Recent studies in poultry calorimetry

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The energy metabolism of poultry has been well reviewed in recent years. Most research has been done on the domestic fowl, mainly because of its commercial importance. Useful introductory reviews are those of Freeman (1971) and Whittow (1976). The more specialist reviews cover: effects of high environmental temperature (Smith & Oliver, 1971; Smith, 1973); principles and assumptions of calorimetry (Farrell, 1974); effects of physical factors (van Kampen, 1974); effects of biological factors (Balnave, 1974) and effects of energy expenditure under productive conditions (Grimbergen, 1974). This paper is a brief review of the field of poultry calorimetry from about 1973 to 1977; it is not comprehensive but deals with some of the more important work reported during this period.

Embryonic gaseous metabolism

Research on gaseous exchange and energy metabolism (mainly of the chick embryo) has been reviewed most recently by Romanoff (1967) and Freeman & Vince (1974). Much of the earlier work (Barott, 1937; Romijn & Lokhorst, (1960, 1962) was concerned with relationships between respiratory metabolism, embryonic age and physical and chemical characteristics of the incubation environment. More recently, the influence of egg-shell characteristics, area, thickness and porosity, all combined in the term gaseous conductance, on respiratory metabolism have been studied (Wangensteen & Rahn, 1970–71; Wangensteen, Rahn, Burton & Smith, 1974; Rahn, Paganelli & Ar, 1974). Wangensteen *et al.* (1970–71) have provided evidence in support of the hypothesis that respiratory gases diffuse through the porous shell along partial pressure gradients. Oxygen tension in the air cell is determined by and influences the rate of oxygen diffusion allowed by the shell oxygen conductance and the oxygen consumption of the embryo. Similar considerations apply to carbon dioxide and water vapour diffusion. Rahn *et al.* (1974) showed, in nine avian species, that the oxygen consumption can be calculated from: $VO_2 = GO_2 . \Delta PO_2$ ml/d, where VO_2 is oxygen consumption ml/d (STPD), GO_2 is oxygen conductance of shell per unit ΔPO_2 in ml/kPa and ΔPO_2 is oxygen partial pressure differential across the shell kPa (i.e., between the air space and ambient air).

Rahn *et al.* (1974) also showed that incubation period is related to oxygen consumption by: $I = K' \frac{W}{VO_2} = K'' \frac{W}{GO_2}$ days, where I is incubation period (d), W is initial egg weight (g), and K' and K'' are constants of proportionality.

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Gaseous conductance of the egg shell, through its effect on gas tensions in the egg, influences metabolic and developmental rates and the timing of certain developmental stages. Visschedijk (1968*a*,*b*) has shown that increased carbon dioxide, or reduced oxygen partial pressure, or both, in the air space advances pipping time.

The limiting effect of gas conductance on metabolic and developmental rates is particularly marked during the later stages of incubation at altitude. Reduced respiratory metabolism at low oxygen tensions has been observed in the laboratory (Lokhorst & Romijn, 1965) and at altitude (Wangensteen *et al.*, 1974; Beattie & Smith, 1975). Wangensteen *et al.* (1974) found that oxygen consumption of 14, 16 and 18 d chick embryos at 3800 m from altitude-adapted hens was 58% of that of unselected eggs at sea level. Total gas conductance was virtually unchanged at altitude, adapted eggs weighed 22% less, gas conductance per unit shell area was 27% greater and oxygen consumption was only 75% of the calculated value for sea-level eggs at sea level. Beattie *et al.* (1975) found no significant difference at sea level between the oxygen consumption from 19 d to hatch of altitude-adapted and sea-level eggs. At 3100 m, adapted and sea-level embryos reduced their oxygen consumption by 9% and 21% respectively. The sea-level eggs and those few chicks which hatched from them were larger than adapted eggs and chicks. It appears that the larger embryos had difficulty in obtaining their greater oxygen requirements because of the low gaseous conductance of the shell per unit mass of embryo.

Age

The heat production of turkeys has been measured most recently by Buffington, Jordan, Junilla & Boyd (1974), Afifi (1975) and Nichelmann, Ellerkamp, Hertrich & Lyhs (1976*a*). Heat losses have been measured by DeShazer, Olson & Mather (1974) and Nichelmann, Ellerkamp, Hertrich & Lyhs (1976*b*). Buffington *et al.* (1974) developed a mathematical model for the total heat production of Wrolstad White Turkeys as a function of age (50–84 d) and weight based on measurements of gaseous metabolism. Afifi (1975) observed that heat production per unit body-weight decreased with age levelling out at about 90 d. Nichelmann *et al.* (1976*a*) fitted a linear log-log function to the relationship between metabolic rate per unit body-weight and age (10–155 d) of White Beltsville turkeys.

Climatic environment

Earlier work on climatic environment and chickens is well covered by the reviews cited. In the USA agricultural engineers have had an important role in this field. They have been particularly concerned to obtain basic information for the design of poultry houses and air-conditioning equipment suitable for the varied macro-climates in different parts of their country. Quite sophisticated calorimeters have been developed and used by them for this purpose. DeShazer, Jordan & Suggs (1970) used a gradient-layer calorimeter to partition the heat losses of hens acclimated to 25° and 35°. Hens acclimated to 35° had a lower heat loss and

maintained heat balance better over the range 25° to 35° than birds acclimated to 25°. Two factors appear to account for these differences: the lower heat production of birds acclimated to 35° is associated with lower body-weight and their evaporative cooling mechanism responds at a lower ambient temperature and with a greater initial sensitivity. As ambient temperature is increased radiative and convective heat losses decrease but increased evaporation maintains heat balance. In birds acclimated to 25° evaporative heat loss does not increase until there has been an appreciable fall in convective and radiative heat loss. Nichelmann, Thomas & Lyhs (1974) maintain that the relationship between metabolic rate (MR) and ambient temperature (T_A) for each of twenty-one different animal species can be defined by a quadratic equation. They have calculated for layers, from the data of Scholander, Hock, Walters, Johnson & Irving (1950), that: $MR_{TA} = 0{\cdot}129T_A^2 - 6{\cdot}86T_A + 180\%$ of minimum MR; and for broilers, from the data of Winkler (1973), that: $MR_{TA} = 0{\cdot}2T_A^2 - 12{\cdot}99T_A + 434\%$ of minimum MR. Misson (1976) measured the metabolic rate of chicks at 1 d in the ambient temperature range 20° to 43°. Chicks, were unable to regulate body temperature outside the thermoneutral zone (34° to 37°). The temperature coefficient of evaporative heat loss increased from 0·024 kJ $kg^{-0{\cdot}75}$ h^{-1} $°C^{-1}$ between 20° and 37° to 6 kJ $kg^{-0{\cdot}75}$ h^{-1} $°C^{-1}$ above 37°. Evaporative heat loss was still not enough to maintain body temperature above 37°. Groups of 20 chicks allowed to huddle reduced heat production per chick by 12·2 and 16·5% at 25° and 20°, respectively, compared with isolated chicks in the same conditions.

DeShazer *et al.* (1974) measured sensible and evaporative heat losses per unit weight of turkey poults at weekly intervals from 0 to 35 d at and 5·6° above and below the recommended brooding temperature for each age. Sensible heat loss at and below the recommended temperature remained fairly constant but above the recommended temperature it increased with age. Evaporative heat losses remained relatively constant over the age range at, above or below the recommended brooder temperature. Nichelmann *et al.* (1976*a*,*b*) fitted quadratic functions to the relationships between heat production (for $weight^{0{\cdot}75}$) and ambient temperature and calculated sensible heat loss (for $weight^{0{\cdot}75}$) at five ages between 10 and 155 d inclusive. There was an exponential relationship between evaporative heat loss and ambient temperature over the same age range.

Smith & Prince (1973) found linear correlations between fasting heat production (FHP) and ambient temperature (range −10° to +20°) for temperature-acclimated male and female mallard ducks. The FHP for unit weight or for $weight^{0{\cdot}75}$ and the temperature coefficient of FHP were greater at all temperatures for the male. The lower critical temperature was 20° and 10° for fasted and fed birds, respectively. Observations on the relationship between heat production and ambient temperature for other species of duck have been reported by Bouverot, Hildwein & LeGoff (1974) and Hagan & Heath (1976).

Feathering insulation

Moulting. Information on the energy cost of moulting in domestic species is

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sparse. Benedict, Landauer & Fox (1932) found metabolic rates from 50 to 100% greater in fasted moulting hens at 18° than in non-moulting hens in the same conditions. Perek & Sulman (1945) obtained values for oxygen consumption during summer laying, autumn moulting and winter laying of 460, 666 and 449 ml/kg per h, respectively, in White Leghorns at 28°. Only the differences between moulting and non-moulting birds were significant. Thomson & Boag (1976) measured pre-moulting, moulting and post-moulting oxygen and metabolizable energy (ME) consumption and crude protein (nitrogen×6·25) intake in Japanese quail (*Coturnix coturnix*) over about 90 d. At an ambient temperature of −10°, peak oxygen consumption averaged 3480 ml/kg per h during moulting and 2100 and 2110 ml/kg per h over the pre- and post-moulting periods respectively. The peak and mean ME during the moult were 25 and 13·6% above pre- and post-moult values. Crude protein intake increased by 17% at peak of moult.

It is not possible, from available results, to partition the energy cost of moulting between increased heat loss due to feather loss, the growth of new feathers and the gain from the cessation of egg production. These costs must depend on the varying critical temperatures throughout the moult, the ambient temperature and the duration of the moult.

Genetically abnormal feathering. Homozygous Frizzle Fowl are characterized by an almost complete lack of feathering in their first year and worn and curly feathers soon after their first moult. Benedict *et al.* (1932) found the average heat production of a group of Frizzle Fowl was 78 and 24% above those of normal Rhode Island Reds at 17·3° and 28° respectively.

Feather deterioration. Olson, DeShazer & Mather (1974) held White Leghorn layers at stocking densities of 1, 2 and 3 birds/cage (0·084, 0·042 and 0·028 m^2/bird) at 22·8° from 38 to 70 weeks of age. There was progressive feather deterioration with age and stocking density. Feather damage was thermally negligible at the lowest stocking density. Sensible heat losses of individual and grouped birds were measured in a direct partitional calorimeter at 69 to 70 weeks. The mean heat losses at 28·3° and 33·9° were 10·4, 11·8 and 13·6 J/s for individual birds previously stocked at 1, 2 and 3 birds/cage, i.e., 13·7 and 31·2% greater for the higher densities. The differences in heat loss between stocking densities were not significant when measured on birds in their original groups. Richards (1977) compared the mean metabolic rates of six normally-feathered, medium-weight layers and six with severe feather loss selected from a battery caged laying flock, at nine different temperatures in the range 0° to 38°. The mean metabolic rate of the poorly feathered groups was significantly higher than that of the control group at temperatures between 0° and 30°, varying from 93 to 26% higher at 0° and 30°, respectively. Differences were not significant at 35° and 38°. The state of feathering was not associated with significant differences in evaporative heat loss at any point in the temperature range. Hartung (1967) measured the effect of quantitative doses of oil applied to the feathers of ducks on their metabolic rates. The heat production of severely oiled birds was more than double that of untreated controls at air temperatures in the range −10° to +20°.

Recovery of insulation was almost complete in 7 d. Survival time was dependent on the size of the body fat reserves rather than on the exposure temperature down to −26°.

Artificial defeathering. O'Neill, Balnave & Jackson (1971) measured fasting heat production, maintenance ME requirements and net availability of ME in two fully feathered and two virtually completely defeathered (clipped and plucked) cockerels over the temperature ranges 15° to 34° and 22° to 38°. At 22°, heat production of defeathered birds was about double that of fully feathered birds and fell steadily with increasing ambient temperature to about the same level for both groups at 34°. The temperature coefficients of metabolic rate over this range (derived from the data of O'Neill *et al.* 1971) for feathered and defeathered birds were approximately −0·05 and −0·28 J/s respectively. Maintenance ME requirements decreased with rising temperature in both groups. The observations on net availability of ME were inconclusive. Brush (1965) found that the oxygen consumption of artificially defeathered Californian quail (*Lophortyx californicus*) at 20° was about double that of normally feathered birds. Between 20° and 37·5° the temperature coefficients of oxygen consumption for feathered and defeathered birds were −68 and −153 ml/kg per h, respectively. In preliminary studies Tullett (personal communication) has measured the oxygen consumption and feed consumption at 20° of normally feathered, neck defeathered and neck and breast defeathered (defeathered by clipping) layers of a brown medium layer strain (Ross Rangers). No significant difference was found in either oxygen or feed consumption of neck defeathered birds compared with normally feathered controls. The oxygen consumption of neck and breast defeathered birds was of the order of 15–20% greater than that of normal controls.

Muscle activity

Posture. When 1-year-old White Leghorn hens were alternately sitting and standing for eight consecutive 30-min periods their mean heat production was 20·5 and 25·0 kJ/kg$^{0.75}$ per h, respectively, an increase of 22% associated with the standing position (van Kampen, 1976*c*). During 2-h periods of standing, heat production in the first and last 30 min was 25 and 16% greater than that calculated for sitting. This 9% reduction with time was associated with a concomitant reduction in the number of head and neck movements. Deighton & Hutchinson (1940) found a mean increase in heat loss of 45% when hens changed from a sitting to a standing position in a direct calorimeter. In this work it is not possible to distinguish between stored heat losses, the energy cost of rising or other muscular activity and the energy cost of maintaining the standing posture.

Walking. Van Kampen (1976*b*) found that the energy cost of walking on a treadmill was a linear function of speed over the range 0·5 to 2·5 km/h. At 0 (measured by extrapolation), 1 and 2 km/h the metabolic rate was 41, 53 and 65% above the measured resting level of 24·59 kJ/kg per h. This implies that the energy cost of walking has two components: a constant walking postural cost and a speed-related cost. Increased stride length and increased stride frequency accounted for

71 and 29% of the increase in speed. Walking involves relatively inefficient reciprocating activity of the limbs so one would expect increasing stride length up to the limit to be the most efficient method of increasing speed.

Activity associated with oviposition. Hens often greatly increase their physical activity before laying (Bessei & Bessei, 1974). Van Kampen (1976*a*) measured the metabolic rate of layers in cages and on litter before and after laying. During the 90 min preceding oviposition the metabolic rate of caged layers was approximately 17% greater than during the corresponding interval on non-laying days. Bessei & Bessei (1974) observed that physical activity was greater in cages than on litter. Van Kampen (1976*a*) found that metabolic rate before oviposition was greater in cages than on litter. Whilst the short-term energy cost of laying in cages may be high it accounts for an increase of only about 0·4% over 24 h.

Eating. Van Kampen (1976*c*) measured the mean heat production associated with eating. It reached a peak value 37% above the resting level during the 15 min when the birds were eating, falling slowly to about 13% above resting level during the next 2 h. It was calculated that feeding activity per se accounted for about 3% of the heat production over 24 h.

Diurnal variations. Buffington, Jordan, Junilla & Boyd (1974) observed that the metabolic rate of turkeys was 33% higher in the light than in the dark. Earlier workers had made similar observations on chicks. Lundy, MacLeod & Jewitt (1977) measured metabolic rates at hourly intervals over 22 h in two commercial layer strains, Warren S.S.L. (a brown, medium-weight strain) and Babcock 300 (a white light-weight strain). Both strains were kept at 20° on a 14 h light 10 h dark lighting cycle. In freely fed and fasted Warrens, heat production was about 41% higher in the light than in the dark. In freely fed and fasted Babcocks it was 35 and 53%, respectively, higher in light than in the dark. Immediately the lights were switched on heat production increased to a peak and then declined over a period of 2 to 4 h. The peak accounted for about 1% of daily metabolism in fasting birds and between 1·8 and 2·6% in fed birds. It appeared to be associated with increased activity.

Shivering. Aulie (1976) measured the oxygen consumption of fasting bantam hens, mean weight 548 g, at 15° and of willow ptarmigan (*Lagopus lagopus*), mean weight 680 g, at −10° to −15°. The heart rate and the electromyograph of pectoral muscles were measured simultaneously. The two groups of birds had been adapted for 6 months to temperatures below their critical temperatures. The ptarmigan shivered for about 16% of the exposure time, mean peak oxygen consumption was about 46% above the resting level of 1180 ml/kg per h. The bantams shivered continuously, oxygen consumption was stable at 36% above the resting level of 720 ml/kg per h. The pattern of heart rate and pectoral muscle activity was similar to that of oxygen consumption in each species.

Nutrition

Calorimetric techniques have been used extensively for nutritional studies on poultry. Most recently work has been done on the effects of energy concentration,

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strain characteristics, energy restriction and certain pathological conditions on the utilization of dietary energy for production.

Energy concentration. Farrell, Cumming & Hardaker (1973), comparing diets of eight different ME concentrations, found that food intake was inversely related to ME concentration. Chickens on medium ME concentrations (about 13·0 MJ/kg) required least ME, had the highest conversion efficiency and the maximum growth rate. Diets of eight different ME concentrations were then fed to groups of five young cockerels in calorimeters (Farrell, 1974). The availability of ME was 80 and 60% when the energy balance was negative and positive, respectively. It was suggested that protein synthesis continued when the chickens were in negative energy balance and that fat was frequently catabolised when they were in positive energy balance.

Strain characteristics. When comparing the energy metabolism of Black Australorps, White Leghorns and Black Australorps×White Leghorns, Farrell (1975) found that the gross efficiency of egg production of the White Leghorn was highest although the crossbred had a higher availability of ME and a higher efficiency of conversion of ME to egg energy than had the other two strains. Pym & Farrell (1977) compared the energy and nitrogen balance of three broiler strains selected for growth rate (W), food consumption (F) and food conversion efficiency (E). Total food and ME intake, maintenance energy requirement, resting and fasting heat production, fasting excretory energy loss, energy balance and carcass fat content were all greater in the F line. Metabolizability of the diet was 0·8% greater in the E line than in the F and control lines.

Energy restriction. MacLeod & Shannon (1978) measured the fasting (FHP) and resting heat production (RHP) of two hybrid laying strains at intervals during 25 weeks post-peak-of-lay. Of each strain, five birds were fed freely and five were restricted to 80% of the free energy intake. In each strain the RHP was about 7% lower in restricted than in control birds but there was no difference in RHP/unit metabolic mass ($kg^{0·75}$). Mean FHP/bird and FHP/$kg^{0·75}$ were 18 and 12% lower in restricted than in control birds. Heat increment of feeding and calculated maintenance energy were higher and net availability of ME for maintenance and production was lower in restricted birds. Gross efficiency of egg production increased in restricted birds. Final liveweight and total carcass energy were 15 and 30% lower in restricted birds of both strains.

Nutritional status and disease. Rajion & Farrell (1976) fed chicks on diets containing 0, 0·7 and 1·2 ppm of aflatoxin. Control chicks were restricted to the same food intake as experimental chicks. In 14 d mortality of experimental chicks was from 53 to 72%. Respiratory metabolism was measured on survivors between 2 and 5 weeks of age. Birds surviving the highest aflatoxin levels grew better, retained more nitrogen, had a better energy balance, a lower FHP (kJ/$kg^{0·75}$) and a higher water consumption than the other two groups. All experimental birds showed typical aflatoxicosis lesions. The major effect of aflatoxicosis was to reduce food intake either through an effect on appetite centres or as a rate-limiting factor in key metabolic pathways in the liver. Walker & Farrell (1976) also used

respiratory calorimetry in association with dietary balance techniques to study the effect of a nematode infection on energy and nitrogen balance of chickens. They found a significant reduction in the metabolizability of dietary energy and nitrogen retention of chicks infected with *Ascaridia galli*. Food utilization was severely reduced. Vitamin A deficiency appeared to reduce the severity of these effects.

Hormonal influences

Thyroid hormones. Bobek, Jastrzebski & Pietras (1977) measured oxygen consumption, plasma triiodothyronine (T_3) and thyroxine (T_4) in White Rock chickens aged 1 d to 8 weeks. They found a good positive correlation (+0·98 to +0·78) between oxygen consumption and T_3 but no systematic relationship between oxygen consumption and T_4. They attribute differences between their findings and those of previous workers to the fact that they were studying endogenous hormone levels, or to differences in experimental conditions.

Norepinephrine and dopamine. Hillman, Scott & van Tienhoven (1977) measured the effects of intraventricular injection of norepinephrine and dopamine, one of its precursors, on heat production and heat loss of White Leghorns at ambient temperatures of 9°, 20° and 35°. Heat production was reduced, about 35% at 9° and 20° and about 15% at 30°, by inhibiting shivering or reducing activity or both. Evaporative heat loss was reduced 3% at 9° and 20° and about 15% at 35°, associated with a reduced respiratory rate. Both drugs produced hyperthermia at 35° and hypothermia at 9°. Hillman *et al.* concluded that it is the physiological effectors on which the drugs act rather than action of the drugs themselves which are influenced by the ambient temperature.

REFERENCES

Afifi, M. A. (1975). *Arch. Geflügelk.* **39**, 347.
Aulie, A. (1976). *Comp. Biochem. Physiol.* **53A**, 347.
Balnave, D. (1974). In *Energy Requirements of Poultry*, p. 25 [T. R. Morris and B. M. Freeman, editors]. Edinburgh: British Poultry Science Ltd.
Beattie, J. & Smith, A. H. (1975). *Am. J. Physiol.* **228**, 1346.
Benedict, F. G., Landauer, W. & Fox, E. L. (1932). *Storrs Agric. Exp. Stn. Bull.* no. 177.
Bessei, H. & Bessei, W. (1974). *Arch. Geflügelk.* **38**, 94.
Barott, H. G. (1937). *Tech. Bull. U.S. Dep. Agric.* no. 553.
Bobek, S., Jastrzebski, M. & Pietras, M. (1977). *Gen. Comp. Endocrinol.* **31**, 169.
Bouverot, P., Hildwein, G. & LeGoff, D. (1974). *Resp. Physiol.* **21**, 255.
Brush, A. H. (1965). *Comp. Biochem. Physiol.* **15**, 399.
Buffington, D. E., Jordan, K. A., Junilla, W. A. & Boyd, L. L. (1974). *Trans. A.S.A.E.* **17**, 542.
Deighton, T. & Hutchinson, J. C. D. (1940). *J. agric. Sci., Camb.* **30**, 141.
De Shazer, J. A., Jordan, K. A. & Suggs, C. W. (1970). *Trans A.S.A.E.* **13**, 82.
De Shazer, J. A., Olson, L. L. & Mather, F. B. (1974). *Poult. Sci.* **53**, 2047.
Farrell, D. J., Cumming, R. B. & Hardaker, J. B. (1973). *Br. Poult. Sci.* **14**, 329.
Farrell, D. J. (1974). *Br. Poult. Sci.* **15**, 341.
Farrell, D. J. (1974). In *Energy Requirements of Poultry*, p. 1 [T. R. Morris and B. M. Freeman, editors]. Edinburgh: British Poultry Science Ltd.
Farrell, D. J. (1975). *Br. Poult. Sci.* **16**, 103.
Freeman, B. M. (1971). In *Physiology of the Domestic Fowl*, p. 279 [D. J. Bell and B. M. Freeman, editors]. London: Academic Press.

Freeman, B. M. & Vince, Margaret, A. (1974). In *Development of the Avian Embryo.* p. 119. London: Chapman & Hall.
Grimbergen, A. H. M. (1974). In *Energy Requirements of Poultry,* p. 61. [T. R. Morris and B. M. Freeman, editors]. Edinburgh: British Poultry Science Ltd.
Hagan, Ann & Heath, J. E. (1976). *Poult. Sci.* **55,** 1899.
Hartung, R. (1967). *J. Wildl. Mgmt.* **31,** 798.
Hillman, P. E., Scott, N. R. & Van Tienhoven, A. (1977). *Am. J. Physiol.* **232,** R137.
Lokhorst, W. & Romijn, C. (1965). In *Energy Metabolism,* p. 419. [K. L. Blaxter, editor]. London: Academic Press.
Lundy, H., MacLeod, M. G. & Jewitt, T. R. (1978). *Br. Poult. Sci.* **19,** (In the Press.)
MacLeod, M. G. & Shannon, D. W. F. (1978). *Br. Poult. Sci.* **19,** (In the Press.)
Misson, B. H. (1976). *J. agric. Sci., Camb.* **86,** 35.
Nichelmann, M., Thomas, E. & Lyhs, L. (1974). *Mh. Vet. Med.* **29,** 656.
Nichelmann, M., Ellerkamp, S., Herntrich, I. & Lyhs, L. (1976*a*). *Mh. Vet. Med.* **31,** 213.
Nichelmann, M., Ellerkamp, S., Herntrich, I. & Lyhs, L. (1976*b*). *Mh. Vet. Med.* **31,** 302.
O'Neill, S. J. B., Balnave, D. & Jackson, N. (1971). *J. agric. Sci., Camb.* **77,** 293.
Olson, L. L., DeShazer, J. A. & Mather, F. B. (1974). *Trans. A.S.A.E.* **17,** 960.
Perek, M. & Sulman, F. (1945). *Endocrinology* **36,** 240.
Pym, R. A. E. & Farrell, D. J. (1977). *Br. Poult. Sci.* **18,** 411.
Rahn, H., Paganelli, C. V. & Ar, A. (1974). *Respir. Physiol.* **22,** 297.
Rajion, M. A. & Farrell, D. J. (1976). *Br. Poult. Sci.* **17,** 79.
Richards, S. A. (1977). *J. agric. Sci., Camb.* **89,** (In the Press.)
Romanoff, A. L. (1967). *Biochemistry of the Avian Embryo,* p. 276. London: John Wiley & Sons.
Romijn, C. & Lokhorst, W. (1960). *J. Physiol.* **150,** 239.
Romijn, C. & Lokhorts, W. (1962). *Proc XII Wld's. Poult. Congr.,* p. 136.
Scholander, P. F., Hock, R., Walters, V., Johnson, F. & Irving, L. (1950). *Biol. Bull.* **99,** 237.
Smith, A. J. & Oliver, J. (1971). *Poult. Sci.* **50,** 912.
Smith, A. J. (1973). *Trop Anim. Hlth. Prod.* **5,** 239.
Thompson, D. C. & Boag, D. A. (1976). *Condor* **78,** 249.
Van Kampen, M. (1974). In *Energy Requirements of Poultry.* p. 47 [T. R. Morris and B. M. Freeman, editors]. Edinburgh: British Poultry Science Ltd.
Van Kampen, M. (1976*a*). *J. agric. Sci., Camb.* **86,** 471.
Van Kampen, M. (1976*b*). *J. agric. Sci., Camb.* **87,** 81.
Van Kampen, M. (1976*c*). *J. agric. Sci., Camb.* **87,** 85.
Visschedijk, A. H. J. (1968*a*). *Br. Poult. Sci.* **9,** 185.
Visschedijk, A. H. J. (1968*b*). *Br. Poult. Sci.* **9,** 197.
Wangensteen, O. D. & Rahn, H. (1970–71). *Resp. Physiol.* **11,** 31.
Wangensteen, O. D., Rahn, H., Burton, R. R. & Smith, A. H. (1974). *Respir. Physiol.* **21,** 61.
Walker, T. R. & Farrell, D. J. (1976). *Br. Poult. Sci.* **17,** 63.
Whittow, G. C. (1976). In *Avian Physiology,* 3rd ed., p. 174 [P. D. Sturkie, editor]. New York: Springer Verlag.
Winkler, G. (1973). In dissertation: *Zum Wärmehaushalt des Broilers,* Biowiss. Fak., Humboldt Universität, Berlin.
Wooley, J. B. & Owen, R. B. (1977). *Comp. Biochem. Physiol.* **57A,** 363.

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