

Body composition of animals during sucking and the immediate post-weaning period

By D. M. WALKER, *Department of Animal Husbandry, University of Sydney, Sydney, New South Wales 2006, Australia*

Postnatal growth immediately after birth is directed towards ensuring the survival of the individual. Widdowson & Crabb (1976) reported that while piglets gain little body-weight during the first 24 h of life, those organs essential for survival gain weight extremely rapidly. Similarly, the postnatal growth of fur or hair in animals born naked, such as rats and mice, and the accumulation of fat in the pig (Elliot & Lodge, 1977) and in other newly-born animals, are protective against the loss of metabolic heat. It has been suggested by de Passillé & Hartsock (1979) that, since piglets have only a limited ability to metabolize fat during the first few days of life (Curtis & Rogler, 1970), an accumulation of fat will occur even when the energy intake is limited. In addition, many young animals are born with reserves of glycogen which provide a short-term but useful energy source in early postnatal life (Shelley, 1969) and reserves of brown fat that produce heat without shivering in the critical period soon after birth. Rowlatt *et al.* (1971) examined 123 mammalian species in the perinatal period for the presence of brown fat, and observed that while it was scarce in some species, it was totally absent in marsupials and edentates.

Composition of the newborn

Widdowson (1950) gave values for the gross body composition of seven species at birth and drew attention to the diversity in the chemical and physical maturity of the newborn. Some more recent values are those of Sawicka-Kapusta (1970) for the common vole; Sheng & Huggins (1971) for the beagle dog; Sawicka-Kapusta (1974) and Fedyk (1974) for the bank vole; Meyer & Ahlswede (1976) for the foal; Kaufman & Kaufman (1977) for the old-field mouse; Holleman & Dieterich (1978) for the brown lemming; and a summary of values for the calf and the lamb by the Agricultural Research Council (1980).

Gross body composition during sucking

The early literature on this subject was reviewed by Spray & Widdowson (1950) and the general picture has changed little since then. During the sucking period the absolute and proportionate fat content of the body increases and, in an inverse relationship, the proportion of water decreases. The ratio, protein:ash also changes as the animal increases in weight, but less sharply than the fat–water relationship.

Norton *et al.* (1970) studied the changes in the gross body composition of the preruminant lamb during the first 8 weeks of life (live-weight range 3–15 kg), when

given milk-substitutes varying in crude protein (nitrogen $\times 6.25$) content from 120 to 460 g/kg, while Searle and colleagues studied the changes in the body composition of lambs whilst with their mothers at pasture, or when given a cow's-milk diet and weaned under pen conditions (Searle, 1970; Searle *et al.* 1972; Searle & Griffiths, 1976). These authors are agreed that when lambs are restricted to a particular diet, such as reconstituted cow's milk, their body composition is closely related to body-weight rather than to age or rate of gain, an observation which is in agreement with the conclusions of Mitchell *et al.* (1928). This relation during the sucking period has also been noted by Morgan (1969) in calves, and by Fraga *et al.* (1978) in rabbits but, as pointed out later, is not applicable to all species.

Effect of plane of nutrition. Campbell & Dunkin (1983) fed groups of sucking pigs on different amounts of milk-substitute of constant composition so that they grew at different rates. They then examined the effect on their body composition when they were slaughtered at the same body-weight. Similarly, Widdowson & McCance (1960) with sucking rats, and Spencer & Hull (1984) with sucking rabbits, were able to increase the milk intakes of individual newly-born young, and thus their rate of gain, by manipulating the number of rat pups suckled per foster mother, or by double-feeding baby rabbits on two does. The results of these experiments with pigs, rats and rabbits showed convincingly that if the voluntary intake of milk can be increased during early life, then the young will not only grow more quickly but will be fatter at any given body-weight than young that have grown more slowly.

In the sucking lamb (Norton *et al.* 1970) and calf (Morgan, 1969), the relation between body-weight and body composition appears to be unaffected by the plane of nutrition, provided that the animals are in positive energy balance (cf. Mitchell & Jagusch, 1972). This lack of response may be accounted for by the relatively-lower voluntary feed intake of preruminant animals, so that no excess energy is available to be stored as fat (Fowler, 1974). In this regard, Hodge (1974) has shown that the voluntary energy intake of sucking pigs exceeds that of preruminant lambs by over 50% during the first 5–8 weeks of life.

Effect of sex. No sex-related differences in body composition have been reported in piglets up to 4 weeks of age, or in rabbits (Spray & Widdowson, 1950), or guinea-pigs (Pitts, 1956) during infancy. However, by 8 weeks of age significant sex-related differences in carcass composition were noted in pigs given high-, but not low-protein diets (Filer *et al.* 1966). Differences in body fat content between sexes were observed in lambs only at body-weights above 14 kg (Searle & Griffiths, 1976).

Effect of dietary protein concentration. This factor has long been known to have an effect on body composition in simple-stomached animals (for example, rats, Forbes *et al.* 1935; pigs, Filer *et al.* 1966; lambs, Norton *et al.* 1970; calves, Donnelly & Hutton, 1976). At low dietary protein concentrations the amount of protein that can be deposited is limited by the supply of amino acids, and excess energy is stored as fat (Fowler, 1974). At high dietary protein concentrations the

supply of non-protein energy is limited, with the result that excess protein is used as a source of energy and fat deposition is restricted. This effect can also be demonstrated in ruminants when they are given diets with a high digestible energy content (for example, sheep, Ørskov *et al.* 1971; cattle, Lindsay & Davies, 1981).

Frequency of feeding. If sucking young are given their daily allowance of milk in one (or two) meals each day, they will have significantly heavier stomachs than animals fed at frequent intervals (cf. rabbits, Davies *et al.* 1964; lambs, Walker *et al.* 1967).

Mineral composition of the body

The changes in the mineral composition of the body during growth have been discussed by Widdowson & Dickerson (1964) for a number of non-ruminant species, and by the Agricultural Research Council (1980) for sheep and cattle. It would seem that, unlike the other gross components of the body, e.g. protein, water, ash and fat, there is no universally-applicable relation between the concentration of individual major minerals and empty-body-weight. However, during the sucking period, when lambs were given a milk-substitute of constant composition, the calcium and phosphorus contents of the body were closely related to empty-body-weight (Walker, 1972).

Slater & Widdowson (1962) drew attention to the reduction in the concentration of Ca and P in individual bones and whole bodies of kittens during the early sucking period, and suggested that the amounts of Ca and P available in mother's milk may be insufficient in a number of species to enable the calcification of the skeleton to keep pace with the increase in size (e.g. puppies, Burns & Henderson, 1936; rabbits, Weidmann & Rogers, 1958; rats, Dickerson & Widdowson, 1960; pigs, Manners & McCrae, 1963). There are no comparable values for sucking ruminants.

In all eutherian mammals so far studied there is a rapid accretion of mineral matter in the skeleton in late pregnancy so that if, for example, the human baby is born prematurely, then it is difficult, due to problems in absorption, to supply a similar amount of Ca as a component of an artificial milk, to that which would normally have been supplied from the maternal blood (Widdowson, 1974). A similar problem would seem to face the pouch-young marsupial, which is born immature and is dependent entirely on the minerals in milk to meet its needs during growth. Although it is not known whether the mineral concentrations reported for the milk of the tammar wallaby (*Macropus eugenii*) are applicable to the milks of all marsupials, it is noteworthy that the concentrations of Ca and P, relative to energy, are not constant but increase during lactation, and are much higher in late lactation than those reported in the milks of eutherian species (Green, 1984).

Body composition during weaning

Under natural conditions the process of weaning from milk on to solid food is a gradual one, and it is to be expected that the changes in body composition will also

be gradual (cf. Searle, 1970). However, with many of our laboratory and domestic animals, weaning is relatively abrupt and is frequently at an earlier stage of growth than would occur in nature.

Many authors have reported a reduction in the rate of deposition of body fat following weaning (e.g. rat, Chanutin, 1931; mouse, Stanier & Mount, 1972), and in some animals this appears to be associated with a negligible change in the rate at which protein is deposited (lambs: Mitchell & Jagusch, 1972; Kellaway, 1973; Searle & Griffiths, 1976; Robelin *et al.* 1977; pigs: Wood & Groves, 1963; Thorbek, 1969). However, all authors are not agreed on this point and there may be some true species differences. For example, Hodge (1974) has studied the effect of energy restriction on sucking pigs and lambs and has shown that restriction to 80% of *ad lib.* intake affects the two species differently. In lambs the rate of deposition of fat and of protein was reduced, whereas in piglets the rate of protein deposition was maintained and only fat deposition was restricted. The difference in response of these two species can be explained on the basis of the observed differences in voluntary food intake (see section on the effect of the plane of nutrition on body composition).

Zucker & Zucker (1963) drew attention to the importance of comparing weights of fat in the whole body, rather than percentages, in analysing the effect of weaning in rats, and this comment is equally applicable to other species. Comparisons on the basis of proportions may lead to the conclusion that animals have lost fat at weaning, whereas they may have actually maintained, or even made slight gains on, the amounts present before weaning.

Whittemore *et al.* (1981), in their studies with baby pigs, have observed that the changes in body composition following weaning are not uniformly distributed throughout all body compartments, but show clear evidence of the protection of 'essential body parts' at the expense of the 'non-essential'. They noted that the fraction containing the essential organs was consistently in positive balance, as also was the muscle and bone fraction, while the fatty fraction was consistently reduced, with a simultaneous loss of fat and a gain in water.

Most newborn animals accumulate fat postnatally, thus the 'physiological undernutrition' of the guinea-pig (Widdowson & McCance, 1955) in the 1st week of life, during which time it loses 70% of the weight of chemical fat present at birth, may appear to be atypical. However, the guinea-pig starts to eat solid food soon after birth so that, in fact, the 1st week of life may be regarded as the time of weaning.

One of the most extreme cases in nature of abrupt weaning occurs with some species of seals (e.g. Atlantic harp seal, Sivertsen, 1941; grey seal, Amoroso & Mathews, 1951; southern elephant seal, Laws, 1959). Bryden (1968) recorded changes in the weight of elephant seal pups during early life and noted that, from a birth weight of about 40 kg, the pups gain weight rapidly so that in 22 d they increase in weight to about 140 kg. At this stage the mothers return to the ocean and the pups are weaned, abruptly. During the next 6–7 weeks the pups starve and their weight drops to about 80 kg. The body fat content of the elephant seal pup

that weighs 40 kg at birth is about 2.4 kg (dissectible), but during sucking this increases to about 70 kg, followed during fasting by a loss of approximately half of this dissectible fat (Bryden, 1968). In contrast to the weaned pig, in which Whitemore *et al.* (1981) showed that much of the loss in weight of fat following weaning is from the carcass fatty tissue (mainly subcutaneous), there is evidence in the harp seal that, during the post-weaning fast, most of the loss in weight is accounted for by a loss of 'core' weight, and that there is actually an increase in the blubber layer (subcutaneous), which has been built up during sucking until it represents some 60% of total body-weight (Stewart & Lavigne, 1980). However, the 'core' contains extensive stores of lipid, as well as protein, to sustain the young seal during the fast of 6 weeks or longer (Worthy & Lavigne, 1983). This would seem to be another clear example of protection, in that the vital insulating layer of blubber is retained at the expense of the dispensable lipid stores in the 'core'.

Growth and development affecting body composition

In just the same way that fat may be retained in the body and perform a protective function in the face of a demand for energy, as in the harp seal, so also may the distribution of protein in certain muscles, or its retention in certain organs, for example, the brain, be of importance in survival. Bryden (1969) and Berg & Butterfield (1976) have related the growth of muscles and their relative weights to the functions that are of importance in survival, whether they be in terms of agility (development of the distal parts of the limbs), or mobility (a greater proportion of the muscles will be found in the whole of the limbs) or, in seals, for swimming (development of the muscles surrounding the spinal column). Furthermore, it has been suggested (R. M. Butterfield, personal communication) that in species which are immobile for many months after birth, e.g. marsupials and humans, the muscle mass represents an increasing proportion of body-weight as the young individuals increase in age (Hopwood, 1976; Malina, 1978) whereas, in species that are mobile at birth, e.g. calves and lambs, the ratio, muscle mass:body-weight remains almost constant from birth to adulthood (Butterfield *et al.* 1971; Lohse, 1971).

The concept of 'adaptive growth' (Goss, 1964) also applies to those species which have a specialized form of digestion, e.g. ruminants and herbivores. Wardrop & Coombe (1960) have shown that although the lamb is almost entirely dependent on milk during the first 3 weeks of life, the organs concerned with the fermentation of food in later life, namely the rumen and reticulum, increase about fivefold in weight while live weight has doubled. By the age of 8 weeks the 'organs of fermentation' have increased fourteenfold since birth, while live weight has quadrupled. Simultaneously, the mucosa of the rumen has developed a papillary structure in response to the food eaten and, while hay alone causes an increase in rumen volume, only those diets that contain a high proportion of readily-digestible nutrients lead to maximum papillary development (Warner *et al.* 1956; Wardrop, 1961).

Digestive enzymes

Eutherians. The development of digestive enzymes in non-ruminants differs considerably from the development in preruminants, particularly of those enzymes concerned with carbohydrate digestion (Bailey *et al.* 1956; Dollar & Porter, 1957; Walker, 1959*a,b*; Manners & Stevens, 1972; Ekstrom *et al.* 1975; Kidder & Manners, 1980). In the pig, for example, while those enzymes concerned with the digestion of maltose, sucrose and starch increase in activity from soon after birth, the ability to digest cellulose in the foregut never develops. On the other hand, in 'foregut fermenters' such as ruminants, and probably also in many marsupials (Hume, 1982), while the enzymes necessary for the digestion of the nutrients in milk are present at birth, the enzymes required for the digestion of maltose and starch are virtually absent, and for sucrose totally absent, so that the utilization of these carbohydrates, and of cellulose, must await the establishment of a microbial population and, in the case of the ruminants, the maturing of the rumen mucosa (Walker & Walker, 1961; Walker & Simmonds, 1962).

Although it is frequently stated that the activity of lactase (*EC* 3.2.1.23) in eutherians decreases with age (de Groot & Hoogendoorn, 1957), this statement, as Widdowson (1984) has recently pointed out, may be misleading. Walker (1959*a*) has shown that if total lactase activity in the intestine is considered, rather than activity per unit weight of tissue, or mucosal protein, then lactase activity in the preruminant lamb and piglet is relatively constant for the first 5 weeks of life. Nevertheless, the total lactase activity in the small intestine of the piglet decreases after weaning, with a concomitant decrease in the weight of the small intestine mucosa and its content of protein (Hampson & Kidder, 1984; McCracken, 1984).

In adult ruminants and ruminant-like mammals there is a symbiotic relation between the host animal and the microbes that live in the foregut. Until recently the mechanism by which these microbes are subsequently digested by the host animal has not been widely known. Thus the observations to be described have particular relevance to this question. Dobson *et al.* (1984) measured the lysozyme *c* activities in the stomach mucosa of twenty-five mammalian species and found that the activities for the ruminants and for a leaf-eating monkey, the langur, are many times higher than those for mammals lacking a foregut. They suggested that stomach lysozyme *c* functions as a major digestive enzyme in ruminant-like mammals, helping to make those bacteria which enter the stomach from the foregut available for hydrolysis by conventional digestive enzymes. Furthermore, they have shown that lysozyme *c*, which is resistant to digestion by pepsin (*EC* 3.4.23.1), appears in the stomach mucosa of the calf before birth. Its activity during development *in utero* is slow initially, being 1% of the adult level in the first 6 months of fetal life, but increasing to 30% by the end of pregnancy, and achieving adult levels by 3 months after birth.

Marsupials. The newborn marsupial is extremely immature and weighs (in the case of the tamar wallaby) only about one-ten-thousandth of its mother's weight. Throughout the majority of the lactation period it is afforded the protection of its mother's pouch, so there is no apparent need for it to accumulate an insulating

layer of fat in the same way as in many newborn eutherian species. Nevertheless, the fat content in late lactation is comparable with that of newborn lambs and calves. Analyses on the whole bodies of grey and red kangaroos, which were furred and aged between 26 and 32 weeks, but not yet completely out of the pouch, gave values varying from 3.5 to 6.5% (D. M. Walker, unpublished results), which are much higher than those of adults of the same species (1.0%; Tribe & Peel, 1963). The newborn tammar wallaby bears a closer resemblance to a fetus than to most eutherian newborn animals, yet is sufficiently developed at birth to be able to utilize a milk that is complex in composition, and which differs markedly from that of the eutherian mammals. In the tammar wallaby the milk in early lactation contains over 50% of the total solids as carbohydrate, largely in the form of neutral oligo- and polysaccharides and sialyl saccharides, whose major monosaccharide is galactose (Messer & Mossop, 1977; Messer & Green, 1979). There is very little lactose in marsupial milk, and pouch-young marsupials are unable to digest lactose to any appreciable extent (Vickery & Walker, 1982). In fact, the digestive process appears to differ in many respects from that of the eutherian. For example, it has been suggested that the galactose polysaccharides in the milk may be absorbed by pinocytosis, before digestion by lactase (Walcott & Messer, 1980), whilst there is evidence that pouch-young tammar wallabies acquire antibodies from milk by absorption through the intestine (Yadav, 1971). During the sucking period of the young marsupial the food supply of the mother is frequently drastically reduced by drought conditions, and the milk supply to the young may cease temporarily, to be resumed when nutritional conditions improve. Janssens (1984) has described how the enzymes associated with gluconeogenesis develop in the young tammar wallaby during pouch life, and are stimulated by fasting, thus ensuring a supply of glucose for vital tissues. This protective mechanism is, however, confined to the young and does not appear to be responsive to fasting in the adult. Thus, in the tammar wallaby, we have yet another example of an adaptation during the sucking period, directed towards ensuring the survival of the individual.

REFERENCES

- Agricultural Research Council (1980). *The Nutrient Requirements of Ruminant Livestock*. Slough: Commonwealth Agricultural Bureaux.
- Amoroso, E. C. & Mathews, J. H. (1951). *Journal of Anatomy* **85**, 427-428.
- Bailey, C. B., Kitts, W. D. & Wood, A. J. (1956). *Canadian Journal of Agricultural Science* **36**, 51-58.
- Berg, R. T. & Butterfield, R. M. (1976). *New Concepts of Cattle Growth*, pp. 65-142. Sydney: Sydney University Press.
- Bryden, M. M. (1968). Study of the biology of the southern elephant seal, *Mirounga leonina* (Linn.): development and growth. PhD Thesis, University of Sydney.
- Bryden, M. M. (1969). *Growth* **33**, 143-156.
- Burns, C. M. & Henderson, N. (1936). *Biochemical Journal* **30**, 1207-1214.
- Butterfield, R. M., Johnson, E. R. & Pryor, W. J. (1971). *Journal of Agricultural Science, Cambridge* **76**, 453-458.
- Campbell, R. G. & Dunkin, A. C. (1983). *British Journal of Nutrition* **49**, 221-230.

- Chanutin, A. (1931). *Journal of Biological Chemistry* **93**, 31–37.
- Curtis, S. E. & Rogler, J. C. (1970). *American Journal of Physiology* **218**, 149–152.
- Davies, J. L., Widdowson, E. M. & McCance, R. A. (1964). *British Journal of Nutrition* **18**, 385–392.
- de Groot, A. P. & Hoogendoorn, P. (1957). *Voeding* **18**, 2–14.
- de Passillé, A. M. B. & Hartsock, T. G. (1979). *Journal of Animal Science* **49**, 1449–1457.
- Dickerson, J. W. T. & Widdowson, E. M. (1960). *Proceedings of the Royal Society B* **152**, 207–217.
- Dobson, D. E., Prager, E. M. & Wilson, A. C. (1984). *Journal of Biological Chemistry* **259**, 11607–11616.
- Dollar, A. M. & Porter, J. W. G. (1957). *Nature* **179**, 1299–1300.
- Donnelly, P. E. & Hutton, J. B. (1976). *New Zealand Journal of Agricultural Research* **19**, 409–414.
- Ekstrom, K. E., Benevenga, N. J. & Grummer, R. H. (1975). *Journal of Nutrition* **105**, 1032–1038.
- Elliot, J. I. & Lodge, G. A. (1977). *Canadian Journal of Animal Science* **57**, 141–150.
- Fedyk, A. (1974). *Acta Theriologica* **19**, 381–401.
- Filer, L. J., Owen, G. M. & Fomon, S. J. (1966). In *Swine in Biomedical Research*, pp. 141–149 [L. K. Bustad, R. O. McClellan and M. P. Burns, editors]. Richland, Washington: Pacific Northwest Laboratory.
- Forbes, E. B., Swift, R. W., Black, A. & Kahlenberg, O. J. (1935). *Journal of Nutrition* **10**, 461–479.
- Fowler, V. R. (1974). In *Meat Animals: Growth and Productivity*, pp. 285–299 [D. Lister, D. N. Rhodes, V. R. Fowler and M. F. Fuller, editors]. New York: Plenum Press.
- Fraga, M. J., Torres, A., Pérez, E., Gálvez, J. F. & De Blas, J. C. (1978). *Journal of Animal Science* **47**, 166–175.
- Goss, R. J. (1964). *Adaptive Growth*. London: Logos.
- Green, B. (1984). *Symposium of the Zoological Society, London* no. 51, 369–387.
- Hampson, D. J. & Kidder, D. E. (1984). *Proceedings of the Nutrition Society* **43**, 18A.
- Hodge, R. W. (1974). *British Journal of Nutrition* **32**, 113–126.
- Holleman, D. F. & Dieterich, R. A. (1978). *Laboratory Animal Science* **28**, 529–535.
- Hopwood, P. R. (1976). The quantitative anatomy of the kangaroo. PhD Thesis, University of Sydney.
- Hume, I. D. (1982). *Digestive Physiology and Nutrition of Marsupials*, pp. 111–158. Cambridge: Cambridge University Press.
- Janssens, P. A. (1984). *Proceedings of the Nutrition Society of Australia* **9**, 68–75.
- Kaufman, G. A. & Kaufman, D. W. (1977). *Journal of Mammalogy* **58**, 429–434.
- Kellaway, R. C. (1973). *Journal of Agricultural Science, Cambridge* **80**, 17–27.
- Kidder, D. E. & Manners, M. J. (1980). *British Journal of Nutrition* **43**, 141–153.
- Laws, R. M. (1959). *Norsk hvalfangsttidende* **48**, 425–452.
- Lindsay, J. A. & Davies, H. L. (1981). *Animal Production* **32**, 85–93.
- Lohse, C. L. (1971). Studies in the quantitative anatomy of Merino sheep. PhD Thesis, University of Sydney.
- McCracken, K. J. (1984). *Proceedings of the Nutrition Society* **43**, 109A.
- Malina, R. M. (1978). In *Human Growth* vol. 2, *Postnatal Growth*, pp. 273–294 [F. Falkner and J. M. Tanner, editors]. London: Baillière Tindall.
- Manners, M. J. & McCrae, M. R. (1963). *British Journal of Nutrition* **17**, 495–513.
- Manners, M. J. & Stevens, J. A. (1972). *British Journal of Nutrition* **28**, 113–127.
- Messer, M. & Green, B. (1979). *Australian Journal of Biological Sciences* **32**, 519–531.
- Messer, M. & Mossop, G. S. (1977). *Australian Journal of Biological Sciences* **30**, 379–388.
- Meyer, H. & Ahlswede, L. (1976). *Übersichten zur Tierernährung* **4**, 263–292.
- Mitchell, H. H., Kammlade, W. F. & Hamilton, T. S. (1928). *University of Illinois Agricultural Experiment Station, Bulletin* no. 314.
- Mitchell, R. M. & Jagusch, K. T. (1972). *New Zealand Journal of Agricultural Research* **15**, 788–794.
- Morgan, J. H. L. (1969). *New Zealand Journal of Agricultural Research* **12**, 75–86.
- Norton, B. W., Jagusch, K. T. & Walker, D. M. (1970). *Journal of Agricultural Science, Cambridge* **75**, 287–292.

- Ørskov, E. R., McDonald, I., Fraser, C. & Corse, E. L. (1971). *Journal of Agricultural Science, Cambridge* **77**, 351–361.
- Pitts, G. C. (1956). *American Journal of Physiology* **185**, 41–42.
- Robelin, J., Theriez, M., Arnal, M. & Ferrara, M. (1977). *Annales de Zootechnie* **26**, 69–81.
- Rowlatt, U., Mrosovsky, N. & English, A. (1971). *Biology of the Neonate* **17**, 53–83.
- Sawicka-Kapusta, K. (1970). *Acta Theriologica* **15**, 67–79.
- Sawicka-Kapusta, K. (1974). *Acta Theriologica* **19**, 27–54.
- Searle, T. W. (1970). *Journal of Agricultural Science, Cambridge* **74**, 357–362.
- Searle, T. W., Graham, N. McC. & O'Callaghan, M. (1972). *Journal of Agricultural Science, Cambridge* **79**, 371–382.
- Searle, T. W. & Griffiths, D. A. (1976). *Journal of Agricultural Science, Cambridge* **86**, 483–493.
- Shelley, H. J. (1969). *Proceedings of the Nutrition Society* **28**, 42–49.
- Sheng, H. P. & Huggins, R. A. (1971). *Growth* **35**, 369–376.
- Sivertsen, E. (1941). *Hvalrådets skrifter, Oslo* no. 26.
- Slater, J. E. & Widdowson, E. M. (1962). *British Journal of Nutrition* **16**, 39–48.
- Spencer, S. A. & Hull, D. (1984). *British Journal of Nutrition* **51**, 389–402.
- Spray, C. M. & Widdowson, E. M. (1950). *British Journal of Nutrition* **4**, 332–353.
- Stanier, M. W. & Mount, L. E. (1972). *British Journal of Nutrition* **28**, 307–325.
- Stewart, R. E. A. & Lavigne, D. M. (1980). *Journal of Mammalogy* **61**, 670–680.
- Thorbek, G. (1969). *European Association for Animal Production Publication* no. 12, pp. 281–289.
- Tribe, D. E. & Peel, L. (1963). *Australian Journal of Zoology* **11**, 273–289.
- Vickery, K. & Walker, D. M. (1982). *Proceedings of the Nutrition Society of Australia* **7**, 141.
- Walcott, P. J. & Messer, M. (1980). *Australian Journal of Biological Sciences* **33**, 521–530.
- Walker, D. M. (1959a). *Journal of Agricultural Science, Cambridge* **52**, 357–363.
- Walker, D. M. (1959b). *Journal of Agricultural Science, Cambridge* **53**, 374–380.
- Walker, D. M. (1972). *Journal of Agricultural Science, Cambridge* **79**, 171–179.
- Walker, D. M., Cook, L. J. & Jagusch, K. T. (1967). *British Journal of Nutrition* **21**, 275–287.
- Walker, D. M. & Simmonds, R. A. (1962). *Journal of Agricultural Science, Cambridge* **59**, 375–379.
- Walker, D. M. & Walker, G. J. (1961). *Journal of Agricultural Science, Cambridge* **57**, 271–278.
- Wardrop, I. D. (1961). *Journal of Agricultural Science, Cambridge* **57**, 343–346.
- Wardrop, I. D. & Coombe, J. B. (1960). *Journal of Agricultural Science, Cambridge* **54**, 140–143.
- Warner, R. G., Flatt, W. P. & Loosli, J. K. (1956). *Journal of Agricultural Food Chemistry* **4**, 788–792.
- Weidmann, S. M. & Rogers, H. J. (1958). *Biochemical Journal* **69**, 338–343.
- Whittemore, C. T., Taylor, H. M., Henderson, R., Wood, J. D. & Brock, D. C. (1981). *Animal Production* **32**, 203–210.
- Widdowson, E. M. (1950). *Nature* **166**, 626–628.
- Widdowson, E. M. (1974). *Proceedings of the Nutrition Society* **33**, 97–102.
- Widdowson, E. M. (1984). *Proceedings of the Nutrition Society* **43**, 87–100.
- Widdowson, E. M. & Crabb, D. E. (1976). *Biology of the Neonate* **28**, 261–271.
- Widdowson, E. M. & Dickerson, J. W. T. (1964). In *Mineral Metabolism: an Advanced Treatise*, vol. 2, part A, pp. 2–247 [C. L. Comar and F. Bronner, editors]. New York: Academic Press.
- Widdowson, E. M. & McCance, R. A. (1955). *British Journal of Nutrition* **9**, 316–321.
- Widdowson, E. M. & McCance, R. A. (1960). *Proceedings of the Royal Society B* **152**, 188–206.
- Wood, A. J. & Groves, T. D. D. (1963). *Annals of the New York Academy of Science* **110**, 349–357.
- Worthy, G. A. J. & Lavigne, D. M. (1983). *Journal of Mammalogy* **64**, 89–96.
- Yadav, M. (1971). *Immunology* **21**, 839–851.
- Zucker, T. F. & Zucker, L. M. (1963). *Journal of Nutrition* **80**, 6–19.