Adaptation to overfeeding in man

By J. A. STRONG, Department of Medicine, Western General Hospital and R. PASSMORE, Department of Physiology, University of Edinburgh

A short account of work carried out by the authors was given. A full presentation will be published (Strong, Shirling & Passmore, 1967). The summary of this paper is as follows:

Food which provided from 2960 to 7880 kcal in excess of requirements was eaten by sixteen subjects, each for a period of 4 days.

The proportion of the nutrients lost in the faeces was not increased during overfeeding.

The metabolic rates were in no case increased by an amount equivalent to more than 15% of the excess calories. The increase could be attributed to the specific dynamic effect of the extra dietary protein.

The gains in weight ranged from 370 to 5460 g/4 days and the calorie equivalent of the weight gained varied from 1.1 to 10.0 kcal/g. These variations can be attributed to variations in the amount of water retained.

Analysis of their respiratory exchanges suggests that most subjects stored from 400 to 1500 g carbohydrate in the tissues, possibly in the form of muscle glycogen.

REFERENCE


The effect of changes in feeding patterns on the performance of pigs

By R. BRAUDE, National Institute for Research in Dairying, Shinfield, Reading

In feeding livestock, three basic questions must be considered: what, how much, and how to feed? The qualitative and quantitative aspects have been studied by many and information has accumulated which, though by no means complete, permits formulation of standards, requirements and allowances. It is only fairly recently that it has become clear that the problem of ‘How should one feed’ is of basic importance in nutrition, and that understanding of it may help to resolve some of the present controversies about feeding standards and requirements. The problem of how to feed is affected by so many factors that it is virtually impossible to arrive at any hard and fast rules or to make valid general recommendations. All one can do in a brief review is to draw attention to the many aspects of the problem and to some of its implications.

In Table I I have listed under three headings, some of the factors which may influence the pattern of feeding: those connected with the animal, those connected with the feed, and those connected with the management. The list is by no means complete, but it points to the complexity of the problem. It becomes even more
complicated if one accepts that the pattern of feeding may, in turn, affect the animal, the utilization of feed or the choice of management. The old question ‘does the pig grow faster because it eats more, or does it eat more because it grows faster’ is still unanswered. The task of collection and interpretation of objective data is a very difficult one, particularly when one recognizes the existence of an unspecifiable number of interactions, the magnitude of which is often impossible to assess.

**Appetite and palatability**

Two of the most fascinating questions in nutrition are, ‘Why does an animal eat?’ and ‘What is the mechanism controlling eating?’ Obviously, in order to live the pig must eat, but when one considers that, by nutritional manipulations, Professor McCance produced pigs weighing about 10 lb at 1 year of age when their normally fed litter-mates weighed more than 200 lb one begins to wonder about factors controlling intake and utilization of feed, especially when one knows that these grossly retarded pigs were rehabilitated within a very short time (McCance & Widdowson, 1955, 1962; McCance, 1960).

It is often said that appetite and palatability govern the voluntary intake of feed. There are many theories about the mechanisms that control appetite and a few selected references could act as an introduction to the subject (Brobeck, 1948; Kennedy, 1953; Mayer, 1953; Quigley, 1955; Anand, 1961).

Variations of feed intake or rejections of one feed in favour of another are attributed to the palatability or acceptability of the feed offered to the pig. There are many reports of experiments designed either to demonstrate that pigs prefer certain diets or to induce pigs to consume more of a particular diet (Bowland, 1957a; Diaz, Grinstead, Hays, Speer & Catron, 1959; Grinstead, Speer, Catron & Hays, 1960; Krüger, Wassmuth & Kirchberg, 1960; Richter & Antoni, 1961; Salmon-Legagneur & Aumaitre, 1961; Thrasher, Henson & Bogdonoff, 1963; Aumaitre & Salmon-Legagneur, 1964; Kare, Pond & Campbell, 1965; Aldinger & Fitzgerald, 1966) (see also p. 170). In this review, when many references are available, only those published since 1955 are quoted.

Pigs often provide clues to their nutritional requirements. A few examples illustrate this: The practice of adding copper sulphate to diets for pigs arose from the observation that pigs sometimes exhibit a craving for copper (cf. Braude, 1965). Recently Wallace, Houser & Combs (1966) described an experiment designed to allow the pig an opportunity to help to define an optimum dietary copper level.

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**Table 1. Factors influencing the pattern of feeding**

<table>
<thead>
<tr>
<th>Animal factors</th>
<th>Feed factors</th>
<th>Management of feeding</th>
</tr>
</thead>
<tbody>
<tr>
<td>Appetite</td>
<td>Palatability</td>
<td>Self choice</td>
</tr>
<tr>
<td>Health</td>
<td>Density</td>
<td>Alternating</td>
</tr>
<tr>
<td>Genetics</td>
<td>Bulk</td>
<td>Ad lib. v. restricted</td>
</tr>
<tr>
<td>Sex</td>
<td>Grinding</td>
<td>Frequency</td>
</tr>
<tr>
<td>Environment</td>
<td>Soaking</td>
<td>Individual v. group</td>
</tr>
<tr>
<td>Behaviour</td>
<td>Heating</td>
<td>Wet v. dry</td>
</tr>
<tr>
<td>Class of pigs</td>
<td>Drying</td>
<td>Trough v. floor</td>
</tr>
<tr>
<td></td>
<td>Pelleting</td>
<td></td>
</tr>
</tbody>
</table>
Table 2. Free choice of diets by pigs. Feed consumption (% of total feed consumed) and average copper consumption with each of five diets of different copper content (from Wallace, Houser & Combs, 1966)

<table>
<thead>
<tr>
<th>Test</th>
<th>0</th>
<th>125</th>
<th>250</th>
<th>500</th>
<th>1000</th>
<th>Added copper in feed (ppm)</th>
<th>Added copper consumed (ppm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>41</td>
<td>42</td>
<td>10</td>
<td>4</td>
<td>3</td>
<td>130</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>48</td>
<td>28</td>
<td>18</td>
<td>3</td>
<td>3</td>
<td>128</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>38</td>
<td>27</td>
<td>25</td>
<td>6</td>
<td>4</td>
<td>161</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>29</td>
<td>15</td>
<td>27</td>
<td>23</td>
<td>6</td>
<td>264</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Average 170</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The pigs had access to five self-feeders which offered a basal diet supplemented with either 0, 125, 250, 500 or 1000 ppm copper as copper sulphate. Table 2 gives the results of four such tests showing clearly that the pigs avoid diets with the higher contents of copper, and on average seek to consume a diet with 170 ppm of copper. Our recommendation has always been 250 ppm.

It has been shown that pigs prefer rolled or pelleted to whole sorghum grain (Koch, Deyoe & Nam, 1963) and that they prefer wet to dry feeds (Siegl, 1962b). The preference of pigs for certain feeds is complicated by the facts that (1) their preference for flavour changes with age (Diaz et al. 1959; Szecsenyi, 1962), (2) they prefer feeds to which they have been accustomed to new ones of the same chemical composition (Fevrier, 1952), (3) they show preferences which depend on previous consumption and performance (Frape, Hays, Speer, Jones & Catron, 1959; Lucas, Calder & Smith, 1959; Lodge & McPherson, 1961, 1963; Lucas, Livingstone & McDonald, 1962; Elsley, 1963; Nielsen, 1964; Fowler, 1965, 1966; Vanschoubroek, de Wilde & van Spaendonck, 1965; Lister, 1966), (4) their appetites depend upon the mode of physiological processes involved in digestion of particular feeds. It is, of course, impossible in this paper to consider the many factors which influence the efficiency of digestion, but one example is chosen to illustrate how important they are in dealing with the question how to feed the pig. It has been demonstrated that the amount of feed may affect the fate of ingesta in various parts of the gut (Gorrill, Bell & Williams, 1960). The speed with which the feed passes through the gut may be affected by the amount consumed, by its chemical composition or texture and by the way it is fed (Castle & Castle, 1956, 1957; Seerley, Miller & Hoefer, 1962).

**Health**

The animal’s health has a considerable influence on its feed consumption. Though it is generally accepted that disease may adversely affect performance, it is not generally appreciated that as great a damage may be caused by chronic ill-health or subclinical disease. Refusal to eat is often the first sign that something is wrong with the pig. Thus, for example, the appetites of pigs infected with enzootic pneumonia are often poor particularly during the periods of so-called ‘secondary breakdowns’.

**Genetics**

Pigs of different genetic make-up respond differently to different feeding patterns.
Diet and pattern of feeding may affect the results of both phenotypic and genotypic selection: a fact which some geneticists have overlooked.

Genetic factors influence feed consumption, both directly and indirectly, and it has been thought that by selection one could produce a pig that would eat only as much as it could efficiently utilize for the production of a lean carcass, but I doubt the possibility of this.

**Sex**

The interaction between sex and performance in pigs has been recognized in practice for a very long time, but there is very little experimental evidence on the interactions between sex, nutrition, and the pattern of feeding. Suggestions have been made that male and female pigs respond differently to different patterns of feeding, so that it might be advantageous to segregate the sexes but there is little evidence on this subject (Fredeen & Jonsson, 1957; Bowland & Berg, 1959; Braude, Mitchell, Cray, Franke & Sedgwick, 1959; Beacom, 1964; Blair & English, 1965; Cole & Holmes, 1965).

**Environment**

That the climate (temperature, humidity, etc.), both inside and outside the piggeries, can influence feed consumption was shown by Gordon & Luke (1955, 1956), Lucas & Calder (1955), Diggs, Jensen, Terrill & Becker (1957), Cooper (1959), Reddy, Lasley & Tribble (1959), Zivkovic (1959), Berg & Plank (1960), Hunter & Jennings (1960), Sørensen (1961, 1962), Plank & Berg (1963), Houghton, Butterworth, King & Goodyear (1964), Holme & Coey (1966) and Mangold (1966). There is very little evidence to indicate to what extent the patterns of feeding contributed to the observed effects.

Few significant observations have been made on the effect of light on the performance of pigs in relation to feed consumption (Braude, Mitchell, Finn-Kelsey & Owen, 1958; Klockova & Emme, 1961; Scholz & Lips, 1964).

**Behaviour**

Knowledge of the interaction of behaviour and nutrition is very limited. Occasionally, attention is drawn to some spectacular detail such as the effect of forcing the pig to eat while standing on its hindlegs by raising the troughs (Heitman & Bond, 1962; Skjervold, Standal & Bruflot, 1963; Heeney, 1965) or making them eat from different types of troughs (Becker, Jensen, Harmon & Norton, 1964) or from the floor (see p. 174). Siegl (1962b) found during every 12 h observation period that there are two periods when pigs prefer to eat. Recently my colleague M. J. Newport (unpublished) made preliminary observations over a continuous 72 h period.
on the voluntary intake of milk by 4-week-old pigs. On the average, each pig drank milk three times per hour, totalling about 200 ml/h, but there was considerable individual variation.

Class of pigs

Different classes of pigs, baby pigs, growing pigs or breeding pigs, react differently to varying patterns of feeding.

The newborn piglet searches for a teat of its dam and is suckled at hourly intervals throughout the day and night. Why nature demanded such a cumbersome routine is by no means clear, but at Shinfield we are studying the effect of level and frequency of feeding on digestion in the young pig (Braude, Medley, Mitchell, Newport & Porter, 1966). There are many other aspects specific to the baby pig which require study, for example the pattern of feeding imposed by different types of feeders used for creep feeding (Schlegel & Ritter, 1960-1).

Pregnant sows are more efficient converters of feed than non-pregnant sows (cf. Salmon-Legagneur & Rerat, 1962) and this fact must inevitably affect the quantitative and qualitative aspects of feeding, and possibly also the pattern of feeding. A few selected references on the effects of feeding patterns on breeding stock are: Self, Grummer & Casida (1955); Dutt & Barnhart (1956, 1959); Casida (1959); Smith (1959); Stevermer, Kovacs, Hockstra & Self (1959, 1961); Hafez (1960); Kuprijanova (1960); Zimmerman, Spies, Rigor, Self & Casida (1960); Lodge & McPherson (1961, 1963); Lidvall & Griffin (1962); Salmon-Legagneur & Rerat (1962); Hoagland, Jones & Pickett (1963); Kaspar (1963); Baird (1966); Mayrose, Speer & Hays (1966); Parker & Clawson (1966).

Density and bulk of feed

The capacity of the alimentary tract of the pig is limited, and it is not equipped to utilize large amounts of bulky feeds. Many tests have shown that increasing the caloric density on the one hand or the bulkiness of the diet on the other hand can affect the intake; for example, addition of fat to the diet causes a reduction in the amount eaten (Kennington, Perry & Beeson, 1958; Sewell, Tarpley & Abernathy, 1958; Asplund, Grummer & Phillips, 1960; Berg, Kuryvial & Bowland, 1960; Pond, Kwong & Loosli, 1960; Clawson, Blumer, Smart & Barrick, 1962; Lowrey, Pond, Loosli & Maner, 1962). By contrast, dilution of the diet with indigestible ballasts usually increases intake, but lowers efficiency of utilization (Axelsson, 1955; Bohman, Hunter & McCormick, 1955; Hansor, Becker, Terrill, Jensen & Norton, 1956; Bowland, 1957b; Merkel, Bray, Grummer, Phillips & Bohstedt, 1958; Bowland & Berg, 1959; Cameron, 1960; Dinusson, Bolin & McIlroy, 1961; Hellberg, 1961; Bednarowska, 1962; Cunningham, Friend & Nicholson, 1962; Cupka & Majerciak, 1962; Pond, Lowrey & Maner, 1962; Schumm & Schremmer, 1962; Siegl, 1962a; Clausen & Nielsen, 1963; Oslage, 1963; Thrasher, Mullins & Newman, 1963; Klay, Weller & Smith, 1964; Todd, 1964; McBee, Anderson & Zinn, 1965). Some workers have diluted pig feed with as much as 40% of sand with benefit at
the lower levels of addition which perhaps aids mixing of ingesta with digestive enzymes (Baker, Becker, Harmon & Nickleson, 1965).

**Water**

Until fairly recently very little attention was paid to the effect of water intake on consumption of feed. We found very little difference in the performance of pigs receiving 1.5, 2.5 or 3 lb of water/lb feed (Barber, Braude & Mitchell, 1958, 1963a). Pigs at the lowest water intake, but having access to additional sources of water, did augment their intake, on the average by about 1 lb/day, their total intake of water being 2.5 lb/lb feed. Pigs with free access to water drank on the average 2.5 lb/lb feed (Braude, Clarke, Mitchell, Cray, Franke & Sedgwick, 1957). Bowland (1965) found no adverse effects when water was restricted to 1.5 lb/lb feed. Cunningham & Friend (1966) found that restriction of water to 1.25 lb/lb feed significantly increased the fat content of the carcass. The digestibilities of dry matter and protein were not affected at any level of restricted imbibition. Braude & Rowell (unpublished) found that the amount of water present in wet feed did not significantly affect the performance of the pigs.

In an unpublished experiment, Barber, Braude & Mitchell compared the water consumptions by pigs which had continuous access to dry feed with those of litter-mates receiving the same amount of dry feed in two portions each day. The mean daily consumption per pig during the period from 40 to 200 lb live weight was 13.4 lb for the former and 10.8 lb for the latter group, but variation in water intake of individual pigs (9.0–16.3 and 7.8–16.3 lb water/pig respectively) deprived these results of statistical significance.

Considerably greater differences between individual pigs were recorded in a recently concluded test in which the effect of the composition of the diet on voluntary water intake was studied. We found that pigs on diets containing either 7 or 17.5% white fish meal drank 13.3 and 13.8 lb water/pig per day respectively, ranging from 6.9 to 37.8 lb water/pig per day irrespective of group.

**Grinding, soaking, heating, pelleting**

It has been generally accepted that pigs cannot efficiently utilize whole grain, though they eagerly consume it. Charlet-Lery & Leroy (1955), Bowland, 1956a, Hebblethwaite (1958), Markovic & Zivkovic (1958), Hillier & Martin (1959), Clawson (1962), Harnisch & Rojahn (1962), Curda, Snopkova, Muzik & Cadkova (1963), Burnett & Neil (1964), Fugate, Pickett, Perry & Curtin (1965), Haugse, Dinusson, Erickson & Bolin (1966) have studied effects of fineness of grinding on intake. Recent reports by Fugate et al. (1965) and Mahan, Pickett, Perry, Curtin, Beeson & Featherston (1965) indicating that oesophagogastric ulcers can result from finely ground feeds certainly added confusion to the issue of what should be the texture of feed given to pigs.

Barber, Braude & Mitchell (1962) and Becker, Jensen, Harmon, Norton & Breidenstein (1963) showed that no advantage resulted from the soaking of feeds. Heating feeds sometimes improved performance (Grigoras, Constantinescu,
Iacomi, Popici & Palade, 1963), as did adding hot water to feed fed wet during the winter (Berek, 1963). For reasons irrelevant to the subject of this review, such as the destruction of a toxic alkaloid in potatoes and of pathogenic bacteria or viruses in swill, cooking of potatoes or swill is essential, and it is generally accepted that the nutritive value of both is improved thereby.

Jensen, Terrill & Becker (1960) studied the effect of different drying temperatures upon the feeding value of maize (reducing moisture content from 21 to 12.4% at 140, 180 or 220°F) and found no effect on either consumption or performance. Subsequently Jensen, Becker & Harmon (1964) used maize dried at very high temperatures (700–900°F for 2.5–7 min) and also observed no effect on performance. On the other hand, Taylor, Pickett, Issacs & Foster (1964) reported impaired performance using maize dried at 290°F as compared with that dried at either 140 or 190°F.

Breidenstein, Garrigan & Humphreys (1964) found the carcasses of pigs fed maize of 25% water content to be of better quality than those of pigs eating maize of 12.2% water content.

Performance on pellets is better than on meal (Tables 3 and 4). Pelleting reduces wastage and may slightly enhance the nutritive value of the feed. However, deterioration in carcass quality due to pelleting the feed has been reported by Bowland, 1956b,

Table 3. Comparison between performances of pigs fed with pellets or meal: classified results from thirty-two papers published since 1955

<table>
<thead>
<tr>
<th>Growth rate</th>
<th>Feed conversion efficiency</th>
<th>No. of reports</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>O</td>
<td>+</td>
<td>5</td>
<td>Rutledge &amp; Teague 1959; Becker, Jensen &amp; Harmon, 1964; Homb et al. 1964; Jensen &amp; Becker, 1965; Meade et al. 1966</td>
</tr>
<tr>
<td>+</td>
<td>O</td>
<td>1</td>
<td>Cameron, 1960</td>
</tr>
<tr>
<td>O</td>
<td>O</td>
<td>4</td>
<td>Teague &amp; Wilson, 1957; Hillier &amp; Martin, 1959; Gorrill et al. 1960; Teague &amp; Rutledge, 1960</td>
</tr>
<tr>
<td>–</td>
<td>–</td>
<td>1</td>
<td>Pickett et al. 1960</td>
</tr>
</tbody>
</table>

+ pellets better; – meal better; O no difference.

Table 4. Comparison between performances of pigs fed with pellets or meal: collected results from the papers listed in Table 3

<table>
<thead>
<tr>
<th>Effect of pellets</th>
<th>Growth rate</th>
<th>Feed conversion efficiency</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Improvement</td>
<td>(no. of papers) 22 26 1 9</td>
</tr>
<tr>
<td></td>
<td>Deterioration</td>
<td>1 1 1 5</td>
</tr>
<tr>
<td></td>
<td>None</td>
<td>1 1 1 5</td>
</tr>
</tbody>
</table>
Hansen (1964), Homb, Lyso & Matre (1964), and Gill (1965), but Hillier & Martin (1959) and Braude & Rowell (1966) found neither benefit nor harm from pellets. In creep-fed baby pigs consumption of pellets is greater than of meal (Lewis, Catron, Combs, Ashton & Culbertson, 1955; Salmon-Legagneur & Fevrier, 1956; Teague & Wilson, 1957; Witt, Andreae & Schröder, 1957; Braude, Townsend & Rowell, 1960; Tardani & Lux, 1963; Schlegel & Kästner, 1965). Though some claim that performance of the pigs is also improved, Horszczaruk, Kotarbinska & Sasorski (1965) found no advantage from creep-feeding with either meal or pellets, and Zausch (1963) attributed adverse effects on growth rate and feed conversion to 'the effect of heating during improvised pelleting'. Chamberlain, Merriman & Lidvall (1965) and Fugate et al. (1965) reported higher incidences of ulcers in the digestive tract with pelleted feed, but these reports still await confirmation.

Methods of feeding

Self-choice. A common method of feeding pigs in the United States is to allow them free access to at least two feeds, usually maize and a protein-mineral-vitamin supplement, in the hope that the pig will adequately balance its own diet. There are many reports pointing to better results with mixed feeds than with self-choice (Bowland, 1956; Brown, 1956; Adams & Ward, 1957; Diggs et al. 1957; Hutchinson, Terrill, Jensen, Becker & Norton, 1957; Conrad & Beeson, 1958; Hillier & Martin, 1959; Rutledge & Teague, 1959; Foster, Jones & Pickett, 1964; Geurin, 1964; Clawson & Otto, 1965). Several reports indicate no difference in performance with the two methods of feeding (Thrasher, Mullins & Newman, 1961; Hoefer, 1963; Ret & Henry, 1964; Supek, Szecsenyi & Levay, 1964; Holck & Tribble, 1965), none giving superiority to the self-choice method. In my opinion, the latter is doomed when very high and efficient performance is aimed at.

However, the question has been raised as to how thorough should be the mixing of dietary ingredients. Eggert, Brinegar & Anderson (1953) reported that, when the protein supplement was added to the feed at intervals of 24 h, the growth and nitrogen utilization were similar to those with balanced feeding. When the intervals between feeding of the supplement were raised to 36 and 48 h, the nitrogen retention was lowered by 7 and 14% respectively. Yeo & Chamberlain (1966) obtained satisfactory results when they gave barley meal at one of the daily feeds and a high-protein mixture at the other. Such alternation of feeds reduces the costs.

Rotermel (1960) claimed that twice weekly alternation of concentrates with bulky feeds improved the performance of the pigs and caused greater development of lungs, liver, kidneys, spleen and stomach.

When Teague, Grifo & Rutledge (1966) studied the effect of intermittent supplementation of the diet with chlortetracycline either continuously or at intervals ranging from 1 week in 2 to 1 week in 8, there was no difference in performance.

Restricted v. ad lib. feeding. Lucas & Calder (1956) reviewed the literature to compare feeding ad lib. with various degrees of restriction; I have classified fifty-four reports published since then (Tables 5 and 6) which indicate that pigs fed ad lib. grow faster, but utilize their feed less efficiently and, if the leanness of the carcass
Feeding pattern and nutrient utilization

Table 5. Comparison between performances of pigs on ad lib. or restricted feeding: classified results from papers published since 1956

<table>
<thead>
<tr>
<th>Growth rate</th>
<th>Feed conversion efficiency</th>
<th>Carcass quality</th>
<th>No. of reports</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>+</td>
<td>+</td>
<td>—</td>
<td>—</td>
<td>29</td>
</tr>
<tr>
<td>+</td>
<td>+</td>
<td>—</td>
<td>1</td>
<td>Geurin et al. 1964</td>
</tr>
<tr>
<td>+</td>
<td>O</td>
<td>—</td>
<td>3</td>
<td>Bradley, 1964; Anderson et al. 1965; Holme &amp; Coey, 1966</td>
</tr>
<tr>
<td>+</td>
<td>O</td>
<td>O</td>
<td>3</td>
<td>Weniger, 1961; Schumm &amp; Kirmse, 1963; Smolinsky et al. 1963</td>
</tr>
<tr>
<td>+</td>
<td>—</td>
<td>O</td>
<td>4</td>
<td>Lenschow, 1959; Shroder, 1963; Otagaki et al. 1963; Koch, 1964</td>
</tr>
<tr>
<td>+</td>
<td>—</td>
<td>N</td>
<td>3</td>
<td>Weber &amp; Kaiser, 1958-9; Lessmann, 1959; Laube &amp; Weissbach, 1963</td>
</tr>
<tr>
<td>+</td>
<td>N</td>
<td>—</td>
<td>3</td>
<td>Keese et al. 1964; Witt et al. 1964; England, Oldfield, Davidson &amp; Copper, 1965</td>
</tr>
<tr>
<td>O</td>
<td>—</td>
<td>—</td>
<td>1</td>
<td>Nikolic &amp; Sreckovic, 1962</td>
</tr>
</tbody>
</table>

+, ad lib. better; —, restricted better; O, no difference; N, no information.

Table 6. Comparison between performances of pigs on ad lib. or restricted feeding: collected results from fifty-three papers published since 1956 (see Table 5)

<table>
<thead>
<tr>
<th>Effect of ad lib. feeding</th>
<th>Growth rate</th>
<th>Feed conversion efficiency</th>
<th>Carcass quality</th>
<th>(no. of papers)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Improvement</td>
<td>52</td>
<td>6</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Deterioration</td>
<td>—</td>
<td>38</td>
<td>40</td>
<td></td>
</tr>
<tr>
<td>None</td>
<td>1</td>
<td>6</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>No information available</td>
<td>—</td>
<td>3</td>
<td>3</td>
<td></td>
</tr>
</tbody>
</table>

is taken as the major criterion, produce carcasses of lower quality. However, I believe that in problems of this kind drawing conclusions from average values, even based on a large number of reports, is not very helpful. There are so many factors interacting which are beyond the control of the workers who carried out these experiments, that it is a hopeless task to attempt to bring them to a common denominator. In addition, the plus–minus classification adopted here, which does not pay attention to the magnitude of observed differences, can be misleading. Comparative tests cannot, in my opinion, answer the question as to whether or not a healthy pig can limit its voluntary feed intake to the amount that it can efficiently utilize. If we assume that the aim of pig-raising is to produce lean meat, the available
evidence does not support the \textit{ad lib.} feeding technique. Quick gains resulting from \textit{ad lib.} feeding conflict with optimum efficiency of feed utilization and lean carcasses. The purpose of restricted feeding is to enhance the last two parameters, partly sacrificing the speed of growth. One should aim at the best of three worlds, efficiency of feed conversion, lean carcass and a good growth rate, in that order.

There are many reports as to what degree of restriction is to be advocated (Smith, 1956; Barber, Braude & Mitchell, 1957; Braude, Townsend \textit{et al.} 1958, 1959; Kirsch, 1960; Lucas \textit{et al.} 1960; Self, Grummer, Hays & Spies, 1960; Hellberg, 1961; Nikolic & Sreckovic, 1962; Abgarowicz, Kotarbinska, Chapulowa & Witczak, 1963; Thrasher, Mullins & Newman, 1963; Watson, 1963; Buchwald & Zalewski, 1964; Witt, Andreae & Schröder, 1964; Bielinska, 1965; England, Oldfield, Davidson & Cooper, 1965; Greer, Hays, Speer, McCall & Hammond, 1965; Orme, Keith, Ball, Baker & Everson, 1965), but no hard and fast rules can be laid down. The guiding principle should be to have as little restriction as possible, and the degree of restriction should be adjusted to the type of pig and the type of diet one is using.

\textbf{Frequency of feeding.} We have recently used for artificially reared pigs equipment which automatically controls feeding (Braude \textit{et al.} 1966), and our results present no advantage, as far as growth rate is concerned, of hourly feeding over twice-daily feeding. There may be a slight improvement in feed conversion. Reports indicate that there is no advantage in frequent feeding of older pigs (Mel’nikov & Struk, 1956; Berg & Bownall, 1958; Cupka & Majerciak, 1962; Friend & Cunningham, 1964, 1965; Hojgaard-Olsen, 1964; Cromwell, Pickett, Foster & Peart, 1965) or in feeding three times daily as compared with twice daily (Majerciak & Peter, 1959; Kotlinski, Juszczak & Gisza, 1960; Majerciak, 1961; Hovorka, 1965; Csire, 1966). Barber, Braude & Mitchell (1961) and Braude, Townsend, Harrington & Rowell (1963) found once-daily, as compared with twice-daily feeding did not adversely affect growth rate, feed conversion or carcass quality. These results have been confirmed by Antoni (1965), Holme & Coey (1966), Richter, (1966), Schreiner (1966) and Todd & Daniels (1966). Twice-daily feeding was found by Pickett, Foster & Peart (1964) and Cromwell \textit{et al.} (1965) to have some advantage.

The omission of one or two feeds per week, but with the same weekly intake, was found by Braude & Rowell (1957), Comberg & Loffelbein (1958) and Lessmann (1959) not to affect performance, but when there was no quantitative compensation the performance was depressed (Szigeti, 1956; Tschilderer, 1956; Landau & Majerciak, 1957; Majerciak & Peter, 1959). Landau & Majerciak (1957) reported that a fast of 18 h each week produced no adverse effects, but if it was extended beyond 18 h the performance suffered. Scholz & Siegl (1955) demonstrated that a day of fasting each week reduced performance, but Hovorka (1960) claimed that such a treatment in fact improved both growth rate and feed conversion efficiency.

Veum, Pond & Walker (1966) subjected pigs to a routine of 1, 2 or 3 days' fasting following 1 day of \textit{ad lib.} feeding and found that growth rate and feed conversion were decreasing with the severity of the restriction. Pigs fed every 2nd day were able partly to compensate for feed withdrawal by consuming more feed when given access to it. (They had access to feed only half of the time and consumed 80% as
much feed as control pigs). The pigs on the more severely restricted diets were unable to compensate by eating more when feed was available.

Psenicnyj (1958) compared feeding twice, three times or four times daily and found that feeding sows twice daily is not only more economical in labour, but also results in more efficient use of the feed. Barber, Braude, Hosking & Mitchell (1960) reported that one afternoon feeding per week could be omitted without adversely affecting either the sow or its litter, provided the amount withheld was distributed between the remaining feeds during each week.

There are two rather intriguing reports which I would like to mention. Chachulowa (1964) reported that feeding three times as compared with twice daily resulted in reduced ammonia production in the caecum; Tomson (1965) claimed that by altering the rhythm of feeding every 6 days (standard amount, 70% and 130%) better growth rate was obtained as compared with that on a continuous standard treatment.

Individual v. group feeding. In practical pig-keeping group feeding is used. For experimental and testing purposes individual feeding has obvious advantages, of which the most important is that it supplies data from which individual feed conversion values can be calculated. Fredeen & Jonsson (1957) and Jonsson (1959), who compared values obtained with individual feeding and with group feeding by the Danish progeny testing stations, recorded a marked reduction of variation in growth rate, conversion and carcass quality with individual feeding. Kirsch, Fender & Werkmeister (1961) compared individual and group feeding and found little difference in carcass quality which, however, improved with individual treatment if the feeding was restricted. Becker, Jensen, Harmon & Norton (1964) found no difference between pigs fed ad lib. individually or in groups, but individual feeding was better when feed intake was restricted. Hale & Coey (1963) reported that pigs kept individually consumed less feed in the final stages of the growing period than pigs fed in groups; Wallace, Palmer, Carpenter, Anh & Combs (1964) found no difference between the two methods of feeding.

Mitchell (1965) determined the amount of feed consumed by individual pigs within a group, and reported that with individual animals the difference between allocated and consumed amounts varied from −10 to +7%.

Dry v. wet feeding. Twenty-seven reports dealing with wet v. dry feeding are classified in Table 7. Table 8 summarizes the results. About half of the reports claim that wet feeding improves growth rate and feed conversion; the other half claim no difference. Improvement associated with dry feeding is certainly an exception. Information about effects on carcass quality is very scanty; three reports claim improvement with wet feeding and four report no difference.

In a recently completed large-scale field trial, Braude & Rowell (1967) showed that pigs given a restricted amount of dry feed but with water always available grew more slowly and utilized their feed less efficiently than their litter-mates given the same amount of feed mixed with water. There were no major effects on carcass quality. When given a choice, pigs prefer their feed wet. Thus those of Siegl (1962b) consumed about two-thirds of their daily feed allowance wet.
Table 7. *Comparison between performance of pigs on wet or dry feeding: classified results from papers published since 1956*

<table>
<thead>
<tr>
<th>Growth rate</th>
<th>Feed conversion efficiency</th>
<th>Carcass quality</th>
<th>No. of reports</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>+</td>
<td>+</td>
<td>+</td>
<td>4</td>
<td>Lips, 1964; Glaps, 1965; Mazaraki, 1965; Roller et al., 1965</td>
</tr>
<tr>
<td>+</td>
<td>+</td>
<td>O</td>
<td>5</td>
<td>Scholz &amp; Siegl, 1958; Milosavljevic et al., 1960; Grigoras et al., 1963; Tardani et al., 1964; Braude &amp; Rowell, 1967</td>
</tr>
<tr>
<td>+</td>
<td>+</td>
<td>N</td>
<td>4</td>
<td>Heitkamp, 1960; Becker et al., 1963; Klay et al., 1964; Zednik, 1964</td>
</tr>
<tr>
<td>+</td>
<td>O</td>
<td>N</td>
<td>1</td>
<td>Becker et al., 1963</td>
</tr>
<tr>
<td>O</td>
<td>O</td>
<td>O</td>
<td>1</td>
<td>Kostic &amp; Zaletel, 1963</td>
</tr>
<tr>
<td>O</td>
<td>O</td>
<td>N</td>
<td>4</td>
<td>Scholz &amp; Siegl, 1959; Duniec &amp; Kaczmarczyk, 1960; Piatkowski &amp; Otto, 1960; Koch, 1964; Bowland, 1965</td>
</tr>
<tr>
<td>O</td>
<td>O</td>
<td>+</td>
<td>1</td>
<td>Raicu et al., 1962</td>
</tr>
<tr>
<td>O</td>
<td>—</td>
<td>N</td>
<td>1</td>
<td>Thrasher et al., 1964</td>
</tr>
<tr>
<td>—</td>
<td>—</td>
<td>O</td>
<td>1</td>
<td>Kornegay &amp; Vander Noot, 1965</td>
</tr>
</tbody>
</table>

+, wet better; —, dry better; O, no difference; N, no information.

The reasons for superiority of wet over dry feeding are by no means clear, but are probably associated with the pig's ability to consume the feed more rapidly, take less time and use up less energy in eating. Knap & Hajek (1964) and Sterba (1964) observed that pigs given wet feed were less active and rested for longer periods. Castle & Castle (1957) found that increasing the ratio of water to feed accelerated rate of passage.

**Pumping of liquid feed.** Braude & Rowell (1967) found that the performance of pigs receiving 4 parts of water to 1 of feed (the ratio for satisfactory pumping of the mixture) was the same as that of litter-mates receiving 2:5 parts of water to 1 of feed.

**Trough v. floor feeding.** In recent years the practice of placing feed on the floor rather than in troughs has been adopted in some piggeries. Barber, Braude & Mitchell (1963b, 1965) found very little to choose between the two methods. Bowland (1964) also found no difference between the two methods of feeding, and Hansen's (1964) observations suggested slightly better results with trough feeding.

In a field experiment, Braude & Rowell (1966) found that pellets were better than meal when the pigs fed from the floor. Floor-fed pigs fared worse with meal than
trough-fed pigs, but there was no difference when pellets were used. Feed wastage accounts for these differences.

Two experiments at present in progress at Shinfield
(Barker, Braude & Mitchell, unpublished)

Expt 1. Four treatments were used, each with ten similar pigs fed individually:
(a) dry feed ad lib. continuously available;
(b) dry feed available ad lib. daily for two periods of 30 min each;
(c) dry feed available for two periods of 30 min each, the quantity being adjusted, depending on whether the trough was emptied or not;
(d) as c but the feed was given ‘wet’, 2.5 lb water/lb feed being added to the trough immediately before feeding.

Treatments c and d are frequently called ‘to appetite’ feeding, and sometimes ‘semi ad lib.’ feeding.

The results were:

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Daily live weight gain (lb)</th>
<th>Feed conversion efficiency (lb feed/lb gain)</th>
</tr>
</thead>
<tbody>
<tr>
<td>a</td>
<td>1.62</td>
<td>3.50</td>
</tr>
<tr>
<td>b</td>
<td>1.15</td>
<td>3.23</td>
</tr>
<tr>
<td>c</td>
<td>0.98</td>
<td>3.38</td>
</tr>
<tr>
<td>d</td>
<td>1.53</td>
<td>2.99</td>
</tr>
</tbody>
</table>

The carcass quality was much worse on treatment a than on the other three treatments, with very little difference between the latter.

Maximum growth, with dry feeding, results when feed is available ad lib. throughout the day and night, but efficiency of feed conversion and carcass quality are not then so good.

There was a considerable difference in performance of the pigs on the two methods of twice daily dry feeding (b versus c), clearly showing that the name ‘to appetite’ is a misnomer.

Treatment b did not satisfy the pigs’ appetites as well as did treatment a; treatment c had an even worse effect on appetite. It is clear that two 30 min periods/day are not long enough for optimal dry feeding. The differences resulting from treatments c and d are very large. The most striking observation in this experiment was the difference between the feed conversion efficiencies with treatments a and d. It is generally believed that ad lib. dry feeding is inefficient, but the differences recorded between treatments a and d in this experiment are astonishing.

Expt 2. This included the following four treatments:
(e) dry feed ad lib. continuously available;
(f) dry feed in the quantity consumed by pigs on treatment e in previous 24 h given in two feeds/day;
(g) as f but given wet in two feeds/day;
(h) wet feed given according to the Shinfield scale (cf. Braude & Rowell, 1966).

There were eleven similar pigs per treatment. Some of the results were:

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Daily live weight gain (lb)</th>
<th>Feed conversion efficiency (lb feed/lb gain)</th>
</tr>
</thead>
<tbody>
<tr>
<td>e</td>
<td>1.55</td>
<td>3.29</td>
</tr>
<tr>
<td>f</td>
<td>1.46</td>
<td>3.15</td>
</tr>
<tr>
<td>g</td>
<td>1.52</td>
<td>3.21</td>
</tr>
<tr>
<td>h</td>
<td>1.39</td>
<td>3.07</td>
</tr>
</tbody>
</table>
The carcass quality was worse on treatment e than on the other three treatments, with very little difference between the latter.

It was observed that pigs on treatment f (dry) required about 90 min to clear their troughs at each of the two daily feeding periods, whereas pigs on treatment g (wet) ate equivalent amounts within 30 min. From a comparison of results with treatments b (Expt 1) and f (Expt 2), it appears that, in order to satisfy its appetite for dry feed, the pig should be able to eat for about 90 min twice daily. It matters little whether the pigs have access to feed throughout the 24 h. Once again evidence is produced that restricted feeding (treatment h), though responsible for a slower growth rate, significantly improves efficiency of feed conversion.

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Effect of frequency of feeding upon food utilization by ruminants

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Introduction

Feeding pattern may be defined as the distribution of food intake over time. As such the term covers many widely divergent aspects of ruminant nutrition.