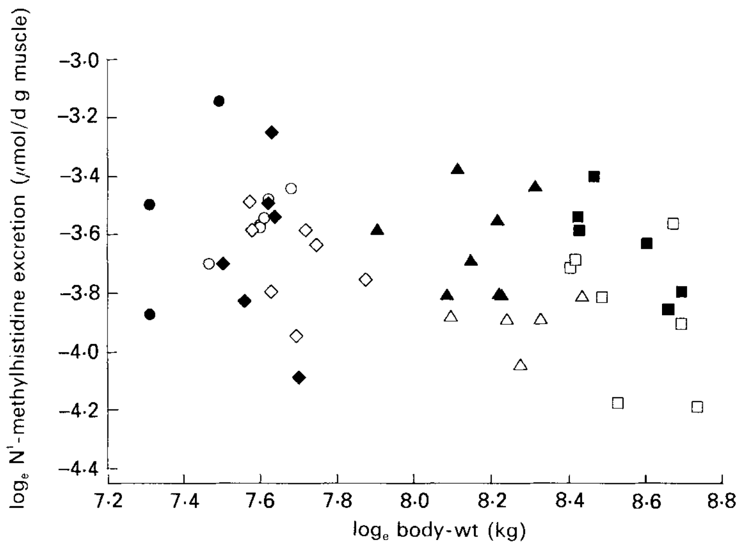

Fig. 4. Expt 2. Log-log plot of the fractional rate of N^t-methylhistidine output per gram of muscle in four strains of adult male chickens fed on two diets of differing protein content. (○, □, ◇, △), 150 g crude protein (nitrogen × 6·25; CP)/kg; (●, ■, ◆, ▲), 100 g CP/kg; (○), egg layer (Ross); (◇), egg layer (S-line); (△), dwarf broiler; (□), normal broiler. For details of birds and procedures, see pp. 392–393.

body-weight was not significantly different from zero. Differences among strains were significant ($P < 0.01$) for $\log_e$ N^{t}MH output but not for the fractional rate. The adjusted mean output of the low-protein diet was lower than that of the high-protein diet ($\log_e$ N^{t}MH 3·27 *v.* 3·21 (SEM 0·04) μmol/d), and the difference was significant ($P < 0.05$) when expressed as the fractional rate of output ($\log_e$ N^{t}MH −3·62 *v.* −3·76 (SEM 0·04) μmol/d per g lean).

Between-group regression coefficients were consistent with the within-group results. The coefficients were 0·56 (SE 0·09) ($P < 0.001$) for $\log_e$ N^{t}MH and −0·19 (SE 0·09) (not significant) for $\log_e$ (N^{t}MH/muscle).

DISCUSSION

N^{t}MH as a measure of protein degradation

The results of Expt 1 do not agree with those of Harris *et al.* (1987) that older broilers do not excrete N^{t}MH quantitatively. At 4 d after injection the broilers had excreted 86% of the radioactivity, which was similar to recoveries of 85 and 89% at 4 and 6 weeks of age in the report by Harris *et al.* (1987) but very different to their recoveries of only 60 and 70% at 12 and 18 weeks of age. Similar measurements were not made on the low-protein diet, but in the absence of evidence to the contrary it is assumed that dietary protein concentration would not significantly influence the recovery of radioactivity.

Similar results to those in the present study were obtained by Saunderson & Leslie (1983) and Tomas *et al.* (1988). The differences between these and the present work and that of Harris *et al.* (1987) warrant further investigation. Since we found that most of the labelled N^{t}MH was excreted after 7 d, it follows that natural N^{t}MH excretion, in the absence of significant contributions from other sources, gives a valid estimate of muscle protein degradation in this experiment. Nishizawa *et al.* (1977) compared N^{t}MH outputs from several organs and concluded that muscle tissue was the major contributor to excreted N^{t}MH in the fowl.

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Table 3. *Adjusted means* and regression coefficients from covariance analyses of the relationship of N^t-methylhistidine (N^tMH) output and N^tMH/lean with body-weight*

(Mean values with their standard errors)

Strain	Dietary crude protein (nitrogen × 6·25) concentration (g/kg): 100 Mean	SE	150 Mean	SE
(a) $\log_e$ N^tMH (μmol/d)				
Egg layer (Ross)	3·15	0·18	3·17	0·12
Egg layer (S-line)	2·98	0·12	3·03	0·10
Dwarf broiler	3·31	0·07	3·17	0·09
Normal broiler	3·62	0·14	3·45	0·14
Regression on $\log_e$ body-wt (g):	0·71	0·24		
(b) $\log_e$ (N^tMH/lean) (μmol/d per g)				
Egg layer (Ross)	−3·61	0·22	−3·62	0·14
Egg layer (S-line)	−3·72	0·14	−3·74	0·12
Dwarf broiler	−3·58	0·08	−3·84	0·11
Normal broiler	−3·55	0·17	−3·78	0·17
Regression on $\log_e$ body-wt (g):	−0·16	0·29		

* Strain means adjusted to the average body-wt of 8·02 on the $\log_e$ scale (3044 g).

Body-weight and protein turnover

The broiler genotypes had large bodies containing proportionally more muscle and more breast in the muscle tissue (Table 2), consistent with other findings (Hocking *et al.* 1985). In general N^tMH output divided by muscle mass was lower in the broiler genotypes (Table 2).

N^tMH output was related to adult body-weight raised to the power 0·71 (Table 3) which is close to the interspecies coefficient of 0·73 (Taylor, 1980). This suggests that normal broilers have a lower rate of muscle protein degradation compared with layers and dwarf broilers in agreement with their larger adult body-weights and that, when scaled by metabolic size, there should be no differences between strains of widely different mature body-weights and selection histories. Higher intercepts for the broiler strains (Table 3) may be a reflection of different body compositions. This conclusion is supported by evidence from the estimated fractional rate of muscle protein turnover. Strain differences disappeared when the relationship between N^tMH/lean and body-weight was analysed (Table 3). The relationship between the N^tMH excretion per unit muscle tissue and body-weight, was −0·16 (SE 0·29) $\log_e$ μmol/g per $\log_e$ body-weight (g). This is consistent with the expected coefficient of −0·27 (since $N^tMH \propto$ body-weight$^{0·73}$, N^tMH/body-weight $\propto$ body-weight$^{0·73-1·00}$). Standard errors for the two coefficients are high and conventional confidence intervals include the values of 1·0 and 0·0, which are consistent with N^tMH output being directly proportional to body-weight and muscle mass respectively. However, the between-group regression coefficients support the suggestion that protein degradation is related to metabolic body-weight. Results from several strains or (avian) species would be needed to resolve this issue.

Modern broilers have an 8-fold greater breast muscle mass compared with layers at 7 weeks of age, whilst there is little difference in body mass at hatch or even 1 week of age (Bulfield *et al.* 1988). Furthermore, Klasing & Jarrell (1985) observed higher rates of

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protein degradation in slow-growing compared with fast-growing muscles. Observed differences in protein degradation at immature ages are consistent with higher growth rates, and differences in body composition, made at this time (Wilson, 1954; Saunderson & Leslie, 1988). It is noteworthy that biochemical differences also occur during this period. Plasma growth hormone levels, for example, are low, and ornithine decarboxylase (*EC* 4.1.1.17) activity (an enzyme implicated in DNA synthesis and cell proliferation) is high in broilers compared with layers between 2 and 8 weeks of age (Bulfield *et al.* 1988; Goddard *et al.* 1988).

The effect of level of dietary protein on $N^{t}MH$ excretion

The significantly higher intercept for the rate of $N^{t}MH$ excretion per unit muscle for the low-protein diet (Table 3) is consistent with other reports that low-protein (or low-lysine) diets increase the rate of muscle protein degradation (Maruyama *et al.* 1978; Tomas *et al.* 1984; Saunderson & Leslie, 1989). Presumably muscle protein degradation is increased to supply deficient amino acids, increasing $N^{t}MH$ output. Eventually a new equilibrium between protein synthesis and degradation is reached at a lower body-weight and muscle mass (Table 2). The results do not support the suggestion that differences in early dietary history have affected the fractional rate of muscle protein degradation.

Guillaume (1976) suggested that dwarf birds may need a higher level of protein in their diet compared with normal broiler breeders because of their higher rate of protein turnover. This conclusion is only valid if food intake does not show a similar relationship to mature-weight as protein turnover. There was no evidence that this was the case in the present experiment (values not shown).

In conclusion, we have shown that lines of mature chickens of widely different body size and composition exhibit rates of muscle protein turnover which differ in proportion to adult body-weight in agreement with the well-established biological principle that larger species have lower rates of various metabolic processes. Clearly, the biological significance of differences in aspects of growth at immature ages should be interpreted with caution.

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